

Changes in memory processing with age

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Over the years, a large body of literature has shown that humans display losses in memory with age, but that not all types of memory are affected equally. Similarly, recent evidence from functional neuroimaging experiments has revealed that, depending on the task, older adults can display greater or lesser activity in task-relevant brain areas compared with younger adults. Recent behavioral and neurophysiological experiments are furthering our understanding of the effects of aging on cognition. It appears that some brain changes seen with age may be compensatory.

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Abbreviations

AD	Alzheimer disease
MRI	magnetic resonance imaging
PET	positron emission tomography
rCBF	regional cerebral blood flow
RT	reaction time
WM	working memory

Introduction

There is general agreement in the literature on cognitive aging that memory performance declines from early to late adulthood, and that such age-related losses in performance are much greater in relation to some tasks than in others. Decrements are typically slight in implicit memory tasks (including priming) in which a stimulus that has been presented previously affects current behavior when presented again, often without the person realizing that the stimulus was encountered beforehand. Age-related declines are also slight both in short-term memory span tasks, in which subjects repeat back a short string of words, letters or numbers, and in many recognition memory tasks, in which previously encountered events (e.g. words, sentences, pictures, faces) are re-presented along with new distractor items of a similar type. In contrast, age-related losses are substantial in tasks involving free or cued recall and those involving recollection of the original context in which an event occurred, as well as in ‘prospective memory’ tasks (i.e. remembering to carry out an action at a future time) and in ‘working memory’ tasks. These last-named tasks usually necessitate the manipulation of information held in mind or the maintenance of some information while dealing concurrently with further incoming stimuli. Evidence in support of these findings is summarized in a number of recent reviews [1•–3•,4].

The fundamental biological changes underlying this pattern of relatively spared versus reduced memory abilities in the elderly are still under active debate, although there is emerging agreement from recent neuroimaging studies that certain cortical areas (such as the prefrontal cortex) are less active in older adults under some conditions, but more active under other conditions. Much of the recent neuroimaging work has been in the area of verbal memory, and a common finding in young adults is that they have increased activity in the left prefrontal cortex during encoding and in the right prefrontal cortex during retrieval (for reviews, see [5,6]). In contrast, older adults often have less activation of left frontal areas during encoding [7], but bilateral prefrontal activation during retrieval [7,8]. Older adults have also been found to have greater activity in left prefrontal cortex during performance of some nonverbal tests of retrieval [9], but not all [10]. These age-related differences in prefrontal activity are probably attributable to some extent to the different task demands involved in the various experiments, but increased left prefrontal activity in older adults may somehow be necessary for them to perform adequately on the tasks. In some cases, the additional recruitment of left prefrontal cortex during retrieval was seen during memory tasks when performance in the older group was comparable to that of younger adults, leading to the suggestion that this recruitment may be a compensatory mechanism [7]. A fundamental issue in this respect is whether the recruitment of additional areas in older adults actually aids their ability to perform the task.

With regard to the theoretical mechanisms underlying age-related memory deficits, current suggestions at the cognitive level include the notions of a general slowing of cognitive operations [11] and an age-related decline in attentional resources [12]. Other researchers have postulated that aging is associated with a reduction in the efficiency of inhibitory processes [13]. It has also been postulated that older adults are impaired in their ability to consciously recollect events and the contexts in which they occurred, but are relatively unimpaired in their experience of the familiarity of a recognized object or person. Thus, when an older individual encounters a slightly known acquaintance, especially in an unusual setting, the acquaintance may seem familiar, but the older person may be unable to recollect where or when they had originally met [14]. Similarly, the influence of learned habits on behavior is unchanged with age, although the older person may be less aware of the original source of the learned information. This last combination of impaired and unimpaired processes means that the cognitive performance of older adults is dominated to a considerable extent by habitual patterns of thought and action [4,15••]. Another popular notion is that older adults have difficulty in associating aspects of an event [16] or in ‘binding’ such aspects into a coherent representation [17].

The present brief review focuses largely on recent studies of the effects of aging on episodic memory for personally experienced events, their neural correlates, and their behavioral manifestations.

Sensory and priming effects

The traditional view that perception and memory involve separate systems is losing support in cognitive psychology in favor of the position that sensation, attention, perception, memory, and higher cognitive processes are strongly associated. One implication of this viewpoint is that at least some of the memory problems experienced by older adults can be attributed to impairments of vision and hearing [18]. The similarities between age-related declines in sensory and intellectual functioning are striking (Figure 1), and it has been reported that visual and auditory acuity, together, account for 93% of the age-related variance in intelligence [19]. It should be noted, however, that measures of sensorimotor functioning (e.g. balance, gait, grip strength) correlate as highly with intellectual functioning as do measures of vision and hearing, so the likely explanation is that sensory acuity is simply one indication of the physiological integrity of the aging brain — the ‘common cause’ hypothesis [19,20]. A more directly causative relation between hearing impairment and memory loss has been demonstrated in a recent study in which the pattern of memory performance shown by older adults was exhibited by younger adults when the items to be remembered were presented in a background of noise [21].

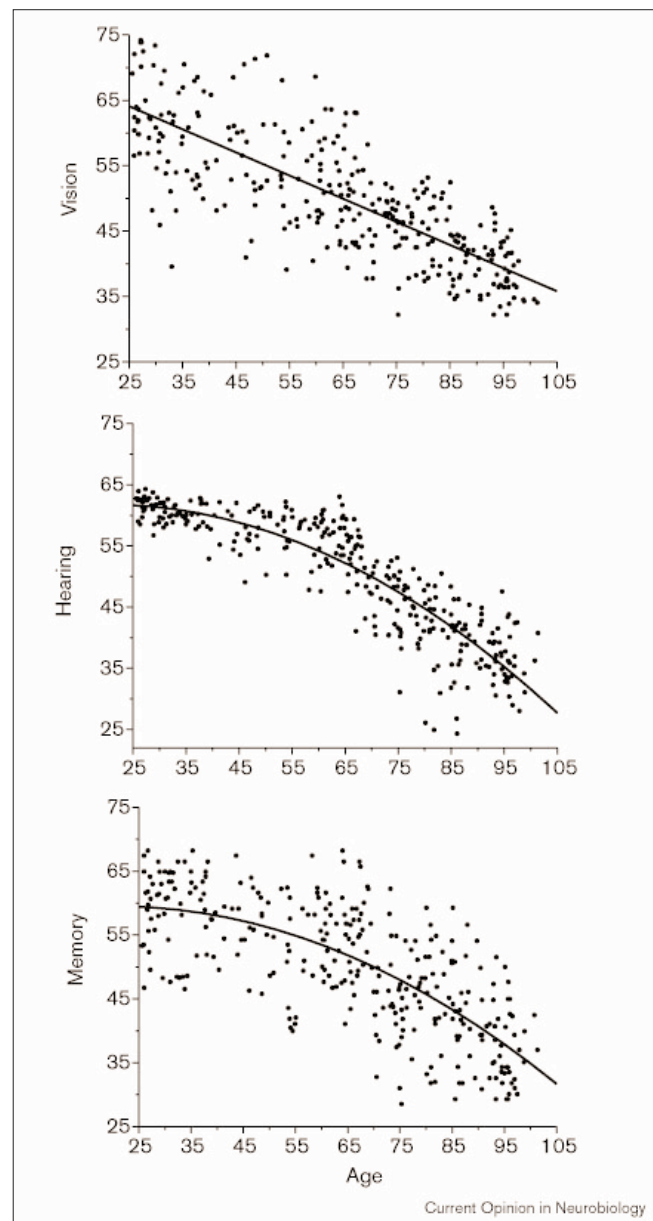
Recent exposure to a stimulus acts to ‘prime’ and thereby facilitate processing of the same stimulus on a second occasion. This type of repetition priming is largely perceptual in nature; greater benefits are typically observed when the stimuli are repeated in the same modality (e.g. visual versus auditory) or in the same form (e.g. pictures versus words). However, stimuli can also prime different targets provided that the stimulus and target are semantically related; thus priming can be both perceptual and conceptual. A recent study has reported age differences in both forms of priming, although the differences were much smaller than those found in explicit tests of memory [22]. Another recent study reported no age differences in the benefits associated with repeating words with the same auditory characteristics [23]. In general, age-related decrements on priming tasks are slight or non-existent.

Tests involving sensory stimuli and tasks involving priming effects both tap relatively low-level cognitive processes, and both sets of tasks show relatively small effects of aging. Larger age-related losses are found with tasks that demand effortful, higher-level cognitive processes [24].

Primary memory and working memory

Age differences are typically slight in tasks requiring the person to hold a sequence of digits, letters, or words in mind for a few seconds before repeating the string in the presented order [24]. Such tasks tap ‘primary memory’ and

Figure 1



Age-related declines in vision, hearing, and memory. Composite measures of vision, hearing, and memory are shown for 315 individuals ranging in age from 25 to 101 years. Results are expressed in the standardized T-score metric (i.e. $M = 50$, $SD = 10$). ‘Vision’ represents visual acuity at 2.5 m and at reading distance. ‘Hearing’ represents pure tone audiometry at eight frequencies ranging from 0.25 to 8.0 kHz. ‘Memory’ represents the combined results of three tests: recall of activities, text, and words. Best-fit functions are linear for vision and quadratic for hearing and memory. Y axes refer to standard T score. Data from [20].

one method of accessing this type of short-term memory is to measure the longest sequence that the person can repeat back without error — the ‘memory span’. If the material held in mind must be manipulated in some way, however, or if the person must process additional information while holding the first set of material in mind, age-related

Table 1**Age differences in recollection and habit*.**

	Young adults		Older adults	
	Non-distinct	Distinct	Non-distinct	Distinct
Recollection	0.44	0.60	0.29	0.30
Habit	0.72	0.70	0.72	0.72

	Older adults			
	3 s response time		Unlimited response time	
	Non-distinct	Distinct	Non-distinct	Distinct
Recollection	0.42	0.48	0.42	0.58
Habit	0.77	0.72	0.72	0.73

*Estimates of recollection and habit (familiarity) as a function of distinctive and non-distinctive information provided at encoding. Top section shows the results for younger and older adults. Bottom section shows the results for older subjects when response time was either 3 s or unlimited. Data from [15**].

decrements are typically found [24]. Such tasks are referred to as 'working memory' (WM) tasks; one example is re-ordering a sequence of presented words mentally then saying them back in alphabetic order, a second example is mental arithmetic. It seems likely that the difference in performance on primary memory and WM tasks is attributable to differences in the complexity of the operations carried out on the information maintained. One recent study exploring age-related differences in verbal and spatial WM tasks reported the surprising finding that individuals with the largest memory spans for their age group suffered the greatest effects of interference when they performed a color-naming task at the same time as the span task. The authors suggest that the mechanisms underlying memory span and information processing are relatively independent [25]. Another line of research examined age-related differences in the extent to which WM performance was reduced by interference from previously processed information of a similar type. The results suggested that older adults are more susceptible to such interference effects, and that this greater vulnerability is one major reason for poorer WM performance in the elderly [1*,26**,27].

The neural correlates of WM have also been examined in older adults. Reuter-Lorenz *et al.* [28*] explored both verbal and spatial WM in young and older adults. Young adults were found to show left-lateralized activity in prefrontal cortex during verbal memory and right-lateralized activity in frontal areas during spatial memory. In contrast, older adults showed bilateral activation of frontal cortex in both memory tasks. Esposito *et al.* [29] examined brain activity during the Wisconsin Card Sort Test (WCST), which depends heavily on WM, although it also involves other cognitive processes such as reasoning. Activation in left dorsolateral prefrontal cortex was negatively correlated with age, indicating that performance of the task in younger adults activated this area to a greater degree. This is a different result from that found by Reuter-Lorenz *et al.* [28*], but is consistent with age-related reductions in left

Table 2**Age differences in recall as a function of activity*.**

	Sitting	Standing	Oval track	Aperiodic track
Young	13.0	13.3	12.9	10.5
Middle	11.7	12.1	9.7	7.9
Older	9.5	9.6	7.2	5.8

*Number of words recalled (out of 16) by young (20s), middle-aged (40s), and older (60s) adults as a function of their activity at the time of encoding the word lists. The conditions were sitting, standing, walking a predictable course (oval track), or walking an unpredictable course (aperiodic track). Data from [35].

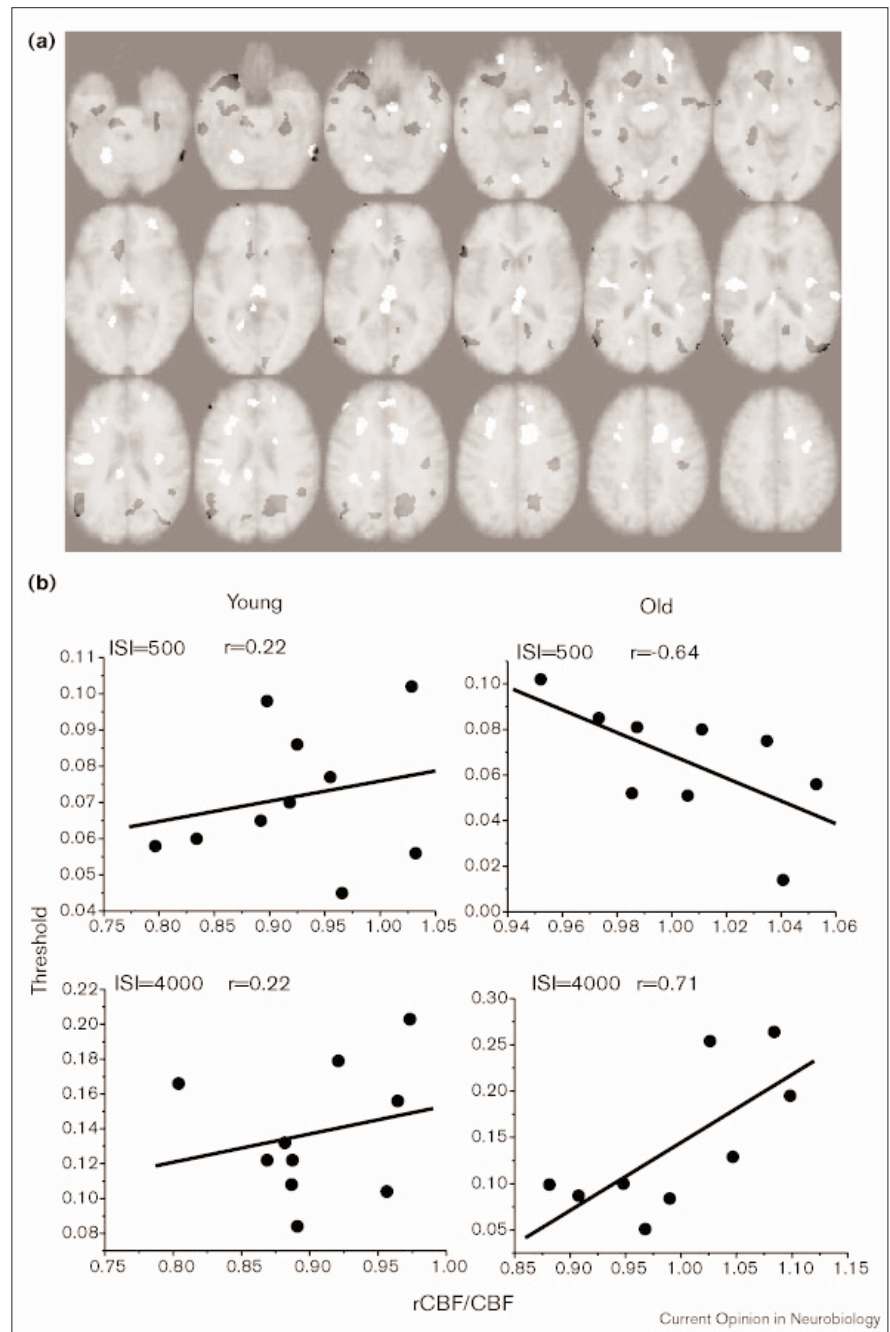
prefrontal cortex in the elderly during encoding of new information into memory [7]. The difference in left prefrontal activity in the elderly participants in these two experiments may be related to their performance on the tasks. In the Reuter-Lorenz study, the older adults performed only slightly below the young adults, whereas in the Esposito experiment, the elderly adults showed more marked deficits in performance. This interpretation is consistent with the idea that recruitment of prefrontal areas during memory tasks may improve older adults' performance.

Encoding and retrieval processes

Encoding and retrieval processes are at the heart of memory research, and there have been several neuroimaging studies that have examined the effects of aging on these processes, which we discuss below. At the behavioral level, Jacoby [30] has provided further proof of the independence of the processes underlying recollection and familiarity. For example, he and his colleagues (see [29]) have shown that whereas repetition of items to be learned enhances both recollection and familiarity, divided attention in young subjects and aging are associated with a reduction in recollection but no change in familiarity [30]. However, older people require more time at retrieval to take advantage of the beneficial effects of repetition. This necessity to support both encoding and retrieval [12] was also shown in a further study [15**] in which pairs of words were presented to be learned; at the time of retrieval the first word in each pair was re-presented and the subject's task was to retrieve the paired word. The first (stimulus) words were homographs, such as 'organ' and 'bank', and each stimulus word was paired with one of two responses that reflected either its two different meanings (e.g. organ–music, organ–heart) or the same meaning (e.g. organ–music, organ–piano). These two conditions represented distinctive and non-distinctive encoding conditions respectively; the distinctive condition was expected to enhance recollection of which word pair had been presented on a specific occasion but have little effect on the familiarity of the stimulus–response pair. As shown in Table 1, a measure of recollection was increased by non-distinctive encoding, but only in younger subjects. The effect was not shown by older subjects unless they had unlimited time to make their retrieval responses. The table also shows that estimates of habit (familiarity)

Figure 2

Age-related differences in the relationship of brain activity to behavior during a perceptual memory task. The task involved presentation of two sine wave gratings that were separated by a delay (interstimulus interval, ISI) of 500 or 4000 ms. The task was to indicate which of the two stimuli had the higher spatial frequency (f). The image shown in (a) depicts the brain areas where activity correlated with behavior in a group of older adults ($p = 0.03$). The areas are shown on a standard structural MRI with slices relative to an imaginary plane defined by the anterior and posterior commissures (AC-PC line). The slices start at 28 mm below the AC-PC line at the top left slice and continue in increments of 4 mm up to 40 mm above the AC-PC line. Left is to the left and the top is anterior in the image. Voxels shown in white had positive correlations between threshold and brain activity in the older adults in the 500 ms ISI condition (poorer performance) and negative correlations in the 4000 ms condition (better performance). Areas shown in black had the opposite pattern. Thus, increased activity in areas such as prefrontal cortex was associated with better performance in the 4000 ms delay condition, whereas increased activity in regions such as the hippocampus and parietal cortex was correlated with better performance in the 500 ms condition. The scatterplots in (b) show the correlation between a measure of brain activity (ratio of regional cerebral blood flow [rCBF] to global CBF) in the left hippocampal region (coordinates X: -26, Y: -12, Z: -24) and memory performance in both young and old groups. Behavioral measures are expressed as the difference in spatial frequency ($\Delta f/f$) necessary for a discrimination between the two stimuli to occur at 80% accuracy (increasing thresholds indicate poorer performance in the task). These plots show that increased hippocampal activity in the 500 ms condition and decreased activity in the 4000 ms condition were associated with lower thresholds in the older group, whereas changes in activity were essentially uncorrelated with performance in the younger group. Data from [54**].



remained remarkably stable across age groups and distinctiveness conditions [15**]. Adequate recollection of an event involves retrieval of some aspects of its original context (e.g. where and when the event took place) and adequate recollection of factual information involves retrieval of the source of the fact (e.g. whether learned in casual conversation or from an authoritative source). The ability to retrieve context or source declines with age, and this decrement has been associated with declining frontal lobe efficiency [31]. A more recent study [32] has provided evidence in support of this conclusion using event-related

potentials (ERPs). It seems possible that the age-related difficulty in retrieving context reflects a more general difficulty in the encoding and retrieval of associative information. Such an 'associative deficit hypothesis' was recently proposed by Naveh-Benjamin [16].

If aging is associated with a reduction in processing resources, then the necessity to perform two tasks concurrently (thereby diverting some attentional resources to a second task) should be especially disadvantageous for older people. Anderson *et al.* [33**] found that when a

memory task was combined with a reaction time (RT) task, performance on the memory task dropped by equivalent amounts in younger and older adults, but that RTs were slowed by a greater amount in the older group. Another study also found no age differences in memory costs or in forgetting rates, but that older people showed greater RT costs [34]. Interestingly, however, an activity as apparently automated as walking can sometimes cause disruption of memory-encoding processes. Lindenberger and colleagues [35] argued that walking (especially perhaps on an unpredictable 'aperiodic' track) requires more control in older than in younger adults, and that this greater need for control would divert attentional resources from memory encoding, resulting in poorer subsequent performance. Their results (Table 2) confirm this hypothesis.

Previous research has shown that older people may be less able to spontaneously initiate adequate encoding strategies, contributing to their reduced memory capacity [36]. Encouraging a 'deep' level of processing during encoding by having people make semantic decisions about the stimuli (e.g. does a word represent something living or non-living) results in better memory than purely perceptual types of processing, so-called 'shallow' processing [37]. This levels-of-processing effect improves memory regardless of age, but may lead to even larger improvements in older adults [38]. One neuroimaging study examined both deep and shallow encoding of words and pictures in young and older adults to determine whether these strategies are implemented differently according to age [39,40]. Both picture and word memory increased after deep encoding in young and old groups, and there was an age-related decrement only in word recognition. During word encoding older adults showed less activity in a number of left hemisphere regions, including prefrontal cortex. However, the two groups had equivalent brain activity during deeper processing of pictures in left prefrontal cortex and in medial temporal areas. This is consistent with the idea that impaired memory in older adults is associated with age-related decrements in activity in the brain networks required to perform the task, whereas during those tasks they perform relatively well, older adults show brain activity equivalent to that of young adults and/or recruitment of additional prefrontal regions. However, a recent study by Madden *et al.* [41], examining brain activity in young and old adults during encoding and recognition of words, showed greater left prefrontal activation in the older adults during recognition but poorer memory performance. This result is similar to the earlier experiment by Cabeza *et al.* [7], but indicates that recruitment of left prefrontal cortex in older adults might not always aid performance.

To examine the issue of age-related deficits in memory for the context of events, or source memory, Cabeza *et al.* [42*] required participants to demonstrate memory for events, or 'items', using a recognition paradigm, and memory for context, defined in this experiment as the order in which the items were presented. In the item recognition condition,

participants were shown one word from a study list, and one new word, and they indicated which word had been on the study list. In the temporal order condition, participants were shown two words from the study list, and they indicated which word had been shown more recently in the list. Older adults had reduced memory for items but an even larger reduction in temporal order memory. During item memory, the older adults showed more left prefrontal activity than their younger counterparts, which is reminiscent of the more extensive retrieval-related networks in older adults reported by others [7,8,41]. In contrast, the temporal order task resulted in significantly less right prefrontal activity for the older than for the younger adults. These results suggest that source memory is impaired because relevant brain regions show less activity, but item memory is relatively spared as a result of the recruitment of left prefrontal cortex.

Thus, one conclusion that can be drawn from these imaging experiments is that left prefrontal cortex is less activated in older adults during many encoding tasks, but more activated during some retrieval tasks. However, it is not clear why this should be the case, or what specifically the left prefrontal area is doing. One possible explanation for the reduced activity during encoding comes from a study by Anderson *et al.* [43] who used a paired associate task to examine verbal memory under conditions of full or divided attention. In this task participants see pairs of words and are instructed to learn both items in the pair by making some association between them. Later testing involves presentation of the first word in each pair and the subject is required to recall the associated second word of the pair. This study was motivated by evidence that younger adults learning under conditions of divided attention have memory impairments that closely resemble those associated with aging [12,33**]. Both aging and divided attention were associated with similar reductions in encoding-related activity in left prefrontal cortex. This suggests that aging may adversely affect memory function because it increases the attentional load of the task in a manner similar to that in which divided attention affects task performance thus reducing the ability to engage in elaborative encoding carried out by left prefrontal cortex. This suggests that aging may adversely affect memory function in a manner similar to the way divided attention affects task performance. Both aging and divided attention may place an increased load on attentional processing, thus reducing the amount of time or processing resources available for encoding, perhaps by reducing activity in left prefrontal regions. Increased left frontal activity in the elderly during retrieval, on the other hand, may reflect additional elaborative processing needed in order to decide whether a particular stimulus has been previously encountered or to recall old information. Alternatively, an experiment by Jonides *et al.* [44] suggests that left prefrontal cortex may be involved in resolving the conflict between competing responses in some types of memory tasks. During such tasks, older adults have reduced left prefrontal activation

and increased amounts of interference from conflicting responses compared to young adults. This result suggests that left prefrontal activation in the elderly during retrieval, in general, may reflect more need to resolve conflicts among competing responses generated during the retrieval search. That is, when attempting to recall items that have been seen previously, older adults may need to generate a number of possible alternatives before they make their retrieval decision, whereas young adults may be able to respond with fewer attempts. This may also account for the longer response times commonly found in older adults.

False memories and prospective memory

In older adults, the reduction in memory for context, and the consequent increased reliance on general familiarity, makes them particularly vulnerable to false recollections [45]. This effect has been shown for photographs of faces — a result that has obvious implications for the use of older witnesses in criminal identification situations [46]. The greater susceptibility of older people to false memories is difficult to eliminate, even by the use of distinctive materials [47], although the likelihood of making false alarms (i.e. false positives) is greatly reduced in adults of all ages when pictures are used instead of words as stimuli in memory tests [48]. One study [49] found that the time of day at which the testing occurred made a large difference to the proportion of false memories produced by older people, whereas testing at non-optimal times produced a false memory rate of 66%; this percentage was reduced to 38% when subjects were tested at their preferred time (typically in the morning).

A final behavioral topic that has received a lot of recent attention is prospective memory; that is, remembering to carry out an intention at a future time. Contrary to earlier reports [50•], older people are usually worse on such tasks, although, interestingly, they are often better than their younger counterparts on such tasks carried out in real-life settings [51], possibly because of their greater motivation to succeed. The cue for carrying out the intended action is sometimes time-based (e.g. “remember to go to your meeting at 3:30 pm”) and sometimes event-based (e.g. “when you next meet Richard, tell him about these latest results”). In general, older people are less penalized in event-based situations, but in laboratory tasks, age-related declines in prospective memory are typically seen [52], even when the prospective action is cued by some external event [53].

Normal versus abnormal aging and the possibility of cortical compensation

Neuroimaging experiments have shown that differential utilization of brain resources in the elderly may sometimes, but not always, be accompanied by spared memory performance, indicating a possible compensatory role under some conditions. When interpreting the consequence of this additional activity in older adults as compensatory, a

crucial issue is determining specifically how activity in the additionally recruited brain areas is related to behavior. That is, we want to know whether increased activity in a particular brain area leads to better performance by those older adults who show the largest increases (i.e. whether activity in this area is related to individual differences in behavior). An experiment that examined this issue reported that older adults were able to perform a memory task for sine wave gratings as well as young adults, but that the neural systems supporting performance differed between young and old individuals [54••]. While there was some overlap in the brain regions supporting performance, old participants recruited unique areas, including medial temporal and dorsolateral prefrontal cortices (Figure 2). Correlations among the activity measures in these unique areas were significantly larger in the older adults and activity in these areas was related to behavior only in older participants. Therefore, these areas may have acted to compensate for reduced interactions among the other brain areas. Similarly, in a further analysis of their reaction time data, Madden *et al.* [55•] separated response times into two parameters, one representing the sensory and motor components of RT and a second that represented the decision-making process. In both young and old adults, activity in right prefrontal cortex during retrieval was correlated with changes in the sensory component, but was correlated with changes in the decision component only in older adults. In addition, older adults had additional correlations between both components and other brain areas. The more diffuse correlational pattern in older adults, and the correlations of right prefrontal cortex with both RT measures, provide further evidence that attentional demands are greater for the elderly and lead to recruitment of additional areas for task performance.

Finally, Small *et al.* [56••] examined brain activity in both elderly individuals who had shown a decline in memory over time but were still judged to be non-demented and a group of patients with Alzheimer disease (AD). Normal elderly subjects without any cognitive decline showed prominent activation in both entorhinal cortex and hippocampus during a face encoding task, whereas AD patients had reduced activity in both regions. Some of the elderly with memory decline had reduced levels of medial temporal activity, similar in severity to that seen in AD patients, whereas others maintained normal levels of activation. These results are consistent with current views of the entorhinal cortex and hippocampus as early sites of abnormality in AD [57], and further suggest that memory decline in some elderly individuals is associated with declining activation in specific medial temporal regions.

Conclusions

Although psychologists have studied the effects of age on memory for decades, the application of neuroimaging techniques to this area of research has only occurred in the past few years. There is thus much work to be done in order to understand the mechanisms underlying behavioral

changes in aging as well as we understand these behavioral changes themselves. In short, we know a lot about the particular aspects of memory that change with age and how they change on a behavioral level, but little about how these changes are mediated by altered function in the brain. The existing evidence suggests that the pattern of impaired versus spared memory abilities seen in older adults may be accompanied by patterns of reductions or increases of activity in brain areas that participate in memory. The challenge is to determine whether the additional activations seen in elderly individuals, such as those in left prefrontal cortex, represent recruitment for compensatory purposes or just more diffuse or 'de-differentiated' activity. The only certain conclusion that can be drawn is that age-related changes in the functional anatomy of memory are complex. Our hope is that in the future, with the increased availability of neuroimaging techniques (particularly fMRI), the community of researchers interested in aging and memory can make more use of these techniques to understand this complexity more fully.

Acknowledgements

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- of special interest
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