Questions of age differences in interference control: When and how, not if?

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ABSTRACT

Declines in the control of attention and working memory are often considered a core feature of cognitive aging. In particular, the idea that older adults are differentially vulnerable to interference from irrelevant information has played an important but sometimes controversial role in guiding research. However, age differences in performance on measures of interference control are sometimes surprisingly small, and in some cases (e.g., mind-wandering and sustained attention), older adults perform better than young adults. Are age differences in interference control more myth than reality? We consider the evidence in light of neurocognitive frameworks that acknowledge the sometimes complex interactions between age-related declines and compensation. When operations can be performed within the focus of attention, age differences in interference control may be more easily detected in neural measures than behavioral ones, whereas behavioral differences are more likely to occur in tasks that require retrieval of information into the focus. Our analysis suggests that age differences in interference control have multiple sources, but also offer multiple opportunities for compensation and intervention.

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1. Introduction

Failures of attention and memory play a pernicious role in what Schacter has playfully termed “memory sins” – the errors and omissions that plague us not just in the lab but in everyday life. Aging is at least colloquially associated with an increase in such transgressions, to the point that they are often referred to as “senior moments”. In a recent survey of older adults’ everyday memory errors, we found that problems with attention-memory interactions leading to absent-mindedness (forgetting where you put something around the house; forgetting what the sentence you have just read was about and having to re-read it) were among the most frequently reported (Ossher et al., 2013). Age differences in cognitive control also play a critical role in age differences on laboratory tasks and in theoretical explanations of cognitive aging. Below we review some of the major findings on age differences in the control of attention, with particular emphasis on age differences in inhibitory control, and suggest that age differences on tasks that emphasize processing stimuli already in the focus of attention are more likely to manifest on neural measures than behavioral ones, whereas situations that require retrieval of relevant stimuli into the focus of attention place a larger demand on working memory and are therefore more likely to show age-related performance declines.

Although most descriptions of cognitive aging include differences in attention and memory as a central feature, it has proven more difficult to define the nature and extent of those differences in detail. At a broad level, age differences in the controlled aspects of attention and/or the executive components of working memory are typically more pronounced than those associated with automatic processing and passive storage (Hasher and Zacks, 1979; Jennings and Jacoby, 1993), but even this distinction is not absolute. One factor making it difficult to pinpoint the cause and nature of age differences in attention and working memory is that these terms are applied, sometimes interchangeably, to multiple stages and levels of processing – for example in discussing dual-task paradigms, one researcher may call the critical construct “divided attention”, another “executive attention”, whereas yet another refers to it as “working memory”.

Furthermore, regardless of what one calls them, processes operating at different stages interact: Failures in early perceptual and selective attention can have cascading effects as noisy or impoverished stimulus information increases the processing load on downstream higher-level identification, storage, and decision processes. As we will describe further below, an individual experiencing such failures in early perceptual or attention processes may recruit more top-down or executive control processes to compensate, but this often comes at a cost of making those processes less available as task demand (e.g., the strength of decision conflict, the number of distractors, the length of the retention interval, or the number of items to be maintained) is increased. There is an increasing awareness of both cognitive and neural pathways of compensation and that older adults may use alternative strategies and circuits to solve what is nominally the same task (e.g., the scaffolding theory of aging and cognition proposed by Park and Reuter-Lorenz (2009); or the shifts from proactive to reactive control described by Braver et al. (2007)).

Resolving these complexities will take a great deal of empirical and theoretical work and is certainly beyond the scope of this review. Instead, this review is intended to take initial steps in addressing seeming inconsistencies in the effects of age-related decline in attention and working memory processes across the literature. We point to recent developments in our understanding of the components of attention-memory interactions, their mutual influence on aging cognition, and their differential effects on behavioral and neural outcome measures. In doing so, we hope to better define the problem space and address some apparent discrepancies and contradictions in the literature: Why do some studies find large age differences in inhibitory control, whereas others do not? If older adults have reduced cognitive control, why do they often report less mind-wandering than young adults, and do better on many tests of sustained attention? In the final section, we consider the potential implications of our ideas for interventions designed to improve the performance of older adults, and how those intervention studies can in turn provide tests of these hypotheses.

We begin by defining the terms as we use them here. Although we subscribe to the idea that a central part of short-term or working memory is the focus of attention (see discussion in Jonides et al., 2008), for the sake of internal consistency here we use the term “attention” to refer to operations that can occur within that focus without additional retrieval, and “working memory” to refer to situations where representations must be retrieved into the focus. We use the term “control” to refer to those operations (e.g., selection, inhibition and sustaining) that determine the contents of attention and working memory. For the moment, we mean the term “representation” to mean the combination of features making up a perceptual or memorial representation, rather than task or goal representations. However, there is some evidence suggesting that similar principles, especially the amplification of age differences in interference susceptibility when representations must be retrieved into the focus of attention, also apply to task-set representations (see Jackson and Balota, 2013).

2. Aging, attention, and cognitive control: Multiple findings, multiple factors?

Although age differences in attention and cognitive control are at the center of many frameworks of cognitive aging, (e.g., levels of processing; Craik and Simon, 1980; inhibitory deficit theory; Hasher and Zacks, 1988), the behavioral evidence for age-related deficits in these functions is somewhat surprisingly mixed, especially for paradigms that emphasize attention with minimal memory demands. For example, in sustained attention or vigilance tasks, older adults sometimes perform as well or even better than young adults (see review by Staub et al., 2013). The relationship between top-down control demands and age differences is at first counter-intuitive: Older adults are more likely to show deficits on traditional vigilance tasks, which require responding to rare
targets and are thus thought to rely more on bottom-up, alerting aspects of attention than on top-down control processes. In contrast, older adults often perform as well or better than young adults on newer vigilance tasks that require responding to frequent nontargets and withholding response or giving a different response to rare targets. Intuitively, the inhibitory or switching requirements in these newer tasks should place higher demands on top-down control. The differential direction of age differences across these two types of task seems to perfectly contradict the idea that aging is associated with reductions in cognitive control and that those reductions are responsible for age-related deficits on a wide variety of tasks.

This apparent paradox may be easier to capture in more complex frameworks (Selection, Optimization, Compensation (SOC), Baltes and Baltes, 1990; Scaffolding Theory of Aging and Cognition (STAG), Park and Reuter-Lorenz, 2009; Growing Of Lifelong Differences Explains Normal aging (GOLDEN), Fabiani, 2012) that consider multiple levels and stages of processing and the potential that aging may be associated with qualitative as well as quantitative shifts in function. Consider first the case of traditional vigilance tasks. As suggested by Staub et al. (2013), compared to newer vigilance tasks, which emphasize response inhibition, traditional tasks place more emphasis on target detection. Performance on these tasks is therefore more heavily influenced by bottom-up sensory salience, and age-related declines in lower-level sensory and perceptual function may put older adults at a disadvantage. This suggestion is supported by findings indicating that for participants of any age group, performance in general, and the ability to sustain attention over time in particular, is impaired when stimuli are perceptually degraded, and older adults are more vulnerable to these effects (e.g., Parasuraman et al., 1989).

In some cases, older adults may attempt to compensate for age-related perceptual declines by engaging more top-down control (Madden et al., 2007, 2005). The Compensation Related Utilization of Neural Circuits (CRUNCH) framework (Reuter-Lorenz and Cappell, 2008; Reuter-Lorenz and Lustig, 2005) applies a similar idea to cognitive tasks more generally, proposing that older adults engage cognitive control at lower objective levels of task load or difficulty to support performance and are earlier to reach a functional ceiling as load increases. Thus, even though young and older adults are nominally doing the same task, it may place higher demands on the cognitive control processes of older adults.

Findings of relatively preserved or sometimes even better performance by older adults on newer vigilance tasks that emphasize withholding the dominant or ongoing response when the rare target appears (e.g., Brache et al., 2010; Carriere et al., 2010; Jackson and Balota, 2012) seem more puzzling, and potentially quite troubling for the suggestion that inhibition is an area of particular difficulty for older adults. However, a closer look provides some explanation. First, although these tasks require restraint of a strong response, they make minimal requirements on working memory, and in particular the inhibition demands appear to be largely at the response level rather than representing a failure to prevent irrelevant information from entering or remaining in the focus of attention, the core deficit proposed by inhibitory deficit theory (Hasher and Zacks, 1988; Lustig et al., 2007). Second, the response patterns of older adults suggest a qualitative age difference rather than a purely quantitative one. Specifically, older adults often show different speed-accuracy tradeoffs in these tasks, with slower response times but fewer errors than young adults (see discussion by Carriere et al., 2010). This suggests that older adults may compensate for difficulties in some aspects of control (i.e., restraint of the strong response) by engaging control at a different level, changing strategies to reduce demands on immediate restraint.

These patterns of deficit, compensation, and qualitative differences in processing described above likely extend beyond sustained attention to a wide variety of attention and working memory tasks. In many cases, these differences in processing by older adults may allow them to maintain surprisingly similar levels of performance compared to young adults. For example, as described above declines in executive function are a major component in many theoretical frameworks of aging cognition, but a review of meta-analyses conducted by his lab led Verhaeghen (2011) to describe the state of executive functioning in older adults as a “demise greatly exaggerated”. He noted that although age differences in response time are often greater for tasks with high rather than low executive demand in absolute terms, these differences are much smaller or even nonexistent when analyzed using Brinley-plot measures: a method which examines performance as a change ratio. In particular, by this metric he found little evidence for an age-related decline in interference control/inhibition and local task-switching, and reliable but small differences in dual-tasking and global task-switching costs.

The results of these meta-analyses are impressive, but a conclusion of no age differences in inhibitory control may also be a bit exaggerated. As noted above, complex patterns of deficit and compensation in older adults can lead to similar performance as young adults but with different processing. In particular, the studies included in these meta-analyses primarily used relatively simple attention tasks that can be performed within the focus of attention and require minimal working-memory retrieval, and relied on central-tendency (mean and median) measures of response time. In contrast, the involvement of working memory and in particular competition between similar items for entry into the focus of attention were a critical part of the original inhibitory deficit theory as proposed by Hasher and Zacks (1988), and some of the strongest evidence for this view has come from measures of accuracy.

In the following section we review the evidence suggesting that when tasks can be performed within the focus, age differences in inhibitory control may be more obvious in neuroimaging measures, whereas when the task requires retrieval into working memory, they can also often be seen in behavior. Here we first review some of the other factors that should be considered when evaluating potential age differences in attention and working memory, focusing on the question of inhibitory control.

The first issue is one of definition. As others have noted (e.g., Aron, 2007), the terms “inhibition” and “interference control” have been applied to a wide variety of functions that have some fundamental differences both conceptually and
empirically, and it has been known for some time that several of these functions do not show large age differences (e.g., Friedman and Miyake, 2004; Kramer et al., 1994). For some tasks, such as the inhibition of return (slower return to a cued position), it is questionable whether they conform with the usual understanding of executive function as “A top-down system that manages and controls other cognitive processes, allowing goal-directed behavior” (Sharman, 2012), rather than more automatic processes, and thus the lack of age differences may not be surprising. Likewise, Kane et al. (1997) pointed out that in many cases of negative priming, another task frequently used to measure inhibitory control, processes are largely automatic – even out of the participant’s awareness - and may rely on processes other than inhibition.

Other inhibitory control tasks, such as the flanker, Stroop, and reading with distraction tasks, are arguably more closely related, as all involve the presentation of some target and irrelevant visual information. In the aforementioned meta-analysis, only reading with distraction showed an exaggerated effect with age. As Verhaeghen (2011) noted, a smaller number of studies here raise some questions about the difference in results. However, reading with distraction also differs from the other two tasks in potentially important ways: (1) the predictability of the distractors’ spatial location, (2) whether distractors are in frank conflict with the target or similar and potentially confusable (see especially Buetti et al. [2014]), and (3) a greater demand on working memory due to the need to retrieve information in order to integrate information across sentences, whereas the flanker and Stroop tasks require resolving conflict within the focus of attention. Conditions such as spatial predictability that make the target and distractor information distinct from each other and thus less likely to be confused provide a form of environmental support that reduces inhibitory demands and thus insulates the performance of older adults (i.e., Carlson et al., 1995; see also Hasher et al., 2001 for discussion of environmental support and inhibitory demands as explanatory constructs in cognitive aging).

To summarize, what at first seem like contradictory findings – poor performance on some vigilance tasks but preserved or even better performance on others; controversies over whether or not there are age deficits in inhibitory control – may be reconcilable within more complex frameworks that consider factors such as the use of top-down control to compensate for failures in bottom-up processing (and the costs of this for other operations requiring top-down control) and the impact of environmental support. Next we turn to the possibility that especially when demands on retrieval are low, age differences in inhibition (and other forms of cognitive control) may be more evident in measures of neural activity than behavior. From a theoretical perspective, however, standard behavioral measures of mean or median accuracies and response times often provide a limited window into cognitive processing – although an increased emphasis on distribution and variability analyses (see discussion by Balota and Yap (2011)) can provide more detailed and specific information about underlying processes. Many recent explanations of cognitive aging, especially those incorporating a neuroscience perspective, emphasize the interactions of multiple processes and stages of processing. The same final behavioral outcome (accuracy score or median RT) might have been reached in very different ways by different groups or individuals.

For example, older adults often fail to engage control proactively, but may compensate for this (not always with complete success) retroactively at later processing stages (Braver et al., 2007; Dew et al., 2012; Velanova et al., 2007). As noted earlier, the Compensated Related Utilization of Neural Circuits (CRUNCH) framework suggests that older adults may engage control at lower levels of task load to preserve performance, making age differences undetectable in behavioral measures (unless one uses a “testing the limits” approach) despite large differences in underlying processing (Reuter-Lorenz and Lustig, 2005; Reuter-Lorenz and Cappell, 2008). Others have noted that these tradeoffs do not affect only older adults but are present throughout lifespan, between individuals with different cognitive profiles, and even within the same individual on a short-term basis as a function of variation in factors such as motivation, fatigue, or sleep deprivation (e.g., SOC, STAC, and GOLDEN).

Even when older adults do not show (differential) behavioral impairments, neural measures often indicate impaired or at least differential processing. Importantly, with regards to potential inhibitory deficits in older adults this may manifest in different ways depending on the type and level of inhibitory demand. In what they called the “expanded inhibitory deficit theory” Dennis and Cabeza (2008) described one potential pattern: Compared to young adults, older adults may show decreased activation in regions associated with inhibitory control (e.g., Jonides et al., 2000), but increased activity in regions that are the targets of that control (e.g., Gazzaley et al., 2005). Interestingly, although each result (decreased activation of inhibitory regions and increased activation of their targets) is frequently reported separately, most reports of both results in the same dataset have the default network as the target of inhibitory control (e.g., Persson et al., 2007; Prakash et al., 2012). As an alternative possibility, based on their meta-analysis findings, Turner and Spreng (2012) proposed that inhibition in older adults was associated with a “young plus” pattern – older adults activated similar inhibitory control regions as young adults (particularly right inferior frontal gyrus), but to a greater degree. This pattern might suggest that older adults find it relatively more demanding to engage inhibitory control, even if their performance is not (differentially) impaired.

3. Neuroimaging insights on inhibitory and executive declines

From a practical perspective, one can argue that what matters is whether older adults show a pattern of preservation, decline, or differential decline (i.e., greater than in other abilities or predicted from overall slowed responding) in behavior. From a theoretical perspective, however, standard behavioral measures of mean or median accuracies and response times often provide a limited window into cognitive processing – although an increased emphasis on distribution and variability analyses (see discussion by Balota and Yap (2011)) can provide more detailed and specific information about underlying processes. Many recent explanations of cognitive aging, especially those incorporating a neuroscience perspective, emphasize the interactions of multiple processes and stages of processing. The same final behavioral outcome (accuracy score or median RT) might have been reached in very different ways by different groups or individuals.

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In contrast, studies manipulating working memory load via variables such as the number of items suggested age differences in network recruitment, with young adults recruiting some areas more than older adults and vice versa.
Sebastian et al. (2013) provided an interesting test of this hypothesis by testing adults age 22–77 years on three tests chosen to vary inhibitory demand: Go/No-Go (the response given on frequent nontarget trials should be withheld for rare target trials; relatively low inhibitory demand), Simon (overcome a habitual response tendency; medium inhibitory demand); and Stop-Signal (cancel a response already in motion; high inhibitory demand). In the Go/No-Go task, which had the lowest inhibitory demands, age correlated with “go” response times, suggesting a possible speed-accuracy tradeoff, but not with the commission errors that are the usual index of failed response inhibition in this task. In the Simon task, age correlated with both overall response time and the Simon effect. (Note that all analyses used z-transformed response times to correct for generalized slowing, see Faust et al., 1999). In both of these tasks, age also showed a positive relationship with activation in regions associated with inhibitory control. In contrast, in the Stop-signal task, age was associated with more commission errors as well as longer stop-signal RTs, and with reduced activation of inhibitory-control regions. As the authors noted, this suggests a CRUNCH-like pattern, with older adults engaging control at lower levels of inhibitory demand but at the cost of slowed responding and greater activation, but reaching a functional ceiling as demand increases, making them more vulnerable to errors.

Although many studies of age differences in inhibitory control focus on frontoparietal networks, age differences are also seen in early sensory processing and likely both contribute to increased demands on control and reflect impairments in that control. Reductions in sensory function starting at the periphery in older adults can reduce the fidelity and discriminability of representation. In turn, items that are harder to discriminate from each other are more likely to compete with each other for the focus of attention, increasing vulnerability to interference and demands on top-down control. In the other direction, evidence especially from ERP studies indicates that in older adults the top-down suppression of distractor processing is impaired at very early stages in the processing stream (e.g., Fabiani and Gratton, 2005; Fabiani et al., 2006; Gazzaley et al., 2008). These suppression deficits often correlate with reduced working memory for the target items, further confirming their role in interference. Although they do not have the same temporal sensitivity, fMRI analyses (e.g., Carp et al., 2011; Park et al., 2012) also indicate less specialized representations in regions associated with higher-level visual processing such as the so-called “fusiform face area” and “parahippocampal place area”.

As mentioned above, in some cases, older brains may compensate for sensory or cognitive-control deficits at earlier stages of processing by increasing activation and engagement of control at later stages. Rather than a simply slowed engagement of the same cognitive control processes used by young adults, there is often a qualitative shift suggesting multiple mechanisms of cognitive control that are differentially engaged by younger and older adults (Braver et al., 2007; Paxton et al., 2008). That is, older adults often engage frontoparietal control networks at different task or processing stages and in response to different cues than do young adults. For example, in task-switching studies, young adults often show greater frontoparietal engagement at the cue signaling an upcoming task change, whereas older adults show greater engagement at the probe item that requires a response (Bugg, 2014; Braver et al., 2007; Martins et al., 2012; see Dew et al., 2012 for similar patterns in a memory-retrieval context). These “load shifts” from early to late processing operations by older adults appear to be especially likely under situations of high demand (Czernochowski et al., 2010; Dew et al., 2012; Velanova et al., 2007).

In summary, measures of neural activity indicate that even in cases where older adults show preserved or at least not differentially-impaired behavioral performance compared to young adults, there may be quite large differences “under the hood”. Peripheral sensory declines may reduce the discriminability of representations and make them more confusable, increasing the likelihood that they will cause interference, and reduced top-down control of sensory function can exacerbate these problems. In the face of the increasing demands imposed by these sensory declines or by task manipulations, older adults often show differential engagement of control, with these differences reflected in amount (greater activation of frontoparietal control networks), location (engagement of regions not engaged by young adults, at least not at that level of demand), and timing (a bias towards greater activation at later, reactive processing stages). However, as demand increases further, these mechanisms may be overwhelmed, resulting in a more global pattern of reduced frontoparietal activation. One hypothesis for future research is whether the first pattern (later and greater activation of cognitive-control networks) is more likely associated with increased response times, whereas the second (reduced activation of such networks) may be more associated with an increase in errors.

4. Mind-wandering and the default network in aging: a case study in complexity

In addition to external stimuli as described above, interference and distraction may arise from internal off-track thoughts. Increases in off-track thoughts and mind-wandering are often thought to be the result of decreased task focus and cognitive control. Although it is not necessarily a one-to-one relationship, generally speaking mind-wandering is thought to be related to activity in a “default network” (Raichle et al., 2001) that is in opposition (“anticorrelated”) with task-active frontoparietal networks (Fox et al., 2005). Given that older adults are typically thought of as having reduced cognitive control compared to young adults, and that neuroimaging evidence suggests that they often suppress the default network during task performance less than young adults do (e.g., Grady et al., 2006; Lustig et al., 2003), the intuitive prediction is that older adults should show more mind-wandering and off-track thought than do young adults. However, a great deal of behavioral evidence suggests otherwise.

How can this be? The answer may lie in the balance of age-related impairments and compensation suggested by the Scaffolding Theory of Aging and Cognition (STAC), Growing Of Lifelong Differences Explains Normal aging (GOLDEN), and
other more complex frameworks of neurocognitive aging and serve as an example of their utility. First, both structural and functional connectivity analyses suggest that the default network itself is impaired or less coherent in older adults, as is its connectivity to frontoparietal control networks (e.g., Damoiseaux et al., 2008; Andrews-Hanna et al., 2007; Spreng and Turner, 2013). Thus, its output may be reduced or less coherent and able to be articulated on the types of questionnaire measures often used to assess mind-wandering.

Second, mind-wandering is thought to occur most often when the central task is not demanding enough to fully engage attention. If older adults engage more attention and cognitive control to perform the main task, as suggested empirically by greater frontoparietal activation and theoretically by CRUNCH and other models, they have less opportunity for mind-wandering. This may be especially the case when the task provides a constant stream of input that occupies the focus of attention, as in the SART and reading tasks used in most studies reporting reduced mind-wandering in older adults. Supporting this idea, Krawietz et al. (2012) found that controlling for older adults’ greater interest in the reading material statistically eliminated age differences in mind-wandering.

The constant inputs used in the SART and reading tasks used in these behavioral studies of mind-wandering contrast with the task conditions in most fMRI studies showing that reduced deactivation of the default network is associated with poor performance. The latter most often use memory or working memory tasks that require retrieving information from episodic or semantic memory into the focus of attention (e.g., Park et al., 2010; Persson et al., 2007; Prakash et al., 2012; Sambataro et al., 2010). This may allow more opportunity for off-track thoughts to enter the focus of attention and disrupt performance. Although we are not aware of an fMRI study of aging and default-network activation that uses online or questionnaire assessments of mind-wandering during the task, Stevens et al. (2008) found that connectivity between the default network and auditory cortex regions mediating distraction from scanner noise was related to poor memory performance in older adults.

To summarize, the seemingly contradictory findings of age-related reductions in both reports of mind-wandering and deactivation of the default network may result from interactions between different tasks and networks. In the tasks often used to assess mind-wandering in behavioral studies, the relatively greater demands on cognitive control for older adults may actually protect them from mind-wandering. The primary task engages attention more fully, leaving less opportunity for mind-wandering, and disrupted connectivity both within the default network itself and with frontoparietal networks may also reduce the degree to which off-track processing emerges to conscious thought. In contrast, age differences in default network deactivation may be related to reduced performance when the primary task requires retrieval into the focus of attention, opening an opportunity for those off-track thoughts (whether they arise internally or are sparked by external distraction, as suggested by Stevens et al., 2008) to compete.

5. Increased interference in older adults: When, not if?

The idea that older adults have more difficulty inhibiting irrelevant information or responses has been both influential and controversial for over 25 years. At the behavioral level, there is a wealth of evidence on both sides: As described above, there is often a lack of large age effects, or at least a lack of a differential age-related reduction in inhibitory performance, on tasks such as Stroop that have strong face value as inhibitory measures (but see Buetti et al. (2014) for an interesting alternative interpretation). On the other hand, there is also a large body of studies demonstrating that older adults are more influenced by putatively irrelevant information, both in positive and negative ways (see Weeks and Hasher (2014) for a recent review).

Given the large age differences and changes (not necessarily in the same regions, see Raz et al. (2010)) in both the white and gray matter of the frontoparietal regions thought to underlie inhibition and other cognitive control functions (see Salami et al. (2014) for a recent study specifically targeting structural and functional correlates of age differences in inhibition), it would be quite remarkable if there were no age deficits in those functions. Indeed, a meta-analysis by Yuan and Raz (2014) found that interference control was one of the constructs showing the strongest relationship with prefrontal volume. Thus, unless one wants to take a dualist perspective, the question of interference-control deficits in aging might be more properly phrased as “when” and “how” rather than “if”.

We suggest that one factor influencing those “when’s and “how’s” may be the degree to which the task involves continuous, ongoing processing that can be performed largely within the focus of attention versus requiring retrieval into that focus. As reviewed above, age differences in behavior appear to be less likely (and sometimes even reversed) in the former situation, such as Stroop, flanker, and mind-wandering tasks. In such cases, age differences may be less evident in typical central-tendency measures of response time and accuracy, although they may be detectable in behavior using more sophisticated variability or distribution analyses (e.g., Spieler et al., 1996). Age effects on these types of task are often more evident in neural measures, at least at lower levels of inhibitory demand. As suggested by frameworks like CRUNCH and results like those of Sebastian et al. (2013), as demands for interference control increase older adults show greater increases in frontoparietal activation and response time, as well as patterns indicating a shift from proactive to reactive control, until reaching a “crunchpoint”, at which young adults’ activation supersedes older adults’ and older adults’ interference vulnerability may start to manifest more in errors.

In contrast, older adults are much more likely to show both positive and negative effects of putatively irrelevant information when the situation requires retrieving information into the focus of attention. For example, older adults benefit more than young adults on working memory, long-term memory, and problem-solving tasks when target information for the critical test is presented as a distractor on a prior test, suggesting that older adults were more likely to
The centrality of attention and working memory to cognitive aging has made them attractive targets for training (e.g., Stepankova et al., 2014; see reviews by Backman and Nyberg, 2013; Lovden et al., 2010; Lustig et al. (2009)). Patterns of improvement and transfer in these interventions also provide clues as to the mechanisms that underlie age effects on cognition. For example, cardiovascular training appears to have its largest effects on executive control (Colcombe and Kramer, 2003), and as expected these effects are mediated by changes in frontoparietal structure and function (e.g., Colcombe et al., 2006; Voss et al., 2013). There is some suggestion that some inhibitory functions, especially the restraint of habitual responses, benefit from strength/resistance training, although potential mechanisms of this remain unclear (Forte et al., 2013; Liu-Ambrose et al., 2010).

A literature search reveals only a few cognitive-training studies specifically targeting interference control in older adults, but they generally fit with a major theme in the training literature (see Lustig et al. (2009) for review): Successful transfer depends on adaptive training programs that develop cognitive processes by gradually increasing demands on those processes rather than task-specific practice or strategies, and on transfer tasks with substantial overlap in those processes and brain mechanisms (e.g., Dahlin et al., 2008). Transfer’s dependence on processing overlap makes it especially critical to consider age and individual differences in different processing components (e.g., bottom-up versus top-down attention) or stages (early stages involved in perceptual selection versus later stages involved in restraint and response control) on both the training and transfer tasks.

This processing-overlap dependence may help explain some of the successes and failures in finding transfer already reported in the literature. For example, Wilkinson and Yang (2012) found that older adults improved performance on Stroop over six sessions, but did not find transfer even to other putative inhibition tasks, perhaps because they tapped different aspects of inhibitory control (control of access to working memory vs restraint of strong responses). In contrast, Berry et al. (2010) found that training perceptual discrimination affected an ERP component (N1) related to early sensory processing and transferred to both interference and non-interference versions of a working memory task. The transfer to interference resistance is especially interesting as it supports the idea that bottom-up difficulties discriminating between representations increase interference on working memory tasks. O’Brien et al. (2013) addressed these factors more directly by adaptively increasing difficulty along a number of dimensions including the number of distractors, and found transfer to an independent visual attention task, along with changes in ERP components related to the control of attention (N2pc and P3b). Together these findings suggest that older adults’ difficulties with interference have multiple sources, and may therefore be addressed through multiple pathways. In addition, they demonstrate the sensitivity of neural measures to training effects and point to the particular usefulness of ERP components in helping to identify the stages of processing that show training-related change.

In addition to exercise and cognitive training interventions, there is an emerging interest in noninvasive brain stimulation (NIBS) methods including transcranial magnetic stimulation (TMS) and transcranial direct current stimulation (tDCS). Thus far only a few studies have addressed working memory in healthy older adults. Taken together, they suggest that stimulation of right prefrontal cortex – an area often associated with inhibitory function (see review by Aron et al. (2014)) – may increase error awareness (Harty et al., 2014) and thereby improve the performance of older adults likely to already be using successful strategies but disrupt the performance of those who are not (Berryhill and Jones, 2012). Further suggesting that NIBS may serve to enhance already-effective processing, Park et al. (2014) found that the effects of encode/less likely to suppress that information in the prior stage (e.g., Biss et al., 2013). As noted earlier, starting from sensory inputs, older adults’ representations may be more cluttered (or ‘richer’, to put a positive spin on it) than those of young adults, and less distinct. As a result, older adults are both less likely to show strong bindings between items and the specific contexts in which they occur and more likely to include related but irrelevant items or features in their representations (Campbell et al., 2014; Fandakova et al., 2014). These are then available to and compete for the focus of attention at later retrieval, and neural evidence also suggests that older adults’ re-activated memory representations are less stimulus-specific than young adults’ (St-Laurent et al., 2014), allowing further opportunity for competition and interference. Across multiple trials, especially with related stimuli, these effects may “snowball” to further increase age differences, as during retrieval young adults suppress related competitors more efficiently than do older adults (Healey et al., 2013).

Besides this major division, a number of other variables influence the size of age differences in inhibition and interference control. One often-overlooked factor in whether nontarget items will cause interference is whether they are similar to the target item in a way that allows them to compete for the focus of attention. If nontargets are made very distinct from targets – for example, by a distinct and predictable spatial location, or with a very different appearance - they typically do not cause competitive interference (e.g., Connelly and Hasher, 1993; Wnuczko et al., 2012). However, if a later cue fits an item that was previously presented as a distractor, older adults are more likely to produce that item, especially if the test is an implicit one (e.g., Biss et al., 2010; Kim et al., 2007; Thomas and Hasher, 2012). Time of day can also play a role in the size of age differences: Most older adults are “morning types” who perform better in the morning than in the evening, and inhibitory function appears to be especially influenced by these circadian rhythms (Anderson et al., 2014; May and Hasher, 1998).

Finally, Guerreiro et al. (2010) have proposed that sensory modality may play an important role, although modality effects do not interact consistently with age and it is unclear what the boundary conditions might be (Guerreiro et al., 2012, 2013, 2014).

6. Interventions and training

The centrality of attention and working memory to cognitive aging has made them attractive targets for training (e.g., Stepankova et al., 2014; see reviews by Backman and Nyberg, 2013; Lovden et al. (2010); Lustig et al. (2009)). Patterns of improvement and transfer in these interventions also provide clues as to the mechanisms that underlie age effects on cognition. For example, cardiovascular training appears to have its largest effects on executive control (Colcombe and Kramer, 2003), and as expected these effects are mediated by changes in frontoparietal structure and function (e.g., Colcombe et al., 2006; Voss et al., 2013). There is some suggestion that some inhibitory functions, especially the restraint of habitual responses, benefit from...
cognitive training were increased by bilateral prefrontal tDCS. Like most stimulation studies, they did not speculate in detail about the cognitive processes underlying their effects. However, it is interesting to note that their effects were largely confined to working memory tests and especially evident on accuracy measures. Taken together with the findings of Harty et al. (2014) and Berryhill and Jones (2012), one possibility is that right prefrontal tDCS enhances error awareness so that older adults who have effective strategies to prevent errors begin to employ them. Speculating further, it may also enhance plasticity by increasing the salience of the prediction errors thought to underlie reinforcement learning (see discussion of such errors by O’Doherty et al. (in press)).

In the process of revising this paper, a reviewer challenged us to take a more prospective view in connecting our points about the necessity of complex frameworks for understanding age differences in attention and working memory, and especially the distinction we draw between operations performed within the focus of attention versus those requiring retrieval into that focus, with implications for training. Since (to our knowledge) that distinction is relatively new, most training studies are not framed in a way that provides a direct test of the idea. However, we tentatively suggest the following: Training regimens that focus on enhancing perceptual discriminability (e.g., Berry et al., 2010; O’Brien et al., 2013) should improve performance on tasks within the focus of attention (if there are age differences) and lead to increases in neural activity measures associated with increased perceptual saliency but decreases in measures associated with (especially late-selection) cognitive control. By making the items to be retrieved from working memory less confusable, they may also enhance performance (especially response time) and reduce cognitive-control activations in tasks that require such retrieval. However, we would expect such transfer to be largely limited to the features (Berry et al., 2010) or dimensions (O’Brien et al., 2013) on which discriminability was improved.

In contrast, to the extent that prefrontal (especially right prefrontal) stimulation acts by improving error awareness, it would be expected to show improvements largely on tasks where late-stage filtering of the correct items from memory into the focus is critical, and possibly on tasks involving response restraint. Neural activation measures associated with cognitive control would be expected to increase, although whether those effects would be seen more in neural correlates of proactive (early stage error prevention) or reactive (late-stage error correction) may depend on the task and individual. As these control processes are typically considered more domain-general, transfer benefits would not be expected to show the same stimulus or dimension-bound properties as those we predict would occur with perceptual discrimination training.

7. Conclusions

Although declines in attentional control and working memory are often considered a central feature of cognitive aging, and inhibitory control may be an area of particular vulnerability, some have questioned whether older adults are really differentially impaired on those fronts. In some cases (e.g., mind-wandering) older adults may actually show less vulnerability than young adults. We have suggested that in tasks that involve applying controlled processing of items already in the focus of attention, age differences are more likely to be seen in neural measures, whereas behavioral differences are more likely when the task requires retrieval into the focus. In such cases, age-related vulnerabilities to interference can arise from both bottom-up and top-down sources governing the discriminability of representations and selection between them. Although these multiple sources of vulnerability pose challenges both to older adults and those who wish to understand cognitive aging, they also provide multiple targets for intervention and training.

References


