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AGE-RELATED CHANGES IN EPISODIC MEMORY

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Memory changes are common in aging, even for older adults unaffected by dementia. Memory impairments are most notable within *episodic memory*, which is the ability to consciously encode and retrieve details and associations that allow us to distinguish one event from another. We discuss the neural factors that contribute to older adults' memory impairments in the first section. We then describe how these factors explain the relative preservation of older adults' emotional memories. In the third section, we discuss recent methods that should provide new insights into age-related memory changes. We conclude by noting the memory benefits to be gained by staying mentally and physically active in old age. Figure 4.1 depicts our conceptualization of age-related changes in episodic memory.

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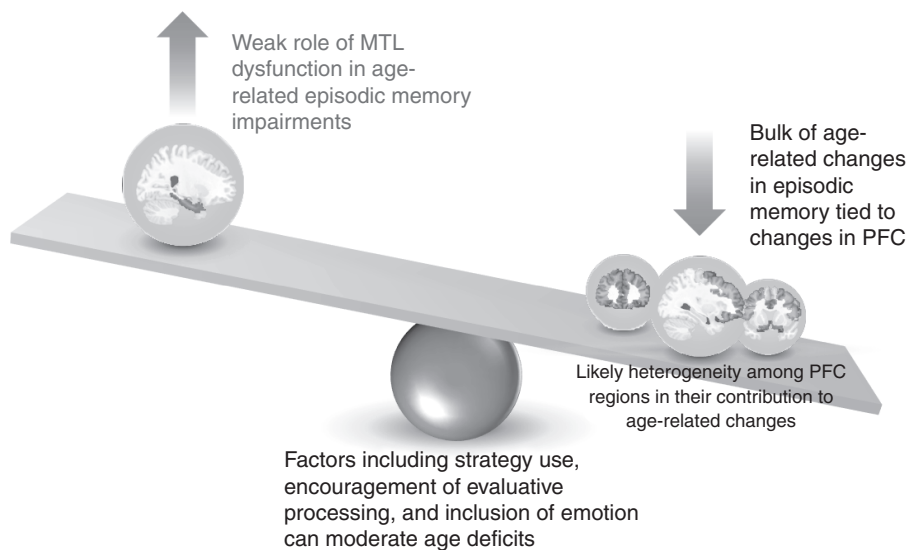


Figure 4.1. Factors including strategy use, encouragement of evaluative processing, and inclusion of emotion can moderate age deficits.

NEUROCOGNITIVE CONTRIBUTIONS TO OLDER ADULTS' MEMORY IMPAIRMENTS

In the laboratory, age-related impairments are most frequently noted on tasks that require older adults to recall specific details of past events or to remember the context in which information was learned. Age-related differences can be minimal on tasks that require only distinguishing events that were experienced from those that are novel, whereas age differences become exaggerated on tasks that require recollection of event details, recounting of contextual elements (Henkel, Johnson, & De Leonardis, 1998), binding of associative detail (Naveh-Benjamin, 2000), or selection of an experienced event among similar lures (Schacter, Koutstaal, & Norman, 1997). Age-related episodic memory impairments have been shown for virtually every stimulus modality and testing procedure. For example, older adults show impairments in source memory tests in which participants are asked to determine which experimentally manipulated details were associated with an item during encoding (e.g., spatial location, color, voice) and in paired associative tests when participants must encode and retrieve stimulus pairs (e.g., face–name, word–word). One exception seems to be episodic memory for emotional or social information, as discussed later in this chapter and in Chapter 6. Nonetheless, given the fairly ubiquitous nature of these impairments, it is likely that they may be explained by age-related changes in brain

regions that support episodic memory in a domain-general manner. Numerous structural and functional imaging studies have investigated the underlying neural factors that contribute to older adults' episodic memory impairments. Most studies have focused on the medial temporal lobe (MTL) and the prefrontal cortex (PFC). In this section, we weigh evidence for the contributions of dysfunction in these regions to age-related memory impairments.

Weak Contribution of Core Episodic Network Dysfunction to Older Adults' Episodic Memory Impairments

Evidence from numerous functional magnetic imaging (fMRI) studies has revealed that episodic memory success is dependent on several regions, including the MTL (hippocampus and parahippocampus) and the highly interconnected posterior parietal cortex (Davachi, Mitchell, & Wagner, 2003; Diana, Yonelinas, & Ranganath, 2007; Mitchell & Johnson, 2009; Uncapher & Wagner, 2009; Vilberg & Rugg, 2008). Furthermore, patient studies suggest that these *core episodic network* regions are necessary for episodic memory function with MTL or parietal damage producing amnesia (reviewed in Benoit & Schacter, 2015; Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Milner, 2005). Several theories have been proposed to explain the functional role of this network in episodic memory. A common view is that the MTL facilitates the binding of multiple features into unique episodic representations during encoding and in the comparison of those representations with retrieval cues during retrieval (Eichenbaum, Yonelinas, & Ranganath, 2007; Sestieri, Shulman, & Corbetta, 2017; Simons & Spiers, 2003). Regions within the posterior parietal cortex serve a less direct role in memory such as accumulating mnemonic evidence for memory decisions (i.e., male or female voice? intact or rearranged pair?; Wagner, Shannon, Kahn, & Buckner, 2005). Consequently, a reasonable prediction is that dysfunction in this network is a major contributor to episodic memory impairments in healthy older adults. Indeed, functional imaging studies have shown age-related differences, primarily under-recruitment of these regions concomitant with older adults' memory impairments (Cansino, Trejo-Morales, et al., 2015; Dennis, Kim, & Cabeza, 2008).

A few points of evidence argue against the role of MTL dysfunction in age-related episodic memory impairments. First, MTL atrophy is not pronounced until the eighth or ninth decade in healthy older adults but the majority of episodic memory studies have assessed older adults between the ages of 60 and 80 (Salami, Eriksson, & Nyberg, 2012). Furthermore, numerous studies have shown age-related sparing of successful encoding and retrieval-related activity in the MTL and parietal cortex (Duarte, Henson, & Graham, 2008; Dulas & Duarte, 2012; S. L. Miller et al., 2008; Morcom, Li, & Rugg, 2007), particularly when memory performance is experimentally or statistically equivalent

equated between age groups (Angel et al., 2013; de Chastelaine, Mattson, Wang, Donley, & Rugg, 2015; Duarte, Ranganath, Trujillo, & Knight, 2006; Duverne, Motamedinia, & Rugg, 2009b; Rugg & Morcom, 2005; Wang, Johnson, de Chastelaine, Donley, & Rugg, 2016). The idea behind equating performance is that group differences in episodic memory activity may be related to dilution by guessing or poor task comprehension rather than aging per se (Rugg & Morcom, 2005). Some studies have implemented study repetitions (Leshikar & Duarte, 2014; Morcom et al., 2007) or reduced memory load (Dulas & Duarte, 2013, 2014) to boost memory performance for older adults, while others have investigated the relationship between neural activity and age after parceling out individual differences in memory performance (de Chastelaine, Mattson, Wang, Donley, & Rugg, 2016). Collectively, these results suggest that dysfunction in the core episodic network is unlikely to be a major contributor to healthy older adults' episodic memory impairments.

Strong Contribution of Prefrontal Dysfunction to Older Adults' Episodic Memory Impairments

Like the core episodic network, the PFC has been implicated in episodic memory success across a number of material domains and task procedures (Blumenfeld, Parks, Yonelinas, & Ranganath, 2011; Gottlieb, Uncapher, & Rugg, 2010; Mitchell & Johnson, 2009). The PFC supports the cognitive control processes that allow information to be processed and behavior to vary in ways that are consistent with one's current task goals (E. K. Miller & Cohen, 2001). Cognitive control functions are diverse and include evaluation of relationships between stimuli or concepts and monitoring retrieved information (Badre, 2008). Damage to the MTL, and potentially also the posterior parietal cortex, results in profound amnesia, whereas damage to the PFC produces subtler episodic memory deficits (Janowsky, Shimamura, & Squire, 1989; Kopelman, Stanhope, & Kingsley, 1997).

Several factors point to PFC dysfunction as a principal source of episodic memory impairments in aging. First, both healthy older adults (Duarte et al., 2006, 2008) and patients with focal lateral or medial PFC lesions (Ciaromelli & Ghetti, 2007; Duarte, Ranganath, & Knight, 2005) can show intact subjective recollection despite impaired objective recollection of experimentally manipulated details. Second, structural imaging studies show disproportionate declines in PFC gray (Raz & Kennedy, 2009) and white matter volume (Nyberg et al., 2010) compared with non-PFC regions across the lifespan. Furthermore, older adults with larger gray matter volumes in lateral PFC regions show better episodic memory performance (Becker et al., 2015). Third, fMRI studies show age-related reductions in PFC activity during encoding (Dennis, Hayes, et al., 2008; Dulas & Duarte, 2011),

and retrieval (Dulas & Duarte, 2012; McDonough & Gallo, 2013; Rajah, Languay, & Valiquette, 2010) despite age-equivalent MTL recruitment. Some neural models predict age-related PFC over-recruitment when cognitive demands are low and underrecruitment when demands are high and performance reduced (Morcom et al., 2007; Reuter-Lorenz & Cappell, 2008). The truth is that both PFC under- and over-recruitment are often observed in the aging literature, and the question of how to interpret these patterns is still under debate (Cabeza et al., 2018). Last, even when memory performance is equated between age groups, PFC activity differences may persist during encoding (de Chastelaine et al., 2015; Dulas & Duarte, 2014) and retrieval (Duarte et al., 2008; Dulas & Duarte, 2014; Wang et al., 2016). Collectively, these findings are consistent with the “frontal aging hypothesis,” which posits that PFC dysfunction underlies many cognitive impairments including but not limited to episodic memory in aging (West, 1996). Other influential cognitive aging theories such as the *inhibitory deficit hypothesis* suggest that older adults’ cognitive impairments arise from an inability to reduce interference from task-irrelevant information (Hasher & Zacks, 1988). Importantly, this theory is not inconsistent with the frontal aging hypothesis. Indeed, it is probable that PFC dysfunction underlies poor inhibitory control and that episodic memory tests that place high demands on inhibition will be particularly difficult for older adults (Jacoby, Bishara, Hessels, & Toth, 2005).

Factors Moderating the Relationship Between the PFC and Episodic Memory in Aging Studies

Our discussion thus far has assumed that young and older adults recruit the same cognitive operations to support their memory performance. Thus, any group differences in neural activity could not be explained by individual differences in the strategies used to encode or retrieve events. However, it is well known that older adults are less likely than young adults to self-initiate effective encoding strategies when they are simply told to memorize events but not given instructional support (Craig & Byrd, 1982; Hertzog, McGuire, Horhota, & Jopp, 2010; Hultsch, Hertzog, & Dixon, 1990; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Naveh-Benjamin, Brav, & Levy, 2007; Perfect & Dasgupta, 1997). Young adults spontaneously use deep encoding strategies such as semantic elaboration and visual imagery, whereas older adults more often use no strategies or shallow ones such as rote repetition, leading to worse memory performance. Importantly, patterns of neural activity underlying these encoding strategies differ in multiple brain regions, including the PFC (Kirchhoff, Anderson, Barch, & Jacoby, 2012; Kirchhoff & Buckner, 2006; Leshikar, Duarte, & Hertzog, 2012). Differential strategy use can also affect neural activity patterns during episodic memory retrieval

(Dulas & Duarte, 2014). Thus, studies that do not constrain the strategies that participants use during encoding or retrieval may conflate age-related differences in strategy utilization with age-related differences in memory-related activity. Indeed, some evidence suggests that when task instructions facilitate elaborative encoding strategies, age-related memory impairments and PFC underrecruitment are reduced (Gutchess et al., 2015; Leshikar & Duarte, 2014; Logan et al., 2002).

Existing findings support the idea that PFC dysfunction is a major contributor to the increasing number of episodic memory failures experienced across the lifespan. However, the PFC is large and functionally heterogeneous. Lesion and human neuroimaging studies suggest dissociations between cognitive control processes within the PFC between hemispheres and along rostral-caudal and dorsal-ventral gradients (Badre, 2008; Petrides, 2005; Ramnani & Owen, 2004; Simons & Spiers, 2003). For example, in most models of PFC function, posterior areas support control over concrete item or action representations (e.g., “Is this a female face?”) while rostral areas support control involving abstract representations or rules (e.g., “Are these two faces alike in the same way as these other two faces?”). Although multiple PFC regions have been implicated in episodic memory through neuroimaging and lesion studies, little work has been done to separate the effects of age on distinct PFC subregions and the control functions they support. Future cognitive aging studies that do so may reveal a more precise role of PFC dysfunction in age-related episodic memory impairments than is currently recognized.

INTERACTIONS BETWEEN EMOTION AND MEMORY

Despite losses in episodic memory for neutral events, older adults' ability to remember emotional events appears to be relatively well preserved. This relative preservation was first revealed when examining memories for highly surprising and personally significant public events, events proposed to trigger “flashbulb memories” (Brown & Kulik, 1977). On the whole, these studies demonstrated that older adults retain the ability to form vivid memories that meet the criteria for “flashbulb memory” (reviewed in Kensinger, Allard, & Krendl, 2014) and suggested that memory deficits can sometimes be mitigated when events are highly emotional (e.g., Kvavilashvili, Mirani, Schlagman, Erskine, & Kornbrot, 2010). Because these highly emotional events differ from more mundane experiences on many factors, extensive laboratory research has been conducted to better delineate the effects of age on emotional memory and to understand their neural underpinnings. In this section, we focus on evidence supporting three conclusions about age-related changes in emotional memory and discuss the proposed mechanisms: First,

older adults' memories prioritize internal states (e.g., thoughts and feelings) more than younger adults' memories. Second, older adults often are more likely to remember the good times than the bad times, in contrast to younger adults who often show a "negativity bias" in memory. Third, when asked to remember a negative life experience, older adults are more likely than younger adults to find a silver lining or to focus on positive aspects, and they often remember negative events less vividly.

Older Adults Prioritize Thoughts and Feelings

When we think back to a prior event, we can remember many types of details: We can recall what happened during an event, we can think about the context in which the event unfolded—where, when, and with whom the event took place—and we can also think about our own internal state, or the internal state of others, during the event. With age, there appears to be a shift toward reflection on these internal aspects of an event. Older adults tend to remember the thoughts or feelings elicited by previous experiences better than they remember perceptual or semantic features of an event. For instance, when asked to self-report the features that comprise a memory, older adults give higher ratings for thoughts and feelings than do younger adults (e.g., Hashtroudi, Johnson, & Chrosniak, 1990), and they are more likely than younger adults to state that they "remember" an item from a study list because they recollect their emotional reaction (Comblain, D'Argembeau, Van der Linden, & Aldenhoff, 2004). Similarly, older adults remember proportionally more emotional information from prose passages than do young adults: They are more likely to recall portions of the narrative related to a character's affect ("looked very searchingly at Mrs. Oliver . . ."; Carstensen & Turk-Charles, 1994).

Age differences at both encoding and retrieval may underlie these behavioral effects. As noted in the previous section, older adults do not spontaneously engage highly effective encoding strategies. During event encoding, older adults often expend more resources on evaluative processing than young adults. Although this is not the most effective encoding strategy, it may boost their ability to encode the thoughts and feelings elicited by that event. A meta-analysis comparing young and older adults' neural recruitment during successful episodic memory encoding revealed that, relative to younger adults, older adults under-recruit perceptual regions and over-recruit regions of the *default mode network* typically linked to evaluative processing, including portions of the medial prefrontal cortex. Importantly, while recruitment of these "default" regions is typically associated with failed encoding in younger adults, older adults recruit these regions in the service of successful encoding (see the meta-analysis by Maillet & Rajah, 2014).

At retrieval, older adults may benefit from the fact that emotional and evaluative information may require less effort to retrieve than other types of episodic information (Clark-Foos & Marsh, 2008; Zajonc, 1980). As noted in the previous section, the *frontal aging hypothesis* proposes that older adults will be particularly disadvantaged on tasks that place heavy burdens on the PFC. Episodic retrieval typically is such a task, with the PFC implicated in the search and monitoring phases, but there is reason to think that PFC demands may be reduced during the retrieval of emotional information. For instance, divided attention has a lesser impact on retrieval of emotional information than neutral information (Clark-Foos & Marsh, 2008), and event-related potential studies have revealed that retrieval of emotional information increases an early-onsetting frontal old–new affect associated with relatively automatic retrieval of familiarity (for review, see van Strien, Cappaert, & Witter, 2009). Because older adults tend to show the most difficulties on tasks with high retrieval demands (Light, 1991), they may recall more affective and evaluative information simply because it is easier for them to retrieve (for a related discussion, see Burke & Light, 1981).

On many tasks, older adults' prioritization of evaluative processing may be to the detriment of their overall memory ability. Often, older adults who show greater over-recruitment of neural regions associated with evaluative processing are those who show poorer memory performance (Duverne, Motamedinia, & Rugg, 2009a; Düzel, Schütze, Yonelinas, & Heinze, 2011). Moreover, older adults who rely on relatively automatic retrieval processes may be those who have a lesser ability to engage controlled retrieval strategies to recall other affective details, consistent with evidence that older adults' focus on affective tone may come at a cost for memory for other types of details (e.g., Comblain, D'Argembeau, & Van der Linden, 2005; Kensinger, Brierley, Medford, Growdon, & Corkin, 2002). Yet other times, this prioritization likely benefits older adults' memories: For example, older adults are as good as younger adults at remembering whether food is safe to eat (May, Rahhal, Berry, & Leighton, 2005) or whether someone is a good or bad person (Rahhal, May, & Hasher, 2002). This focus on thoughts and feelings also may help to explain why older adults readily form "flashbulb memories" despite their general deficits in creating detailed, episodic memories (reviewed in Kensinger et al., 2014). Thus, older adults' evaluative focusing may be a double-edged sword, enabling them to remember some types of events, or event details, at the cost of others.

Older Adults Remember the Good More Than the Bad

Although the previous section has emphasized that older adults' memories prioritize thoughts and feelings, it is not the case that all types

of emotional events are prioritized equally. The *positivity effect* is a widely discussed consequence of aging: While younger adults often show a *negativity bias* in memory, consistent with proposals that “bad is stronger than good” (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001), older adults do not show the same degree of bias toward the negative, and in fact they often remember positive information more readily than negative (see Chapter 6, this volume).

One of the more surprising revelations about the positivity effect is that it occurs most readily in older adults who have the most cognitive control resources to devote (Knight et al., 2007; Mather & Knight, 2005). Thus, it is the higher functioning older adults who show a memory pattern that diverges from younger adults, while lower functioning older adults are more likely to show the negativity bias typical in younger cohorts. This pattern has led to the proposal that the effect reflects an adaptive change in the way that information is remembered, enabling high-functioning older adults to focus on content that will maximize their well-being and support their emotion-regulation goals (Nashiro & Mather, 2011; Reed & Carstensen, 2012).

This regulatory account has been supported by evidence that not only do older adults sometimes recruit prefrontal regions more on memory tasks than younger adults (as reviewed in the preceding subsection), prefrontal regions are engaged and connected differently depending on the valence of information being remembered. Most notably, aging is associated with greater increases in prefrontal recruitment during negative relative to neutral (Murty et al., 2009) and positive event retrieval (Ford, Morris, & Kensinger, 2014). These effects of age are present over relatively short retention delays, but they may become exaggerated over longer delays (Kalpouzos, Fischer, Rieckmann, Macdonald, & Bäckman, 2012). At least some of the time, these prefrontal processes appear to dampen activity in medial temporal-lobe regions, including both the amygdala (St. Jacques, Dolcos, & Cabeza, 2009) and hippocampus (Ford et al., 2014), broadly consistent with a regulatory account.

Three studies incorporating assessments of individual differences also revealed evidence consistent with a regulatory account. In one study (Erk, Kleczar, & Walter, 2007), older adults who endorsed using reappraisal strategies more frequently showed reduced amygdala activity to negative stimuli. In another study (Waldinger, Kensinger, & Schulz, 2011), only older adults who rated themselves to have high life satisfaction showed stronger connectivity between the amygdala and other nodes of an emotional memory network when successfully encoding positive compared to negative images. Individual differences in neural connectivity also can relate to the prevalence of the positivity effect. Sakaki, Nga, and Mather (2013) demonstrated that the older adults most likely to show enhanced connectivity between the PFC

and amygdala at rest (i.e., when no task is instructed) also are those who are most likely to remember positive information disproportionately.

However, there are some lines of work that suggest a regulatory account may not be the sole mechanism of the positivity effect. Most notably, age-by-valence interactions have been revealed early in the time course of retrieval (Newsome, Dulas, & Duarte, 2012), before regulatory processes would be likely to be implemented, as measured with electroencephalography (EEG). Although these early changes could reflect age differences in the processing of an emotional retrieval cue, rather than in mnemonic content elicited by it, they emphasize the need for further research to elucidate whether there are circumstances when older adults' prefrontal engagement is less likely to be tied to regulatory actions.

Older Adults Reflect on Past Negative Events Differently

The previous subsection emphasized that negative events often are less likely to come to mind for an older adult than for a younger adult. Even when they do come to mind, however, age can affect the way that individuals reflect on those past bad experiences. Two primary changes have been noted in this domain. First, older adults are better able to find the good to remember. For instance, when asked to describe autobiographical events from their past, older adults use more positive words to describe a past negative event than do younger adults. Relatedly, when young and older adults were asked to report how often they thought about positive and negative aspects of a highly negative event (the bombings at the 2013 Boston Marathon), older age increased the likelihood of thinking about the positive aspects (e.g., heroism, town pride, capture of suspect) but had no effect on the likelihood of thinking about the negative aspects. Second, older adults can remember negative events less vividly than younger adults, and this reduced memory vividness can be connected to their recruitment of prefrontal regions (Ford & Kensinger, 2018). Specifically, older adults often show an inverse relation between prefrontal activity and medial temporal-lobe activity during the retrieval of negative information, and the recruitment of the prefrontal regions that show this inverse relation with hippocampal activity is both disproportionate during the retrieval of negative information and linked to lower ratings of subjective vividness for those negative memories (Ford & Kensinger, 2018). It is well known that older adults choose to avoid situations that they know will evoke negative affect: *In the moment*, age increases disengagement from offending situations (Charles & Carstensen, 2008). These results may be intertwined with this phenomenon, suggesting that age also increases the likelihood that individuals disengage from remembering events in ways that will evoke negative affect.

CONCLUDING REMARKS

Although we have learned a great deal about age-related changes in episodic memory from neuroscience research to date, there are several relatively unexplored questions that will be important to address in the coming years. For example, human neuroscience methods and analyses are developing exponentially, but many of these approaches have only recently been applied to age-related memory research. In this section, we discuss some of these approaches and offer suggestions for how they might be used to advance the field of age-related memory research.

Implications

The research reviewed in this chapter may elucidate an apparent contradiction: Laboratory assessments paint a somewhat bleak picture of older adults' memory capabilities, yet the older adult participants in these studies lead independent lives and contribute meaningfully to society, often taking on roles (e.g., caretaking) that have high memory demands. What may account for this contradiction?

First, many laboratory assessments exaggerate age-related differences due to a combination of factors. The sterile and potentially intimidating laboratory environment and long lists of briefly presented, unimodal (usually visual), unrelated stimuli may curtail the evaluative and motivationally relevant processes that older adults would excel at using in everyday life (see Chapter 5, this volume, for more on motivated learning). These factors also may exaggerate the attentional and interference-resolution demands of learning and retrieving beyond those typical in everyday life. As technological advances improve the ability to enrich learning contexts and to tailor learning tasks to the experience and goals of each participant, laboratory assessments should better approximate the learning environments of older adults' day-to-day experience. This may provide new insights into the patterns of age-related preservation and decline.

Second, a fundamental insight to be gained from a cognitive neuroscience perspective is that older adults often remember information by recruiting different strategies than those engaged by younger adults, consistent with the centrality of compensation to the conceptualization of cognitive aging (Baltes & Lindenberger, 1997). The efficacy of these compensatory processes can be shaped by the experiences achieved over a lifetime and by the degree of cognitive or brain reserve available to an older adult (Park & Reuter-Lorenz, 2009). As discussed earlier, more longitudinal aging research is necessary to determine whether differential neural recruitment in the PFC or other areas in aging reflects functional compensation. Nonetheless, these

age differences should not always be cast as deficits. As we have described, older adults' shift toward evaluative processing can help them to remember the thoughts and feelings associated with past events. Similarly, older adults' shift toward pattern completion or toward gist-based memory can lead them to be more likely than younger adults to extract the high-level importance of an event, including its implications (McGinnis, Goss, Tessmer, & Zelinski, 2008). These shifts may also enable older adults to note connections across experiences, often are considered part of the "wisdom" acquired with age (Baltes & Staudinger, 2000).

Moreover, it is increasingly recognized that the brain retains plasticity into older age, and that older adults can continue to benefit from life experiences (Lövdén, Bäckman, Lindenberger, Schaefer, & Schmiedek, 2010). Newer lines of research suggest a potential for lifestyle interventions—many focused on improving fitness levels, nutrition, and social engagement (for review, see Williams & Kemper, 2010) to benefit older adults' cognitive performance. Similarly, there is speculation that personalized cognitive training interventions may benefit older adults (for commentary, see Mishra & Gazzaley, 2014). Although many open questions remain regarding the efficacy of these interventions (for a review, see Salthouse, 2015), two broad points can be made. First, there are more interconnections between our mental and physical health than many older adults realize, enabling interventions known to convey benefits in one domain (e.g., increased fitness improving physical health) to potentially deliver benefits in the other. Second, a beneficial cycle may be created whereby those older adults who seek new learning opportunities to allow them to stay cognitively active, physically fit, and socially engaged may be those who will find it easier to continue to learn from these experiences.

Future Directions for Age-Related Memory Research

Most neuroimaging and EEG studies have used univariate analyses, which are excellent for determining whether a particular brain region or EEG signal contributes to memory or is affected by age but do not allow for assessments of brain networks. Multivariate analyses, by contrast, can be used to characterize how aging affects functional coherence within and between networks. For example, consistent with older adults' cognitive control impairments, univariate analyses show age-related decreases in lateral PFC recruitment during attempts to perform cognitively demanding emotion regulation strategies, namely, reappraisal (Opitz, Rauch, Terry, & Urry, 2012; Winecoff, Labar, Madden, Cabeza, & Huettel, 2011). Multivariate analyses, however, show that both young and older adults

recruit a coherent network of PFC regions while engaging in reappraisal of negative events (Allard & Kensinger, 2014). This example highlights the potential divergence in conclusions reached by univariate and multivariate analyses. Thus, while univariate analyses might suggest reduced availability of PFC regions to support episodic memory functioning in older adults, multivariate analyses show that functional communication between these regions can support memory performance across age. Recently, analyses grounded in graph theory have been used to show that aging is associated with reduced segregation of functional brain networks that support distinct high-order cognitive functions, which in turn is related to impaired long-term memory performance (Chan, Park, Savalia, Petersen, & Wig, 2014). Age-related reductions in within-network connectivity together with increases in between-network connectivity (i.e., segregation) have largely been assessed for resting state data and in association with memory performance measured offline (Antonenko & Flöel, 2014). It will be important for future studies to determine whether age-related desegregation of functional brain networks affects the recruitment of these networks during performance of episodic memory tasks.

Machine-learning-based analyses such as multivariate pattern analysis (MVPA) have become popular in recent years for their ability to detect patterns of activity, within and across brain areas, that are indicative of different cognitive states (reviewed in Norman, Polyn, Detre, & Haxby, 2006). MVPA has been used in young adults to reveal the specificity, measured as the degree of matching between encoding and retrieval brain activity patterns, with which episodic memories are retrieved (Liang & Preston, 2017; Staresina, Henson, Kriegeskorte, & Alink, 2012; Xiao et al., 2017). Specifically, MVPA results show that successful retrieval of previous events is associated with neural reactivation of category (e.g., scene, face, word) or context (e.g., orienting tasks) representations that were observed during encoding (Kuhl, Bainbridge, & Chun, 2012). Even more interestingly, MVPA evidence shows that successful retrieval of word–scene pairs (i.e., “apple”–nature scene) is accompanied by reactivation of encoding activity associated with that specific pair above and beyond reactivation of the category level representations common to all retrieved pairs (Staresina et al., 2012). To date, one study has used MVPA to show category level reinstatement for recollected items is unaffected by age (Wang et al., 2016). As discussed within this chapter, aging is associated with declines in recollection for specific details of previously encoded events. This conclusion has been drawn largely from studies in which memory for details such as spatial location or stimulus color or category is tested, but these are relatively coarse measures. We know little about whether age-related recollection impairments stem

from dysfunction in neural reinstatement of specific encoding-related activity or constructive processes that support specific memory retrieval. Brain pattern analyses may prove promising for addressing this issue, but to date, few studies have applied such analyses to aging data.

The majority of aging studies have been cross-sectional and have not examined memory performance and related neural activity in middle-aged adults. Consequently, we know relatively little about what underlies episodic memory changes in middle age or when many of the aforementioned age-related changes in emotional memory begin to emerge. Evidence from lifespan cross-sectional studies suggests that changes in PFC recruitment during encoding (Cansino, Estrada-Manilla, et al., 2015) and retrieval (Ankudowich, Pasvanis, & Rajah, 2016; Cansino, Hernández-Ramos, & Trejo-Morales, 2012; Cansino, Trejo-Morales, et al., 2015; Kwon et al., 2016) contribute to episodic memory decline even in mid-life (~40–60 years of age). It is not clear from this work whether the mechanisms underlying memory decline in middle age are the same as those in old age. Arguably the best approach to investigate neural changes underlying episodic memory decline across the lifespan would be longitudinal assessments of individuals over an extended period of time. Although such studies are costly and face unique issues including subject attrition and practice effects (Salthouse, 2014), a few longitudinal studies have revealed some important findings regarding aging and memory. For example, longitudinal evidence suggests that findings of age-related PFC over-recruitment in cross-sectional studies may be overestimated and that PFC under-recruitment during encoding or retrieval is a more typical response (Nyberg et al., 2010). Furthermore, PFC over-recruitment may be more likely related to declining memory function than to a compensatory mechanism that supports memory performance in older adults (Pudas, Josefsson, Rieckmann, & Nyberg, 2018). With regard to affect, longitudinal behavioral evidence substantiates the decline in negativity bias across the lifespan that has been observed in numerous cross-sectional studies (Charles, Reynolds, & Gatz, 2001). Longitudinal work is needed, however, to determine what underlying neural changes contribute to this positivity shift. We would argue that longitudinal research is needed to more accurately characterize the neural basis of age-related episodic memory decline and the factors that contribute to these changes (i.e., lifestyle, genetics). This is not to suggest that cross-sectional aging studies have no value. Indeed, cross-sectional research is arguably the best method for dissociating cognitive mechanisms that contribute to memory performance, including recollection, familiarity, and various cognitive control operations, and identifying the brain areas and networks that support these mechanisms. A combination of cross-sectional and longitudinal research may be the strongest approach to tackling questions about lifespan changes in memory function.

REFERENCES

- Allard, E. S., & Kensinger, E. A. (2014). Age-related differences in functional connectivity during cognitive emotion regulation. *The Journals of Gerontology: Series B. Psychological Sciences and Social Sciences*, *69*, 852–860. <http://dx.doi.org/10.1093/geronb/gbu108>
- Angel, L., Bastin, C., Genon, S., Balteau, E., Phillips, C., Luxen, A., . . . Collette, F. (2013). Differential effects of aging on the neural correlates of recollection and familiarity. *Cortex*, *49*, 1585–1597. <http://dx.doi.org/10.1016/j.cortex.2012.10.002>
- Ankudowich, E., Pasvanis, S., & Rajah, M. N. (2016). Changes in the modulation of brain activity during context encoding vs. context retrieval across the adult lifespan. *NeuroImage*, *139*, 103–113. <http://dx.doi.org/10.1016/j.neuroimage.2016.06.022>
- Antonenko, D., & Flöel, A. (2014). Healthy aging by staying selectively connected: A mini-review. *Gerontology*, *60*, 3–9. <http://dx.doi.org/10.1159/000354376>
- Badre, D. (2008). Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends in Cognitive Sciences*, *12*, 193–200. <http://dx.doi.org/10.1016/j.tics.2008.02.004>
- Baltes, P. B., & Lindenberger, U. (1997). Emergence of a powerful connection between sensory and cognitive functions across the adult life span: A new window to the study of cognitive aging? *Psychology and Aging*, *12*, 12–21. <http://dx.doi.org/10.1037/0882-7974.12.1.12>
- Baltes, P. B., & Staudinger, U. M. (2000). Wisdom. A metaheuristic (pragmatic) to orchestrate mind and virtue toward excellence. *American Psychologist*, *55*, 122–136. <http://dx.doi.org/10.1037/0003-066X.55.1.122>
- Baumeister, R. F., Bratslavsky, E., Finkenauer, C., & Vohs, K. D. (2001). Bad is stronger than good. *Review of General Psychology*, *5*, 323–370. <http://dx.doi.org/10.1037/1089-2680.5.4.323>
- Becker, N., Laukka, E. J., Kalpouzos, G., Naveh-Benjamin, M., Bäckman, L., & Brehmer, Y. (2015). Structural brain correlates of associative memory in older adults. *NeuroImage*, *118*, 146–153. <http://dx.doi.org/10.1016/j.neuroimage.2015.06.002>
- Benoit, R. G., & Schacter, D. L. (2015). Specifying the core network supporting episodic simulation and episodic memory by activation likelihood estimation. *Neuropsychologia*, *75*, 450–457. <http://dx.doi.org/10.1016/j.neuropsychologia.2015.06.034>
- Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience*, *27*, 14415–14423. <http://dx.doi.org/10.1523/JNEUROSCI.4163-07.2007>
- Blumenfeld, R. S., Parks, C. M., Yonelinas, A. P., & Ranganath, C. (2011). Putting the pieces together: The role of dorsolateral prefrontal cortex in relational memory encoding. *Journal of Cognitive Neuroscience*, *23*, 257–265. <http://dx.doi.org/10.1162/jocn.2010.21459>

- Brown, R., & Kulik, J. (1977). Flashbulb memories. *Cognition*, 5, 73–99. [http://dx.doi.org/10.1016/0010-0277\(77\)90018-X](http://dx.doi.org/10.1016/0010-0277(77)90018-X)
- Burke, D. M., & Light, L. L. (1981). Memory and aging: The role of retrieval processes. *Psychological Bulletin*, 90, 513–514. <http://dx.doi.org/10.1037/0033-2909.90.3.513>
- Cabeza, R., Albert, M., Belleville, S., Craik, F. I. M., Duarte, A., Grady, C. L., . . . Rajah, M. N. (2018). Maintenance, reserve and compensation: The cognitive neuroscience of healthy ageing [erratum at <http://dx.doi.org/10.1038/s41583-018-0086-0>]. *Nature Reviews Neuroscience*, 19, 701–710. <http://dx.doi.org/10.1038/s41583-018-0068-2>
- Cansino, S., Estrada-Manilla, C., Trejo-Morales, P., Pasaye-Alcaraz, E. H., Aguilar-Castañeda, E., Salgado-Lujambio, P., & Sosa-Ortiz, A. L. (2015). fMRI subsequent source memory effects in young, middle-aged and old adults. *Behavioural Brain Research*, 280, 24–35. <http://dx.doi.org/10.1016/j.bbr.2014.11.042>
- Cansino, S., Hernández-Ramos, E., & Trejo-Morales, P. (2012). Neural correlates of source memory retrieval in young, middle-aged and elderly adults. *Biological Psychology*, 90, 33–49. <http://dx.doi.org/10.1016/j.biopsycho.2012.02.004>
- Cansino, S., Trejo-Morales, P., Estrada-Manilla, C., Pasaye-Alcaraz, E. H., Aguilar-Castañeda, E., Salgado-Lujambio, P., & Sosa-Ortiz, A. L. (2015). Brain activity during source memory retrieval in young, middle-aged and old adults. *Brain Research*, 1618, 168–180. <http://dx.doi.org/10.1016/j.brainres.2015.05.032>
- Carstensen, L. L., & Turk-Charles, S. (1994). The salience of emotion across the adult life span. *Psychology and Aging*, 9, 259–264. <http://dx.doi.org/10.1037/0882-7974.9.2.259>
- Chan, M. Y., Park, D. C., Savalia, N. K., Petersen, S. E., & Wig, G. S. (2014). Decreased segregation of brain systems across the healthy adult lifespan. *Proceedings of the National Academy of Sciences of the United States of America*, 111, E4997–E5006. <http://dx.doi.org/10.1073/pnas.1415122111>
- Charles, S. T., & Carstensen, L. L. (2008). Unpleasant situations elicit different emotional responses in younger and older adults. *Psychology and Aging*, 23, 495–504. <http://dx.doi.org/10.1037/a0013284>
- Charles, S. T., Reynolds, C. A., & Gatz, M. (2001). Age-related differences and change in positive and negative affect over 23 years. *Journal of Personality and Social Psychology*, 80, 136–151. <http://dx.doi.org/10.1037/0022-3514.80.1.136>
- Ciaramelli, E., & Ghetti, S. (2007). What are confabulators' memories made of? A study of subjective and objective measures of recollection in confabulation. *Neuropsychologia*, 45, 1489–1500. <http://dx.doi.org/10.1016/j.neuropsychologia.2006.11.007>
- Clark-Foos, A., & Marsh, R. L. (2008). Recognition memory for valenced and arousing materials under conditions of divided attention. *Memory*, 16, 530–537. <http://dx.doi.org/10.1080/09658210802007493>
- Comblain, C., D'Argembeau, A., & Van der Linden, M. (2005). Phenomenal characteristics of autobiographical memories for emotional and neutral

- events in older and younger adults. *Experimental Aging Research*, 31, 173–189. <http://dx.doi.org/10.1080/03610730590915010>
- Comblain, C., D'Argembeau, A., Van der Linden, M., & Aldenhoff, L. (2004). The effect of ageing on the recollection of emotional and neutral pictures. *Memory*, 12, 673–684. <http://dx.doi.org/10.1080/09658210344000477>
- Craik, F. I. M., & Byrd, M. (1982). Aging and cognitive deficits: The role of attentional resources. In F. Craik & S. Trehub (Eds.), *Aging and cognitive processes* (pp. 191–211). New York, NY: Springer.
- Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 2157–2162. <http://dx.doi.org/10.1073/pnas.0337195100>
- de Chastelaine, M., Mattson, J. T., Wang, T. H., Donley, B. E., & Rugg, M. D. (2015). Sensitivity of negative subsequent memory and task-negative effects to age and associative memory performance. *Brain Research*, 1612, 16–29. <http://dx.doi.org/10.1016/j.brainres.2014.09.045>
- de Chastelaine, M., Mattson, J. T., Wang, T. H., Donley, B. E., & Rugg, M. D. (2016). The neural correlates of recollection and retrieval monitoring: Relationships with age and recollection performance [erratum at <https://www.sciencedirect.com/science/article/pii/S1053811917301763?via%3Dihub>]. *NeuroImage*, 138, 164–175. <http://dx.doi.org/10.1016/j.neuroimage.2016.04.071>
- Dennis, N. A., Hayes, S. M., Prince, S. E., Madden, D. J., Huettel, S. A., & Cabeza, R. (2008). Effects of aging on the neural correlates of successful item and source memory encoding. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 34, 791–808. <http://dx.doi.org/10.1037/0278-7393.34.4.791>
- Dennis, N. A., Kim, H., & Cabeza, R. (2008). Age-related differences in brain activity during true and false memory retrieval. *Journal of Cognitive Neuroscience*, 20, 1390–1402. <http://dx.doi.org/10.1162/jocn.2008.20096>
- Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, 11, 379–386. <http://dx.doi.org/10.1016/j.tics.2007.08.001>
- Duarte, A., Henson, R. N., & Graham, K. S. (2008). The effects of aging on the neural correlates of subjective and objective recollection. *Cerebral Cortex*, 18, 2169–2180. <http://dx.doi.org/10.1093/cercor/bhm243>
- Duarte, A., Ranganath, C., & Knight, R. T. (2005). Effects of unilateral prefrontal lesions on familiarity, recollection, and source memory. *The Journal of Neuroscience*, 25, 8333–8337. <http://dx.doi.org/10.1523/JNEUROSCI.1392-05.2005>
- Duarte, A., Ranganath, C., Trujillo, C., & Knight, R. T. (2006). Intact recollection memory in high-performing older adults: ERP and behavioral evidence. *Journal of Cognitive Neuroscience*, 18, 33–47. <http://dx.doi.org/10.1162/089892906775249988>
- Dulas, M. R., & Duarte, A. (2011). The effects of aging on material-independent and material-dependent neural correlates of contextual binding. *NeuroImage*, 57, 1192–1204. <http://dx.doi.org/10.1016/j.neuroimage.2011.05.036>

- Dulas, M. R., & Duarte, A. (2012). The effects of aging on material-independent and material-dependent neural correlates of source memory retrieval. *Cerebral Cortex*, *22*, 37–50. <http://dx.doi.org/10.1093/cercor/bhr056>
- Dulas, M. R., & Duarte, A. (2013). The influence of directed attention at encoding on source memory retrieval in the young and old: An ERP study. *Brain Research*, *1500*, 55–71. <http://dx.doi.org/10.1016/j.brainres.2013.01.018>
- Dulas, M. R., & Duarte, A. (2014). Aging affects the interaction between attentional control and source memory: An fMRI study. *Journal of Cognitive Neuroscience*, *26*, 2653–2669. http://dx.doi.org/10.1162/jocn_a_00663
- Duverne, S., Motamedinia, S., & Rugg, M. D. (2009a). Effects of age on the neural correlates of retrieval cue processing are modulated by task demands. *Journal of Cognitive Neuroscience*, *21*, 1–17. <http://dx.doi.org/10.1162/jocn.2009.21001>
- Duverne, S., Motamedinia, S., & Rugg, M. D. (2009b). The relationship between aging, performance, and the neural correlates of successful memory encoding. *Cerebral Cortex*, *19*, 733–744. <http://dx.doi.org/10.1093/cercor/bhn122>
- Düzel, E., Schütze, H., Yonelinas, A. P., & Heinze, H. J. (2011). Functional phenotyping of successful aging in long-term memory: Preserved performance in the absence of neural compensation. *Hippocampus*, *21*, 803–814.
- Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*, 123–152. <http://dx.doi.org/10.1146/annurev.neuro.30.051606.094328>
- Erk, S., Kleczar, A., & Walter, H. (2007). Valence-specific regulation effects in a working memory task with emotional context. *NeuroImage*, *37*, 623–632. <http://dx.doi.org/10.1016/j.neuroimage.2007.05.006>
- Ford, J. H., & Kensinger, E. A. (2018). Older adults use a prefrontal regulatory mechanism to reduce negative memory vividness of a highly emotional real-world event. *Neuroreport*, *29*, 1129–1134. <http://dx.doi.org/10.1097/WNR.0000000000001084>
- Ford, J. H., Morris, J. A., & Kensinger, E. A. (2014). Neural recruitment and connectivity during emotional memory retrieval across the adult life span. *Neurobiology of Aging*, *35*, 2770–2784. <http://dx.doi.org/10.1016/j.neurobiolaging.2014.05.029>
- Gottlieb, L. J., Uncapher, M. R., & Rugg, M. D. (2010). Dissociation of the neural correlates of visual and auditory contextual encoding. *Neuropsychologia*, *48*, 137–144. <http://dx.doi.org/10.1016/j.neuropsychologia.2009.08.019>
- Gutchess, A. H., Sokal, R., Coleman, J. A., Gotthilf, G., Grewal, L., & Rosa, N. (2015). Age differences in self-referencing: Evidence for common and distinct encoding strategies. *Brain Research*, *1612*, 118–127. <http://dx.doi.org/10.1016/j.brainres.2014.08.033>
- Hasher, L., & Zacks, R. (1988). Working memory, comprehension, and aging: A review and a new view. In G. Bower (Ed.), *The psychology of learning and motivation* (pp. 193–225). San Diego, CA: Academic Press. [http://dx.doi.org/10.1016/S0079-7421\(08\)60041-9](http://dx.doi.org/10.1016/S0079-7421(08)60041-9)

- Hashtroudi, S., Johnson, M. K., & Chrosniak, L. D. (1990). Aging and qualitative characteristics of memories for perceived and imagined complex events. *Psychology and Aging, 5*, 119–126. <http://dx.doi.org/10.1037/0882-7974.5.1.119>
- Henkel, L. A., Johnson, M. K., & De Leonardis, D. M. (1998). Aging and source monitoring: Cognitive processes and neuropsychological correlates. *Journal of Experimental Psychology: General, 127*, 251–268. <http://dx.doi.org/10.1037/0096-3445.127.3.251>
- Hertzog, C., McGuire, C. L., Horhota, M., & Jopp, D. (2010). Does believing in “use it or lose it” relate to self-rated memory control, strategy use, and recall? *The International Journal of Aging & Human Development, 70*, 61–87. <http://dx.doi.org/10.2190/AG.70.1.c>
- Hultsch, D. F., Hertzog, C., & Dixon, R. A. (1990). Ability correlates of memory performance in adulthood and aging. *Psychology and Aging, 5*, 356–368. <http://dx.doi.org/10.1037/0882-7974.5.3.356>
- Jacoby, L. L., Bishara, A. J., Hessels, S., & Toth, J. P. (2005). Aging, subjective experience, and cognitive control: Dramatic false remembering by older adults. *Journal of Experimental Psychology: General, 134*, 131–148. <http://dx.doi.org/10.1037/0096-3445.134.2.131>
- Janowsky, J. S., Shimamura, A. P., & Squire, L. R. (1989). Source memory impairment in patients with frontal lobe lesions. *Neuropsychologia, 27*, 1043–1056. [http://dx.doi.org/10.1016/0028-3932\(89\)90184-X](http://dx.doi.org/10.1016/0028-3932(89)90184-X)
- Kalpouzos, G., Fischer, H., Rieckmann, A., Macdonald, S. W., & Bäckman, L. (2012). Impact of negative emotion on the neural correlates of long-term recognition in younger and older adults. *Frontiers in Integrative Neuroscience, 6*, 74. <http://dx.doi.org/10.3389/fnint.2012.00074>
- Kensinger, E. A., Allard, E., & Krendl, A. C. (2014). The effects of age on memory for socioemotional material: An affective neuroscience perspective. In P. Verhaeghen & C. Hertzog (Eds.), *The Oxford handbook of emotion, social cognition, and problem solving in adulthood* (pp. 26–46). Oxford, England: Oxford University Press.
- Kensinger, E. A., Brierley, B., Medford, N., Growdon, J. H., & Corkin, S. (2002). Effects of normal aging and Alzheimer’s disease on emotional memory. *Emotion, 2*, 118–134. <http://dx.doi.org/10.1037/1528-3542.2.2.118>
- Kirchhoff, B. A., Anderson, B. A., Barch, D. M., & Jacoby, L. L. (2012). Cognitive and neural effects of semantic encoding strategy training in older adults. *Cerebral Cortex, 22*, 788–799. <http://dx.doi.org/10.1093/cercor/bhr129>
- Kirchhoff, B. A., & Buckner, R. L. (2006). Functional–anatomic correlates of individual differences in memory. *Neuron, 51*, 263–274. <http://dx.doi.org/10.1016/j.neuron.2006.06.006>
- Knight, M., Seymour, T. L., Gaunt, J. T., Baker, C., Nesmith, K., & Mather, M. (2007). Aging and goal-directed emotional attention: Distraction reverses emotional biases. *Emotion, 7*, 705–714. <http://dx.doi.org/10.1037/1528-3542.7.4.705>
- Kopelman, M. D., Stanhope, N., & Kingsley, D. (1997). Temporal and spatial context memory in patients with focal frontal, temporal lobe, and dience-

- phalic lesions. *Neuropsychologia*, 35, 1533–1545. [http://dx.doi.org/10.1016/S0028-3932\(97\)00076-6](http://dx.doi.org/10.1016/S0028-3932(97)00076-6)
- Kuhl, B. A., Bainbridge, W. A., & Chun, M. M. (2012). Neural reactivation reveals mechanisms for updating memory. *The Journal of Neuroscience*, 32, 3453–3461. <http://dx.doi.org/10.1523/JNEUROSCI.5846-11.2012>
- Kvavilashvili, L., Mirani, J., Schlagman, S., Erskine, J. A., & Kornbrot, D. E. (2010). Effects of age on phenomenology and consistency of flashbulb memories of September 11 and a staged control event. *Psychology and Aging*, 25, 391–404. <http://dx.doi.org/10.1037/a0017532>
- Kwon, D., Maillet, D., Pasvanis, S., Ankudowich, E., Grady, C. L., & Rajah, M. N. (2016). Context memory decline in middle aged adults is related to changes in prefrontal cortex function. *Cerebral Cortex*, 26, 2440–2460. <http://dx.doi.org/10.1093/cercor/bhv068>
- Leshikar, E. D., & Duarte, A. (2014). Medial prefrontal cortex supports source memory for self-referenced materials in young and older adults. *Cognitive, Affective & Behavioral Neuroscience*, 14, 236–252. <http://dx.doi.org/10.3758/s13415-013-0198-y>
- Leshikar, E. D., Duarte, A., & Hertzog, C. (2012). Task-selective memory effects for successfully implemented encoding strategies. *PLoS One*, 7, e38160. <http://dx.doi.org/10.1371/journal.pone.0038160>
- Liang, J. C., & Preston, A. R. (2017). Medial temporal lobe reinstatement of content-specific details predicts source memory. *Cortex*, 91, 67–78. <http://dx.doi.org/10.1016/j.cortex.2016.09.011>
- Light, L. L. (1991). Memory and aging: Four hypotheses in search of data. *Annual Review of Psychology*, 42, 333–376. <http://dx.doi.org/10.1146/annurev.ps.42.020191.002001>
- Logan, J. M., Sanders, A. L., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2002). Under-recruitment and nonselective recruitment: Dissociable neural mechanisms associated with aging. *Neuron*, 33, 827–840. [http://dx.doi.org/10.1016/S0896-6273\(02\)00612-8](http://dx.doi.org/10.1016/S0896-6273(02)00612-8)
- Lövdén, M., Bäckman, L., Lindenberger, U., Schaefer, S., & Schmiedek, F. (2010). A theoretical framework for the study of adult cognitive plasticity. *Psychological Bulletin*, 136, 659–676. <http://dx.doi.org/10.1037/a0020080>
- Maillet, D., & Rajah, M. N. (2014). Age-related differences in brain activity in the subsequent memory paradigm: A meta-analysis. *Neuroscience and Biobehavioral Reviews*, 45, 246–257. <http://dx.doi.org/10.1016/j.neubiorev.2014.06.006>
- Mather, M., & Knight, M. (2005). Goal-directed memory: The role of cognitive control in older adults' emotional memory. *Psychology and Aging*, 20, 554–570. <http://dx.doi.org/10.1037/0882-7974.20.4.554>
- May, C. P., Rahhal, T., Berry, E. M., & Leighton, E. A. (2005). Aging, source memory, and emotion. *Psychology and Aging*, 20, 571–578. <http://dx.doi.org/10.1037/0882-7974.20.4.571>
- McDonough, I. M., & Gallo, D. A. (2013). Impaired retrieval monitoring for past and future autobiographical events in older adults. *Psychology and Aging*, 28, 457–466. <http://dx.doi.org/10.1037/a0032732>

- McGinnis, D., Goss, R., Tessmer, C., & Zelinski, E. M. (2008). Inference generation in young, young-old, and old-old adults: Evidence for semantic architecture stability. *Applied Cognitive Psychology*, *22*, 171–192. <http://dx.doi.org/10.1002/acp.1367>
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202. <http://dx.doi.org/10.1146/annurev.neuro.24.1.167>
- Miller, S. L., Celone, K., DePeau, K., Diamond, E., Dickerson, B. C., Rentz, D., . . . Sperling, R. A. (2008). Age-related memory impairment associated with loss of parietal deactivation but preserved hippocampal activation. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 2181–2186. <http://dx.doi.org/10.1073/pnas.0706818105>
- Milner, B. (2005). The medial temporal-lobe amnesic syndrome. *Psychiatric Clinics of North America*, *28*, 599–611, 609. Retrieved from <https://www.sciencedirect.com/science/article/pii/S0193953X05000560?via%3Dihub>
- Mishra, J., & Gazzaley, A. (2014). Closed-loop rehabilitation of age-related cognitive disorders. *Seminars in Neurology*, *34*, 584–590. <http://dx.doi.org/10.1055/s-0034-1396011>
- Mitchell, K. J., & Johnson, M. K. (2009). Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory? *Psychological Bulletin*, *135*, 638–677. <http://dx.doi.org/10.1037/a0015849>
- Morcom, A. M., Li, J., & Rugg, M. D. (2007). Age effects on the neural correlates of episodic retrieval: Increased cortical recruitment with matched performance. *Cerebral Cortex*, *17*, 2491–2506. <http://dx.doi.org/10.1093/cercor/bhl155>
- Murty, V. P., Sambataro, F., Das, S., Tan, H. Y., Callicott, J. H., Goldberg, T. E., . . . Mattay, V. S. (2009). Age-related alterations in simple declarative memory and the effect of negative stimulus valence. *Journal of Cognitive Neuroscience*, *21*, 1920–1933. <http://dx.doi.org/10.1162/jocn.2009.21130>
- Nashiro, K., & Mather, M. (2011). Effects of emotional arousal on memory binding in normal aging and Alzheimer's disease. *The American Journal of Psychology*, *124*, 301–312. <http://dx.doi.org/10.5406/amerjpsyc.124.3.0301>
- Naveh-Benjamin, M. (2000). Adult age differences in memory performance: Tests of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*, 1170–1187. <http://dx.doi.org/10.1037/0278-7393.26.5.1170>
- Naveh-Benjamin, M., Brav, T. K., & Levy, O. (2007). The associative memory deficit of older adults: The role of strategy utilization. *Psychology and Aging*, *22*, 202–208. <http://dx.doi.org/10.1037/0882-7974.22.1.202>
- Newsome, R. N., Dulas, M. R., & Duarte, A. (2012). The effects of aging on emotion-induced modulations of source retrieval ERPs: Evidence for valence biases. *Neuropsychologia*, *50*, 3370–3384. <http://dx.doi.org/10.1016/j.neuropsychologia.2012.09.024>
- Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*, 424–430. <http://dx.doi.org/10.1016/j.tics.2006.07.005>

- Nyberg, L., Salami, A., Andersson, M., Eriksson, J., Kalpouzos, G., Kauppi, K., . . . Nilsson, L. G. (2010). Longitudinal evidence for diminished frontal cortex function in aging. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 22682–22686. <http://dx.doi.org/10.1073/pnas.1012651108>
- Opitz, P. C., Rauch, L. C., Terry, D. P., & Urry, H. L. (2012). Prefrontal mediation of age differences in cognitive reappraisal. *Neurobiology of Aging*, *33*, 645–655. <http://dx.doi.org/10.1016/j.neurobiolaging.2010.06.004>
- Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*, *60*, 173–196. <http://dx.doi.org/10.1146/annurev.psych.59.103006.093656>
- Perfect, T. J., & Dasgupta, Z. R. (1997). What underlies the deficit in reported recollective experience in old age? *Memory & Cognition*, *25*, 849–858. <http://dx.doi.org/10.3758/BF03211329>
- Petrides, M. (2005). Lateral prefrontal cortex: Architectonic and functional organization. *Philosophical Transactions of the Royal Society of London: Series B. Biological Sciences*, *360*, 781–795. <http://dx.doi.org/10.1098/rstb.2005.1631>
- Pudas, S., Josefsson, M., Rieckmann, A., & Nyberg, L. (2018). Longitudinal evidence for increased functional response in frontal cortex for older adults with hippocampal atrophy and memory decline. *Cerebral Cortex*, *28*, 936–948. <http://dx.doi.org/10.1093/cercor/bhw418>
- Rahhal, T. A., May, C. P., & Hasher, L. (2002). Truth and character: Sources that older adults can remember. *Psychological Science*, *13*, 101–105. <http://dx.doi.org/10.1111/1467-9280.00419>
- Rajah, M. N., Languay, R., & Valiquette, L. (2010). Age-related changes in prefrontal cortex activity are associated with behavioural deficits in both temporal and spatial context memory retrieval in older adults. *Cortex*, *46*, 535–549. <http://dx.doi.org/10.1016/j.cortex.2009.07.006>
- Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience*, *5*, 184–194. <http://dx.doi.org/10.1038/nrn1343>
- Raz, N., & Kennedy, K. M. (2009). A systems approach to the aging brain: Neuroanatomic changes, their modifiers, and cognitive correlates. In W. J. Jagust & M. D'Esposito (Eds.), *Imaging the aging brain* (pp. 43–70). New York, NY: Oxford University Press. <http://dx.doi.org/10.1093/acprof:oso/9780195328875.003.0004>
- Reed, A. E., & Carstensen, L. L. (2012). The theory behind the age-related positivity effect. *Frontiers in Psychology*, *3*, 339. <http://dx.doi.org/10.3389/fpsyg.2012.00339>
- Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, *17*, 177–182. <http://dx.doi.org/10.1111/j.1467-8721.2008.00570.x>
- Rugg, M. D., & Morcom, A. M. (2005). The relationship between brain activity, cognitive performance and aging: The case of memory. In R. Cabeza, L. Nyberg, & D. C. Park (Eds.), *Cognitive neuroscience of aging: Linking cognitive and cerebral aging* (pp. 132–154). New York, NY: Oxford University Press.

- Sakaki, M., Nga, L., & Mather, M. (2013). Amygdala functional connectivity with medial prefrontal cortex at rest predicts the positivity effect in older adults' memory. *Journal of Cognitive Neuroscience*, *25*, 1206–1224. http://dx.doi.org/10.1162/jocn_a_00392
- Salami, A., Eriksson, J., & Nyberg, L. (2012). Opposing effects of aging on large-scale brain systems for memory encoding and cognitive control. *The Journal of Neuroscience*, *32*, 10749–10757. <http://dx.doi.org/10.1523/JNEUROSCI.0278-12.2012>
- Salthouse, T. A. (2014). Why are there different age relations in cross-sectional and longitudinal comparisons of cognitive functioning? *Current Directions in Psychological Science*, *23*, 252–256. <http://dx.doi.org/10.1177/0963721414535212>
- Salthouse, T. A. (2015). Do cognitive interventions alter the rate of age-related cognitive change? *Intelligence*, *53*, 86–91. <http://dx.doi.org/10.1016/j.intell.2015.09.004>
- Schacter, D. L., Koutstaal, W., & Norman, K. A. (1997). False memories and aging. *Trends in Cognitive Sciences*, *1*, 229–236. [http://dx.doi.org/10.1016/S1364-6613\(97\)01068-1](http://dx.doi.org/10.1016/S1364-6613(97)01068-1)
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2017). The contribution of the human posterior parietal cortex to episodic memory. *Nature Reviews Neuroscience*, *18*, 183–192. <http://dx.doi.org/10.1038/nrn.2017.6>
- Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews Neuroscience*, *4*, 637–648. <http://dx.doi.org/10.1038/nrn1178>
- St. Jacques, P. L., Dolcos, F., & Cabeza, R. (2009). Effects of aging on functional connectivity of the amygdala for subsequent memory of negative pictures: A network analysis of functional magnetic resonance imaging data. *Psychological Science*, *20*, 74–84. <http://dx.doi.org/10.1111/j.1467-9280.2008.02258.x>
- Staresina, B. P., Henson, R. N., Kriegeskorte, N., & Alink, A. (2012). Episodic reinstatement in the medial temporal lobe. *The Journal of Neuroscience*, *32*, 18150–18156. <http://dx.doi.org/10.1523/JNEUROSCI.4156-12.2012>
- Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic encoding: Insights from fMRI subsequent memory effects and dual-attention theory. *Neurobiology of Learning and Memory*, *91*, 139–154. <http://dx.doi.org/10.1016/j.nlm.2008.10.011>
- van Strien, N. M., Cappaert, N. L., & Witter, M. P. (2009). The anatomy of memory: An interactive overview of the parahippocampal-hippocampal network. *Nature Reviews Neuroscience*, *10*, 272–282. <http://dx.doi.org/10.1038/nrn2614>
- Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, *46*, 1787–1799. <http://dx.doi.org/10.1016/j.neuropsychologia.2008.01.004>
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, *9*, 445–453. <http://dx.doi.org/10.1016/j.tics.2005.07.001>
- Waldinger, R. J., Kensinger, E. A., & Schulz, M. S. (2011). Neural activity, neural connectivity, and the processing of emotionally valenced information in older

- adults: Links with life satisfaction. *Cognitive, Affective & Behavioral Neuroscience*, 11, 426–436. <http://dx.doi.org/10.3758/s13415-011-0039-9>
- Wang, T. H., Johnson, J. D., de Chastelaine, M., Donley, B. E., & Rugg, M. D. (2016). The effects of age on the neural correlates of recollection success, recollection-related cortical reinstatement, and post-retrieval monitoring. *Cerebral Cortex*, 26, 1698–1714. <http://dx.doi.org/10.1093/cercor/bhu333>
- West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin*, 120, 272–292. <http://dx.doi.org/10.1037/0033-2909.120.2.272>
- Williams, K. N., & Kemper, S. (2010). Interventions to reduce cognitive decline in aging. *Journal of Psychosocial Nursing and Mental Health Services*, 48, 42–51. <http://dx.doi.org/10.3928/02793695-20100331-03>
- Winecoff, A., Labar, K. S., Madden, D. J., Cabeza, R., & Huettel, S. A. (2011). Cognitive and neural contributors to emotion regulation in aging. *Social Cognitive and Affective Neuroscience*, 6, 165–176. <http://dx.doi.org/10.1093/scan/nsq030>
- Xiao, X., Dong, Q., Gao, J., Men, W., Poldrack, R. A., & Xue, G. (2017). Transformed neural pattern reinstatement during episodic memory retrieval. *The Journal of Neuroscience*, 37, 2986–2998. <http://dx.doi.org/10.1523/JNEUROSCI.2324-16.2017>
- Zajonc, R. B. (1980). Feeling and thinking. Preferences need no inferences. *American Psychologist*, 35, 151–175. <http://dx.doi.org/10.1037/0003-066X.35.2.151>