

CHAPTER 10

Item and Associative Memory Decline in Healthy Aging

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INTRODUCTION

When considering age-related deficits in episodic memory, nearly countless factors ranging from individual differences to memory instructions to type of memory test used have been shown to influence age differences in behavior (for extensive reviews see Cabeza, Nyberg, & Park, 2005; Craik, Anderson, Kerr, & Li, 1995; Dixon, Small, MacDonald, & McArdle, 2012; Zacks, Hasher, & Li, 2000). The following review will focus on a handful of such factors that have been shown to influence behavior in item memory and associative memory, as well as those investigated using functional neuroimaging. Item and associative memory represent key areas of research within the context of memory and aging. The former refers to memory for an individual item or episode, whereas the latter refers to memory for the relationship between two or more items or

between an item and its context. Although item memory represents a large majority of the original research examining memory deficits in aging, associative memory is generally considered a more difficult memory task and more reflective of real-world experiences. When possible, we will draw links between findings identified in the behavioral literature and those in the neural literature. We will also explore how results fit with existing theories of cognitive aging and identify future work necessary to integrate the current set of findings. Finally, we will explore means by which memory deficits have been mitigated in aging and the neural underpinnings of such memory improvements.

BEHAVIORAL EVIDENCE FOR AGE-RELATED DECLINE IN ITEM MEMORY

Item memory refers to the process of remembering a single unit or piece of information, such as a word or a picture. Within the context of aging, several factors have been identified as having significant impacts on age differences in performance, including the type of stimuli being tested, the testing format, the depth of processing, the encoding task, and the contributions of recollection and

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familiarity to memory. In reviewing these findings, we will also identify how relatively simple modifications to stimuli presentation, memory instructions, or strategy use can have significant benefits to performance in older adults.

Encoding

Although it is often difficult, from a behavioral perspective, to isolate age differences in memory with respect to memory phase (encoding or retrieval), several studies have manipulated variables within each stage in order to isolate the contributions a given stage has to overall memory performance. With respect to encoding, several studies have suggested that age deficits in perception may lead to reduced visual input during encoding (for a review of perceptual deterioration and its implications for aging, see Schneider & Pichora-Fuller, 2000). Age deficits in sensory processing, specifically in the visual and auditory domains, are well established (e.g., Cruickshanks et al., 1998; Schneider & Pichora-Fuller, 2000; Surprenant, 2007). Thus, with regard to the study phase of memory, it has been suggested that age deficits in memory are due, in part, to the fact that older adults encode less detailed information (e.g., Anderson & Craik, 2000; Glisky, Rubin, & Davidson, 2001; Hess & Slaughter, 1990; Koutstaal, Schacter, Galluccio, & Stofer, 1999) and to some degree rely on more general or *gist* information (Brainerd, Reyna, & Kneer, 1995; Reyna & Brainerd, 1995). Support for this theory comes from studies that find that degrading the quality of information (e.g., visually degraded stimuli) (e.g., Anstey, Butterworth, Borzycki, & Andrews, 2006; Harley, Dillon, & Loftus, 2004) provided to younger adults equates memory performance between age groups (Craik & Rose, 2012; Murphy, Craik, Li, & Schneider, 2000; Rabbitt, 1968; Schneider & Pichora-Fuller, 2000).

To this end, older adults exhibit minimal age deficits when the encoding material involves perceptually rich stimuli such as pictures or scenes compared to the use of words (e.g., Craik & Byrd, 1982; Grady, McIntosh, Rajah, Beig, & Craik, 1999; Hale et al., 2011; Rose, Myerson, Sommers, & Hale, 2009). There is an inherent element of environmental support when pictures are rich and detailed. Unlike in words or other verbal memory tasks, in which individuals must largely rely on self-generation to elaborate and encode, detailed pictures provide perceptual detail and content supportive of deep, semantic encoding (e.g., Smith, Park, Cherry, & Berkovsky, 1990). For example, Smith and colleagues (1990) used visual details (see Figure 10.1 for example) to convey complex perceptual information (complex or detailed pictures versus simple pictures) as well as the propositional content to vary the linguistic meaningfulness (concrete versus abstract). Results showed no age-related differences in memory for complex-concrete pictures yet an age deficit in memory for simple pictures. Similar to this finding, it has been shown that information that lacks an inherent perceptual meaning or semantic labels (i.e., random visuospatial patterns or unclassifiable material) is generally poorly remembered and shows relatively large age deficits in memory (e.g., Hale et al., 2011; Rose et al., 2009). Taken together, results suggest that perceptual detail during encoding enhances memory performance in older adults, mitigating age differences that arise when information lacks such meaning.

Inherent in the foregoing results, it is posited that such perceptually rich stimuli carry enhanced meaning and implicitly engage deep encoding processes that support subsequent memory. Research has shown that younger and older adults benefit from deep versus shallow encoding and that these benefits may reduce age differences in

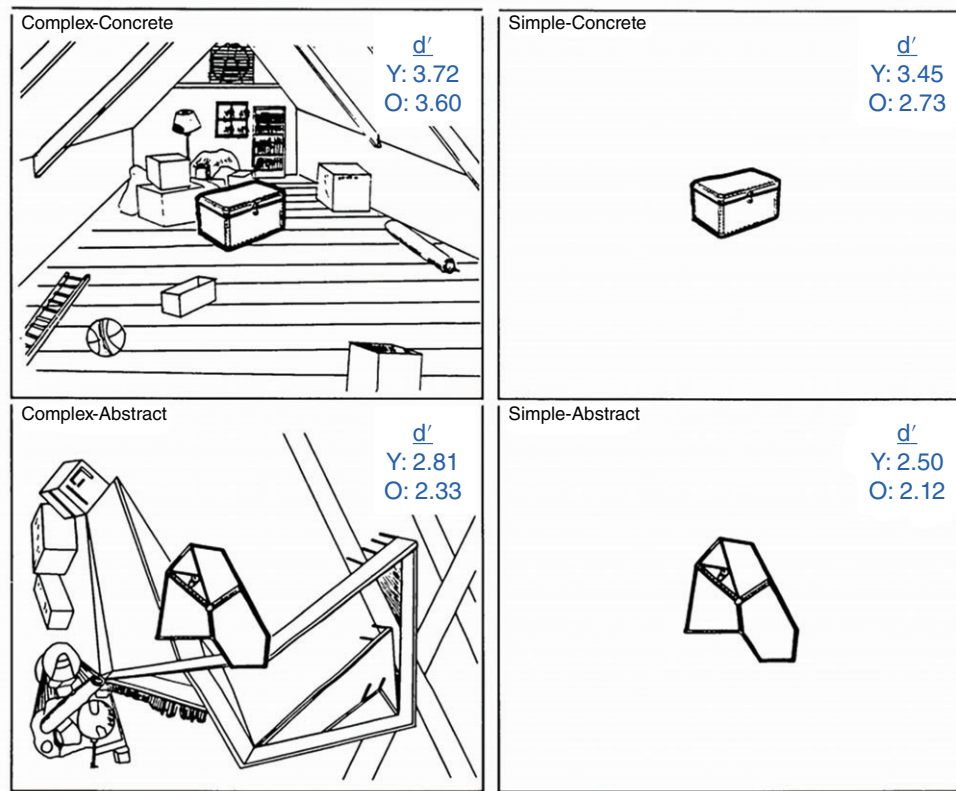


Figure 10.1 An example of simple and complex pictures exemplifying how memory support delivered through varying degrees of visual detail can lead to enhanced memory in older adults. Top right of each panel shows d' values for younger (Y) and older (O) adults.

SOURCE: Adapted from Smith et al. (1990). Age differences in memory for concrete and abstract pictures. *Journal of Gerontology*, 45(5), 205–210, by permission of Oxford University Press.

memory (e.g., Bäckman, 1986; Grady, Bernstein, Beig, & Siegenthaler, 2002; Troyer, Hafliger, Cadieux, & Craik, 2006). Additionally, when encoding incorporates the use of semantic processes—processes that exhibit little to no decline in aging (Craik, 2000; Light, 1992; Light & Burke, 1988)—memory deficits are minimized (Hill, Allen, & Mcwhorter, 1991; Hill, Storandt, & Simeone, 1990). For example, Troyer and colleagues (2006, Experiment 1) found that memory performance for names taken from a phonebook increased when encoding utilized semantic meaning compared to encoding instructions that focused on phonemic or physical characteristics of the names. Moreover,

results showed that semantic processing benefited memory performance in older adults more so than in younger adults. Similarly, Froger, Taconnat, Landre, Beigneux, and Isingrini (2009) demonstrated that younger and older adults showed increased memory performance for semantic versus shallow encoding. In shallow conditions, participants determined if a presented word's first or last letter was an *E*. In the semantic condition, participants made a judgment as to whether or not the word was a concrete or abstract entity.

Although deep encoding clearly provides memory benefits compared to shallow encoding, older adults often fail to spontaneously adopt a deep encoding strategy and thus do

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not take advantage of these benefits. That is, research has shown that memory tests employing incidental encoding typically result in information being processed in less elaborate and meaningful manners in older compared to younger adults (Craig, 1983, 1986, 2002; Rabinowitz, Craig, & Ackerman, 1982). This trend largely holds true for intentional encoding as well (Hultsch, Hertzog, & Dixon, 1990; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Sanders, Murphy, Schmitt, & Walsh, 1980; Witte, Freund, & Sebb, 1990). Even with the understanding of intentional encoding, some older adults report the absence of any strategy use (Devolder & Pressley, 1992; Perfect & Dasgupta, 1997; Rowe & Schnore, 1971). As to why this is the case, it is often theorized that, due to limited resources in aging, older adults are unable to spontaneously engage in the necessary, effortful processes that will lead to deep, meaningful encoding (Craig & Byrd, 1982; Perlmutter & Mitchell, 1982).

Supporting this theory, when studies tax resources in younger adults either by divided attention tasks (e.g., Anderson, Craig, & Naveh-Benjamin, 1998; Lindenberger, Marsiske, & Baltes, 2000) or limiting the time available to complete encoding operations (e.g., Paivo & Csapo, 1969; Salthouse, 1996; Simon, 1979) younger adults' memory performance often reflects that typically observed in aging. Together, this evidence has led to the idea that an inability to spontaneously adopt an effective encoding strategy may be linked to age-related decline in frontal functioning (Kapur et al., 1994; Tulving, Kapur, Craig, Moscovitch, & Houle, 1994). However, this conclusion should be taken with caution given that when encoding strategies are provided to older adults, they tend to perform on par with younger counterparts (e.g., Cheke, 2016; Craig & Rose, 2012; Perfect & Dasgupta, 1997; Perfect, Williams, & Anderton-Brown, 1995). Thus,

it is more likely the case that older adults' deficits do not lie in the execution of the encoding strategy (which would point to a functional issue) but rather with spontaneous engagement of an effective encoding strategy.

Taken together, the aforementioned findings highlight the role of encoding and the influence of stimulus detail and encoding instructions to memory performance in older adults. Specifically, research finds that older adults benefit from being provided with detailed and meaningful stimuli at encoding and an explicit encoding strategy that taps into semantic processing. Interestingly, the fact that older adults tend not self-initiate meaningful encoding strategies, but can use them when instructed to do so, suggests that their memory deficit is not one of execution but rather one of initiation and may arise due to resource limitations that prevent older adults from searching for the most effective encoding strategy when presented with a memory task. Thus, with respect to item memory, the provision of encoding support is able to ameliorate age deficits by enabling older adults to engage cognitive resources at their disposal and form a rich memory trace.

Retrieval

Importantly, factors that affect age-related memory deficits are not limited to encoding but have also been examined at retrieval. Research examining retrieval-related factors influencing age differences in item memory has focused on factors such as testing methods, environmental support, retrieval support, and specificity of retrieval strength (i.e., recollection or familiarity). With respect to the influence of testing method and environmental support, item memory is typically evaluated using free recall and recognition tests. Broadly speaking, the former refers to a process of generating previously encountered information from memory in the absence

of environment support, whereas the latter involves making a judgment as to whether an item was previously encountered. As such, free recall requires the need to self-initiate strategic search processes in order to retrieve previously encountered information. Similar to self-initiated encoding, such a process can be taxing on older adults' limited resources (e.g., Craik & Byrd, 1982), leading to large age deficits because older adults are unable to identify a strategy that supports memory success (Botwinick, 1978; Burke & Light, 1981; Craik, 1977). Supporting this notion, work by Craik and McDowd (1987) found that age deficits were not only larger for a cued recall test than for a recognition test but also that cued recall was associated with significantly longer response times than that for recognition, concluding that recall required more cognitive resources in older adults. Similarly, Macht and Buschke (1983) had participants perform a recall task while simultaneously performing a reaction time task in which they were required to press a button each time a light bulb turned on. Older adults exhibited significant increases in reaction time compared to younger adults, which the authors interpreted as reflecting the effortful and taxing nature of recall in aging.

Although recall tasks are taxing for older adults, numerous studies have demonstrated that age differences are significantly smaller for recognition tests (compared to recall tests), in which there exists retrieval support and a clearer retrieval strategy (Botwinick & Storandt, 1980; Craik, 1977; Craik & Jennings, 1992; Craik & McDowd, 1987; LaVoie & Light, 1994; Old & Naveh-Benjamin, 2008; Schonfield & Robertson, 1966; Wahlin, Bäckman, & Winblad, 1995; Whiting & Smith, 1997; Yonelinas, 2002). The previously described work by Craik and McDowd (1987) demonstrated that the older adults had a greater age difference for words

during a recall task as compared to words during a recognition task (e.g., 4% difference for recognition and 13% difference for recall). In another study, Bastin and Van der Linden (2006) examined face memory within a forced-choice recognition task. In such a test, younger and older adults displayed near-ceiling memory performance, indicating that retrieval and contextual support provided by a recognition test can be a key factor to mitigating age differences in item memory.

Within the context of retrieval, results have also shown that age deficits are mitigated when items are tested in the same modality as they were studied (e.g., Larsson & Bäckman, 1998; Lehman & Mellinger, 1984; Light, LaVoie, Valencia-Laver, Owens, & Mead, 1992; Naveh-Benjamin & Craik, 1995). For example, Naveh-Benjamin and Craik (1995) had participants encode words presented visually. A recognition task was then administered in either the same modality (i.e., visually) or in an auditory format. Younger and older adults showed greater memory performance when the words were presented in the reinstated modality, with a smaller age-difference for the reinstated modality. Such context reinstatement findings fall within the contextual support argument, suggesting that older adults are able to take advantage of contextual support when provided in memory tests, but they do not generate this information on their own, thereby lending to much of the memory deficits observed in the literature.

Another factor that has been shown to have a significant influence on memory performance in older adults is the specific memory process that is engaged during retrieval, with the most studied processes being recollection and familiarity (Atkinson & Juola, 1974; Jacoby & Dallas, 1981; Mandler, 1980; Reder et al., 2000; Tulving, 1985; Yonelinas, 1994, 2002). Recollection is defined as remembering specific aspects associated with a prior episode such as perceptual details,

temporal ordering, internal thoughts or feelings, or the source of the information. In contrast to recollection, familiarity involves memory in the absence of such details. Whether recollection and familiarity are two discrete processes or simply a continuum of a single process has been debated (Buchner, Erdfelder, & Vaterrodt-Plunnecke, 1995; Curran & Hintzman, 1995; Graf & Komatsu, 1994; Jacoby, Yonelinas, & Jennings, 1997; Joordens & Merikle, 1993; Toth et al., 1995). However, with respect to aging, each has provided unique profiles of behavior.

Specifically, aging is typically marked by deficits in recollection often in the presence of intact or a greater reliance on familiarity (e.g., Anderson et al., 2008; Cohn, Emrich, & Moscovitch, 2008; Jennings & Jacoby, 1997; Luo, Hendriks, & Craik, 2007; Wolk, Mancuso, Kliot, Arnold, & Dickerson, 2013; Yonelinas, 2002). Although estimates of recollection and familiarity obviously follow from the retrieval test itself, it has been suggested that such differences may arise because of poor encoding. This is evidenced by the fact that recollection deficits are reduced when studies are able to control for encoding strategies (e.g., Perfect & Dasgupta, 1997; Perfect et al., 1995). The extent to whether age differences in recollection and familiarity are an encoding or a retrieval issue cannot be completely elucidated at the behavioral level. However, imaging work does enable us to take a more nuanced look at the issue by obtaining separable measurements of encoding and retrieval processes (see the following discussion).

Item Conclusions

Thus far, we have reviewed a body of behavioral literature that has sought to provide an understanding of age-related differences in performance of item memory. We have highlighted overarching themes to encoding and retrieval, including encoding support,

resource allocation, and testing format. From the onset at encoding, we reported the impact of declining sensory process and the importance of rich, detailed stimuli. Importantly, older adults have much to gain from contextual support and use of semantic processing during encoding. Inherent to the benefits provided by such support is a reduction in cognitive resources necessary to effectively initiate useful memory strategies. A similar resource depletion account may also be at play with regard to retrieval, whereby older adults fail to retrieve encoding details, yet fare better on tasks that include contextual support. Here we now turn to associative memory, and we continue a discussion of many of the points raised in item memory and introduce challenges unique to the memory of associative information.

BEHAVIORAL EVIDENCE FOR AGE-RELATED DECLINE IN ASSOCIATIVE MEMORY

Whereas item memory focuses on memory for a single object or word, everyday memory often deals with more complex structures such as associations between items. Associative memory concerns itself with the binding together of individual items or items with a context. As such, associative memory enables us to remember everything from face-name associations to the correspondence between different medicines and their specific dosage schedule. Thus, associative memory errors can lead to a spectrum of negative consequences ranging from experiencing embarrassment (face-name association failure) to poor health or even death (medicine-dosage association failure). Aging research has shown that age-deficits in associative memory exceed those in item memory and thus may represent the foundation of age deficits in memory performance. Furthermore, association memory shares a common

profile to recall and recollection memory with respect to retrieval demands. That is, to the extent that recollection relies on memory for contextual information, recollection and associative memory may be tapping into the same retrieval processes. We will explore more of this discussion after we have presented behavioral findings pertaining to associative memory.

With regard to aging, a wealth of research has shown age-related deficits in associative memory exceed those observed in item memory (see Figure 10.2) (e.g., Bender & Raz, 2012; Naveh-Benjamin, 2000; Ratcliff & McKoon, 2015; Silver, Goodman, & Bilker, 2012). For example, Chalfonte and Johnson (1996) asked individuals to study drawings of objects, each of which was placed in its own square on a 7×7 grid, with grid squares identifiable by location and colored boundaries. They found that although older adults performed comparable to younger with respect to item memory, when the test

required knowledge of the object and the color or location of the square, older adults showed substantial age-related reductions in performance. Similarly, Simons, Dodson, Bell, and Schacter (2004) assessed age differences in memory for the content of sentences as well as the speaker's voice (i.e., source) of the sentences. Although older adults performed similarly to younger with respect to item memory, they exhibited substantial decline in performance when the test required knowledge of the sentence and the speaker's identity. The results suggest that the associative deficit in aging is not predicated on reductions in item memory but stems from deficits in forming associations among discrete pieces of information.

Research has further shown that age-deficits in associative memory are not unique to specific types of associations but are observed across multiple types of associations, including item-list associations (e.g., Trott, Friedman, Ritter, & Fabiani, 1997;

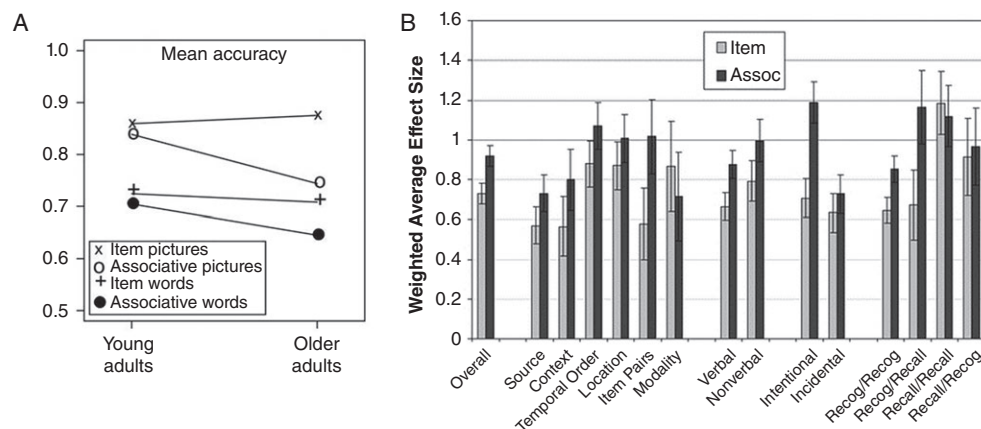


Figure 10.2 A. Plot of accuracy for item and associative memory for pictures and words in younger and older adults. B. Results from associative memory paradigms exemplifying the age-related associative memory deficit. Recog = recognition.

SOURCE: Panel A is adapted from Ratcliff and McKoon (2015). Aging effects in item and associative recognition memory for pictures and words. *Psychology and Aging*, 30(3), 669, with permission from the American Psychological Association. Panel B is reproduced from Old and Naveh-Benjamin (2008). Differential effects of age on item and associative measures of memory: a meta-analysis. *Psychology and Aging*, 23(1), 104, with permission from the American Psychological Association.

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Wegesin, Friedman, Varughese, & Stern, 2002; Wegesin, Jacobs, Zubin, Ventura, & Stern, 2000); item-location associations (e.g., Light & Zelinski, 1983; Pezdek, 1983; Puglisi, Park, Smith, & Hill, 1985); source retrieval (e.g., Ferguson, Hashtroudi, & Johnson, 1992; Glisky et al., 2001); word pairs (e.g., Naveh-Benjamin, 2000; Naveh-Benjamin, Guez, & Shulman, 2004); and speaker identity (Naveh-Benjamin & Craik, 1995). These represent just a small sampling of the various associative memory tasks present in the literature (see Old & Naveh-Benjamin, 2008). Such ubiquitous findings led researchers to suggest that age-related memory impairments are due to a global deficit in forming associations (i.e., the associative deficit hypothesis; Naveh-Benjamin, 2000). To this end, the associative deficit hypothesis is an extension of previous work suggesting that older adults exhibit difficulty binding features together in memory (e.g., Chalfonte & Johnson, 1996). Moreover, the associative deficit hypothesis highlights the comparison of item and associative memory, pinpointing older adults' memory deficits specifically to the formation of associations among units.

With respect to the underlying cause for this associative deficit, several theories have been posited, including cognitive slowing, deficits in attentional processes, failure to form semantic structure during encoding, and deficits in strategy. Cognitive slowing is predicated on the findings that, as individuals age, cognitive processes slow (Light, 1991; Myerson, Hale, Wagstaff, Poon, & Smith, 1990; Park, 2000). From this slowing a series of implications arise for human cognition, including a reduction in working memory capacity and attention (e.g., Salthouse, 1992, 1994). The binding of information required in associative memory tasks requires individuals to hold multiple items in working memory while manipulating the information to form associations. With a deficit at the level of working memory and executive

processes (Moscovitch, 1992; Moscovitch & Winocur, 1992), the reduction in capacity may result in less information that can be simultaneously held and available to form associations. Supporting this theory, Bender and Raz (2012) found reductions in working memory capacity with age were associated with worst performance in the recognition of word pairs.

Age-related declines in attentional processes have also been posited to play a role in associative memory deficits. Specifically, it has been suggested that age-related reduction in attentional resources (e.g., Craik, 1983; Craik & Byrd, 1982; Craik & Simon, 1980) may hinder older adults' ability to attend to multiple pieces of information in order to bind them into a rich episodic memory. Although a handful of studies have shown that divided attention at encoding reduces associative memory performance in younger and older adults (e.g., Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Kim & Giovanello, 2011a), several others have found that reducing attentional resources in younger adults does not produce performance deficits that mirror those observed in older adults (e.g., Castel & Craik, 2003; Kilb & Naveh-Benjamin, 2007; Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003). However, a recent study by Kim and Giovanello (2011a) showed that it may depend on the specific type of attention being tapped that is critical for producing age-related associative memory deficits. Specifically, the researchers showed that attentional demands that tapped into relational memory processing disproportionately impaired associative (versus item) memory in younger adults. Further, unlike previous findings, the observed deficits mirrored performance in older adults under full attention conditions.

Another well-examined theory focuses on the encoding processes undertaken by older adults in order to form meaningful associations among items. Similar to the encoding

deficits previously described in item memory, researchers have suggested older adults fail to engage in encoding processes that will lead to the formation of meaningful associations (Chalfonte & Johnson, 1996; Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000; Naveh-Benjamin, 2000; Ryan, Leung, Turk-Browne, & Hasher, 2007). This is supported by evidence showing that older adults have increased difficulty in associative memory tasks when the to-be-associated elements are unrelated to one another (i.e., semantically unrelated word pairs) (e.g., Naveh-Benjamin, Brav, & Levy, 2007; Naveh-Benjamin et al., 2003). For example, Naveh-Benjamin et al. (2003) found that older adults showed a disproportionate deficit in associative memory for unrelated word pairs compared to related word pairs. The authors ascribe the better performance for related pairs to the semantic nature of the pairs and ability to tap into semantic memory during encoding. With the two words being semantically related, it creates a more cohesive binding between the two separate entities, assisting the formation of the association. This finding is further supported by results from a meta-analysis of the associative deficit in aging that indicates that

the greater the similarity between the context and the item, the better the subsequent memory (Spencer & Raz, 1995). Taken together, results suggest that the degree to which disparate pieces of information are unrelated to one another incurs greater strategic processing in order to associate them.

As reviewed, older adults incur difficulty initiating such encoding strategies in associative memory tasks (Hertzog, McGuire, Horhota, & Jopp, 2010; Naveh-Benjamin, 2000; Naveh-Benjamin et al., 2007; Perfect & Dasgupta, 1997; Verhaeghen & Marcoen, 1994). Despite this difficulty in initiating effective encoding strategies, research has shown that, similar to item memory, providing older adults with an associative encoding strategy can enhance memory performance (e.g., Coane, 2013; Dunlosky & Hertzog, 1998; Naveh-Benjamin et al., 2007). For example, several studies have found that by instructing participants to mentally generate sentences using the to-be-associated word pairs, older adults improve their performance on associative memory performance as compared to older adults who are not provided an encoding strategy (Giovanello & Schacter, 2012; Naveh-Benjamin et al., 2007) (see Figure 10.3 for evidence from

		Intentional learning (No Strategy Provided)		Associative strategy provided at encoding		Associative strategy provided at encoding and retrieval	
Self-reported strategy use		Young adults	Older adults	Young adults	Older adults	Young adults	Older adults
Relational strategies	Creating a sentence	0.63	0.00	0.92	1.00	0.88	1.00
	Creating interactive mental imagery	0.29	0.00	0.04	0.00	0.00	0.00
	Using associations	0.08	0.11	0.04	0.00	0.12	0.00
Non- relational strategies	Rehearsal	0.00	0.67	0.00	0.00	0.00	0.00
	No strategy	0.00	0.22	0.00	0.00	0.00	0.00

Figure 10.3 In the absence of a provided strategy, younger adults spontaneously use relational strategies in an associative memory task, whereas older adults do not. Yet, when provided relational strategies, older adults can adopt such strategies.

SOURCE: Adapted from Naveh-Benjamin et al. (2007). The associative memory deficit of older adults: The role of strategy utilization. *Psychology and Aging*, 22(1), 202, with permission from the American Psychological Association.

Naveh-Benjamin et al., 2007). Such an encoding task enhances memory performance by encouraging individuals to connect or associate the disparate units of information (word pairs) in meaningful ways.

Related to the aforementioned strategy is the notion of “unitization” (Graf & Schacter, 1989), which involves strengthening the relationship between items (or items and contexts) during encoding so that the two items (or an item and context) to be bound are perceived as a single entity. As such, unitization promotes the use of familiarity in associative recognition because the two disparate pieces of information are viewed as a cohesive unit and thus can be processed similarly to a single item as opposed to two individual items requiring binding. Research in younger adults has shown that encoding manipulations that enable participants to encode an item and source or two items as a single unit resulted in increased familiarity during recognition (Diana, Yonelinas, & Ranganath, 2008; Giovanello, Keane, & Verfaellie, 2006; Yonelinas, Kroll, Dobbins, & Soltani, 1999). Similar benefits have been shown for older adults as well. To this end, unitization provides a critical strategy for ameliorating age-related declines in associations because it takes advantage of the relatively preserved nature of item memory and allows for retrieval to tap into familiarity processes, which are retrieval processes that show stability in aging.

The ability to rely on familiarity processes during associative memory retrieval may be a critical method for ameliorating age deficits in associative memory. At its base, associative memory is posited to rely on recollection, not familiarity processes (Yonelinas, 2002). This is due to the fact that associative memory is tested using cued recall tests or rearranged lures at retrieval, and familiarity is not a viable or efficient option for basing one’s memory decision. For example, in the case of rearranged lures, familiarity with both

items is insufficient to remembering whether the two items were studied together (see also Old & Naveh-Benjamin, 2008). Thus, it is not surprising that many cognitive and neural factors that govern age-related deficits in recollection are mirrored in associative memory. Age deficits in associative memory may be substantially reduced by encouraging older adults to rely on familiarity processing, which exhibits relatively small declines in aging. For example, Bastin et al. (2013) used the concept of unitization to enhance associative memory for item-source information. Specifically, they instructed participants to encode a noun in the likeness of the background color on which it was presented (e.g., the word *turtle* superimposed on a red background required participants to imagine a red turtle). Results showed that compared to instructions that didn’t promote unitization, the unitization instructions eliminated the age deficit in associative memory. Overman and Stephens (2013) also showed that a visualization strategy reduced age-related differences in associative memory. In their study, participants were asked to encode face-occupation associations by imagining the individual performing a task related to the identified occupation. Interestingly, in addition to enhancing item-item performance, the unitization instruction also eliminated the age difference in memory for the context (study list) in which the face-occupation pairs were originally presented. Thus, unitization appears to have benefits to associative encoding beyond even the targeted association.

Associative Conclusions

Here we have reviewed and highlighted a number of findings from behavioral studies evaluating associative memory and aging. Similar to our discussion of item encoding, it is important to note the many overarching themes. Critically, we have pointed to evidence that has documented the role

of inefficient strategy use during encoding as an underlying cause for age deficits in associative memory. Interestingly, similar to our discussion in item memory, it has been suggested that the observed age deficits do not lie in the execution of the encoding task but in the initiation of an effective encoding strategy. Taken together, these points converge to form a strategy-related account for the associative memory deficit. Faulty strategies (e.g., rehearsal), or a lack thereof, result in poor memory performance in older adults compared to their younger counterparts. But there remains encouraging evidence that associative deficits can be attenuated or even eliminated through supportive strategies such as utilization. In addition to discussing this strategy-related account, we have also provided evidence for several other possible explanations for the age deficit found for associative memory, including the slowing of cognitive processes and a reduction in available resources. Furthermore, research in associative memory, similar again to item memory, suggests that older adults benefit when they can rely on familiarity processes in lieu of more resource-demanding recollection processes. Promising work is being done to better understand which strategies are most effective, including a growing body of literature studying unitization. Finally, several of the themes explored in behavioral work have also been investigated using fMRI. In the following sections we will discuss how the imaging work can further shed light on the cognitive basis of age differences in item and associative memory.

fMRI STUDIES OF ITEM MEMORY

The foregoing behavioral findings provide a critical foundation for identifying various age-related differences in memory performance. They have also afforded researchers the opportunity to identify a multitude of cognitive processes that influence memory

behavior. As noted, one of the advantages of using neuroimaging to investigate memory and age differences therein is the fact that, although behavioral studies are unable to separate encoding and retrieval processes, neuroimaging methods can isolate memory processes at each stage. In doing so, fMRI can identify age-related decline as well as compensatory shifts in neural processing that support encoding separate from that of retrieval. To this end fMRI studies have also been able to investigate the neural basis of many of the same factors that affect aging and memory that were previously described (e.g., levels of processing, recollection and familiarity, attention, and unitization). Thus, fMRI affords researchers the ability to gain further insights into the neural mechanisms that underlie age-related differences in memory.

Encoding

A major benefit of functional neuroimaging is its ability to allow investigators to isolate age-related differences at each memory stage. With respect to encoding, early imaging studies assessed study-related activity within the context of a blocked design. As such, the studies were able to identify age-related differences in neural activity corresponding to task-related activity, yet not necessarily encoding success (see the following overview of event-related designs). The most consistent finding across blocked designs has been an age-related reduction in recruitment of the left prefrontal cortex (PFC) (Anderson et al., 2000; Cabeza et al., 1997; Grady et al., 1995, 2002; Logan et al., 2002; Morcom, Good, Frackowiak, & Rugg, 2003; Nyberg et al., 2003; Rosen et al., 2002; Stebbins et al., 2002). In many studies, this reduction was coupled with an age-related increase in recruitment of the right PFC (Anderson & Craik, 2000; Cabeza et al., 1997; Grady et al., 1995; Logan et al., 2002). To that end, it has been suggested that a more bilateral pattern of frontal activation may serve as a means to

compensate for the functional deficit incurred in the left PFC in aging. This compensatory theory was introduced by Cabeza (2002) as part of the HAROLD model (*hemispheric asymmetry reduction in older adults*).

This compensatory interpretation of bilateral activity in aging (particularly in the PFC) is supported by numerous studies that find bilateral activity accompanied by successful memory performance (for a review, see Dennis & Cabeza, 2008). Furthermore, this pattern is often more prevalent in high-performing compared to low-performing older adults (e.g., Cabeza, Anderson, Locantore, & McIntosh, 2002; Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003; Rosen et al., 2002). However, an alternative account in the literature posits that more widespread activation in older adults reflects an age-related difficulty in engaging specialized neural mechanisms (e.g., Li & Lindenberger, 1999; Logan et al., 2002). This *dedifferentiation account* is consistent with age-related increases in correlations across tasks (Lindenberger & Baltes, 1994) and is defined by the inability of older adults to selectively allocate resources (Logan et al., 2002). Konishi, Donaldson and Buckner (2001) believed that dedifferentiation demonstrated the inability to activate the appropriate brain region amid early competition of neural resources. Whereas younger adults early in a task may have engaged numerous brain regions that could potentially prove useful, they quickly inhibit unnecessary regions and utilize the most efficient regions. Older adults, by contrast, do not engage in this inhibition, thus resulting in the widespread activity observed across many studies.

With the advent of event-related designs, neuroimaging studies are able to separate encoding trials into those that lead to successful and unsuccessful subsequent memory. As such, neuroimaging analyses are able

to identify age-related differences in neural mechanisms that mediate subsequent memory success. Unlike blocked studies, results from event-related designs tend to exhibit age-related increases in left and right PFC activity (e.g., Cabeza & Dennis, 2012; Dennis, Kim, & Cabeza, 2007; Gutchess et al., 2005; Logan et al., 2002; Morcom et al., 2003). These findings were confirmed in a meta-analysis (Maillet & Rajah, 2014) in which age-related increases in subsequent memory were observed across several prefrontal regions including bilateral medial, superior, and middle frontal gyri. Interestingly, such frontal recruitment occurred in regions that were not recruited in younger adults, suggesting that older adults did not simply exhibit over-recruitment of regions critical to memory performance in younger adults because of inefficiency of using these regions but rather recruited brain regions that younger adults tend not to use for memory success. Such a pattern suggests that older adults need to use additional resources than those that are typically found to support memory encoding in younger adults.

Although the available evidence tends to be more consistent with the compensation account, several studies have found age-related increases in activity that were accompanied with poorer task performance in older adults (e.g., de Chastelaine, Wang, Minton, Muftuler, & Rugg, 2011; Duverne, Motamedinia, & Rugg, 2009; Düzel, Schutze, Yonelinas, & Heinze, 2011; Miller et al., 2008). For example, using an incidental encoding task, Duverne et al. (2009) found that over-recruitment of right PFC in older adults actually led to worse, not better, subsequent memory performance. Although the exact mechanism of this activation has yet to be understood, the results reflect possible dedifferentiation, whereby such differences in aging are deleterious to cognition. Thus, it is critical to take into consideration the

pattern of activation and behavioral profile when labeling age-related differences in neural activation as either compensation or dedifferentiation (Dennis & Cabeza, 2008).

A second major finding arising from subsequent memory studies has been the identification of age-related reductions in medial temporal lobe (MTL) activity (e.g., Daselaar et al., 2003; Dennis, Kim, et al., 2007; Grady et al., 2002; Gutchess et al., 2005; Iidaka et al., 2002). Functional decline in the MTL mirrors structural decline also observed in this region (e.g., Raz, 2005). Deficits in MTL function are posited to reflect deficits in the encoding of episodic details of an event that are necessary for later retrieval (e.g., Davachi, 2006; Diana, Yonelinas, & Ranganath, 2007; Squire, Stark, & Clark, 2004). Moreover, decreases in MTL activity in aging have been accompanied not only by increases in frontal activations, but also by a significant negative relationship between activation across the two regions (Grady, McIntosh, & Craik, 2003; Gutchess et al., 2005; McIntosh et al., 1999; Park et al., 2003). For example, Gutchess and colleagues (2005) found that reduced recruitment of the parahippocampal gyrus (PHG) in aging was correlated with increased engagement of the bilateral inferior PFC during successful encoding. These results support the compensation account of PFC recruitment in aging, and identify a specific mechanism of compensation (i.e., that PFC compensation is linked to MTL deficits) by which older adults maintain memory function.

Interestingly, two recent meta-analyses found opposing results with respect to age differences in the MTL associated with encoding (Maillet & Rajah, 2014; Spreng, Wojtowicz, & Grady, 2010). Specifically, although Spreng et al. (2010) found age-related under-recruitment of the right PHG, Maillet and Rajah (2014) failed to find age differences in any MTL region associated

with successful encoding. By contrast, the latter results pointed to age-invariant findings within the right PHG and hippocampus and two separate foci in the left PHG. One notable difference between the meta-analyses was the fact that the former included blocked and event-related designs, whereas the latter focused solely on subsequent memory studies. As such, the results suggested that age-related decline in MTL function might have a stronger relationship with task set as opposed to memory success. However, this explanation still cannot account for the large number of subsequent memory studies that have found age-related deficits in MTL recruitment (e.g., Dennis, Daselaar, & Cabeza, 2007; Gutchess et al., 2005; Kensinger & Schacter, 2008; St Jacques, Dolcos, & Cabeza, 2009). One possibility is that differences, although present, are interspersed across MTL subregions and thus are not detectable in the typical meta-analysis. This could stem from differences in stimuli (e.g., verbal, spatial), which have been known to recruit different MTL subregions (e.g., Ekstrom & Bookheimer, 2007; Kennepohl, Sziklas, Garver, Wagner, & Jones-Gotman, 2007), as well as differences with respect to the specific contrast used to examine subsequent memory effects (e.g., hits versus misses opposed to high-confidence hits versus low-confidence hits). Further studies are needed to clarify the exact contribution of the MTL to successful encoding in aging and to identify any specificity with respect to age differences within MTL subregions.

Age differences in MTL function during encoding have also been assessed via functional connectivity methods. In one of the first studies to examine age-related differences in functional connectivity during episodic encoding, Grady et al. (2003) found that hippocampal connectivity showed a ventral-to-dorsal shift in functional coupling. Specifically, younger adults exhibited greater

functional coupling between activity in the hippocampus and activity in the ventral PFC and the extrastriate cortex, whereas older adults exhibited greater functional coupling between hippocampal activity and activity in the dorsolateral PFC and the parietal cortex. The authors concluded that this age-related shift in hippocampal connectivity was reflective of a shift from perceptual-based processing in younger adults to higher-order or top-down processing in aging. Other encoding studies have observed a shift in MTL connectivity from more posterior to more anterior regions (Addis & Schacter, 2011; Murty et al., 2009; St Jacques et al., 2009). Taken together, results suggest that not only do older adults differ with respect to the overall recruitment of the MTL in encoding but also in the functional network to which the MTL is related.

Age-related under-recruitment during successful encoding has also been observed in parietal (Iidaka et al., 2001; Schiavetto, Kohler, Grady, Winocur, & Moscovitch, 2002) and occipital cortices (Gutchess et al., 2005; Iidaka et al., 2001; Meulenbroek, Petersson, Voermans, Weber, & Fernandez, 2004; Schiavetto et al., 2002). Age-related deficits in occipital activity have been posited to reflect reduced item-specific processing and encoding of details critical to forming rich memories (e.g., Dennis et al., 2007; Gutchess et al., 2005). Similar to the aforementioned relationship between MTL and frontal recruitment in aging, deficits in occipital cortex are also often coupled with increases in frontal recruitment (Cabeza, Anderson, Houle, Mangels, & Nyberg, 2000; Grady et al., 1994; Gunning-Dixon & Raz, 2003; Gutchess et al., 2005; Iidaka et al., 2002; Levine et al., 2000). Taken together, reduced recruitment of posterior regions (i.e., MTL, visual cortex) and increased recruitment of frontal regions (i.e., PFC) has led to a second model of neural aging—the

posterior-to-anterior shift in aging (PASA) (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Dennis & Cabeza, 2008; Grady et al., 1994). Similar to HAROLD, PASA is also generally regarded as reflecting compensatory processing in aging because it too is often accompanied by successful memory performance.

In addition to task-positive effects, researchers have investigated negative subsequent memory effects in which activity is greater for subsequently forgotten, compared to subsequently remembered, information. In younger adults, negative subsequent memory effects are typically found in regions associated with the default mode network (DMN), wherein greater suppression of the DMN typically is associated with better subsequent memory performance (e.g., Clark & Wagner, 2003; Daselaar, Prince, & Cabeza, 2004; Otten & Rugg, 2001; Reynolds, Donaldson, Wagner, & Braver, 2004; Wagner & Davachi, 2001). However, these effects have often been found to be reserved in older adults (e.g., de Chastelaine et al., 2011; Duverne et al., 2009; Miller et al., 2008; Park, Kennedy, Rodrigue, Hebrank, & Park, 2013) such that the extent to which older adults are unable to suppress activity in the DMN is correlated with poorer memory performance. Reductions in the ability to suppress DMN activity and engage task-related neural regions are reflective of older adults' inability to fluently transfer between processing states in service of completing tasks goals.

Although numerous behavioral studies have investigated factors supporting enhanced performance in older adults, only a handful of imaging studies have followed this trend. For example, as noted in the behavioral section, providing older adults with supportive encoding strategies has been shown to improve episodic encoding, yet only a few fMRI reports have evaluated similar efforts (Kirchhoff, Anderson, Barch, & Jacoby, 2012;

Nyberg et al., 2003). A recent study by Kirchhoff, Anderson, Barch, et al. (2012) found that although semantic training increased recognition memory performance in older adults, equating performance to that of younger adults, it also resulted in increased neural activity in several brain regions, including the medial superior frontal gyrus, right precentral gyrus, and left caudate. However, because these regions were also over-recruited prior to training, results suggest that training may not have necessarily increased the efficiency of the regions. Individual differences

analyses showed positive correlations between older adults' ability to benefit from semantic encoding strategy training and training-related increases in medial superior frontal, left middle precentral, left inferior frontal, and left lateral temporal cortices (see Figure 10.4). Taken together, the results were encouraging because they suggested that older adults were capable of utilizing encoding training to self-initiate effective encoding strategies and that neural recruitment could be modulated to benefit memory performance even in advanced aging.

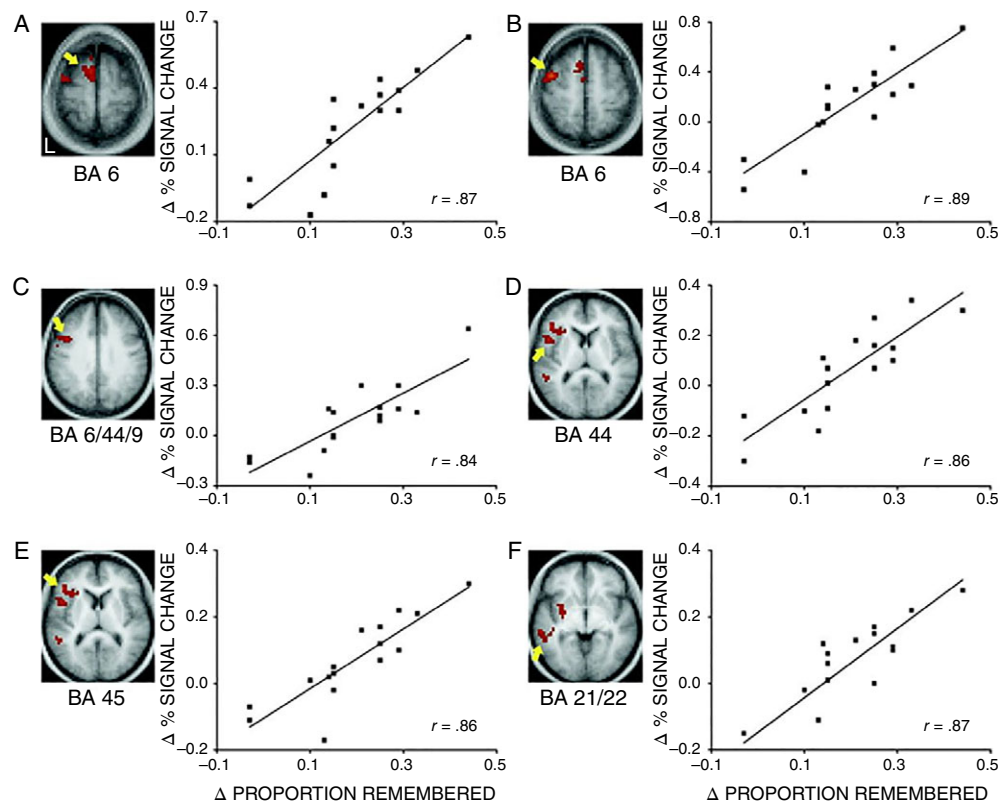


Figure 10.4 Results showing individual differences in older adults' ability to benefit from semantic encoding strategy training. Specifically results show training-related changes in recognition memory that correlate with activity in the A. medial superior frontal, B. left middle frontal/precentral, C. left dorsal posterior inferior frontal, D. left ventral posterior inferior frontal, E. left anterior inferior frontal, and F. left middle/superior temporal.

SOURCE: Reproduced from Kirchhoff, Anderson, Barch, et al. (2012). *Cerebral Cortex*, 22(4), 788–799, by permission of Oxford University Press.

In the behavioral encoding studies previously discussed, we described studies that evaluated shallow and deep encoding, highlighting the fact that memory performance in young and old is enhanced and age difference mitigated when deep encoding is used but that older adults show a marked decrement in self-initiation of such strategies. A handful of fMRI studies have investigated the neural correlates associated with benefits provided from such deep encoding strategies (Daselaar et al., 2003; Logan et al., 2002; Mandzia, Black, McAndrews, Grady, & Graham, 2004; Rosen et al., 2002; Stebbins et al., 2002). Often deep encoding is accompanied by enhanced frontal and MTL activation, as well as the amelioration of age differences. For example, Logan and colleagues (2002) found that in the absence of environmental encoding support (i.e., deep semantic processing), older adults demonstrated under-recruitment and nonselective activity in frontal regions. The under-recruitment was reversed when a deep encoding strategy was encouraged, but nonselective activation persisted. Along with other studies that have also observed increased frontal activation in aging when a deep semantic encoding task is provided, it is unclear the extent to which increases are reflective of focused processing supporting enhanced encoding and which may be reflective of general effort- or task-based processing. Future work investigating methods for improving memory in older adults should correlate neural activity and behavior in order to identify the extent to which increased processing reflects improvements in behavior as opposed to general increases associated with the introduction of the task itself.

Retrieval

Similar to encoding studies, many retrieval studies exhibit HAROLD and PASA activation patterns. For example, although several

early blocked studies exhibit bilateral frontal changes in aging (HAROLD) (e.g., Bäckman et al., 1997; Cabeza et al., 1997, 2002; Madden et al., 1999), many other retrieval studies show general increases in frontal recruitment coupled with decreased activation in more posterior brain regions (e.g., occipital cortex [PASA]) (e.g., Anderson et al., 2000; Cabeza et al., 2000, 2004; Davis et al., 2008; Grady et al., 2002). Similar to the interpretation posited at encoding, such patterns have been interpreted as compensatory because they are often associated with retrieval success. For example, Davis and colleagues (2008) found that the strength of the observed age-related increases in PFC activity in older adults was negatively correlated with the strength of occipital decreases in this same group. Moreover, age-related increases in frontal activity were positively correlated with performance. This finding is consistent with the idea that older adults attempt to compensate for occipital decline by recruiting additional resources in the PFC and that their ability to do so can positively affect memory performance. However, not all increases in frontal activation have been linked to occipital decreases or to enhanced memory performance in older adults (see Cabeza & Dennis, 2012). When frontal increases are associated with poorer, not better, performance in older adults (e.g., Persson, Kalpouzos, Nilsson, Ryberg, & Nyberg, 2011; Stevens, Hasher, Chiew, & Grady, 2008; see also de Chastelaine et al., 2011, for encoding example), they are considered to reflect a greater demand on processing resources, less-efficient processing (Grady, 2012), or attempted, yet unsuccessful compensation (Cabeza & Dennis, 2012). This work continues to highlight a critical point to the interpretation of neural differences in aging—the fact that an accurate interpretation of the differences must take into account behavioral performance (Cabeza & Dennis, 2012; Grady, 2012).

With respect to age differences in MTL recruitment, results have been mixed, with some studies identifying under-recruitment of the MTL (e.g., Dew, Buchler, Dobbins, & Cabeza, 2012; Ramsøy et al., 2011), age-equivalent recruitment (Persson et al., 2011), and yet others reporting over-recruitment (Bäckman et al., 1997; Cabeza et al., 2004; Maguire & Frith, 2003; Meulenbroek et al., 2004; Schiavetto et al., 2002; Tromp, Dufour, Lithfous, Pebayle, & Despres, 2015). Such differences may have arisen from a lack of specificity in accounting for separable components of memory retrieval or a lack of specificity with respect to identifying separable roles of MTL subregions. That is, many of the original retrieval studies assessed age differences by collapsing across different types of memory strength (i.e., confidence rating or recollection and familiarity) and comparing successful to unsuccessful memory. However, as noted in the previous behavioral review, recollection and familiarity exhibit different aging profiles. Additionally, neuroimaging studies in younger adults have shown that recollection and familiarity rely on different neural substrates, with recollection being mediated by the hippocampus and familiarity being mediated by the rhinal and perirhinal cortices (see Figure 10.5 for visualization of MTL recollection and familiarity subdivisions) (e.g., Diana et al., 2007; Ranganath et al., 2004). To this end, more recent studies have focused on the distinction between the two memory processes.

In line with behavioral evidence finding greater age-related impairments in recollection compared to familiarity, research has shown greater age deficits in hippocampal recruitment compared to cortical MTL regions (Cabeza et al., 2004; Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Giovanello, Kensinger, Wong, & Schacter, 2009). Given that the dissociation within the MTL with regard to each memory process, this neural shift supports the findings

from behavioral studies, suggesting that older adults may be relying to a greater extent on familiarity processing to compensate for deficits in recollection. For example, Daselaar et al. (2006) found a double dissociation in the MTL with age-related decreases in recollection-related activity in the hippocampus and age-related increases in familiarity-related activity in rhinal cortex. Additionally, regression analyses showed that although trial-by-trial changes in hippocampal activity predicted memory performance across both age groups, only changes in rhinal activity predicted performance in older adults.

An alternative view regarding this subdivision of the MTL has also emerged, focusing on the role of memory strength and attributes of memory experience (for a review, see Squire & Wixted, 2011; Wixted & Squire, 2011). Such research argues that recollection and familiarity studies do not take into account memory strength so that they often are comparing strong recollection versus weak familiarity, whereas, once equated, strong recollection and strong familiarity elicit hippocampal activity (for further discussion of this alternative, see Smith, Wixted, & Squire, 2011; Wais, Squire, & Wixted, 2010). Research supporting the memory strength account further argues that a discussion of MTL subdivisions are best characterized by focusing on neuroanatomical and neurophysiological distinctions with respect to memory attributes (see Wixted & Squire, 2011). Several studies have explored this account of MTL function in younger adults (Wais, 2008; Wais et al., 2010); however, it has yet to be applied to the interpretation of aging data. Future research should seek to differentiate between these two theoretical perspectives with respect to age differences in item and associative memory.

Achieving equal memory performance in younger and older adults has been another

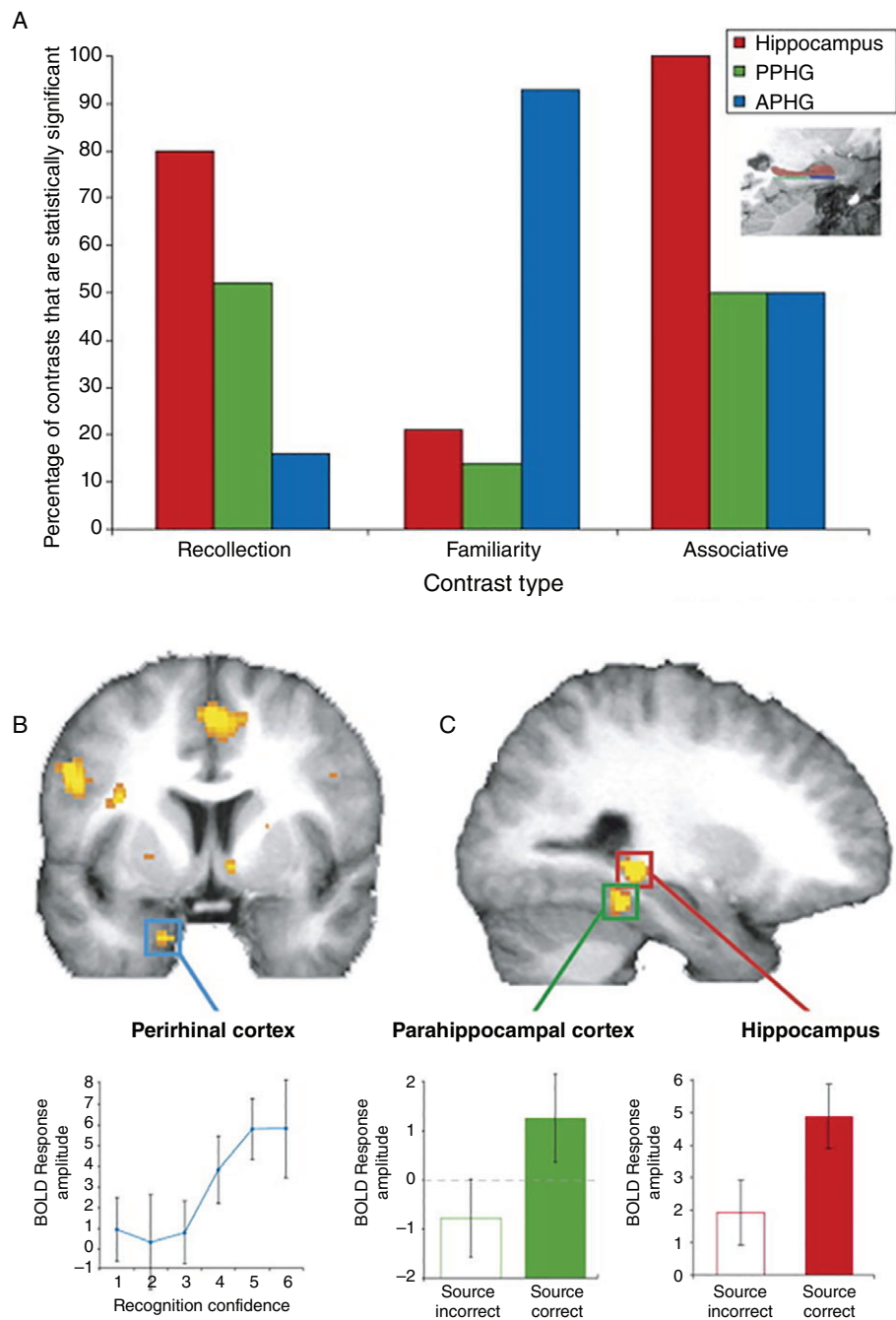


Figure 10.5 A. Count of papers reporting suprathresholded activation in MTL subregions, showing a dissociation between recollection and associative memory in the hippocampus and posterior parahippocampal gyrus (PPHG) and familiarity in the anterior parahippocampal gyrus (APHG). B. Neural activity in the perirhinal cortex tracking memory strength and posited to reflect familiarity. C. The hippocampus and PPHG showing the involvement of the regions in source accuracy, posited to reflect recollection.

SOURCE: Reprinted from Diana et al. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, 11(9), 379–386, with permission from Elsevier.

approach to studying age-related differences in neural recruitment. For example, in the study by Daselaar et al. (2006), older adults were provided the study list twice in order to equate memory performance with younger adults (see also Li, Morcom, & Rugg, 2004; Morcom, Li, & Rugg, 2007). Others have also found enhanced recruitment of brain regions supporting memory retrieval following memory training (Belleville et al., 2011; Hampstead et al., 2012; Kirchhoff, Anderson, Smith, Barch, & Jacoby, 2012). For example, Kirchhoff, Anderson, Smith, and colleagues (2012) also examined the effects of their semantic-encoding strategy on retrieval-related activity. Similar to encoding, several regions showed positive benefits of training. Specifically, training-related increases in recollection (yet not familiarity) were correlated with changes in activity in the bilateral hippocampus (see Figure 10.6) (see also Belleville et al., 2011; Hampstead et al., 2012). Results suggest that, despite age-related volume loss in this region (e.g., Raz et al., 2005), the hippocampus can show functional benefits from cognitive training.

In addition, encoding activity in prefrontal and left lateral temporal regions supporting encoding was also found to be correlated with retrieval-related hippocampal activity. The author suggested that training-induced changes in these regions during encoding served to alter subsequent recruitment of the hippocampus at retrieval (as opposed to directly effecting hippocampal functioning). This conclusion is consistent with a more general assumption in aging that memory impairments are more pronounced during encoding. Thus, encoding support has the potential to alert down-stream memory operations (i.e., consolidation, retrieval).

With respect to age-related differences in functional connectivity during retrieval, similar to encoding, retrieval studies have observed greater MTL-PFC connectivity (e.g., Daselaar et al., 2006; Dew et al., 2012). For example, Daselaar and colleagues (2006) showed that reductions in hippocampal activity were accompanied by reductions in functional connectivity between the hippocampus and the retrosplenial and parietotemporal cortices. Yet, older adults

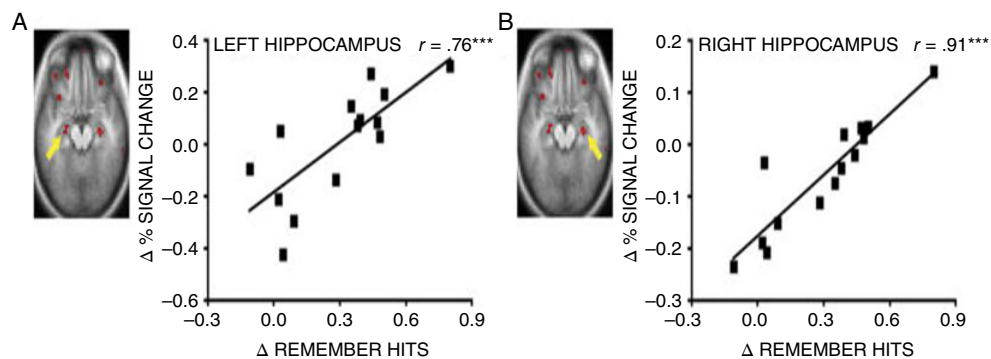


Figure 10.6 Results showing individual differences in changes in neural recruitment underlying recollection following semantic training. Specifically, better recollection post-training was associated with changes in activation in the A. left and B. right hippocampus.

SOURCE: Reprinted from Kirchhoff, Anderson, Smith, et al. (2012). Cognitive training-related changes in hippocampal activity associated with recollection in older adults. *NeuroImage*, 62(3), 1956–1964, with permission from Elsevier.

exhibited increased rhinal activity during recollection and increased connectivity between the rhinal cortex and the bilateral frontal cortices. Once again, results suggested that top-down modulation by frontal regions might serve a compensatory mechanism. To that end, Dew et al. (2012) showed that although younger adults exhibited greater MTL-PFC connectivity during retrieval preparation, older adults exhibited greater MTL-PFC connectivity during the execution of successful retrieval trials. As such, results suggested that this shift to top-down modulation might be responsive to the demands of the retrieval task itself and successful execution of tasks demands.

Item Conclusions

Taken together, functional neuroimaging studies investigating item memory have identified several findings. First, encoding and retrieval research has found increased frontal activity and more bilateral frontal activation in older adults (e.g., HAROLD, PASA). Although this pattern of activation is often interpreted as compensatory, as we have discussed, an ongoing debate in the literature remains as to whether this finding is always one of compensation or rather one of dedifferentiation. We note that this distinction should be based not only on the pattern of neural activity but also with respect to the behavioral performance in older adults and differences in behavior between age groups. With respect to age differences in the MTL, although encoding studies have shown relatively ubiquitous functional declines in MTL activity, retrieval studies have shown a mix of results. This has been taken as evidence supporting the notion that age deficits in item memory are greater at encoding than during retrieval. But again, correlations with behavior should be investigated before such an interpretation is

accepted. In addition to pure activation differences within the MTL, results also suggest that MTL connectivity is disrupted in aging. Together with over-recruitment of the PFC, this MTL connectivity deficit may represent disruptions to the core item-memory network in aging. Furthermore, although much of the review focused on the MTL and the PFC, we also note age-related under-recruitment in the parietal and occipital cortices across item encoding and retrieval. Together with the aforementioned MTL and PFC results, results suggest that age-related declines in visual and attentional processes may result in weaker input into and processing by the MTL during memory tasks, thereby creating the need for a shift from more bottom-up to more top-down processes to support memory. Finally, although the investigation of deep versus shallow encoding explores the issue of strategy use, as noted, few neuroimaging studies have explicitly investigated the neural underpinnings related to the enhancement of strategy use in older adults. Those that have (e.g., Kirchhoff, Anderson, Barch, et al., 2012; Kirchhoff, Anderson, Smith, et al., 2012) have found correlations between behavioral gains and neural recruitment. Such findings suggest that the neural plasticity, present throughout the life span, is an advantage in enhancing memory performance. Future research should continue to investigate the full extent of this plasticity.

fMRI STUDIES OF ASSOCIATIVE MEMORY

In a previous section, we discussed a wealth of behavioral findings that identified an associative deficit in older adults' memory. This deficit was particularly apparent when associative memory was compared to item memory. In our review, we explored the various cognitive explanations for these

differences with regards to age. We also discussed the role of strategies in accounting for age deficits in associative memories. Here, we extend this discussion to include the neural findings associated with these previously raised themes. Within the context of neuroimaging studies, associative memory success is measured by the neural differences between remembering the correct associative pair compared to remembering a mismatched pair. It is critical to note that, by and large, the same regions that support item memory also support associative memory. Additionally, to the extent that associative memory represents a more difficult task than item memory and also is more analogous to recollection, most of the imaging research investigating age deficits in associative memory has also focused on the function of the PFC and MTL.

Encoding

With respect to the involvement of the MTL in associative memory encoding, research in younger adults has shown that, although the perirhinal cortex supports item memory and associations between items, the hippocampus proper plays a critical role in the formation of item context associations (e.g., Diana, Yonelinas, & Ranganath, 2010, 2012). Given that the structure and function of MTL subregions are differentially affected by aging (e.g., Daselaar et al., 2006; Raz et al., 2005), age differences in associative memory, similar to that of item memory, have been shown to exhibit mixed results with regard to age differences in MTL activation. Specifically, although a number of studies have identified age-related deficits in hippocampal recruitment during successful associative encoding (e.g., Anderson & Craik, 2000; Daselaar et al., 2003; Dennis et al., 2008; Mitchell, Johnson, Raye, & D'Esposito, 2000; Sperling et al., 2003), many others

have suggested that there is no age-related difference in hippocampal activation (e.g., Addis, Giovanello, Vu, & Schacter, 2014; Duverne et al., 2009; Kim & Giovanello, 2011b; Persson et al., 2011), whereas others find age-related over-recruitment of the MTL (e.g., Dulas & Duarte, 2011). Although results may appear to be a mixed bag at first glance, a finer evaluation of the aforementioned studies may be able to clarify the apparent incongruity.

To this end, studies finding hippocampal deficits in associative memory tasks in aging (e.g., Dennis et al., 2008; Giovanello, Kensinger, Wong, & Schacter, 2010; Mitchell, Johnson, Raye, & D'Esposito, 2000) are often accompanied by significant age-related deficits in associative memory performance. For example, using incidental encoding, Dennis and colleagues (2008) had younger and older adults encode faces, scenes, and face-scene pairs. They found that older adults demonstrated worse performance for associative memory compared to item memory and found an age-related reduction in activity for source compared to item memory in the left hippocampus. Studies that have observed no age-related differences in hippocampal recruitment are often those that provided participants with strong explicit encoding strategies (e.g., Addis et al., 2014; Miller et al., 2008) as a means for overcoming age-related deficits. For example, Addis et al. (2014) presented individuals with word triads that differed with respect to the number of semantic associations that existed between the words (e.g., TOYS-lily-wool; BEVERAGES-milk-beer). They found that as the encoding support increased with the number of semantic links, so did hippocampal recruitment. Moreover, this up-regulation of hippocampal activity did not differ between younger and older adults, suggesting that, when older adults were provided apt encoding support, they were able to engage

the hippocampus as well as younger adults in support of successful associative encoding (but see the following for PFC deficits under the same conditions).

One pattern of activation that has not been observed in associative encoding studies is that of age-related compensation within the MTL complex. That is, although item studies have found that age-related deficits in hippocampal activation can be compensated by age-related increases in other MTL subregions (e.g., perirhinal cortex; Daselaar et al., 2006), the same has not been shown in associative memory. It may be that the burden of associative memory on the MTL complex is so great in aging that there are not adequate resources to compensate for declining function. It may also be the case that there is a power issue contributing to the observation of a shift in MTL recruitment. Alternatively, the resolution presently employed in associative memory studies may be insufficient to identify age-related shifts in recruitment within such a small region. Although some multivariate approaches are making progress in this domain (e.g., Stark, Yassa, & Stark, 2010; Yassa & Stark, 2011), additional research is needed to understand such nuanced differences.

In addition to MTL involvement, research has focused on the role of the PFC in associative encoding. Specifically, a meta-analysis of episodic memory in younger adults (Spaniol et al., 2009) found that activity in the left ventrolateral and dorsolateral prefrontal cortex (VLPFC, DLPFC) plays a critical role during associative encoding, supporting later memory success. Moreover, research in younger adults has found that activity in the VLPFC is disproportionately active for associative compared to item encoding (e.g., Achim & Lepage, 2005; Addis & McAndrews, 2006). This is especially true for when there is a need to generate semantic associations between to-be-remembered

items (e.g., Achim & Lepage, 2005; Addis et al., 2014; Fletcher, Shallice, & Dolan, 2000). In contrast to item encoding, associative memory studies rarely find age-related increases in PFC activity but rather age deficits (Anderson et al., 2000; Cabeza et al., 1997; Dennis et al., 2008; Mitchell, Johnson, Raye, & D'Esposito, 2000; Sperling et al., 2003; see also Kim & Giovanello, 2011b, for example of no frontal activity supporting associative encoding). Thus, whereas younger adults are specifically up-regulating activity throughout the PFC to meet the added demands of associative memory, older adults are not and may actually under-recruit frontal resources during associative encoding. The finding of age-related under-recruitment of prefrontal regions in associative encoding, together with over-recruitment observed in item encoding, can be reconciled within the context of the scaffolding model (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014). The scaffolding theory posits that older adults over-recruit neural resources at lower levels of task difficulty (e.g., item memory) as a compensatory mechanism in order to maintain performance. However, that leaves diminished resources available as task demands increase (e.g., associative encoding). Thus, age-related deficits in frontal recruitment may reflect diminished resources in aging and an inability to keep up with task demands as task requirements and difficulty increase.

In addition to PFC recruitment for associative compared to item tasks, studies have also investigated the role of task difficulty within an associative memory task. Interestingly, in the foregoing study by Addis and colleagues (2014) in which individuals were presented with word triads that differed with respect to the number of semantic associations that existed between the words, younger adults exhibited up-regulation of the VLPFC as the generative demands increased, whereas older

adults exhibited constant VLPFC activation across all levels of task difficulty. The authors interpreted this finding as reflecting reduced efficiency of the VLPFC in aging. That is, older adults may have needed to sustain activity in this region in order to form associations across repeated presentations, whereas younger adults were able to form associations more efficiently (with fewer presentations). Age differences in VLPFC activity have also been found in studies that attempt to enhance associative encoding in older adults by providing repeated presentations of the to-be-remembered associations (face-name pairs; Rand-Giovannetti et al., 2006; Sperling et al., 2003). In this work, although younger adults exhibit VLPFC activity during the first presentation of the face-name pairs, older adults exhibit sustained activity in this region throughout the subsequent encoding presentations. Because increased presentations led to enhanced performance in older adults, this up-regulation of VLPFC was suggested to function in a compensatory capacity. The inability to modulate frontal activity across task demands in associative memory further suggests that associative memory demands push the limits of functional resources in older adults.

Similar to interpretations put forth in item memory studies, frontal activation has been linked to attentional processes necessary for successful encoding. For example, following up on their behavioral study examining the role of attention in age-related associative memory deficits, Kim and Giovanello (2011b) found that younger adults with depleted attentional resources exhibited equivalent patterns of neural recruitment with that observed in older adults under full attention conditions. Specifically, both groups exhibited reduced recruitment of VLPFC and DLPFC, parietal cortex, and hippocampus compared to younger adults under full attention. Similar to the foregoing

behavioral studies, results suggested that reduced resources in aging might be a significant contributing factor to age-related reductions in neural recruitment in aging. The results further added to a resource theory of aging (e.g., Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Lustig, 2005) suggesting that, when task demands are sufficiently high, the absence of available resources limits their ability to recruit compensatory processes. In another attention-related study, Dulas and Duarte (2014) found that directing attention to the associative link during encoding led to enhanced activation in the parahippocampal cortex as well as better associative memory accuracy in younger and older adults. Despite enhanced MTL processing across groups, attentional instructions failed to enhance recruitment of the lateral anterior PFC in older adults (whereas younger adults showed instructional benefits in this region). Given the critical role of frontal cortices in associative memory, results suggest that attentional support may be insufficient to support the encoding of contextual details necessary for successful associative memory in aging.

In addition to age differences in task positive activations, a number of studies have investigated age differences in task-negative activations that support associative encoding (de Chastelaine, Mattson, Wang, Donley, & Rugg, 2015; de Chastelaine et al., 2011; Mattson, Wang, de Chastelaine, & Rugg, 2014; Miller et al., 2008), finding mixed results with respect to age-related attenuation of negative memory effects. For example, de Chastelaine et al. (2011) found that negative effects, which were mainly localized to DMN regions in younger adults, were reversed in the older group. Furthermore, individual differences analyses showed that the size of the reversal correlated negatively with memory performance. As such, the results support those of item encoding, suggesting that, during associative encoding, older adults

exhibit difficulty disengaging the DMN and reallocating processing to the task of encoding. In contrast to this finding, Mattson et al. (2014) found the typical age-related attenuation of negative item effects, yet age-invariant negative associative memory effects. Specifically, negative associative effects were observed mainly in “task-positive” frontal regions, including the left middle frontal gyrus, the bilateral insula, and the right anterior cingulate cortex, as well as the right posterior cingulate and parietal cortices. Furthermore, in both age groups, the magnitude of the effect correlated with associative memory performance.

With respect to the mixed findings, Mattson et al. (2014) suggest that a better understanding of behavioral differences across studies can clarify matters. That is, in the de Chastelaine et al. (2011) study older adults exhibited significantly lower associative memory performance compared to younger adults, whereas older adults in the Mattson et al. (2014) study exhibited matched memory performance to that of younger adults. Thus, differences in negative subsequent memory effects may reflect differences in the ability to modulate the network with respect to overall encoding success. This explanation is supported by Miller et al. (2008), who found that older adults with the poorest associative memory performance were also those that failed to deactivate DMN regions during encoding. However, this explanation is in contrast to item encoding findings, in which memory is typically matched more closely between age groups than in associative memory tasks (yet negative effects are typically greater in older adults). Although differences in the negative memory effect across task may account for this difference, more research is needed to fully elucidate how negative subsequent memory effects support successful associative encoding in older adults.

Finally, to date only a relatively small number of studies have investigated age-related differences in functional connectivity within the associative encoding network. Assessing whole brain connectivity with the hippocampus during associative encoding, Dennis et al. (2008) showed that older adults exhibited enhanced functional connectivity between the hippocampus and the PFC but reduced connectivity with perceptual processing regions. In conjunction with age-related deficits in behavioral performance, this was interpreted as reflecting more efficient use of bottom-up, perceptually driven processes supporting binding in younger adults (see also Tompary, Duncan, & Davachi, 2015) and attempted, yet unsuccessfully, frontally mediated compensation in older adults. In contrast to the foregoing result, Wang and colleagues (2010) showed that enhanced intrinsic connectivity between the hippocampus and the posterior parietal cortex was associated with better memory performance in older adults. Furthermore, results suggest that such intrinsic connectivity may underlie individual differences in memory success among older individuals. Far more studies are needed in this domain before any strong conclusions can be made as to the overall structure and functional state of the associative encoding network in aging. Potential future studies should include employing multivariate approaches to examining network connectivity as well as examining connectivity post-encoding to investigate consolidation effects.

Retrieval

Similar to the described encoding studies, studies examining successful associative retrieval in aging have focused analyses on hippocampal and PFC activity (Dulas & Duarte, 2011; Giovanello & Schacter, 2012; Persson et al., 2011; Tsukiura et al., 2011).

Findings with regard to age differences in the hippocampus differ depending on whether studies measure task-related activity or success-related activity. That is, examining face-name associations in a block design, Persson and colleagues (2011) observed equivalent behavior and equivalent recruitment of bilateral hippocampus during retrieval in younger and older adults. However, Tsukiura et al. (2011) found that although both age groups exhibited significant hippocampal activity supporting successful associative memory, younger adults outperformed older adults and exhibited greater hippocampal recruitment. Although the former study concluded that hippocampal functioning is preserved in aging, the latter concluded that hippocampal function displays an age-related decline. Finally, Dulas and Duarte (2011) found age-equivalent activity in the hippocampus yet age-related increases in the perirhinal cortex that correlated with performance, which the authors attribute to compensation in aging. With no clear conclusion to be drawn across studies, results serve to highlight the need to consider behavior and task design in interpreting age differences in neural functioning as well as the need for additional research in this area.

With respect to age differences in the PFC, several studies have reported age-related under-recruitment or negative correlations between PFC engagement and associative retrieval. For example, the foregoing study by Dulas and Duarte (2011) found age-related under-recruitment of right lateralized PFC regions when compared to younger adults. The authors suggested that given the region's role in inhibiting irrelevant information and monitoring retrieval processes, coupled with the observation of decreased behavior success in older adults, older adults are less able to correctly monitor and evaluate the retrieval of source information in support of making

correct associative decisions. Similar results were reported by Tsukiura and colleagues (2011). Specifically, older adults in their study showed an age-related decrease in activation of the right middle frontal gyrus. They too suggested that their results reflect age-related deficits in monitoring retrieval output necessary for successful associative memory judgments. Interestingly, in a study by Persson and colleagues (2011) older adults also exhibited enhanced activation of left dorsolateral frontal cortices, but the activity negatively correlated with performance in aging. The authors interpret this finding as a failed attempted compensation mechanism in low-performing older adults. Taken together, results suggest that, similar to associative encoding, older adults are not able to engage PFC regions to successfully meet the needs of demanding associative memory tasks.

In addition to the attentional instructions provided by Dulas and Duarte (2011), other studies have attempted to enhance associative memory performance in aging through the use of encoding support (Giovanello & Schacter, 2012; Leshikar & Duarte, 2014). Using encoding instructions that promoted unitization, Giovanello and Schacter (2012) found associative retrieval success activity in the left ventrolateral PFC, the left dorsolateral PFC, and the right hippocampus in younger and older adults. However, although younger adults showed greater recruitment in the foregoing regions for associative compared to item retrieval, older adults exhibited equivalent activity in all regions for item and associative retrieval. The authors ascribed their results to a decline in regional specialization with age. More work focusing on the role of memory instructions and promoting the use of encoding strategies is needed to ascertain a more complete understanding of age differences in associative retrieval and the extent to which older adults may be able to exhibit persevered or

compensatory functioning. Leshikar and Duarte (2014) used self-referencing encoding instructions to enhance associative memory in younger and older adults. Self-referencing behavior is a form of deep encoding in which participants encode stimuli with regards to one's self-schema. Results showed that self-referencing led to matched associative memory performance between age groups as well as age-equivalent recruitment throughout the associative memory network. Taken together, results suggest that when sufficient support is provided to older adults so that performance can be equated to younger adults, age deficits in neural recruitment can be ameliorated.

Associative Conclusions

Encoding and retrieval studies investigating associative memory have identified many similar findings. Regarding frontal activation, associative memory studies typically find age-related under-recruitment of lateral frontal cortices, with decreased activity corresponding to reduced associative memory in aging. This pattern of activity is often interpreted as reflecting reductions in neural resources that are required for successful age-related compensation in the face of increased task difficulty. However, given that supportive encoding instructions that promote unitization and self-referential processing result in enhanced frontal recruitment in both age groups as well as mitigate age differences in frontal recruitment, it may be true that, similar to item results, age deficits in associative memory are related more to an age-related decline in recruiting necessary resources than a decline in the availability of the resources themselves. Future work should investigate the extent to which observed decreases in frontal activation are an availability or accessibility issue. Additionally, given the small number of studies examining

the neural mechanisms supporting strategy use in associative memory task in older adults, more research is needed to explore the extent to which shifts in neural recruitment associated with the implementation of strategies lead to enhanced associative memory in aging. Regarding the MTL, evidence was relatively mixed, with some studies finding that aging is associated with under-recruitment of the hippocampus and others showing no decline in MTL activation. Thus, it is currently unclear as to the distinction between these two sets of results. Future work examining the contribution of MTL subregions to associative memory in aging are needed to further clarify differences focusing on the dual process model of memory as well as the memory strength account.

CONCLUSION

Overall, several themes have emerged across the foregoing review of behavioral and imaging studies. First and foremost, the age deficit for associative memory exceeds that of item memory. This has been observed at the behavioral level and with respect to neural differences. Although associative memory clearly represents a more difficult task compared to item memory, it is unclear the extent to which age differences reflect mere increases in difficulty or are specific to the associative binding components of the memory task. Second, despite the observed age deficits across tasks, research has shown that age deficits can be ameliorated through the use of focused encoding instructions that tap into deep encoding processes. With respect to associative memory, unitization has shown to be a useful encoding strategy that not only enhances behavior in older adults but also enhances and mitigates age differences in neural recruitment. Unfortunately, research has also indicated that

older adults are typically unable to engage such encoding strategies on their own. Thus, results support the idea that age deficits in task performance and under-recruitment of neural processes often reflects accessibility of resources and are not reflective of issues of availability so that when encoding support is provided, older adults are able to utilize the necessary resources for carrying out task objectives. To this end, results suggest that age differences in item and associative memory are not an inevitable consequence of aging but can be mitigated under numerous circumstances.

FUTURE DIRECTIONS

In addition to the future directions listed throughout the chapter itself, we note a few additional lines of research that should be explored with respect to aging and episodic memory. As noted, behavioral research has identified a handful of factors that serve to enhance memory function. Future research should continue to examine what encoding strategies most benefit older adult aging as well as what types of processes are adaptable at the neural level to support successful item and associative memory in older adults. For example, to the extent that unitization allows for familiarity in associative retrieval, this may prove an effective strategy from a neural perspective because it may shift neural recruitment to more preserved subregions within the MTL (e.g., the perirhinal cortex). This would contribute to a growing body of literature that is seeking to better understand how more effective use of strategies can enhance memory performance in older adults. As mentioned previously, the pace at which the behavioral literature has continued to advance its understanding of different strategies affecting associative memory has eclipsed the pace found in the neuroimaging

field. There are many factors that can contribute to this, but there is no doubt that the field of cognitive aging will benefit from more neuroimaging studies exploring factors supporting enhanced memory performance. Additionally, a growing body of literature is investigating basic associative processes in younger adults. Future work needs to establish a firmer understanding of these same associative processes in aging (e.g., differences between item-item and item-context associations). Once identified, future work can continue to find ways to ameliorate age deficits under the guidance of identified neural systems, especially given age-related frontal compensation.

Although the aforementioned review focused on differences between younger (typically 18–30-year-olds) and older adults (>60 years), an emerging number of studies are beginning to focus on processing in middle-aged adults (e.g., Cansino et al., 2013, 2015; Kwon et al., 2015). Given that aging is a developmental process, more research needs to focus on mechanisms that examine how and when the foregoing age-related shifts in processing occur. Incorporation of a middle age group and the use of age as a covariate in analyses would bolster our knowledge as to the developmental trajectory of the underlying mechanisms mediating age differences in memory.

Additionally, several studies allude to a shift in neural processing within the MTL and PFC. To that end, the use of high-resolution fMRI and multivariate analyses such as a multi-voxel pattern analysis will serve to better identify and characterize this shift. Finally, we cannot emphasize enough the need to continue to incorporate behavior into memory analyses. This is especially critical when considering differences between groups—especially groups that may differ in base rates of performance and in variability among individuals.

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