Working Memory in Older Age

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Synonyms

Working memory capacity; Short-term memory; Working memory updating; Updating and monitoring

Definition

Working memory (WM) refers to the immediate and limited memory system that is responsible for maintaining, processing, and updating information flexibly and for brief periods of time. WM is sometimes used interchangeably with short-term memory in the literature, although WM is often considered more active and dynamic than the more passive short-term memory. The construct has been fundamental to researchers' understanding of age-related changes in a broader range of other cognitive abilities, such as fluid intelligence (i.e., abstract reasoning) and long-term episodic memory (i.e., retrieval of information that is no longer held in working memory). This chapter reviews several important life-span models of WM from the literature and their supporting evidence, while also considering other aspects of WM, such as methodologies for testing WM capacity in older adults, the neural signatures of WM in the aging brain, and whether it is possible to train WM in order to yield improvements to other areas of cognition across the life-span.

Introduction

In daily life, we are regularly required to briefly hold some information in an accessible state for an ongoing task. While planning a trip, for example, it is often the case that we must consider the prices of several hotels to make comparisons between them, perhaps while also considering their relative distances to a desirable location in the city. The immediate memory system thought to underlie such tasks is called *working memory (WM)*, a concept that has been fundamental to many theories regarding age-related changes in cognition due to its hallmark responsibility of maintaining information available for processing.

Working memory capacity refers to the maximum amount of information that a person can maintain efficiently in WM. It is well known that WM capacity is limited: The system can become quickly overloaded (e.g., considering the prices of a large number of hotels), resulting in considerably impaired performance. Moreover, WM capacity only becomes more constrained with increased age: Older adults show worse performance on WM tests compared to younger adults

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(Bopp and Verhaeghen 2005; McCabe et al. 2010; Park et al. 1996). This fact is particularly important because the functioning of WM has a large impact on many other forms of complex cognition. Individual differences in WM capacity correlate highly with success on other cognitive tasks, such as tests of long-term episodic memory and of reasoning ability. Moreover, individual variation in WM capacity accounts for a large proportion of age-related variance in cognitive abilities such as episodic memory (McCabe et al. 2010; Park et al. 1996). In other words, how much individuals of different ages vary in their episodic memory performance can largely be ascribed to their variation in performance on the WM measure. For that reason, WM has been a core construct at the center of research on age-related decline in higher-order cognition.

The explanation that many researchers offer for such findings is that the mechanisms underlying WM are similarly required during tasks measuring other forms of higher-order cognition. However, researchers have disagreed about what causes the limitations in WM and why WM capacity predicts other cognitive functions. In the aforementioned example of maintaining hotel prices and locations for a trip, it could be that younger adults excel at this task relative to older adults because: (1) they are just generally faster and therefore more efficient at the task (*processing-speed hypothesis*); (2) they are better able to disregard irrelevant information (e.g., checking emails, distracting music) during the task (*inhibitory-deficit hypothesis*); (3) they are better able to flexibly coordinate between the different subtasks involved (*coordination and task-switching hypotheses*); or (4) they are more effective at integrating the hotel price and location information into a cohesive unit (*binding-deficit hypothesis*). Accordingly, age differences in one of these predicted underlying functions in WM are thought to be similar in other tasks of higher-order cognition (e.g., episodic memory) that likewise rely on the same function.

The goal of this section is to review several frameworks and concepts that have been important to explaining age-related differences in WM and elucidating its role in higher-order cognition. Important findings from the neuroscientific literature concerning age-related changes in the brain that correspond to changes in WM performance are also reviewed. Furthermore, findings from the relatively recent field of WM training are also considered. Prior to these overviews, a summary of the typically used empirical methods in the field of cognitive aging and WM is presented.

Empirical Methodologies and Working Memory Measures

There is a wide range of commonly used empirical methods in the study of WM across the lifespan. The use of any one of these particular methods depends on the research question of the researcher, and unfortunately, sometimes the convenience and cost of the study. Furthermore, the WM literature in general is rife with discussion on the best tasks to use to properly assess WM capacity. Much of the research attempts to balance the practical importance of utilizing well-established and reliable tasks with the aim to use theoretically informative tasks that could adjudicate between purported mechanisms of WM. A thorough consideration of these empirical and task-specific methodologies is essential for any study on WM in older adults.

Empirical Methods. As is the case in many areas concerning development, studies of WM generally fall under the umbrellas of either cross-sectional or longitudinal designs. Both types of designs either recruit participants for a continuous age sample (e.g., adults aged 18–80 with the ages more or less equivalently represented) or recruit participants to represent prearranged and discrete or extreme age groups (e.g., younger adults aged 18–30 vs. older adults aged 65–80). Cross-sectional studies compare adults of various ages or age groups at the same singular time point. Thus, cross-sectional studies assess interindividual variability, or how WM differs between these disparate age groups. Conversely, longitudinal studies examine adults representing one or several age groups across at least two time points. Thus, longitudinal studies are primarily concerned with intraindividual variability, or how WM differs within a person across different points in time. Whereas cross-sectional designs tend to show a steep linear decline from age 20 on in a host of cognitive functions including WM (McCabe et al. 2010; Park et al. 1996), longitudinal designs usually show much more modest rates of decline in WM (Hertzog et al. 2003). Within either cross-sectional or longitudinal designs, researchers typically implement experimental or individual differences methods, or a combination of the two, depending on their research question. Experimental research questions concern the effect of manipulating one or several factors on subsequent performance. In cross-sectional designs, for example, researchers may examine whether increasing the amount of information (i.e., load) in WM yields different patterns of brain activity in the prefrontal cortex in younger and older adults (Daselaar and Cabeza 2014). Experimental studies very commonly test for age × variable interactions, such that effect of manipulating a variable (such as WM load) is more pronounced for one age group than another.

As will be discussed more thoroughly in the overview of theories of WM age differences, such interactions can be informative for differentiating key aspects underlying age-related changes in WM. However, many age × variable interactions are ordinal, and as such, are uninformative because they depend on the scale of measurement. Several methods have been developed to address this issue. First, a Brinley plot is a scatterplot wherein older adults' mean performance is plotted as a function of that of younger adults' for the same task condition. The regression line represents the relation between young and old adults' performance scores across a number of tasks and experimental conditions. A meaningful interaction between age and the variable of interest can be inferred if two separate regression lines are necessary to explain the young-old relation in two conditions (e.g., a baseline condition and a critical experimental condition). Two lines would suggest that there is a specific age-related deficit associated to the experimental condition over and above the age deficit observed in the baseline condition. Conversely, if only one regression line is necessary to explain the relationship between younger and older adults' performance on the different task conditions, then it can be inferred that the age-related deficit can be reduced to a single underlying variable that accounts for the age effects in all task conditions.

In a similar vein, state-trace plots also examine interactions between age and a variable of interest by plotting performance on one task (e.g., the baseline condition) against performance on another task (e.g., the experimental condition) in order to ascertain if the relationship between these tasks differs between younger and older adults. Similar to Brinley plots, an age × variable interaction can be inferred if two regression lines (one for either age group) are necessary to explain the performance relations between the tasks. However, if only one regression line is necessary, then it can be concluded that the relationship between the tasks can be reduced to a single variable that changes across the lifespan. Thus, Brinley plots and state-trace plots can be very informative to indicate whether an underlying process or mechanism is uniquely deficient in older age or not.

Individual-differences research asks to what extent differences between individuals on a particular task or set of tasks covary with differences on other measures. Because no single task is a pure measure of a construct, it is increasingly common to administer a number of tests that purportedly measure the same underlying construct, such as WM capacity. The construct is represented by the latent factor that reflects the common variance of all the WM tests. Researchers then use structural-equation modeling (SEM) to examine how these latent constructs correlate with other constructs, such as fluid intelligence. These methods are important for assessing the contribution of WM in explaining age-related variability in other complex cognition. For example, in a longitudinal design, one could examine how changes in WM performance from age 64 to 70 accounts for the changes shown in other variables like episodic memory (Hertzog et al. 2003). Analogous analyses in cross-sectional designs using path models examine how WM accounts for age-related variability in other measures (McCabe et al. 2010; Park et al. 1996). Individual differences methods like hierarchical linear regression and SEM can be useful for comparing alternative models to each other, but such methods applied to cross-sectional designs are inadequate to infer that age-related changes in one construct (such as WM) are causally responsible for age-related changes in other constructs (Lindenberger and Pötter 1998).

Working Memory Measures. Most researchers agree that WM is a system that briefly maintains, manipulates, and updates information. Given this characterization of WM as a construct, researchers have created a plethora of tasks that aim to assess these functions.

Complex span tasks have dominated the literature: They require participants to briefly maintain information (e.g., in verbal complex span tasks, digits, letters, or words) while concurrently engage in other processing activities (e.g., in operation span, arithmetic problems, such as "$4 \times 6 = 24$?"). Typically, after 2–7 memoranda have been presented, participants are asked to recall them in their original order of presentation. Other WM tasks emphasize the updating function of WM, such that initially presented information (e.g., the digits 4 2 9 presented across three frames) is updated using new incoming information (e.g., successively presented operands such as +2, +1, and −3, to be applied to the first, second, and third digit, respectively). Other studies, especially neuroscientific studies using fMRI, commonly use *n*-back tasks. In the n-back paradigm, participants observe a long series of items and decide for each presented item (e.g., letters) whether it matches the item presented *n* steps back (e.g., in a 2-back with letters, the sequence L-R-L-Q would require "yes" to the second presentation of L but "no" to Q). Neuroscientific and behavioral studies have also commonly employed immediate short-term recognition or probed-recognition paradigms: A set of stimuli is presented, followed by a brief delay. WM is then tested by presenting a probe stimulus and requiring participants to decide whether it was included in the memory set, or whether it matches one particular stimulus in the memory set.

There are several methods of determining whether various measures of WM capacity are good indicators of the construct as well as informative about the nature of WM itself (Oberauer 2005b). These methods are not necessarily specific to WM research but have been immensely informative for the literature in general and for considering age-related changes in WM performance. As discussed previously, researchers often use factor analysis to the benefit of understanding how these WM measures share common variability at the latent level. That is, if different kinds of measures of WM capacity load on the same factor, then it can be concluded that only one factor of common variability is necessary to explain performance on the tasks (i.e., construct validity). Furthermore, the different WM measures should correlate to the same extent with other criterion measures commonly associated to WM, such as fluid intelligence (i.e., convergent validity). Conversely, the measures should not predict performance on other tasks that are theoretically assumed to be unrelated with the construct, such as visual search (i.e., discriminant validity). Finally, the measures should be similarly affected by experimental manipulations and by age at both the behavioral and neural level, especially as predicted by the theoretical understanding of the construct. While it is greatly important to establish the reliability and validity of these different measures, the selection of any one of them thereafter depends on the research questions of the study. Specifically, the selection of one task over another is motivated by the task characteristics that allow one to test the underlying mechanisms of interest.

Theoretical Accounts for Age-Related Decline in Working Memory

Given the many proposed models of WM (Miyake and Shah 1999), it is not surprising that there are a variety of corresponding theoretical accounts for age-related differences in WM. Some of these theoretical accounts have focused on interpreting age-related deficits in WM as deficits in more basic functions (i.e., processing speed, binding), whereas others have emphasized the importance of cognitive control in WM (i.e., inhibition of irrelevant information, coordinative ability).

Processing Speed. Among the earliest and arguably the most profoundly influential explanations for age-related decline in WM, and fluid cognition in general, was the *processing-speed hypothesis* (Salthouse 1996). It is regularly observed that older adults process and respond to information much more slowly than younger adults. For example, on a typical processing speed measure (e.g., letter comparison), the speed with which one decides whether a string of consonants matches another string of consonants (e.g., LHQFPY – LHRFPY) tends to increase with increasing age. The processing speed hypothesis states that information in WM declines over time. Therefore, adults' slower speed of processing means that fewer cognitive operations on information in WM can be completed before that information is lost. Moreover, less information is simultaneously accessible in WM because encoding and rehearsal of information is also slowed, compared to younger adults. Thus, processing speed is argued to cause the age-related decline in performance in WM tasks. Evidence for the processing-speed hypothesis comes from the well-established finding that the negative correlation between age and measures of WM capacity is substantially attenuated when measures of processing speed are statistically controlled for, particularly in cross-sectional studies.

Despite consistent evidence that processing speed shares a large proportion of age-related variance with performance on tasks of higher order cognition, age differences in WM capacity cannot be reduced to mere speed of processing. A number of studies varying different dimensions of task complexity have shown that age differences in speed of processing depend on the demands of the task: As task complexity increases, the ratio of average response times between old and young adults increases from about 2:1 to about 4:1 (Oberauer 2005a). This suggests that the age difference in speed is not a cause but a consequence of the age difference in WM capacity: With reduced WM capacity all task-relevant representations – including task sets that implement the goals and instructions – are represented less robustly, resulting in slower processing, and that effect is exacerbated the more WM is loaded. Further evidence has indicated that older adults' comparatively slower processing speeds are largely due to different speed-accuracy trade-offs between younger and older adults: Older adults are more likely to prioritize accurate responses at the cost of response times, whereas younger adults tend to balance speed and accuracy to achieve the most correct responses per unit of time (Starns and Ratcliff 2010). Therefore, much of the age-related slowing observed in response times does not reflect slowing of information processing.

From an individual differences perspective, WM and processing speed at the latent level are often strongly related but still distinguishable constructs. Moreover, structural-equation models including both WM and processing speed as separate predictors of higher-order cognition (e.g., episodic memory) have provided better fits of the data than models that only used speed as a predictor variable and WM as a measure of general memory ability (McCabe et al. 2010; Park et al. 1996). Thus, although processing speed is an important factor in age-related decline in cognitive abilities, research from experimental and individual differences perspectives alike show the unique predictive utility of a WM factor that cannot be entirely reduced to processing speed.

Inhibition. The *inhibitory-deficit hypothesis* attributes age-related changes in WM to a decreased ability to keep irrelevant information out of WM, and thereby prevent it from interfering with the task at hand (Hasher et al. 2007). According to this view, age differences in WM arise not because older adults are less capable than young adults of maintaining information in WM; rather, there is *too much* irrelevant information cluttering their WM that disrupts the maintenance and processing of relevant information and consequently yields worse performance.

The evidence for inhibition as a crucial factor in WM stems from a number of different paradigms that infer successful inhibition from the contrast of two experimental conditions. Inhibition can be inferred from slower response times to information assumed to be suppressed previously, less priming of suppressed information, or fewer intrusions of information that was deemed irrelevant to the task, compared to a baseline condition in which suppression is unnecessary (Hasher et al. 2007). Compared to younger adults, older adults have shown diminished inhibitory ability in each of these regards. The paradigms developed to test inhibitory functioning have included negative priming, directed forgetting, and resistance to prepotent responses (e.g., antisaccade, Stroop), among many others. In many of these paradigms, the crucial measure is the relative difference in response times during the critical task that requires inhibition of irrelevant information compared to a baseline condition. For example, the negative priming task simultaneously presents two stimuli and requires a response to the predetermined relevant stimulus (e.g., name the red letters) while also ignoring the irrelevant distracter (e.g., a superimposed green letter). Negative priming effects are shown when response times are differentially slower when the irrelevant distracters are repeated as relevant stimuli on the following trial, compared to a baseline condition wherein none of the distracters are repeated. Thus, *smaller* negative-priming effects indicate failures to inhibit the irrelevant stimulus, whereas in other paradigms, which measure the influence of distraction or prepotent responses (e.g., antisaccade, Stroop), *larger* effects indicate failures to inhibit distracting or irrelevant stimuli compared to the neutral baseline. Accordingly, proponents of the inhibitory-deficit hypothesis have shown that older adults show less evidence of inhibiting the distracting or irrelevant stimuli in these paradigms compared to younger adults (Hasher et al. 2007).

A recent meta-analysis has cast doubt on inhibitory functioning as the main culprit of age differences in WM (Verhaeghen 2011). This is largely demonstrated by using Brinley plots that plot older adults' response times as a function of younger adults' response times for the aforementioned baseline and critical conditions. If increased age is associated with impaired inhibitory function, then the function relating older adults' response times to those of younger adults in the critical condition should have a higher intercept, or a steeper slope (or both), than the function for the baseline condition. However, as the meta-analysis showed, older adults' relatively slower response times in the baseline conditions were not further exacerbated in the critical conditions requiring inhibition. This result contradicts the assertion that older adults suffer from a specific deficit in inhibitory function. Furthermore, critics have questioned whether inhibition is really necessary to explain the results of the studies that purportedly support deficient inhibition in older adults (Oberauer 2005a). As will be discussed in a later section, it is possible that intrusion errors or slower response times to irrelevant information may not reflect inhibitory failures per se, but rather poor discrimination of the proper source context of the information due to failures of binding (Oberauer 2005a).

Coordination and Task Switching. Another explanation of age differences in WM is the relatively diminished ability to coordinate or switch between different subcomponents of a task. Research on coordination between tasks in WM has utilized dual-task paradigms, wherein performance on a single-task condition (e.g., responding to visually presented stimuli) is compared to performance when that task is performed concurrently with an additional task (e.g., also responding to auditorily presented stimuli). A meta-analysis has indicated that the relative cost of performing the dual-task relative to the single-task is reliably larger in older adults than younger adults, although the effect is relatively small (i.e., an age difference of 36 ms) (Verhaeghen 2011).

Somewhat relatedly, the ability to switch between tasks has also been a considered source of age-related differences in WM. This ability can be tested with the task-switch paradigm, in which participants must perform one of two tasks on successively presented stimuli, with a task cue informing participants on each trial about the task to be carried out. As in the dual-task paradigm, these tasks are first performed alone (pure blocks; e.g., reporting the parity of a digit vs. reporting its magnitude relative to 5) and then together (mixed block; e.g., report the parity of the digit if the digit is red, report the magnitude if the digit is blue). Two measures of interest are assessed: the *local task-switching cost* associated with switching tasks within the mixed block (i.e., switch vs. nonswitch trials) and the *global task-switching cost* associated with the general requirement of switching (i.e., pure vs. mixed blocks). Global task-switching costs are larger for older than younger adults, whereas local task-switching costs are similar in both age groups (Verhaeghen 2011). Thus, age differences appear to be largest when participants must maintain two distinct task sets, as is required during dual-task and global task-switching paradigms.

Whereas this research demonstrates age-related differences in cognitive control as manifested by task coordination and global task-switching, correlations between measures of WM capacity and task-switching are typically low (Oberauer 2005a). If age differences in WM arise from differences in the ability to coordinate and switch between tasks, then these variables should be highly correlated, and account for similar variance in other measures of higher-order cognition. However, the aforementioned meta-analysis showed that a latent construct representing task-switching and coordination did not explain additional variance in complex cognition (representing reasoning, episodic memory, and spatial ability) over and beyond the influence of WM and processing speed (Verhaeghen 2011). Thus, age differences in these abilities likely do not reflect the differences shown in WM capacity.

Binding. Another potential source of age-related decline in WM concerns whether older adults are specifically impaired in their ability to establish temporary bindings between information and their contexts within a common cognitive coordinate system (Oberauer 2005a). Much of this research is guided by the premise that WM tasks require robust bindings between contents (e.g., information to remember, such as words) and their contexts (e.g., the relative positions of the words in the trial), as do other complex cognitive tasks with which WM is correlated (Oberauer 2005a). This conception of age differences in WM also corresponds to evidence from the episodic memory literature: Older adults exhibit a specific deficit in the retrieval of information on the basis of associations (Old and Naveh-Benjamin 2008) or recollection of specific details (Jacoby and Rhodes 2006), both of which presumably require some binding of that information during encoding.

Research testing the *binding-deficit hypothesis* has focused on the importance of constructing, maintaining, and dissolving temporary bindings among representations in WM and their temporal-spatial source contexts (Oberauer 2005a). The contribution of bindings in WM can be measured through short-term recognition paradigms that separate two contributions to the recognition decision: (1) recollection, reflecting memory for which content was presented in which context, based on temporary bindings, and (2) familiarity, reflecting memory for which content was presented without memory for its context, which merely requires the activation of content representations but no bindings. The two contributions can be measured separately by recognition paradigms in which participants must decide whether the test probe has been presented in a particular context. For instance, in the local-recognition paradigm a set of words is presented across a row of boxes, and a recognition probe appears in one box, requiring a decision whether the probe matches the memory word in that box. In this paradigm there are two kinds of to-be-rejected probes: new probes, not included in the memory set, and intrusion probes, which were in the memory set but in a different box (i.e., a different context). Whereas new probes can be rejected based on their lack of familiarity alone, rejection of intrusion probes requires bindings between the words and their boxes. Older adults exhibit disproportionately larger costs for intrusions probes compared to new probes, as predicted by the assumption that their recollection is impaired by a binding deficit. In contrast, older adults were much less impaired in rejecting new probes, suggesting that their ability to use familiarity for recognition decisions is largely intact (Fandakova et al. 2014; Oberauer 2005a).

The disproportionate intrusion costs for older adults cannot be explained by an inhibitory deficit (Oberauer 2005a). Rather, the intrusion costs reflect an age-related deficit in binding information in WM. In addition to the aforementioned meta-analysis concluding that older adults do not exhibit deficient inhibitory control, these studies have further supported the notion that the source of intrusion costs commonly attributed to inhibitory failures may in fact be due to relatively deficient binding in WM. Furthermore, age-related deficiencies in building or maintaining bindings in WM connects the age differences exhibited in WM to the specific age-related impairment of retrieving associative information from episodic memory (Jacoby and Rhodes 2006; Old and Naveh-Benjamin 2008).

Working Memory in the Aging Brain

The advent of neuroscientific techniques has also been considerably important to scientists' understanding of the underlying brain mechanisms that correspond to age-related change in WM performance. Neuroimaging techniques include positron emission tomography (PET), functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and transcranial magnetic stimulation (TMS). Researchers have also been interested in the role of neurotransmitters, especially dopamine, associated with age-related changes in WM.

Much of the neuroscientific research has centered on the frontal lobe, especially the prefrontal cortex, and its interactions with other brain regions in supporting WM functioning. Among other regions, the frontal lobes are known to decline in structural integrity with increased age. Thus, researchers have been interested in whether these structural changes correspond to functional decline in WM capacity with older age (Daselaar and Cabeza 2014; Nagel and Lindenberger 2014; Nyberg et al. 2012; Reuter-Lorenz and Cappell 2008). Much of this research has been guided by examinations of how neural activity differs between younger and older adults on WM tasks, especially as the tasks increase in attentional demand or WM load. There are a number of studies indicating underactivation of task-relevant neural regions in the prefrontal cortex in older adults, whereas other studies have suggested overactivation relative to younger adults (Daselaar and Cabeza 2014; Nagel and Lindenberger 2014; Nyberg et al. 2012; Reuter-Lorenz and Cappell 2008). Underactivation occurs when older adults activate a brain region to a lesser extent than younger adults, whereas overactivation often manifests as bilateral activation of the prefrontal cortex, or activation of the mirror area in the opposite hemisphere in older adults that is unilaterally active in younger adults (i.e., Hemispheric Asymmetry Reduction in Older Adults, or HAROLD (Daselaar and Cabeza 2014)). Both patterns can occur in the same task, especially when WM load is varied: Whereas younger adults show increasing activity with increasing load, older adults show overactivation under low WM loads and underactivation at higher loads relative to younger adults. Underactivation is typically interpreted as an age-related functional deficiency in the processes that rely on the particular neural substrate. The interpretation of overactivation in the HAROLD pattern, however, is less clear than underactivation, primarily due to conflicting results regarding the performance associated with this activity.

Some studies have shown that overactivity is correlated with higher performance in older adults, indicating that the recruitment of additional brain regions may serve a compensatory role in WM and other cognitive functions (Daselaar and Cabeza 2014; Reuter-Lorenz and Cappell 2008). These studies are commensurate with the compensation-related utilization of neural circuits (CRUNCH) hypothesis (Reuter-Lorenz and Cappell 2008). Specifically, in order to meet task demands, older adults recruit more neural circuits than younger adults to compensate for declining neural efficiency. However, older adults appear to reach their maximal capacity of compensatory function at low WM loads, and therefore show underactivation during high loads relative to younger adults. The pattern of overactivation has been linked to successful aging in that older adults who more strongly show overactivation are more likely to exhibit greater WM performance relative to those who do not (Daselaar and Cabeza 2014; Reuter-Lorenz and Cappell 2008). However, others have interpreted the HAROLD pattern as dysfunctional; that is, older adults with preserved WM should be more similar to younger adults in terms of patterns of brain activity (Nagel and Lindenberger 2014; Nyberg et al. 2012). Overactivation may rather be more indicative of increased effort, and those who are successfully aging would not need to recruit additional neural regions if their performance was comparable to that of younger adults. Accordingly, some studies have shown that the older adults with the highest WM capacities had more similar patterns of activation in the prefrontal cortex to younger adults than low performers (Nagel and Lindenberger 2014; Nyberg et al. 2012). Moreover, increasing prefrontal activity was related to increasing WM recall accuracy in younger and older adults when an index of responsivity was considered (i.e., subtracting the signal change in the lowest from that of the highest load). Thus, the causative role of overactivity in regions of the prefrontal cortex in older adults' behavioral WM performance is presently to be determined.

Other research has indicated that WM age differences are not solely localized to the prefrontal cortex. In addition to its interaction with the parietal cortex, the circuitry between the prefrontal cortex and the medial temporal lobe has more recently received much attention. Activity in the medial temporal lobe is more traditionally linked to episodic memory. However, more recent research has suggested that the medial temporal lobe is additionally important during visual-spatial WM tasks, particularly when the tasks involve binding between spatial/pictorial elements of the memoranda (Daselaar and Cabeza 2014). These studies indicated greater age-related underactivation of the hippocampus when the WM tasks explicitly required binding (e.g., an object in its location) relative to maintenance of item-specific information (e.g., just the object or just its location) (Daselaar and Cabeza 2014). Such studies converge with the previously described behavioral studies showing that the age differences in WM may be attributable to older adults' relative inability to bind information in WM (Fandakova et al. 2014; Oberauer 2005a).

Finally, a number of studies have also investigated the functional role of dopamine (DA) activity in the age-related decline in WM. There is much evidence that both presynaptic (i.e., the DA transporter) and postsynaptic markers (i.e., D1 and D2 receptors) deteriorate with increasing age (Nyberg et al. 2012). Among other cognitive functions, age-related decline in D1 receptor binding potential in the caudate nucleus and the prefrontal cortex have been associated with underactivation of fronto-parietal regions and corresponding reduced performance in older adults during WM tasks (Nyberg et al. 2012). Specifically, statistically controlling for D1 binding in the caudate and prefrontal cortex fully mediated the age-related underactivation in the left prefrontal cortex and partially mediated the age-related underactivation in the right prefrontal and left parietal regions (Nyberg et al. 2012). Moreover, simulating older adults' DA activity in young adults by allocating a D1 antagonist induced increased frontal bilateral connectivity in younger adults that significantly predicted WM performance (Nyberg et al. 2012), supporting a compensatory view of the previously described HAROLD pattern exhibited by older adults (Daselaar and Cabeza 2014; Reuter-Lorenz and Cappell 2008).

Training Working Memory

An increasingly important topic in the cognitive aging literature is whether the effects of age-related cognitive decline can be circumvented by training older adults on these cognitive functions, especially WM. Given its aforementioned importance for a wide range of higher-order cognition, many researchers have focused on WM as an access point to generalizing the benefits of increased WM capacity. If WM accounts for substantial age-related variability in other factors (e.g., fluid intelligence), then perhaps training WM could improve older adults' performance in these other cognitive functions (i.e., *far transfer effects*). However, it may also be that the effects of training are only specific to the trained task (i.e., *trained task effects*) or, at best, other measures of

WM capacity (i.e., *near transfer effects*). Finding that WM training does not improve broader cognitive functions would undermine the practical utility of training WM in older adults.

Although rising in popularity, the question of whether older adults' WM capacity can be improved and can show generalizable benefits to other forms of cognition is still not settled. Theoretically speaking, it is not clear which aspects of WM that training actually improves, and further still, how improvements to those aspects bring about improvements in other far transfer tasks. Further complicating matters, assessments of the effectiveness of WM training vary substantially across studies, with some showing massive near and far transfer effects after only several sessions whereas others only indicate improvements to the trained task, but no transfer, even after extensive training. This complication is compounded when one considers the bias toward publishing statistically significant rather than null results, thereby increasing the visibility of training-related gains in the literature that may in actuality overestimate the true effectiveness of training.

A recent meta-analysis of 61 training experiments with older adults who received WM training (Karbach and Verhaeghen 2014) showed significant improvements to performance (i.e., pre- vs. post-test) on the trained tasks (effect size = 0.91), near transfer tasks (effect size = 0.47, corrected for publication bias), and far transfer tasks (effect size = 0.38). Moreover, these improvements were similar to those shown in younger adults and reliably larger than the improvements shown in the active and passive control groups, who generally showed statistically indistinguishable effects. Thus, although the improvements of training WM were largest for the trained tasks, there was still a modest improvement even in tasks representing other cognitive functions (e.g., fluid intelligence, episodic memory).

Conclusions

Although the book is far from closed as to what underlies the age differences exhibited in WM capacity and the construct's importance for other age-related cognition, the field has made important strides toward this goal. A bird's-eye view of the literature taken through meta-analyses helps to identify sources of age-related variability that are correlated with WM capacity, most notably processing speed, and others that are uncorrelated with WM capacity (e.g., task switching). Moreover, age-related declines in inhibitory functions do not go beyond declines in general speed. Together, these findings rule out the task-switching/coordination hypothesis and the inhibition-deficit hypothesis of age-related declines of WM capacity. The speed hypothesis provides at best an incomplete explanation because age-related slowing accounts at best for a part of the age-related decline in WM capacity. A deficit in maintaining temporary bindings is likely to be one factor responsible for that decline. Neuroscience research has shown that older adults recruit WM-related neural networks less effectively when WM is challenged by a high load; at the same time, older adults recruit a larger network at lower levels of load, perhaps to compensate for reduced neural efficiency. Reduced sensitivity to dopamine appears to be one factor responsible for the deterioration of neural efficiency in the WM system. Training studies have yielded promising results showing that performance in WM tests can be improved in old adults as much as in young adults, but it remains an open question how far these training gains transfer to performance in other tasks. These findings collectively demonstrate the importance of understanding age-related changes in WM capacity, especially as they relate to those of other areas in complex cognition.

Cross-References

- ▶ Memory: Episodic
- ▶ Cognitive Control and Self-regulation
- ▶ Brain Training Games
- ▶ Aging and Inhibition
- ▶ Cognition
- ▶ Individual Differences
- ▶ Executive Function
- ▶ Cognitive Resource Theories

- ▶ Process and Systems Views of Aging and Memory
- ▶ Attention
- ▶ Inhibitory Decline Theories of Behavior and Cognition
- ▶ History of Cognitive Slowing Theory and Research
- ▶ History of Cognitive Aging Research
- ▶ Response Time

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