

Memory: Behavior and Neural Basis

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WHAT IS MEMORY, AND WHAT IS AGING?

A Martian attempting to understand the human condition might be rather baffled to discover that we use the same term—“memory”—to describe the processes that allow us to ride a bicycle, know that the sound “bahy-si-kuhl” refers to that contraption, recount the story of our last ride, and successfully meet our friends at the correct time and place for the next journey. Likewise, as discussed in Chapters 1–3,

“aging” is a complex, multidimensional term that varies in both its theoretical scope and in how it is operationally defined across studies (e.g., healthy vs. normal vs. preclinical; cross-sectional vs. longitudinal; chronological age as time from birth vs. time to death).

Despite these complexities, a review of some of the major meta-analyses of different aspects of memory and aging (Bopp & Verhaeghen, 2005; Fleischman & Gabrieli, 1998; Henry, MacLeod, Phillips, & Crawford, 2004; Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995;

Uttl, 2011; Verhaeghen, Steitz, Sliwinski, & Cerella, 2003) reveals several consistent themes. From a task perspective, major factors influencing the presence and size of negative age differences include demands on controlled versus automatic processing, demands for associative versus item processing, and the opportunity for use of environmental support or compensation. Age-related declines are not uniform in size, nor are they universal—especially in the domains of prospective memory and emotional memory there is an increasing emphasis on findings indicating preserved or even better performance by older adults. As research increases on genetic and lifestyle influences on aging, as well as on interventions to preserve and improve the performance of older adults, there is a corresponding emphasis on understanding the component processes and biological mechanisms that underlie memory performance and individual differences in their efficiency and use.

Below we start with a brief discussion of the major findings on age-related memory preservation and decline and how they may be related to different brain structures. This discussion starts from the traditional systems' view of different types of memory that has guided much of this research. Such views provide an easy introductory framework, but upon closer examination quickly prove inadequate for describing the complexity of findings. In recent years, the field has increasingly moved to a consideration of how different processes that may be implicated in a variety of memory tasks are affected by age as well as situation factors.

BRAIN AGING AND MEMORY: A COMPLEX AND DYNAMIC RELATIONSHIP

At a broad level, patterns of structural brain change follow a “front to back” or “last in, first out” pattern (Raz, 2000). That is, the prefrontal

areas that are among the last to reach full maturity are also those that show the earliest age-related decline, whereas posterior sensory regions that reach mature states within the first few years of life show relatively little decline in healthy aging. Studies of the hippocampus and medial temporal regions most strongly associated with episodic memory have yielded mixed results, with the head and body more likely to show age differences than the tail (Gordon, Blazey, Benzinger, & Head, 2013).

These patterns fit well with a broad view of age differences in memory. Working memory tasks that require the executive functions supported by prefrontal cortex show large age-related declines, whereas declines in sensory memory and passive short-term storage, which rely primarily on the activation and maintenance of representations in posterior cortex, are relatively small. In episodic memory, simple item recognition shows only minor declines, with the size of age-related declines increasing with demands for prefrontal control processes (e.g., free recall) and association processes that depend on the hippocampus and other medial temporal lobe structures. In contrast, semantic memory is preserved and may even increase until the final decades of life, consistent with the relatively preserved volume of the anterior temporal lobes (Taki et al., 2011).

However, the picture quickly becomes more complicated when looking at a finer grain of detail. For example, although the word retrieval might be considered an index of semantic memory, tip-of-the-tongue errors are a common complaint for older adults, and appear to be linked to age-related declines both in regions involved in phonological processing—which may increase the likelihood of such errors—and prefrontal regions involved in the selection and inhibition processes needed to resolve them (Galdo-Alvarez, Lindin, & Diaz, 2009; Shafto, Burke, Stamatakis, Tam, & Tyler, 2007). There is also substantial regional heterogeneity in the patterns of age-related volume differences and

change. For example, [Raz, Ghisletta, Rodrigue, Kennedy, and Lindenberger \(2010\)](#) found that lateral prefrontal cortex showed substantial cross-sectional age differences but little longitudinal change, whereas orbitofrontal cortex had the opposite pattern. Of course, gray matter volume changes are only one aspect of brain aging; changes in white matter volume, integrity, and connectivity and in neurotransmitter function also play important roles (see Chapter 6 on plasticity).

Rather than a simple mapping of types of memory task (e.g., working memory, episodic memory, semantic memory) to specific brain systems, a neurocognitive approach to age effects on memory considers that any memory task requires multiple processing components ([Cabeza & Moscovitch, 2013](#)) and that young and older adults often differ not only in the efficiency of specific components but also the degree to which they rely on them. Not surprisingly, these differences are reflected in measures of brain function, and one of neuroimaging's most compelling contributions to research on aging is the rejection of a simple "lesion" model in which older adults' brains are characterized by reduced activity, especially in prefrontal regions associated with cognitive control.

Instead, especially in memory tasks (working memory tasks with exceptionally high executive demands may be an exception), older adults often show more activation, especially of prefrontal regions, and this is often associated with better performance within the older adult group ([Cabeza et al., 2002](#); [Reuter-Lorenz, Stnczak & Miller 1999](#); [Rosen et al., 2002](#); see [Eyler, Sherzai, Kaup, & Jeste, 2011](#), for a review)—though some longitudinal studies suggest that this pattern may be driven by a subset of participants ([Nyberg et al., 2010](#)) or even reflect impending decline ([Persson et al., 2006](#)). There are a number of frameworks describing age-related differences in activation and their links to behavior, some emphasizing

specific spatial or temporal patterns (e.g., HAROLD (Hemispheric Asymmetry Reduction in the Old), [Cabeza, 2002](#); PASA (Posterior to Anterior Shift in Aging), [Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008](#); ELSA (Early to Late Shift in Aging), [Dew, Buchler, Dobbins, & Cabeza, 2012](#)), and others the interactions between external task demands and internal processing and activations (e.g., CRUNCH (Compensated Related Utilization of Neural Circuits Hypothesis), [Reuter-Lorenz & Cappell, 2008](#); STAC (Scaffolding Theory of Aging and Cognition), [Park & Reuter-Lorenz, 2009](#); GOLDEN (Growing of Lifelong Differences Explains Normal aging), [Fabiani, 2012](#)).

CONTROL AND ASSOCIATION: MAJOR INFLUENCES ON AGE DIFFERENCES IN MEMORY

Despite these complexities, it is possible to derive consistencies in the interactions between memory and aging—especially when one takes the perspective of examining components that may play into multiple memory systems, as described above. Here we summarize some of the major themes driving research on memory and aging. In some cases age differences in neural structure and function have a fairly straightforward relationship to differences in memory performance, but in others they suggest that age differences in memory processing may be quite a bit more complex than suggested by typical central-tendency measures of accuracy or response time.

The Controlled Processing Paradox: Important and Impaired

At a heuristic level, older adults often perform as well as young adults on memory tasks that rely largely on automatic processing, and the young-adult advantage increases with demands on controlled processing ([Jennings](#)

& Jacoby, 1993; Spencer & Raz, 1995). In addition to having reduced cognitive control, older adults are often more reliant on top-down control at earlier stages of processing and lower levels of task difficulty, possibly in partial compensation for sensorimotor deficits (Carp, Park, Hebrank, Park, & Polk, 2011; Fabiani & Gratton, 2005; Fabiani, Low, Wee, Sable, & Gratton, 2006; Gazzaley et al., 2008).

Repetition priming (facilitated or biased processing as a result of prior exposure) is a prototypical example of automatic processing: It occurs even if the participant is not consciously aware of the connection between the prior exposure and current task. As expected, it is largely preserved in aging, but even here there is some variance in control demands and age differences: simple identification and decision priming tasks (e.g., faster perceptual or semantic decisions for repeated than novel stimuli) rarely show declines in healthy adults, and it has been suggested that when impairments are found, they indicate subclinical or impending dementia (Fleischman, 2007). In contrast, age differences are more frequently found on tasks that require more controlled processes such as production or selection among competing alternatives (e.g., category exemplar production or word stem completion where the stems have multiple potential completions in addition to the target). As is also the case on explicit memory tasks, older adults are more impaired by interference from such competing alternatives (Ikier, Yang, & Hasher, 2008; Lustig & Hasher, 2001).

As in behavioral studies, age differences in priming-related neural activity reductions are influenced by control demands. Furthermore, stimulus repetition can have independent effects on different brain regions and networks (Wig, Buckner, & Schacter, 2009), not all of which contribute to behavioral priming effects. For example, Lustig and Buckner (2004) reported that older adults had similar repetition-related reductions in left inferior frontal cortex during a semantic decision task, and that these activity

reductions correlated with response-time reductions, indicating functional significance. This basic finding replicates across studies that use similar tasks (Ballesteros, Bischof, Goh, & Park, 2013; Bergerbest et al., 2009; Gold, Andersen, Jicha, & Smith, 2009; Soldan, Gazes, Hilton, & Stern, 2008), although some of these have found age differences in other areas, especially right prefrontal and inferior temporal regions that may have reflected engagement and repetition-related change in compensatory processing. Such compensatory processing may be especially prevalent in studies that used relatively simple (e.g., MMSE score cutoffs) rather than extensive screens for subclinical dementia (see discussion by Fleischman, 2007). As noted earlier, tasks such as word stem completion that require selection among competing alternatives are more likely to show behavioral differences, and they likewise are associated with age differences in the neural correlates of priming (Bäckman et al., 1997; Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2005).

Other aspects of nondeclarative memory (e.g., procedural memory, probabilistic learning) follow the same pattern. Older adults show generally preserved benefits from experience, but age differences in behavioral and neural effects grow with demands on controlled processing or the possibility for competing alternatives, and similar behavioral patterns for young and old adults can mask substantial differences in neural activity and brain volume (Fera et al., 2005; Howard & Howard, 1992; Kennedy, Rodrigue, Head, Gunning-Dixon, & Raz, 2009). Put in more neural terms, the likelihood of age-related deficits increases the more that experience-related change *depends on* regions (e.g., prefrontal cortex, striatum, medial temporal lobe) associated with controlled processing and age-related decline rather than *reducing demand on* those regions (see Howard & Howard, 2013, for discussion relevant to procedural learning).

Controlled and automatic processing also show different patterns in episodic memory,

where distinctions are made between *familiarity*—the subjective feeling that the item or event has been previously experienced, and *recollection*—the retrieval of details associated with that previous experience. Familiarity is usually considered to rely on automatic processes, whereas recollection is most often characterized by controlled, effortful retrieval (see reviews by [Wixted, 2007](#); [Yonelinas, 2002](#)). One caveat to this distinction is that recollection also has a less-discussed automatic form (“noncritical recollection,” or details that come to mind spontaneously; [Yonelinas & Jacoby, 1996](#)). At the behavioral level, older adults show relatively intact familiarity and rely on it more than (effortful) recollection, which is also more likely to be impaired in older adults ([Jennings & Jacoby, 1993](#)). The neuroimaging findings are broadly consistent with this view, as older adults show increased activity in rhinal cortex regions associated with familiarity and reduced activity in hippocampal regions associated with recollection ([Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006](#)).

However, age differences in familiarity-related activity and functional connectivity of other brain regions, especially prefrontal and parietal regions associated with cognitive control suggest that for older adults the familiarity signal may be less specific, increasing vulnerability to false memories ([Dennis, Bowman, & Peterson, 2014](#); [Duarte, Graham, & Henson, 2010](#)). Some ERP evidence also suggests that preserved behavioral familiarity in older adults relies on different neural signals than for young adults ([Wang, de Chastelaine, Minton, & Rugg, 2012](#); see review by [Friedman, 2013](#)). Consistent with the idea that controlled processing may be more demanding for older adults, when young and old adults are matched for recollection performance, older adults show more extensive activation than do young adults, especially in prefrontal and parietal regions, perhaps in compensation for reduced modulation of other regions ([Angel et al., 2013](#); [Morcom, Li, & Rugg,](#)

[2007](#)). Interpretation is further complicated by the different methods used to assess familiarity and recollection across studies (e.g., remember-know vs. requiring detail identification vs. the process dissociation procedure) that may rely on different brain networks and be differently affected by aging and cognitive status ([Duarte, Henson, & Graham, 2008](#)).

Before it can be retrieved, information must first be encoded and stored. Storage or consolidation processes are difficult to study directly. However, changes in several neurobiological systems, including changes in cholinergic systems linked to reduced sleep quality in older age, appear to reduce the efficiency and duration of consolidation (see [Gold & Korol, 2014](#), for a recent review). More relevant to our discussion of controlled versus automatic processing, older adults’ reduced engagement of controlled processing at encoding is central to several major theories of age-related reductions in episodic memory. This reduction in controlled processing at encoding can result in less distinct, elaborated representations of the to-be-remembered item ([Craik & Byrd, 1982](#); [Craik & Rose, 2012](#)) and in the “accidental” encoding of putatively irrelevant items, which compete with the target and interfere with its retrieval ([Hasher & Zacks, 1988](#); [Lustig, Hasher, & Zacks, 2007](#)).

The neuroimaging evidence also suggests that older adults are less likely to self-initiate the encoding processes that support later episodic memory, perhaps due to structural and functional declines, especially in prefrontal cortex, but can bring them into play with instruction or training. In one of the first neuroimaging studies of cognitive aging, [Grady et al. \(1995\)](#) found that under intentional learning instructions (i.e., participants are told to learn items in preparation for a later memory test), older adults did not show activation in a number of regions associated with successful encoding in young adults, especially left inferior prefrontal cortex. This pattern was

replicated in a number of subsequent studies and fit well with a “frontal lesion” model of aging. However, later studies showed that when participants were given a task (e.g., non/living or abstract/concrete judgments) that required semantic processing at encoding, older adults engaged these regions to nearly the same degree as young adults—and also showed activation in additional regions, especially right prefrontal cortex (Logan, Sanders, Snyder, Morris, & Buckner, 2002; Morcom, Good, Frackowiak, & Rugg, 2003).

Although there are some exceptions, such additional activation is often associated with better performance in older adults (see review by Eyler et al., 2011), raising the question of what it is compensating for. There are a number of possibilities that are not mutually exclusive. The most obvious, especially when older adults show bilateral prefrontal recruitment where young adults are lateralized, is that age-related structural and functional declines have reduced the efficiency or power of the cognitive control regions recruited by young adults. In such cases, the homologous region of the other hemisphere may be recruited to “help out.” In addition, cognitive control regions may be recruited to help compensate for declines in more memory-specialized networks; for example, Salami et al. (2012) found that increasing age was negatively associated with activation of a memory-specific network including hippocampus and positively associated with activation of a more general frontoparietal cognitive control network. A third related possibility is both control and memory-specific processes are operating on degraded representations—for example, reduced sensory function in aging may make the features of an item less distinctive—creating greater demands on cognitive control downstream. In addition to sensory declines, older adults also have less specialized neural representations in regions associated with higher-level visual (and likely other sensory) processing (Carp et al., 2011; Park et al., 2012). To summarize, additional recruitment in

older brains may reflect compensation both for reduced function in the regions young adults engage for cognitive control and increased demands on such control due to dysfunction in other systems.

Associational Memory May Be Especially Impaired in Aging

The associative deficit hypothesis (Naveh-Benjamin, 2000) posits that demands for associative processing are another major factor in age differences in memory (see also earlier work by Chalfonte & Johnson, 1996). The strong version of this hypothesis predicts that older adults will have difficulty not only connecting items to either items (e.g., paired associate memory) or to the context (e.g., source memory) and but also with binding together the features of an item (e.g., font, color, modality, and size). However, a meta-analysis by Old and Naveh-Benjamin (2008) comparing the size of age differences for item versus associational memory found greater age deficits for associational memory only for item associations with other items or with context (Spencer & Raz, 1995) and not for intra-item features.

As Old and Naveh-Benjamin (2008) noted when discussing the results of their meta-analysis, from a neurobiological perspective there may be (at least) two major components to older adults’ associative memory deficits (see Sander, Lindenberger, & Werkle-Bergner, 2012 for a more detailed discussion). One is the frontally mediated cognitive control component that also applies to item memory as described above. This component may explain why the size of the associative memory deficit is influenced by factors such as the number of items to be associated (i.e., interference or fan effects), encoding instructions, test format, and meta-memory (see also Bender & Raz, 2012). It may also explain why Campbell, Trelle, and Hasher (2014) found evidence for what they termed “hyper-binding”. After studying a series of

paired associates, older adults were more likely than young adults to incorrectly identify as “old” unstudied pairs that re-arranged items temporally close together on the study list. In this case, it may not have been the associative process itself that was dysfunctional in older adults, but instead the cognitive control processes influencing which items were still active in attention and working memory and thus candidates for binding. The binding/association process itself is likely more strongly influenced by a medial temporal lobe/hippocampal component that is relatively automatic. This component also likely undergoes some degradation with age, though not to the same degree as the frontal component (Raz et al., 2010). Age-related declines in medial temporal structures also seem to show larger individual differences (Raz et al., 2010), which may be related to pathological but preclinical conditions such as iron concentration (Rodrigue, Daugherty, Haacke, & Raz, 2013) or amyloid (Doré et al., 2013).

Default Network Dysregulation

In addition to the age differences in task-related activation described above, research over the past decade has established that older adults also have reduced deactivation of the “default network”—a relatively consistent set of regions thought to support processes preferentially involved in task-unrelated, unconstrained thought. In contrast to the varied findings of age-related reductions versus increases in activation found in task-positive regions, age differences in default network deactivation are almost always in the direction of reduced deactivation by older adults. This pattern was first described in the context of a semantic judgment task used to encourage deep incidental encoding (Lustig et al., 2003), and has since been demonstrated across a wide array of both memory and non-memory tasks (see reviews by Grady, 2012; Hafkemeijer, van der Grond, & Rombouts, 2012).

Although its activity is modulated when engaging in a wide variety of tasks (Shulman et al., 1997), the default network plays a special role in memory–cognitive control interactions. The posterior cingulate/retrosplenial cortex is a primary hub of the network, and is also heavily interconnected with medial temporal and frontal regions (see Buckner, Andrews-Hanna, & Schacter, 2008, for an extensive review of research on the default network). Studies in nonhuman primates (Pandya, Van Hoesen, & Mesulam, 1981) also indicate connections with lateral prefrontal cortex though this has not been as clearly established in humans. These connections put it in a privileged position with regards to memory and cognitive control, and are disrupted in older adults (Andrews-Hanna et al., 2007). Furthermore, posterior cingulate/retrosplenial cortex shows a unique activation pattern in memory processing known as the “encoding–retrieval flip”: decreases in activity during successful encoding, increases in activity during episodic retrieval. Both sides of the flip are smaller in older adults, but age deficits in the encoding–deactivation component appear especially large (Vannini et al., 2013) and linked to reduced subsequent memory in older adults (de Chastelaine, Wang, & Rugg, in press; de Chastelaine & Rugg, 2014; Miller et al., 2008).

Serious investigation of the default network is a relatively recent phenomenon (sparked by Gusnard & Raichle, 2001), and there are still many questions about its function and alteration with age. However, it appears to make at least two major contributions to age differences in memory. First, failures to deactivate during encoding are linked to failures to encode regardless of age (Daselaar, Prince, & Cabeza, 2004); as mentioned earlier these failures are more common in older adults. These age differences increase with demands for control (Persson, Lustig, Nelson, & Reuter-Lorenz, 2007) and are often interpreted to reflect a failure to disengage from task-unrelated thought.

Thus, failures to deactivate the default network may be related to older adults' increased distractibility. In a particularly interesting study supporting this idea, [Stevens et al. \(2008\)](#) found that during unsuccessful encoding older adults showed increased connectivity between default network regions and auditory cortex, suggesting that they were distracted by irrelevant thoughts about the scanner noise. Second, the ongoing activity of the default network may serve an important role in consolidation and integrating new learning into existing knowledge structures ([Albert, Robertson, & Miall, 2009](#); [Lewis, Baldassarre, Comitteri, Romani, & Corbetta, 2009](#)). Disruptions of this network in older adults may therefore contribute to reductions in associational memory and delay-related memory impairments in older adults. Disruptions in default network activity are especially pronounced in older adults with amyloid deposition and/or genetic risk for Alzheimer's disease, another strong indicator of its role in age-related memory declines.

MODIFYING FACTORS: QUALITATIVE AND QUANTITATIVE EFFECTS

A number of variables can affect the size and direction of age differences in memory. As described above, these include task demands for controlled or associative processing, and individual differences influenced by lifestyle and genetics (see [Raz & Lustig, 2014](#), for recent work on the latter front). More subjective factors including emotion and strategy use also have important effects. Findings that older adults' performance can be influenced by the degree to which task instructions invoke negative stereotypes about memory and aging ([Hess, Auman, Colcombe, & Rahhal, 2003](#); [Rahhal, Hasher, & Colcombe, 2001](#)) initially led to the hypothesis that participants from Eastern (and American Deaf) cultures, thought to have

more positive stereotypes about aging, might show fewer age-related declines in memory ([Levy & Langer, 1994](#)). However, later studies failed to find strong support for this idea. Instead, culture may have greater effects on qualitative aspects of memory. That is, rather than affecting how much people remember, cultural influences may be more evident in what they pay attention to (e.g., the aspects of an item that differentiate it from or associate it with other members of a category) and thus later remember. There is still some debate as to whether the size of these cultural differences is larger or smaller in older adults as compared to younger ones: on the one hand, older adults have spent longer internalizing their own culture and thus may be more strongly influenced by it; on the other hand, age-related declines in neuroplasticity and distinctiveness may become a more overwhelming contributor to individual differences in brain structure and function (see reviews by [Gutchess & Huff, in press](#); [Park, 2002](#); [Park & Gutchess, 2006](#)).

Age differences in emotion-memory interactions are robust and represent an interesting exception to age-related reductions in cognitive control (see [Mather, 2012](#), for an extensive review). Compared to young adults, older adults show a bias towards remembering positive information. This appears to be a controlled, strategic process aimed at maintaining positive mood and emotional balance in the face of limited (life) time ([Carstensen, 1993, 2006](#)). For example, the effect is eliminated or even reversed under divided attention ([Knight et al., 2007](#)), and older adults show reduced subcortical but increased cortical responses to emotional stimuli, suggesting top-down regulation of the emotional response (see review by [Samanez-Larkin & Carstensen, 2011](#)). In addition, some of the prefrontal regions associated with emotional control show less structural decline in aging than do those associated with other forms of cognitive control ([Fjell et al., 2009](#); [Salat, Kaye, & Janowsky, 2001](#)). [Mather](#)

(2012) suggests that older adults may engage emotional regulation more consistently than young adults in everyday life as well as in the lab, which could lead to a positive feedback loop of “use it and don’t lose it” between structure and function and explain the generally lower rates of depression in older adults. However, if those structures are damaged, for example by cardiovascular disease, the resulting impairment may make depression particularly severe and resistant to treatment.

Emotion effects on memory represent a special case of older adults increasing their exercise of control and, like cultural effects, may have a greater impact on what is remembered rather than how much. In contrast, increasing environmental support affects the size of age differences in memory. As described previously in the section on controlled processing and encoding, changing the task or environment to reduce demands on self-initiated processing—for example, asking participants to engage in a semantic decision task that encourages deep processing rather than simply telling them to memorize items—often differentially improves the performance of older adults. However, care must be taken that the guided, supposedly supportive task does not itself place high demands on cognitive control, or the effects may be reversed and exacerbate age-related performance deficits (Luo et al., 2007). In some cases, environmental support at either encoding or retrieval can result in older adults’ brain activity, as well as behavior, more closely resembling that of young adults (Angel et al., 2010; Logan et al., 2002).

Older adults’ use of environmental support and other compensatory strategies in everyday life may help explain why, despite the apparently large age-related declines in memory and other cognitive functions on laboratory tasks, older adults often perform as well or even better than young adults in real-world situations (Ng & Feldman, 2008; Verhaeghen, Martin, & Sedek, 2012). This is demonstrated dramatically

in the domain of prospective memory: In naturalistic settings, where older adults can make use of environmental supports such as notes and calendars, they reliably outperform young adults. In the lab, where subjects are typically denied such supports, young adults have the advantage (see meta-analysis by Henry et al., 2004). Likewise, when examining the everyday memory errors most commonly reported by older adults (Ossher, Flegal, & Lustig, 2012), the most frequent errors were those least amenable to environmental support, such as tip-of-the-tongue errors or forgetting the name of a new acquaintance. In contrast, errors were very rare in situations where routine, reminders, or maps could provide supportive guidance or cues.

Putting aside the task and the environment, one of the most important factors in determining memory performance is the individual. Nyberg, Lövdén, Riklund, Lindenberger, and Bäckman (2012) describe large longitudinal studies in which some older adults show little or no evidence of memory decline. They suggest a distinction between brain or cognitive *reserve*, which allows an individual to maintain good performance despite age-related pathology (Stern, 2002), and brain *maintenance* factors that protect from such pathology. Genetics and lifestyle impact both, but through different pathways. Reserve factors may provide a larger bank of neural or cognitive resources that can be drawn down by pathology before reaching clinical levels, or methods of compensation for pathological decline. Brain maintenance factors, in contrast, prevent that pathology from occurring in the first place.

INTERVENTIONS: HOPE FOR IMPROVEMENT?

In addition to reserve or maintenance, intervention programs often aim for a third possibility: brain and/or cognitive *enhancement*. Although there is an increasing interest in

combined, multimodal interventions, most studies can be roughly divided into those that target brain function directly through exercise, nutrition, or pharmaceuticals, and those that use behaviorally based training, targeting one or more cognitive domains. Cardiovascular training has attracted the most attention, with modest but reliable effects on memory, perhaps in part through its larger effects on executive function and cognitive control (see [Smith et al., 2010](#), for a recent meta-analysis); it also improves hippocampal size as well as frontal function ([Erickson et al., 2011](#); [Weinstein et al., 2012](#)). The effectiveness of behaviorally based interventions has been questioned, but recent meta-analyses indicate small but significant effects on a number of cognitive functions including memory ([Au et al., 2014](#); [Gross et al., 2012](#); [Kelly et al., 2014](#)). On the other hand, most researchers still advise strong caution when considering the often-exaggerated claims of commercially based programs (e.g., Stanford Center on Longevity, 2014), especially when it comes to the transfer of training benefits to other tasks.

Two developments may help improve the reliability of training and transfer. One is a shift away from training specific strategies and towards training processes, with the idea that the likelihood of benefits transferring from the training task to other tasks increases with the overlap in processing demands. Many early studies of memory training started from the premise of older adults' failure to self-initiate the deep, elaborate encoding processes thought to support later memory, and were designed to teach these strategies. For example, as part of what is to date the largest clinical trial of different behavioral training methods, the ACTIVE study gave older adults instruction and practice on memory strategies including categorization, visualization, and mnemonics (e.g., method of loci). This resulted in moderate benefits to memory performance that lasted for 5 (though not 10) years ([Rebok et al., 2013, 2014](#)). These

benefits were for the most part restricted to certain closely related laboratory memory assessments, and did not show significant effects on everyday function ([Willis et al., 2006](#)). Similar findings of improvements on the training task and closely related tasks but very limited transfer have been found in most studies of strategy-based training (see [Lustig, Shah, Seidler, & Reuter-Lorenz, 2009](#), for review).

The desire for broader transfer has led to an increased emphasis on training processes or abilities (see reviews by [Lustig et al., 2009](#); [Klingberg, 2010](#)). A number of investigators focus on the executive functions of working memory, as these are thought to underlie performance on a wide range of tasks both in and out of the laboratory ([Dahlin, Neely, Larsson, Bäckman, & Nyberg, 2008](#); [Stepankova et al., 2014](#); see [Morrison & Chein, 2011](#), for review). Dahlin et al. leveraged neuroimaging data to provide strong evidence for the notion that transfer depends on processing overlap. For young adults training on a letter-updating task that activated striatum transferred to another working memory task (n-back) that also activated striatum, but not to another task (Stroop) that also had high executive demands but of a different sort (conflict processing/inhibition rather than updating) and did not activate striatum. Further, older adults did not activate striatum for the updating task prior to training and did not show transfer, suggesting that this overlap was a critical contributor to the transfer effects seen in young adults. This use of neuroimaging to identify shared neurocognitive processing components between training tasks and potential transfer tasks holds powerful promise for demonstrations of transfer within the lab, though it faces obvious practical difficulties for transfer to real-world memory situations that typically are not amenable to neuroimaging.

With regards to training episodic memory, [Ranganath, Flegal, and Kelly \(2011\)](#) noted that the memory processes mediated by the medial temporal lobe (e.g., association and

binding) are thought to be largely nondeliberate and ongoing, and thus unlikely to be further improved by training. Instead, most episodic memory training programs focus on improving its inputs at encoding or the downstream processing of its outputs at retrieval. At encoding, these interventions may take either a bottom-up approach of trying to improve perceptual processing and thus the distinctiveness of to-be-encoded representations (Mahncke et al., 2006), or top-down approaches that try to train older adults to engage more attention and control (presumably supporting deeper, more elaborative processing) at encoding (Bissig & Lustig, 2007; Lustig & Flegal, 2008; see also Paxton, Barch, Storandt, & Braver, 2006, for a non-memory example). At retrieval, training may focus on recollection processes that help distinguish between cue-appropriate responses and other items that are familiar but incorrect (Jennings & Jacoby, 2003; Jennings, Webster, Kleykamp, & Dagenbach, 2005). Both of these methods have shown transfer to other laboratory episodic memory tasks, and encoding training has been linked to reductions in self-reported everyday memory (Lustig & Flegal, 2008), but further testing of real-world outcomes is needed to establish their value long term.

The other development that may improve training outcomes is increased attention to individual differences. In cardiovascular training, several studies now suggest that the benefits are especially large for those at genetic risk for dementia (Ferencz et al., 2014; Head, Bugg & Goate, 2012; see Raichlen & Alexander, 2014, for a review). In cognitive training studies, findings have been mixed as to whether greater benefits accrue to those who started with high or low baseline function. This variance is most likely caused by interactions between the individual's ability and the difficulty and range of both the training and outcome tasks. Greater benefits may accrue to high-ability participants if low-ability participants have difficulty with the training task itself. On the other hand, if

they are able to master the training task, those with lower baseline ability have the most room for improvement. Adaptive programs that allow the participant to begin at a high level of performance and gradually increase demand on the to-be-trained processes as performance improves may help foster benefits in both groups.

One intriguing possibility is that increased attention to individual differences may be combined with initially structured adaptive training to help improve training and transfer. Kirchhoff, Anderson, Barch, and Jacoby (2011) and Kirchhoff, Anderson, Smith, Barch, and Jacoby (2012) found that at baseline, many older adults reported not using any strategy at all during an intentional encoding task. However, after a series of training sessions that exposed them to a number of encoding strategies (e.g., pleasantness ratings, self-relevance, sentence generation) they increased strategy use on an intentional encoding task administered approximately 2 weeks later, even without specific instructions to do so. They also increased prefrontal brain activity during the encoding task, recollection-related hippocampal activity during the retrieval task, and their recollection performance after intentional encoding improved to the level of young adults. Importantly, after initial exposure to the different encoding strategies, participants were allowed to choose which they chose to practice, which may have enhanced both their ability to master the strategy and the likelihood that they would use it in other circumstances. Consistent with this interpretation, performance and brain activity improvements were specific to the intentional encoding condition and did not generalize to an untrained semantic encoding task (abstract/concrete judgments). Thus, the improvements most likely stemmed from an increased self-initiation of preferred deep encoding processes after training. Likewise, Lustig and Flegal (2008) found that training task improvements were related to reductions

in self-reported everyday memory errors when the training task enforced adequate encoding time but allowed participants to choose their own strategies, but not when a specific strategy was enforced.

Together, these findings suggest that providing constraints—which might alternatively be termed “environmental support”—that cue deep encoding but providing latitude in how that deep encoding is implemented may bridge the heretofore troublesome gap between improving older adults’ memory abilities and getting them to self-initiate the transfer and use of those improvements. Bottiroli, Cavallini, Dunlosky, Vecchi, and Hertzog (2013) also found promising results using an even more proactive approach to the mastery and transfer of successful encoding: participants who received training in successful encoding strategies, including how to implement those strategies, and discussed with the trainer how they could be adapted to other tasks showed the greatest transfer, even to tasks that were not specifically discussed. Orthogonal to the question of training strategies or abilities, training older adults’ metacognition and self-initiation may prove critical for promoting transfer.

SUMMARY AND CONCLUSIONS

Our bodies—including our brains—change with time, and so do the strengths and weaknesses of our memories. A neurocognitive approach to the study of memory and aging highlights the role of processing components that may be differently weighted in different individuals and situations to result in decline, preservation, or even improvement. Controlled and associative processes appear to be the most vulnerable, corresponding to age-related declines in the prefrontal and medial temporal lobe regions that subserve them. Memory tasks that rely heavily on controlled processes may take an especially large hit, as these processes

are dependent on the brain regions that show some of the largest age-related declines and also under increasing pressure to compensate for age-related declines in sensory or bottom-up processing. On the other hand, time also grants a wealth of experience and semantic knowledge that is largely preserved, and that may contribute to a prioritization of controlled processing towards maintaining stable, positive emotion.

Thus, the picture that emerges from the study of memory and aging is not one of gloom and inevitable decline. Longitudinal studies indicate that some older adults maintain relatively high levels of performance even in advanced age, and even those that are not so privileged can often perform as well or even better than young adults by making use of environmental support. Furthermore, the knowledge gained from studies of memory and aging guides the design of interventions. Our understanding of how to preserve or improve the memories of older adults is still relatively rudimentary, but meta-analyses suggest positive effects overall and point to promising directions for future research. As controlled and associative processes play an important role in age-related memory declines, they are also important targets for intervention. Because medial temporal-lobe-mediated associative processes are relatively automatic, they do not provide easy footholds for behaviorally based training, but may be improved by cardiovascular training and other biologically based means. In contrast, age differences in controlled processing offer a number of targets for intervention: demands on them can be reduced by improving bottom-up processing, by increasing the efficiency of controlled memory processes such as elaborative encoding and recollection, and by increasing their use via improved metacognition. It has been said that happiness at all ages is “good health and a bad memory,” but we would argue for good health and a memory that is well-controlled.

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