

Evidence for Frontally Mediated Controlled Processing Differences in Older Adults

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Advanced aging is associated with slower and less flexible performance on demanding cognitive tasks. Here we used rapid event-related functional magnetic resonance imaging to explore differences between young ($n = 65$) and older adults ($n = 75$) during memory retrieval. Methods were optimized to afford exploration of both amplitude and timing differences in neural activity. Although many correlates of retrieval were similar between the groups, including medial and lateral parietal responses to successful recognition, older adults showed increased recruitment of frontal regions relative to young adults when retrieval demanded heavy use of control processes. This effect was not significant during less effortful retrieval. Moreover, the timing of increased recruitment in older adults occurred at relatively late stages of the retrieval event, suggesting a strategy shift. One possibility is that older adults fail to engage appropriate top-down attentional sets at early stages of the retrieval event; as a consequence, frontally mediated processing is extended at late stages to compensate. This strategy shift, which we conceptualize in a framework called the “load-shift” model, may underlie the often observed retention of high-level cognitive function during advanced aging but at the cost of less flexible and slower performance on demanding cognitive tasks.

Keywords: aging, cognitive control, compensation, executive function, fMRI, recognition memory

Introduction

Older adults with no signs of clinical impairment commonly show less flexible and slowed performance on tasks that place high demands on control processes (Zacks and Hasher 1994; Moscovitch and Winocur 1995; Craik and Salthouse 2000; Craik and Grady 2002). Memory performance is often lower as compared with young adults. Memory tasks such as free recall and source retrieval are prototypical examples (e.g., Craik and McDowd 1987; Glisky and others 2001; see also Spencer and Raz 1995). Subclinical disruption of white matter tracts, neurotransmitter depletion, and atrophy within frontal-striatal systems are the most likely underlying causes of executive change in aging (Volkow and others 2000; Buckner 2004; Hedden and Gabrieli 2004; Raz 2005). These structural changes presumably lead to functional differences in how frontal systems mediate controlled processing. The goal of the present series of studies was to explore age-associated differences in control processes during memory retrieval using functional neuroimaging. Of particular interest is the possibility that older adults adopt different strategies than younger adults as a means to compensate for changes in available cognitive resources.

A consistent observation from prior neuroimaging studies of controlled task performance is that older adults paradoxically increase activity in frontal regions relative to young adults, sometimes in regions minimally active in young adults performing the same task (e.g., Cabeza and others 1997; Reuter-Lorenz and others 2000; Logan and others 2002; Morcom and others 2003). Recent findings further suggest increased recruitment may reflect a productive response to detrimental changes in aging, serving to mitigate performance decline (e.g., Cabeza and others 2002; Rosen and others 2002; Grady and others 2003; see also Reuter-Lorenz 2001). An open question is what mechanisms underlie increased recruitment in older adults. In this paper, we examine the temporal characteristics and boundary conditions for increased recruitment by older adults and propose a mechanistic hypothesis for how such increases might benefit performance.

Theoretical models of how control processes operate during tasks provide a basis for our analyses. Most models of cognitive control and attention include some concept of early versus late selection (e.g., see Kahneman and Treisman 1984). The basic idea is that an attentional set can supply a “top-down” bias signal that gates perceptual (and perhaps cognitive) inputs prior to their being extensively processed in an elaborated, sequential fashion (Desimone and Duncan 1995; Miller and Cohen 2001). To the degree that task-relevant stimuli and processing demands can be anticipated, top-down attentional sets that filter incoming information will be efficient. By contrast, late-selection processes can be applied to edit and elaborate on information as appropriate to task goals.

Variations of such attentional models have been applied to understand memory retrieval (e.g., Burgess and Shallice 1996; Jacoby and others 1999; Rugg and Wilding 2000). In particular, models of remembering typically include an attentional set, often referred to as a “retrieval mode,” that guides retrieval. Rugg and Wilding (2000) expanded on this idea in the concepts of retrieval orientation, retrieval effort, and post-retrieval monitoring. Retrieval orientation refers to control processes put in place in advance of specific retrieval trials based on anticipated retrieval demands; retrieval effort refers to processes engaged to access past information during the isolated memory event; and post-retrieval monitoring refers to processes engaged at the back end of retrieval to evaluate the appropriateness of the recollected information and guide further decision making.

Relevant to aging, these theoretical models suggest possibilities for how increased recruitment might arise during retrieval. One possibility is that older adults increase frontal recruitment in anticipation of retrieval demands (a difference in anticipatory

processing associated with retrieval mode or orientation). A second possibility is that access to memory traces requires greater effort during the early stages of the retrieval event and, hence, increased recruitment. Finally, it is also possible that frontal recruitment increases at the back end of the retrieval event to compensate for less efficient processing during early stages.

In the present studies, event-related functional magnetic resonance imaging (fMRI) methods able to accurately estimate temporal evolution were employed to examine the temporal characteristics of increased recruitment by older adults and the conditions under which such increased recruitment occurs (Friston and others 1999; Menon and Kim 1999; Miezin and others 2000). We base these studies on 2 observations about controlled retrieval in young adults. First, specific frontal regions along inferior frontal gyrus associate with controlled processing demands. These regions increase their activity levels as controlled processing demands increase, often independent of whether retrieval is successful. Controlled processing demands and associated frontal activations can be manipulated both by instructions at retrieval (e.g., source versus item memory tasks [Dobbins and others 2002; Cabeza and others 2003]) and by manipulating the depth or quality of initial encoding (Velanova and others 2003; Wheeler and Buckner 2003). Second, a network of regions, prominently including those in precuneus and lateral parietal cortex, is more active when items are correctly recognized (e.g., Habib and Lepage 1999; Henson and others 1999; Konishi and others 2000; Shannon and Buckner 2004; for review, see Wagner and others 2005), and activity in this network correlates with recognition performance (Wheeler and Buckner 2003; Kahn and others 2004). Thus, regions comprising this network can index processes associated with the successful recovery of information. Here we manipulated controlled processing demands across retrieval tasks and explored differences in activity between young and older adults in regions participating in control processes and in regions associated with successful retrieval. Importantly, we also examined the temporal characteristics of activity so as to constrain hypotheses about mechanisms of compensatory recruitment in older adults.

Methods

Overview

Functional anatomic correlates of memory retrieval were studied across 2 between-group fMRI experiments of young and older adults. The goal of the first experiment was to contrast recognition in young and older adults, with an emphasis on frontal regions implicated in controlled processing demands and parietal regions implicated in retrieval success. Based on the results of experiment 1, a second experiment was conducted to replicate the findings and also contrast high- and low-control retrieval conditions created by manipulating encoding. Data from the young participants in experiment 2 have been reported previously (Velanova and others 2003). Methods common to both experiments are described first, followed by experiment-specific methods.

Participants

A total of 140 paid adults participated in accordance with the guidelines of the Washington University Human Studies Committee. Older adults were recruited either from the local Alzheimer's Disease Research Center (ADRC) or through advertisements to the Washington University community. When recruited through the ADRC, only nondemented individuals were enrolled, as assessed by the clinical dementia rating (CDR) scale (all CDR 0) (Morris 1993), and therefore would be considered atypically healthy "high-functioning" older adults, exhibiting

no signs of even mild cognitive impairment. Older adults recruited through the broader community were administered neuropsychological tests that also revealed a high level of functioning (see Neuropsychological Testing below). Young adults were recruited through advertisements. All participants were right handed, native English speakers and reported no history of neurological problems. Vision was normal or corrected to near normal using magnet-compatible glasses or contact lenses.

fMRI Data Acquisition

Data were acquired using a Siemens 1.5-tesla Vision System (Erlangen, Germany) with a standard circularity-polarized head coil. Pillows and thermoplastic facemasks minimized head movement. Headphones dampened scanner noise and allowed communication with participants. A power Macintosh computer (Apple, Cupertino, CA) and PsyScope software (Cohen and others 1993) controlled stimulus display and recorded responses from a magnet-compatible fiber-optic key-press device. An LCD projector (Epson 500C LCD, Sharp LCD PG-C20XU) projected stimuli onto a screen at the head of the bore, viewable via a mirror attached to the head coil. Participants were fitted for magnet-compatible lenses based on autorefractor readings (Marko Technologies, Jacksonville, FL, model 760A) and subjective reports of improved acuity. For experiment 1, participants not needing vision correction wore plain lenses without refraction. For experiment 2, only older participants not needing vision correction wore plain lenses.

Structural images were acquired first, using a sagittal magnetization prepared rapid gradient echo (MPRAGE) T_1 -weighted sequence (repetition time [TR] = 9.7 ms, echo time [TE] = 4 ms, flip angle α = 10°, inversion time = 20 ms, voxel size = 1 × 1 × 1.25 mm). Functional images were acquired using an asymmetric spin-echo echo planar sequence (Conturo and others 1996) sensitive to blood oxygenation level-dependent (BOLD) contrast [T_2^*] (TR = 2.5 or 2.36 s [for experiments 1 and 2, respectively], TE = 50 or 37 ms, flip angle = 90°, voxel size = 3.75 × 3.75 mm in-plane resolution [Kwong and others 1992; Ogawa and others 1992]). For experiment 1, participants performed 2 functional runs (preceded by 4 related runs reported elsewhere). For experiment 2, participants performed 4 functional runs (prior to performance of an additional experiment, reported separately). During each run, 116 (experiment 1) and 128 (experiment 2) sets of 16 contiguous 8-mm-thick axial images were acquired parallel to the anterior commissure-posterior commissure plane. All functional runs began with 4 "dummy" image acquisitions to allow stabilization of longitudinal magnetization.

General fMRI Data Analyses

Data were preprocessed to remove noise and artifacts. Motion was corrected within and across runs using a rigid-body rotation and translation algorithm (cf., Friston and others 1996; Snyder 1996). Image slices were realigned in time to the midpoint of the first slice (using sinc interpolation) to account for differences in acquisition timing across slices. Data were normalized to a whole run mean magnitude of 1000. Data were then resampled into a standardized atlas space using 2-mm isotropic voxels (see Maccotta and others 2001) and smoothed with a Gaussian spatial filter (2 mm full width half maximum). To accommodate structural differences associated with aging, the atlas representative target image was composed of a merged young adult/older adult reference (Buckner and others 2004).

Preprocessed data were analyzed using the general linear model (Friston and others 1995; Worsley and Friston 1995; Zarahn and others 1997; Miezin and others 2000) implemented in an in-house analysis and display package. Analyses were performed to separate transient BOLD responses to each trial type (i.e., responses associated with "hits", "misses", "correct rejections (CRs)" and "false alarms" in each experiment and in each retrieval condition) in addition to coding for the effects of a linear trend (to account for within-run drift) and constant term (to account for run mean) (Donaldson, Petersen, Ollinger, and Buckner 2001; Visscher and others 2003). Effects for all analyses are described in terms of percent signal change, defined as signal magnitude divided by the mean of the estimated constant terms (one per run).

For each participant, the response to each trial was estimated by coding a different regressor (i.e., delta function) for each of the eight time points (i.e., image acquisitions) immediately following each stimulus onset. Regressors were also coded to account for the visual

prompts at the beginning of each task block in experiment 2. This estimation produced one time course estimate (over 8 time points covering 17.5 s in experiment 1 and 16.52 s in experiment 2) per voxel, per trial condition. Separate estimates were computed for trials occurring within “low-control” and “high-control” blocks in experiment 2 (see behavioral methods below). Full time course estimates were entered into a priori analyses using specific regions of interest (see Hypothesis-Directed Analyses).

Hypothesis-Directed Analyses

Specific regions of interest in frontal cortex associated with controlled retrieval were defined a priori based on literature reviews and recent work in our laboratory (for prior use of these regions, see Gold and Buckner 2002; Logan and others 2002; Velanova and others 2003; Lustig and Buckner 2004). Controlled retrieval is associated with the recovery of episodic information, and consequently with the explicit awareness that information is old. Thus, neural correlates of “retrieval success” were also examined. Particular focus was given to parietal regions that have been associated with the successful recovery of episodic information (Henson and others 1999; Konishi and others 2000; McDermott and others 2000; Donaldson, Petersen, and Buckner 2001; Donaldson, Petersen, Ollinger, and Buckner 2001; see also Wagner and others 2005).

Frontal regions associated with controlled processing were exactly as used in Logan and others (2002), defined about peak locations at 1) -43,

3, 32 (labeled left Brodmann area [BA] 6/44); 2) -45, 29, 6 (labeled left BA 45/47); and 3) 43, 3, 32 (labeled right BA 6/44). Parietal regions associated with retrieval success were taken directly from Konishi and others (2000) defined about peak locations 1) -39, -55, 36 (labeled BA 39/40, near the intraparietal sulcus) and 2) -7, -73, 34, (labeled BA 7, near precuneus). Region labels use BA names as a reference; these should only be considered as heuristics. The anatomical location and spatial extent of the specific regions can be visualized in Figures 1 and 2.

For each experiment, estimates of event-related responses were averaged across all voxels within each region and submitted to analyses based on a mixed-effects model, with subjects as a random factor. For both experiments, analyses were performed to determine whether activity modulated among trial types (in particular, hits versus CRs) and, for experiment 2, between conditions (low control versus high control). Sphericity corrected levels of significance are reported.

Exploratory Analyses

To further explore the data, maps of voxelwise activity change were constructed in an exploratory manner. To produce whole-brain statistical maps comparing activity in the high- and low-control conditions of experiment 2, magnitude estimates of the BOLD response were obtained for high- and low-control trials (summing across hits, CRs, and error trials). Magnitude estimates were computed for each trial condition as the inner product of the estimated time course and

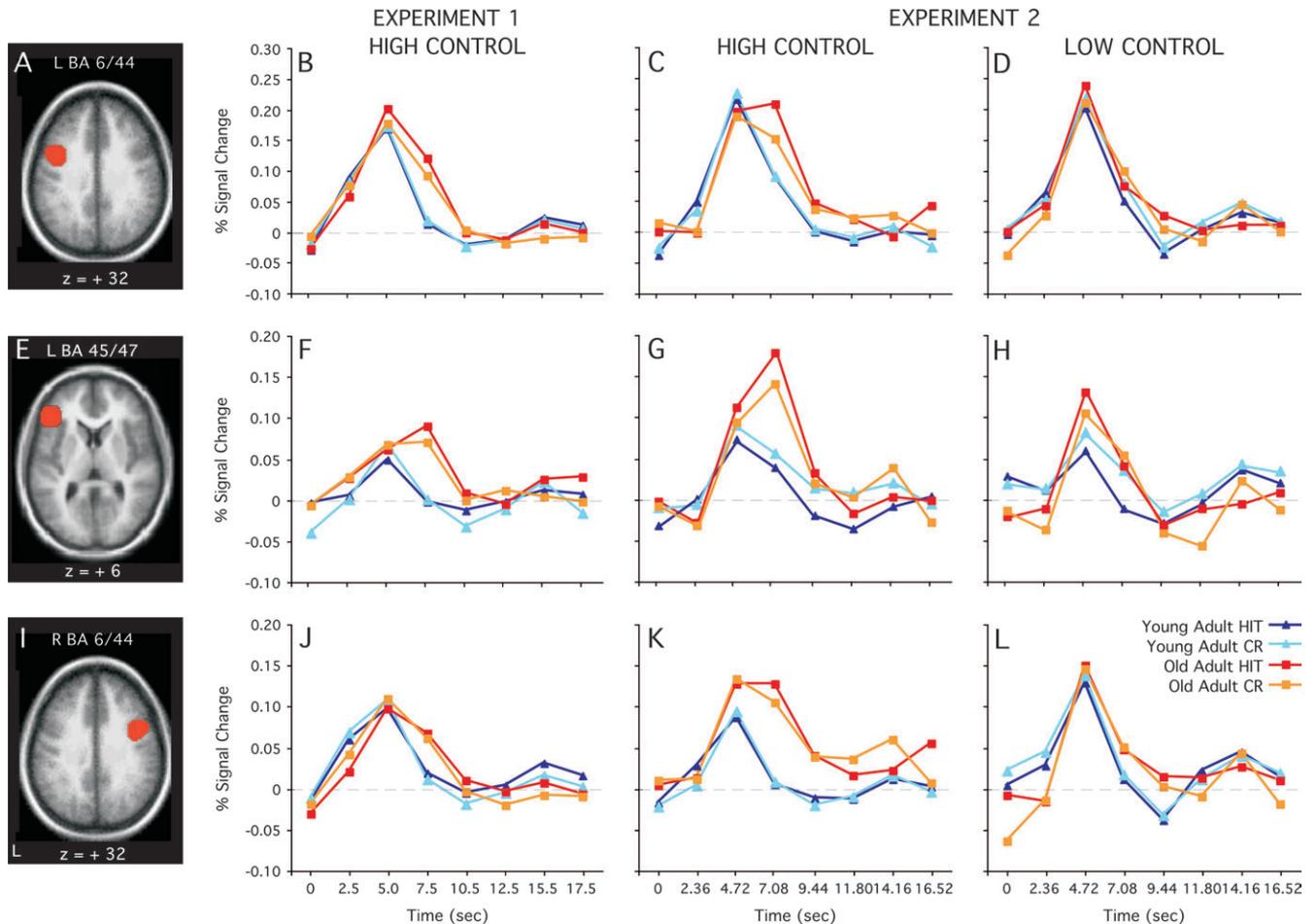


Figure 1. Frontal regions increase activity in older adults preferentially during retrieval tasks that place high demands on controlled processing. (A) A horizontal section shows the left BA 6/44 region, selected a priori, overlaid onto a standardized anatomical image ($z = +32$). (B) Time course estimates of signal change in left BA 6/44 in experiment 1 across retrieval conditions. No modulation by response type was observed in either age group. Rather, older adults showed more persistent activity relative to young adults. (C) Time course estimates of signal change in left BA 6/44 in the high-control condition of experiment 2. Results parallel those found in experiment 1 (see panel B), with older adults showing more persistent activity relative to young adults. (D) Time course estimates of signal change in left BA 6/44 in the low-control condition of experiment 2. The time course of activity in older adults mirrored that for young adults. Panels (E), (F), (G), and (H) and (I), (J), (K), and (L) are similar in layout to panels (A), (B), (C), and (D), respectively, except that the displayed regions represent left BA 45/47 ($z = +6$) and right BA 6/44 ($z = +32$). In all panels displaying time courses, time point 1 (at 0 s) designates the time at which the retrieval cue was presented.

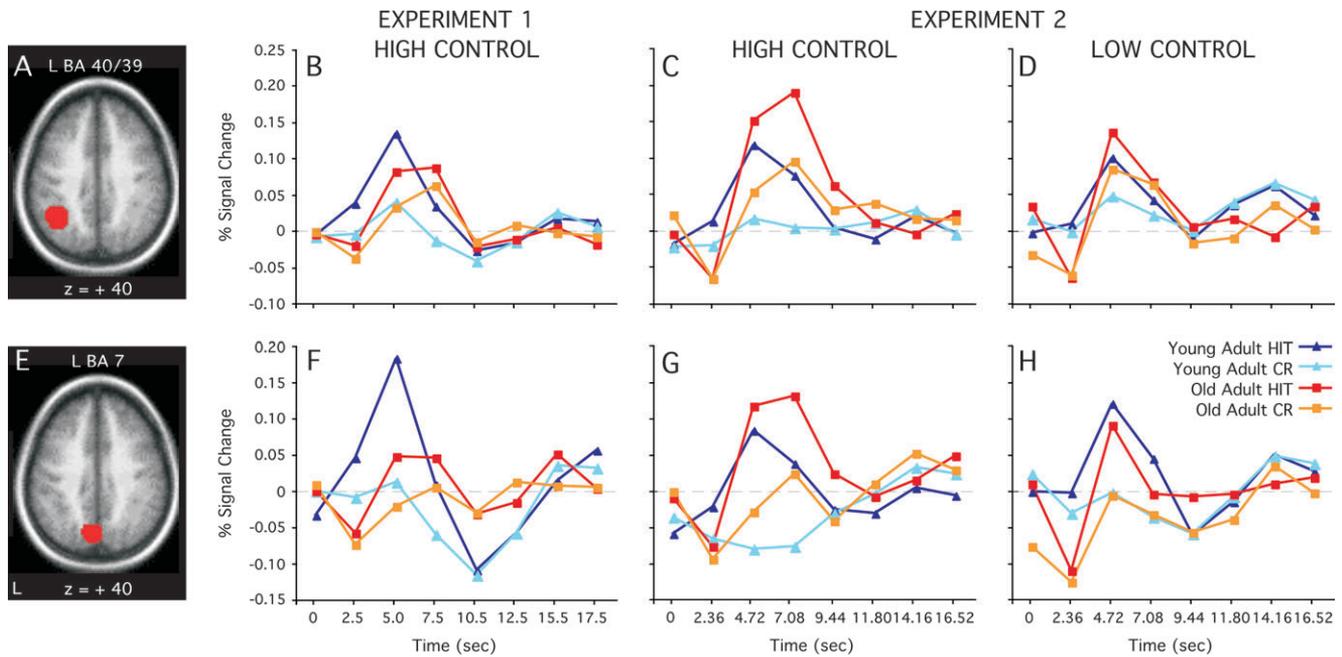


Figure 2. Parietal regions show retrieval success effects for both young and old adults and augmented overall activity in older adults. Left BA 39/40 (panels A, B, C, and D) and BA 7 (panels E, F, G, and H) showed greater modulation for hits relative to CRs for both age groups. In experiment 2, hits tended to produce greater signal modulation in the high-control condition relative to the low-control condition. The panel layout parallels that of Figure 1.

a vector of contrast weights modeling the hemodynamic response function. Contrast weights were derived from gamma functions with delays of 2, 3, 4, 5, and 6 s and a time constant of 1.25 s (Boynton and others 1996). By definition, the contrast weights summed to zero and were normalized to have a magnitude of one. Estimates were obtained at multiple delays so that the evolution of activity in frontal regions could be observed. These summary cross-correlation magnitude estimates were obtained for each participant at each voxel and were submitted to paired *t*-tests within each group. The resulting *t*-statistics were converted to *z*-statistics and plotted over the whole brain. We note, however, that all theoretically interpreted results were established using the a priori regions described above based on a mixed-effects model.

Neuropsychological Testing

Neuropsychological tests were administered to older adults participating in experiment 1 as part of their ongoing participation for the ADRC. Older adults participating in experiment 2 were tested separately (using a separate neuropsychological battery) in a 2-h session. For experiment 1, memory was assessed with the Wechsler Memory Scale (WMS) Associate Recall subscales (paired associate learning) (Wechsler and Stone 1973). Forward and Backward Digit Span and Mental Control from the WMS were also assessed. Participants in experiment 1 were also administered the Word Fluency Test (Thurstone and Thurstone 1949). General intelligence measures included 3 subtests of the Wechsler Adult Intelligence Scale (Wechsler 1955): Information, Block Design, and Digit Symbol. Visual perceptual motor performance was assessed by Trail Making forms A and B. Finally, participants in experiment 1 completed the Boston Naming Test (Goodglass and others 1983), which reflects semantic-lexical retrieval processes in naming simple line drawings.

Participants in experiment 2 were administered a battery assessing executive (frontal) function as described by Glisky and others (1995). The battery comprised 5 tests; 1) the modified Wisconsin Card Sorting Test (Hart and others 1988), 2) the Controlled Oral Word Association Test (Benton and Hamsher 1976), 3) Mental Arithmetic from the Wechsler Adult Intelligence Scale-Revised (Wechsler 1981), 4) Mental Control from the Wechsler Memory Scale-Revised (WMS-R; Wechsler 1987), and 5) Backward Digit Span from the WMS-R. Additionally, participants in experiment 2 completed Trail Making forms A and B, the

Table 1

Demographic and neuropsychological test data for participants in experiments 1 and 2

	Mean	SD	Mean	SD
Experiment 1	Old (<i>n</i> = 38, 13 male)		Young (<i>n</i> = 36, 18 male)	
Age	75.9	7.5	22.3	3.6
Education	14.5 ^a	2.9		
MMSE	28.7 ^a	1.2		
WAIS information	21.0	3.8		
WAIS block design	32.4	8.2		
WAIS digit symbol	46.5	8.4		
Boston naming	56.4	3.1		
Word fluency (letters: s,p)	31.6	9.0		
WMS mental control	7.2	1.7		
WMS backward digit span	5.1	1.1		
WMS logical memory	9.5	3.8		
Trail making A	34.7	12.7		
Trail making B	93.9	35.4		
Experiment 2	Old (<i>n</i> = 37, 11 male)		Young (<i>n</i> = 29, 10 male)	
Age	74.3	5.2	21.2	2.8
Education	15.3	2.5		
Glisky battery				
Modified Wisconsin card sort	4.4	1.5		
Word fluency (letters: F, A, S)	41.8	13.0		
WAIS-R mental arithmetic	12.5	3.7		
WMS-R mental control	27.8	6.7		
WMS-R backward digit span	6.4	2.3		
Weighted average	−.23	0.77		
Stroop interference (Golden 1978)	5.5	6.4		
Trail making A	30.4	9.3		
Trail making B	86.1	45.9		
Shipley vocabulary raw score	35.4	3.1		

Note: Means and standard deviations (SDs) for demographic variables and neuropsychological test performance. MMSE, Mini Mental State Exam; WAIS, Wechsler Adult Intelligence Scale; WAIS-R, Wechsler Adult Intelligence Scale-Revised.

^aData from 11 participants were unavailable.

Golden Stroop test (Golden 1978), and the Shipley Vocabulary test (Shipley 1940).

Neuropsychological test results for older participants are summarized in Table 1.

Experiment 1

Thirty-six younger adults (mean age = 22.3 years, range 18–34 years; 18 male) and 38 older adults (mean age = 75.9 years, range 60–91 years; 13 male) participated in experiment 1. The basic design consisted of deep incidental encoding followed by 2 scanned event-related recognition runs.

Encoding before the High-Control Retrieval Condition

During incidental deep encoding, participants made living/nonliving judgments on visually presented words (right button press with the right hand for living, and left button press with the left hand for non-living). Seventy-two relevant words were each presented for 2000 ms, followed by 500 ms of fixation. Brain activity associated with the presentation of these words, which served as study words for the present exploration of memory retrieval, has been previously described in the context of repetition priming (Lustig and Buckner 2004). The fMRI data reported here do not overlap with that of the prior study.

Scanned Retrieval

Following the semantic classification task, the critical recognition task was performed in 2 event-related runs. Each run consisted of 116 time points: 4 dummy fixation trials to allow the MR signal to stabilize, 108 intermixed “old”, “new”, and “fixation” trials of the recognition memory task, and 4 ending fixation trials to capture the full extent of the hemodynamic response. On old trials, items that appeared once during the semantic classification task were presented. New words, occurring nowhere else in the experiment, were presented during new trials, and a fixation crosshair appeared during fixation trials. Each trial had a duration of 2500 ms consisting of one of the 3 item types (old words, new words, and fixation crosshairs) presented for 2000 ms, followed by 500 ms of fixation. Old word, new word, and fixation trials were presented equally often in a pseudorandom order such that the interval between successive word stimuli ranged from 500 to 8000 ms, with shorter intervals more frequent than long (counterbalanced using the procedure developed in Buckner and others 1998).

Word stimuli consisted of 168 nouns (range 3–10 letters; mean frequency 29 per million, range 1–147 per million) selected from the Kucera and Francis (1967) norms. These words were subdivided into 14 lists of 12 words each with lists matched for word length and frequency. These lists were then rotated through conditions so that each served equally often as old or new items.

All stimuli were presented in uppercase white type on a black background in Geneva 48 font. Participants’ task was to distinguish old from new words by pressing the right button for old and the left button for new. To increase hemodynamic sampling, one run was synced to begin with the first MR pulse/trial, whereas the other run began 1250 ms after the first pulse/trial (Miezin and others 2000). The order of delayed versus nondelayed runs was counterbalanced across participants.

Experiment 2

Twenty-nine younger adults (mean age = 21.2 years, range 18–31 years; 10 male) and 37 older adults (mean age = 74.3 years, range 66–84 years; 11 male) participated. Parietal data from one older participant were not included in analyses because of insufficient coverage. Experiment 2 was conducted over 2 days, with scanning occurring on day 2. The experiment included 2 different encoding conditions that markedly varied the extent and depth of study. During scanning, each of 4 event-related runs included old items from only one of the 2 study conditions yielding distinct low- and high-control retrieval conditions (adapted from Velanova and others 2003).

Encoding before the Low-Control Retrieval Condition

On day one, participants repeatedly studied and were tested on one set of 60 words during each of 3 study blocks; these words subsequently became part of the low-control condition in the scanner. During each block, the same set of 60 words was presented 5 times. Words were presented for 1000 ms followed by a 500 ms intertrial fixation interval. Participants were instructed to read words aloud and to remember them for a later memory test. Recognition tests included the 60 study words randomly intermixed with 60 new words (that differed for each test) and 60 fixation trials. All test stimuli were presented for 1500 ms,

followed by an 860-ms fixation crosshair. Participants responded “old” or “new” to each test word by pressing keys on the computer keyboard, with the mapping of hand (right versus left) to response counter-balanced across participants. This study–test procedure was repeated 3 times such that, on day one, participants studied each of the 60 target words 15 times causing their recognition responses to become highly overlearned. On day 2, prior to scanning, participants performed one more study session (as above), intended to refresh their memory for the words presented on day one.

Encoding before the High-Control Retrieval Condition

On day 2, immediately following the study session above, participants performed a semantic judgment task in which they judged the pleasantness of 60 words (not presented elsewhere in the experiment) presented once each. These words became the old items in the high-control retrieval scans. Each word was appearing for 1000 ms, followed by an intertrial fixation crosshair (of varying duration). Participants read each word aloud and then made a pleasantness judgment by stating aloud “pleasant” or “unpleasant”. The experimenter keyed in each response, thus initiating the next trial.

Scanned Retrieval

Following encoding, participants performed recognition during 4 fMRI runs (following a 20- to 25-min delay). Across runs, the nature of the old words was manipulated. For 2 low-control runs, old words were those that had been repeatedly studied using intentional encoding and repeated tests. For the 2 high-control runs (paralleling experiment 1), old words were those presented in the incidental deep encoding task. Participants were explicitly informed about the source of the old words to be tested prior to each run. The order of low- and high-control runs was counterbalanced across participants.

The scanned portion of the experiment was conducted as a mixed blocked/event-related design such that, during each run, participants alternated between blocked periods of the recognition task and blocked periods of fixation (Chawla and others 1999; Donaldson, Petersen, Ollinger, and Buckner 2001). Within task blocks, trials were temporally jittered as in a rapid event-related design (Dale and Buckner 1997). Each block period began with a visual prompt, either “FIXATE!” or “OLD?” (of 2360 ms duration). Fixation blocks lasted 23.6 s during which a fixation crosshair was continuously displayed. Recognition blocks lasted for 106.2 s during which stimuli were presented (15 old word trials, 15 new word trials, 15 fixation trials). The presentation of test items was time locked to the onset of successive whole-brain image acquisitions. Trial order within each recognition block was pseudorandomized as in experiment 1 such that the interval between successive word stimuli ranged from 860 to 10300 ms, with shorter intervals more frequent than long. We note that, as in experiment 1, task timing was demanding and likely more so for older adults given their generally slower response times.

Following the 4 functional runs relevant to this experiment, an additional 4 runs were acquired as part of an unrelated study. At the completion of scanning, participants returned to the behavioral laboratory for a surprise lure recognition task to probe whether different levels of controlled processing were applied during the scanned recognition tasks (adapted from Buckner and others 2001). During this task, 240 words were presented at participant-controlled durations, each followed by a 500 ms blank intertrial fixation. These words comprised the 60 lures (new words in the recognition task) presented in low-control retrieval runs, the 60 lures presented in high-control retrieval runs, and 120 new words (not presented elsewhere in the experiment). Participants’ task was to identify lures presented in the scanner by pressing 1 of 4 colored keys on the computer keyboard, corresponding to “definitely old” (dark red), “probably old” (red), “probably new” (green), and “definitely new” responses (dark green). Postscan lure recognition data for one young participant was not collected.

For experiment 2, word stimuli consisted of 540 nouns (range 3–10 letters; mean frequency 12 per million, range 5–25 per million) selected from the Kucera and Francis (1967) norms. These words were subdivided into 9 lists of 60 words with lists matched for word length and frequency. Mapping of lists to encoding condition (low control and high control) and item type (targets and lures) was counterbalanced across participants.

Results

Experiment 1 Behavioral Results

In experiment 1, 2 event-related recognition runs followed an incidental deep encoding task. Both young and older adults were accurate in making living/nonliving judgments during encoding, correctly categorizing 92% and 94% of words, respectively. Recognition results are summarized in Table 2. Young adults were more likely than older adults to correctly identify old items (hits) and new items (CRs; $P < 0.001$). Older adults were slower to respond, resulting in a significant main effect of age group ($P < 0.001$). For both age groups, hits were faster than CRs (both $P < 0.001$). There was no significant interaction of age group with response type ($F < 1$).

Experiment 1 fMRI Results

Regions selected for analysis were defined a priori to include 3 frontal regions associated with controlled processing and 2 regions consistently implicated in retrieval success (taken directly from Logan and others 2002 and Konishi and others 2000, respectively). Analyses asked 1) to what degree each region responded to the recognition task generally (across both hit and CR trials), 2) whether each region showed differential activity between the hit and CR trials, and 3) whether young and older adults differed in their response patterns. For clarity, we describe the analyses within each group first (to emphasize similarities between the groups) and then present direct between-group tests that explore age differences using a mixed-effects model.

Frontal Regions Show Greater and Prolonged Responses during Retrieval in Older Adults

Frontal regions, heuristically labeled left BA 6/44, left BA 45/47, and right BA 6/44 (Fig. 1), showed robust recruitment for both age groups and response types, consistent with their role in

responding to controlled processing demands. For both young and old adults, left BA 6/44 (Fig. 1, panel A) and BA 45/47 (Fig. 1, panel E) showed significant activity for both hits and CRs, as indicated by main effects of time (all $P < 0.001$), and no effects of response type (all $F < 1$).

Of most interest, age differences were noted in left BA 6/44 and, to a lesser extent, in BA 45/47. For left BA 6/44, when both age groups were entered into the analysis, the main effect of time was modified in a time by age group interaction ($F_{7,504} = 3.42$, $P < 0.05$), indicating that the older adult response differed from that for young adults. This interaction was marginal for left BA 45/47, $F_{7,504} = 1.87$, $P = 0.09$. Examination of the time course of responses reveals that the older adults showed greater and more persistent activity than did the young adults (see Fig. 1).

Older adults frequently show greater activation in right frontal regions on verbal tasks than do young adults (see reviews by Park and others 2001; Reuter-Lorenz 2001; Cabeza 2002; Buckner 2004). In the current data set, right BA 6/44 showed a similar pattern as the left frontal regions, with significant main effects of time for both age groups (both $P < 0.0001$) and no modulation by response type ($P > 0.20$ for both groups). With both groups entered into analysis, the main effect of time was modified by a significant time by age group interaction ($F_{7,504} = 2.72$, $P < 0.05$). An examination of time courses (see Fig. 1) again revealed that the older adults showed greater and more persistent responses than did the young adults.

Parietal Regions Show Retrieval Success Effects for Both Young and Older Adults

A second set of analyses focused on regions associated with retrieval success (Fig. 2). A frequent finding in the literature is that a left lateral parietal region at or near BA 39/40 and medial parietal regions at or near BA 7 and precuneus increase activity when items are correctly remembered on tests of episodic memory (e.g., Habib and Lepage 1999; Henson and others 1999;

Table 2

Behavioral results from the scanned recognition tasks in experiments 1 and 2

	Recognition accuracy (SD)					
	Low control			High control		
	Hit	CR	d'	Hit	CR	d'
Experiment 1						
Young adults	~	~	~	0.83 (0.15)	0.78 (0.13)	2.04 (0.74)
Older adults	~	~	~	0.72 (0.15)	0.72 (0.13)	1.42 (0.54)
Experiment 2						
Young adults	0.96 (0.05)	0.96 (0.05)	3.78 (0.62)	0.89 (0.09)	0.86 (0.10)	2.63 (0.52)
Older adults	0.92 (0.08)	0.86 (0.14)	2.99 (0.96)	0.85 (0.09)	0.71 (0.19)	1.91 (0.79)
	RT in ms (SD)					
	Low control			High control		
	Hit	CR		Hit	CR	
Experiment 1						
Young adults	~	~		954 (121)	1067 (134)	
Older adults	~	~		1161 (167)	1282 (181)	
Experiment 2						
Young adults	735 (87)	819 (127)		872 (87)	952 (113)	
Older adults	858 (115)	1043 (155)		1073 (128)	1217 (149)	

Note: Means and standard deviations (SDs, in parentheses) for performance variables across experiments 1 and 2. The table shows that across experiments, young adults made faster responses and were better able to correctly categorize items as old (hit) or new (CR) relative to older adults. Comparisons of performance in the high- and low-control conditions of experiment 2 suggest that participants adopted different retrieval sets for the 2 types of runs and that recognition was more controlled in runs in which once presented, incidentally encoded, items appeared. Across age groups, responses during these runs were slower and less accurate, with recognition of new items being disproportionately poor in older adults. d' scores (corrected for ceiling performance) for the 2 age groups are also provided (Macmillan and Creelman 1991). RT, response time.

Konishi and others 2000; Shannon and Buckner 2004; for review, see Wagner and others 2005). Regional analyses in experiment 1 replicated this basic finding in young adults and further demonstrated that this modulation to old information can occur in older participants.

For BA 39/40, young adults showed increased responses for hits relative to CR trials, reflected in a time by response type interaction, ($F_{7,245} = 9.85, P < 0.0001$). Older adults showed a trend toward a similar interaction, ($F_{7,259} = 1.89, P = 0.09$). For BA 7, young adults again demonstrated a time by response type interaction, ($F_{7,245} = 14.01, P < 0.0001$). The time by response type interaction was also significant for older adults in this medial region, ($F_{7,259} = 2.36, P < 0.05$).

With both age groups entered into the analysis for BA 39/40, the interaction of time and response type was significant ($F_{7,504} = 7.93, P < 0.0001$), as was the interaction of time and age group ($F_{7,504} = 3.24, P < 0.01$). BA 7 showed similar effects and also a significant 3-way interaction of age group, time, and response type ($F_{7,504} = 2.35, P < 0.05$) that reflected a reduced retrieval success effect for the older adults. Inspection of the time courses (Fig. 2) suggests that the overall evolution of the time course for the older adults was delayed as compared with the young adults, similar to the pattern found for the frontal regions. However, for both parietal regions, the timing of the “retrieval success effect” (point of maximal difference between the response for hits and CRs) was similar across the 2 age groups.

Two important observations stem from these results. First, parietal retrieval success effects are apparent in both age groups, although they may be slightly attenuated in older adults. Second, although the peaks of the individual parietal responses are delayed for older adults compared with young adults, the retrieval success effect has a similar timing for the 2 groups and occurs before the peak frontal response in older adults. In experiment 2, we replicate these findings in a new sample of young and old adults and ask how the frontal and parietal effects modulate with demands for control during retrieval.

Experiment 2 Behavioral Results

Experiment 2 created 2 retrieval conditions that differed with respect to the level of control required. To this end, prior to the scanned recognition tests, participants encoded 2 lists of words in different ways. In the high-control condition, the list was presented only once in a deep encoding task, paralleling the procedure used in experiment 1. By contrast, in the low-control condition, the list was studied 20 times (total) and was tested 3 times prior to scanning. Participants' mean response accuracy and response times generally improved across these 3 tests, suggesting that the repetition manipulation was successful in reducing control demands during retrieval (Table 3).

Behavioral results from the scanned retrieval tasks are summarized in Table 2. When analyzed separately, performance in both the high- and low-control scanned retrieval tests replicated standard findings of differences in response times for hits and CRs and of age-related differences in response time and accuracy. Both retrieval conditions showed main effects of response type (both $P < 0.0001$), with hits faster than CRs, and of age (both $P < 0.0001$), with older adults slower than young adults. Older adults were disproportionately slower on CR trials, as shown by significant age group by response type interactions ($P < 0.01$ for the high-control condition and $P < 0.001$ for the low-control condition). Young adults were more likely than

Table 3

Mean response accuracy and response times (RTs) for the 3 prescan tests of recognition for words to be presented in the low-control condition of experiment 2

	Recognition accuracy (SD)		RT in ms (SD)	
	Hit	CR	Hit	CR
Young adults				
Test 1	0.94 (0.07)	0.92 (0.07)	744 (126)	836 (138)
Test 2	0.97 (0.04)	0.95 (0.09)	684 (109)	757 (149)
Test 3	0.97 (0.05)	0.97 (0.10)	676 (129)	713 (142)
Older adults				
Test 1	0.94 (0.05)	0.86 (0.14)	792 (97)	1056 (167)
Test 2	0.97 (0.03)	0.93 (0.11)	754 (91)	915 (119)
Test 3	0.98 (0.03)	0.95 (0.10)	741 (88)	861 (119)

Note: The table shows that participants' responses became faster and more accurate from test 1 to test 3, that hits were typically faster than CRs, and that the speeding of CRs occurred at a faster rate than that for hits. Young adults were reliably faster than older adults; however, the 2 groups were comparable in their accuracy by tests 2 and 3. SD, standard deviation.

older adults to correctly identify both new and old items regardless of retrieval condition, ($P < 0.001$ for both the high- and low-control conditions). Replicating typical findings in the aging literature (Balota and others 1999; Jacoby 1999; Karpel and others 2001), the age group by response type interaction was significant ($P < 0.05$) in both retrieval conditions, with older adults making a disproportionate number of false alarms.

Including retrieval condition as a factor in analyses revealed that participants likely adopted different retrieval sets across conditions, with more extensive processing of both targets and lures in the high-control condition (Jacoby and others 2005). Both age groups were less accurate and slower in the high-versus low-control conditions (main effects of control condition for accuracy and response times, both $P < 0.0001$). Young adults' subsequent memory for lures was better for items presented in the high- relative to the low-control condition (Fig. 3, panel A; $P < 0.0001$). Older adults, in a separate analysis, also showed better memory for lures presented in the high- relative to the low-control condition (Fig. 3, panel B; $P < 0.01$). We note that the effect of condition on memory for lures is larger for young adults than for older adults, reflected in a significant control condition by age group interaction ($P < 0.01$) when both age groups were entered into analysis. These results, however, suggest that both age groups engaged less elaborative retrieval processes in the low-control condition.

Experiment 2 fMRI Results

The previous experiment demonstrated greater and prolonged frontal responses during controlled retrieval in older adults relative to young adults, as well as the presence of retrieval success effects in parietal regions. Experiment 2 replicated these findings and further asked to what degree differences between young and older adults were preferential to controlled, as opposed to more automated, retrieval decisions. The frontal and parietal a priori regions were again the bases for analysis.

Greater and Prolonged Frontal Responses in Older Adults Are Preferential to Controlled Retrieval

Inspection of the time courses for the 3 a priori frontal regions suggested that the pattern for the high-control condition in experiment 2 replicated the age differences found in experiment 1 (Fig. 1). In left and right BA 6/44, significant time by age group interactions were observed ($F_{7,448} = 2.52, P < 0.05$ and

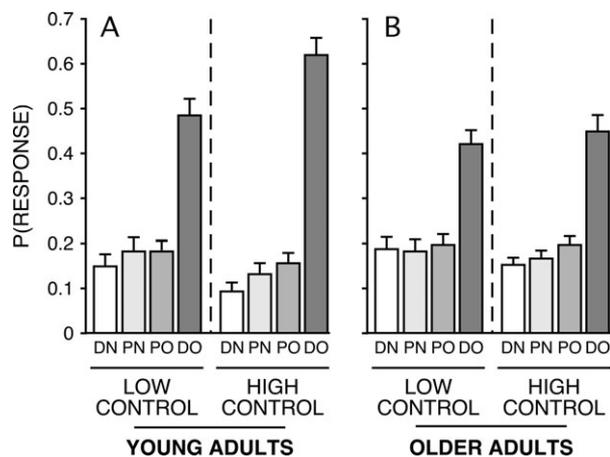


Figure 3. Subsequent memory for lures. In experiment 2, participants' subsequent memory for lures presented during the critical scanned tests was better for items presented in the high-control condition relative to items presented in the low-control condition. Panels (A) and (B) show results for young and older adults, respectively. Young adults showed better memory for lures than older adults, particularly in the high-control condition where they were more likely to respond with high confidence. (DN, PN, PO, and DO refer to participants' identifying critical lures as definitely new, probably new, probably old, and definitely old, respectively.)

$F_{7,448} = 2.30, P < 0.05$, respectively). In left BA 45/47, the time by age group interaction did not reach significance, $F_{7,448} = 1.43, P = 0.20$, although the time courses suggest a delayed peak for older adults. There were no effects of response type within either the young or older adult groups, again suggesting a processing role independent of retrieval outcome. Thus, across 2 independent studies, frontal regions implicated in controlled processing during retrieval showed significantly extended activation in older adults.

Analysis of the frontal regions in the low-control condition revealed a considerably greater degree of similarity between the young and older adults. For left BA 6/44 and left BA 45/47, only main effects of time were observed (see Fig. 1, panel D; both $P < 0.0001$). There was no modulation by age group, and the time courses were nearly identical. This result provides evidence that the differences in time courses between age groups observed in the high-control condition (above and in experiment 1) were selective to the task demands. Right BA 6/44 behaved similarly between the groups, although a time by age group interaction was observed ($F_{7,448} = 2.26, P < 0.05$, modifying a main effect of time, $F_{7,448} = 17.51, P < 0.0001$) (Fig. 1, panel L). No modulation by response type was observed in any of the frontal regions in the low-control condition.

The 3-way interaction of age group, time, and retrieval condition did not reach significance for the a priori frontal regions, but this may have been due to a lack of power to detect a higher order effect at these sample sizes.

Parietal Regions Again Show Retrieval Success Effects for Both Young and Older Adults

In the high-control condition, for both BA 39/40 and BA 7, hits showed greater responses than CRs for both the young and older adult groups, all $P < 0.001$. With both age groups entered into analyses, time by response type interactions were observed in both regions (both $P < 0.0001$). In BA 39/40, an age group by time interaction was also obtained ($F_{7,441} = 3.05, P < 0.01$)—a

consequence of older adults showing greater peak activity for both hits and CRs, that, additionally, showed a delay, relative to young adults. Although this same pattern was observed in medial parietal cortex, the interaction of age group and time did not reach significance ($F_{7,441} = 1.41, P = 0.21$). Thus, retrieval success effects were again observed in both age groups in the context of overall augmented parietal responses in older adults.

In the low-control condition, a similar pattern emerged, however, retrieval success effects were somewhat attenuated. For both BA 39/40 and BA 7, hits again showed greater modulation over time than did CRs for young (both $P < 0.01$) and older adults (both $P < 0.05$). With both age groups entered into analyses, 3-way interactions of time, response type, and age group were observed in both parietal regions (BA 39/40: $F_{7,441} = 2.30, P < 0.05$; BA 7: $F_{7,441} = 2.60, P < 0.05$). The data patterns presented in Figure 2 suggest that the differences between hits and CRs may be slightly less for older adults than young adults, but we do not interpret this strongly.

The Temporal Evolution of Parietal Retrieval Success and Frontal Control Effects

The above analyses yielded 2 important, convergent observations. First, older adults showed greater and prolonged responses in frontal regions during controlled retrieval as compared with young adults. Second, older adults showed parietal retrieval success effects in that responses were greater for hit than CR trials. Both these effects were independently replicated across the 2 experiments.

In order to isolate these effects and directly plot their temporal relations (Miezin and others 2000; Maccotta and others 2001), a post hoc data reduction was performed: 1) The parietal retrieval success effect (i.e., the hit - CR difference) was plotted separately for young and older adults and 2) the high-control frontal response, pooled across all trial types, was plotted as the difference between older and young adults. For both analyses, mean responses were pooled within the sets of parietal and frontal regions from Figures 1 and 2. In this manner, the temporal evolution of the retrieval success effect could be observed separately and contrasted for young and older adults (Fig. 4A,B). For frontal regions, the temporal evolution of the frontal response difference between older and young adults could also be observed in a comparable manner (Fig. 4C,D). Although qualitative, this procedure provided a means to visualize temporal offsets and replicate their appearance across independent data sets, providing some confidence in their reliability.

A clear pattern emerged across both experiments: the greater and prolonged frontal response in older adults was delayed relative to the similarly timed parietal retrieval success effect for both age groups. That is, the retrieval success effect, or the difference in the parietal regions' response to hit as compared with CR trials, evolved with a roughly similar, rapid time course in both young and older adults. (Note that this result was obtained despite older adult hit and CR trials individually showing delayed peak responses relative to young adults.) By contrast, the extended frontal response in older adults occurred relatively late. This offset was most impressive in experiment 2 where young and older adults showed similar retrieval success effects in the high-control condition. This replicable, but nonetheless qualitative, observation suggests that increased frontal contributions to control processes in older adults occur at a relatively late stage of retrieval.

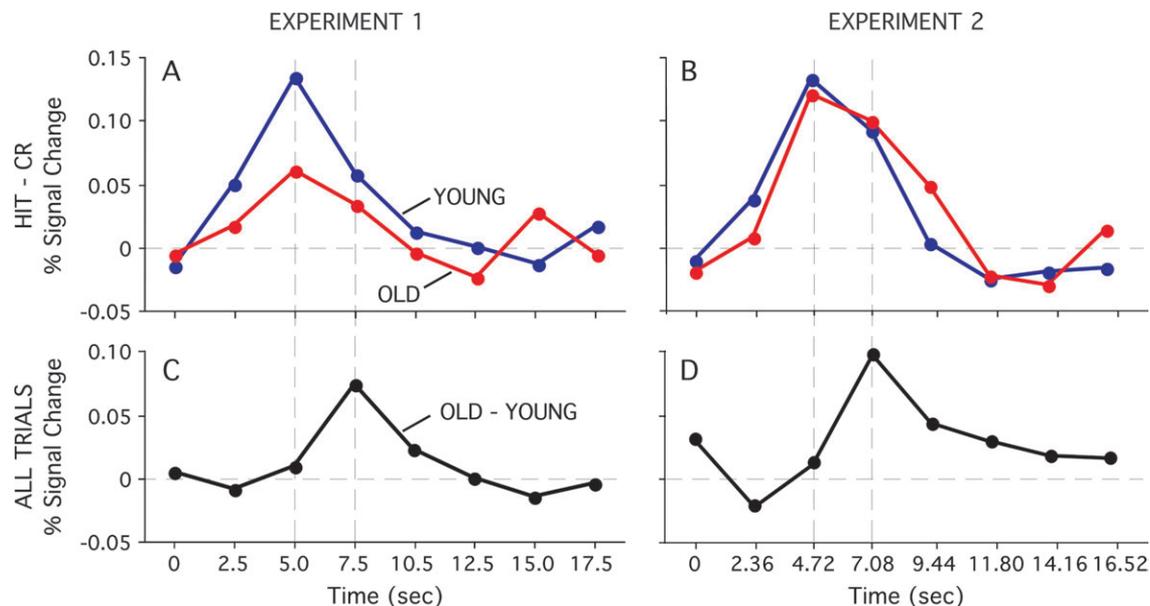


Figure 4. Relative comparisons of hemodynamic response profiles suggest age-associated frontal increases occur temporally late during controlled task performance. Parietal regions are displayed in panels A and B, and frontal regions in C and D. In high-control retrieval conditions, BOLD signal modulation in parietal regions was greater for hits than CRs, with the greatest difference in modulation occurring at analogous time points for young and older adults. In frontal regions, maximal activity in older adults was observed at a point later in time relative to young adults. (A) Mean BOLD signal differences between hits and CRs for young and older adults in experiment 1. Differences for each age group are plotted across time and represent the mean estimate across both BA 39/40 and BA 7. (B) Similar to Panel (A), mean BOLD signal differences between hits and CRs for young and older adults in the high-control condition of experiment 2. (C) Mean BOLD signal differences between young and older adults, summing across hits and CRs, in experiment 1. Differences between age groups are plotted across time and represent the mean estimate across the 3 a priori frontal regions; left BA 6/44, left BA 45/47, and right BA 6/44. (D) Similar to Panel (C), mean BOLD signal differences between young and older adults, summing across hits and CRs, in the high-control condition of experiment 2.

Confirmation Using Exploratory Analyses

The a priori frontal regions were chosen because of their strong association with controlled memory processes (Demb and others 1995; Wagner and others 2001; Dobbins and others 2002; Gold and Buckner 2002; Nyberg and others 2003; Velanova and others 2003; Wheeler and Buckner 2003). To further verify the presence of delayed activation by older adults, exploratory whole-brain activation maps were constructed to visualize the temporal evolution of control processes. For this analysis, trials from the low-control condition were directly subtracted from the high-control condition for each age group. Based on analyses of Schacter and others (1997), maps were constructed separately for multiple temporal delays of the hemodynamic response (from 2 to 6 s). Figure 5 plots the results. Two notable results are evident. First, clear activation of frontal regions can be observed in both young and older adults, with their anatomical locations similar to those predicted by the a priori regions. Second, the activations associate with later temporal regressors in older adults (peak at 4 and 5 s) relative to young adults (peak at 3 s). Note that overall parietal responses parallel frontal responses in their temporal delay; it is the retrieval success effects that evolve rapidly.

In summary, the results of this whole-brain analysis converged with the previous analyses to build confidence that an age-increased frontal response occurs at relatively late stages of retrieval processing and associates with high-control demands. First, temporally extended responses were observed for older adults in the high-control conditions of both experiments 1 and 2 but not in the low-control condition (Fig. 1). Second, the extended frontal response by older adults continued after the maximal parietal retrieval success effect (Fig. 4). Third,

the frontal high-low contrast had a slower temporal evolution for older adults than for young adults (Fig. 5). Taken collectively, these results provide strong convergent evidence that increased recruitment of frontal regions in older adults occurs at late stages of retrieval processing.

Discussion

Change in executive function is common in advanced aging and affects performance on demanding cognitive tasks including remembering (Hasher and Zacks 1988; Moscovitch and Winocur 1995). Older adults are typically slower and less flexible than young adults, and age differences are increasingly evident with increased demands on control processes. In the present studies, activity patterns were contrasted between young and older adults during memory retrieval tasks that varied controlled processing demands. Our goal was to characterize age differences in the implementation of control. Results indicated that 1) relative to young adults, older adults increased recruitment of frontal regions associated with control processes, 2) increased recruitment was attenuated during less effortful, familiarity-based retrieval, and 3) the temporal dynamics of increased recruitment revealed greater and more prolonged hemodynamic responses in the older adults. In particular, the temporal evolution of the hemodynamic response in frontal regions was temporally lagged relative to the evolution of parietal correlates of retrieval success. This finding of an increased response on the back-end of trial processing is consistent with increased recruitment reflecting a change in strategy to one that augments late-stage selection processes.

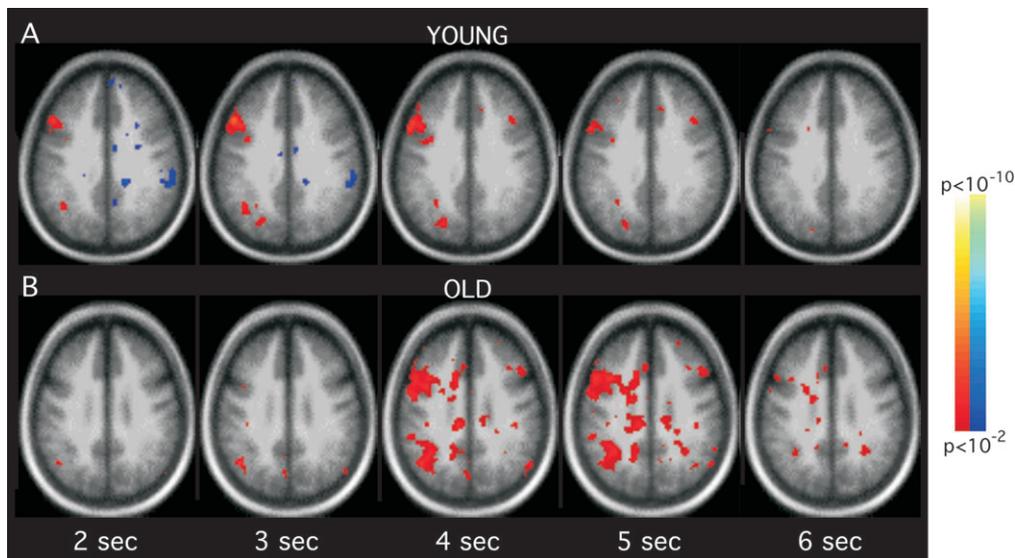


Figure 5. Exploratory activation maps show that the evolution of control-related activity in frontal cortex is delayed in older adults relative to young adults. (A) Panels show activity in high- relative to the low-control runs at $z = +32$ for young adults. Activity is shown at 2, 3, 4, 5 and 6 s delays following cue onset. (B) Similar to (A) for older adults. Activation maps are shown overlaid on averaged anatomical images for the relevant age group. Level of significance (based on the t -statistic) is shown in the color scale bar at the right of the figure.

Older Adults Increase Frontal Recruitment Preferentially during Controlled Forms of Retrieval

Older adults often show increased recruitment of frontal regions, among others, during performance of demanding cognitive tasks (Cabeza and others 1997; Reuter-Lorenz and others 2000; Logan and others 2002; for reviews, see Reuter-Lorenz 2001; Cabeza 2002; Buckner 2004; Reuter-Lorenz and Lustig 2005). Consistent with prior studies, the present study generalizes and replicates this finding across a series of tasks that demand controlled memory retrieval. Of importance, the present studies also show that minimizing the controlled processing demands of the task largely reverses the relative increase in recruitment. When the demand for controlled processing was reduced via practice (experiment 2), the age-associated increase in frontal recruitment was strongly reduced as well. The reversible nature of the recruitment difference suggests that it cannot be accounted for solely by age-related changes in vasculature that might affect properties of the hemodynamic response (D'Esposito and others 1999, 2003; Buckner and others 2000). Instead, the responsiveness of age-related increases in recruitment to encoding manipulations suggests that the determining factors are task demands for control.

At least 3 previous studies of normal aging have shown empirical links between increased recruitment and better performance in older adults, suggesting that such increases reflect a form of compensation (Reuter-Lorenz and others 2000; Cabeza and others 2002; Rosen and others 2002). Recently, Persson and others (2005) showed that older adults who experience the greatest longitudinal cognitive changes are those most likely to show frontal white matter disruption, medial temporal atrophy, and increased frontal recruitment. In the following sections, we discuss a mechanistic hypothesis for how increased recruitment might aid performance, suggesting that it may reflect a strategy shift to increased "late" or "back-end" processing to compensate for age-related declines at earlier stages of retrieval that rely on top-down attentional sets. Although the present study explored memory retrieval, we

suspect the effect is more general as increased recruitment has been observed across a wide range of task forms.

Increased Recruitment Occurs at Late Stages of Trial Processing

Control processes influence separate components of task processing that are distinguished by their temporal characteristics, among other properties. A long-standing theoretical distinction has been made between early- and late-selection processes. Heuristically, early-selection processes are those that are set up in advance of individual processing events to produce top-down bias and filter information before it is extensively processed at high levels. By contrast, late-selection processes operate on information in a sequential, slow series of extended processes. An efficient system is one that optimally constrains incoming information early and then devotes maximal resources, as needed, to elaborate on and edit information that survives early-selection processes. Increased recruitment in aging could potentially relate to any or all these control processes. For example, because of deficiencies in executive processing systems, older adults might increase effort to implement early-selection processes. Alternatively, increased recruitment could reflect augmented processing at late-selection stages. For this reason, the specific temporal profiles of hemodynamic responses that associate with increased recruitment are theoretically informative.

Our results strongly suggest that, during demanding memory retrieval tests, frontal response increases reflect relatively late recruitment. Three empirical observations support this conclusion. First, at an observational level, frontal responses evolved with a temporally extended profile in older adults relative to younger adults (Fig. 1). Second, exploratory maps of differential recruitment between the high- and low-control conditions showed a temporal lag between young and older adults (Fig. 5). This result converges with those from the a priori regional analyses but, critically, makes no assumption about timing differences or regional specificity. Nonetheless, frontal

recruitment during retrieval was lagged and the anatomical effect was largely selective to those regions tested in a hypothesis-directed manner. Finally, analyses of “relative” temporal offsets between controlled processing effects (in frontal regions) and retrieval success effects (in parietal regions) showed that age-increased frontal recruitment was temporally delayed relative to parietal retrieval success effects (Fig. 4). This finding replicated across experiments. The most parsimonious explanation is that increased frontal recruitment by older adults reflects an augmentation of control processes associated with late selection. In the next section, we propose a theoretical framework within which to consider late recruitment as a compensatory mechanism associated with a shift in executive processing strategy in older adults.

The Load-Shift Model of Executive Function in Aging

The present results provide a beginning set of constraints on how executive function might change in aging. We conceptualize these findings within a “load-shift model” (Fig. 6). Optimal executive function is presumably accomplished by an efficient and flexible collection of control processes that can constrain processing through top-down mechanisms prior to engaging individual processing events (early selection), as well as sequential, elaborated processes that edit information (late selection). Depending on task goals, young adults likely place emphasis on one or both of these control strategies, with maximal use of early-selection processes. In aging, executive function diminishes. The present results are consistent with a shift to greater resources being devoted to back-end (late selection) processes. One possibility is that executive resources have diminished, and older adults are less effective at implementing early-selection processes to constrain retrieval: as a compensatory mechanism they shift to cognitively expensive late-selection processes.

We refer to this as load shifting, reflecting the change in balance between early and late allocation of resources with aging (Fig. 6). Our proposal draws on the related concepts of postaccess monitoring (e.g., Jacoby and others 2005), retrieval monitoring (e.g., Henson and others 2000), and post-retrieval monitoring (e.g., Schacter and others 1997; Rugg and Wilding 2000). According to these formulations, control processes are employed late during retrieval events to monitor recovered memory content, verifying whether it satisfies current task demands. In young adults, such monitoring processes are thought to be engaged in situations where recovered information is impoverished or degraded, in situations of uncertainty, and when relying on memories lacking contextual content. Because of age-related declines in the ability to constrain and filter retrieval at early stages, our model suggests that the implementation of such monitoring processes can provide a route to preserved task performance in older adults. We note that the load-shift model is proposed as a hypothesis, not a conclusion, and suspect such changes in executive strategy will apply to many task forms that extend beyond memory retrieval. Further explorations will be required to test the utility and generality of the load-shift model.

An age-related shift to late-selection processing may be a general principle that can capture results from low-level perception (Park and others 2004) to high-level social functioning (Jacoby and others 1999). A number of different findings, in addition to the current data set, support its influence on memory. For example, Jacoby and others (2005) demon-

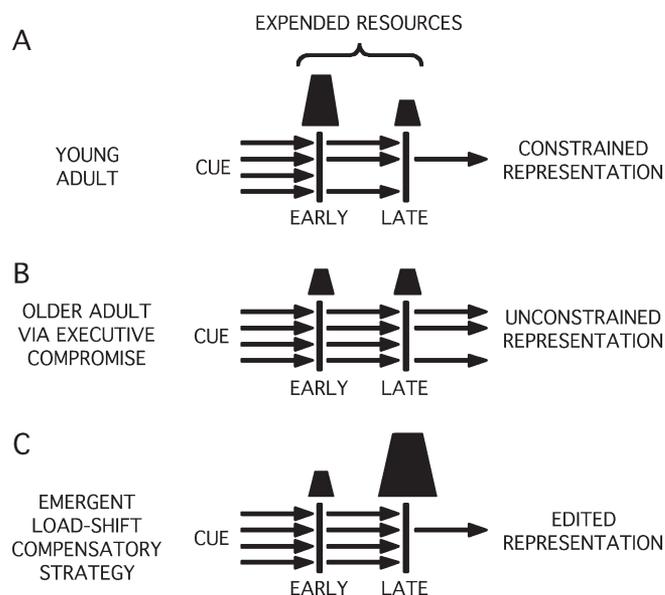


Figure 6. The load-shift model of executive function in aging. Memory retrieval is heuristically conceived as a set of processes automatically elicited by a cue that are constrained by early-selection processes and edited by late-selection processes. Resources, represented by polygons, can be expended at early- and late-selection stages to aid effective memory retrieval. (A) Young adults are hypothesized to rely on a combination of early- and late-selection processes with considerable resources expended to constrain processing through top-down mechanisms at early-selection stages. (B) Due to compromise in frontal-striatal systems involved in executive function, older adults fail to constrain processing at the early-selection stage. As a result, poorly constrained representations are accessed. (C) To compensate, older adults expend greater resources to edit the retrieval event at late-selection stages. The shift from expending front-end resources to mediate early-selection processes to those applied at the back-end to implement compensatory late-selection processes is the load shift. This model is one possible account of the present data and should be considered a hypothesis.

strate that, relative to young adults, older adults show poor subsequent memory for lures initially presented during a recognition task. They suggest that older adults’ poor subsequent memory performance stems, in part, from a failure to constrain retrieval to a relevant encoding context and that older adults instead rely on late-selection control processes. Kelley and Sahakyan (2003) make a similar argument regarding older adults’ poor source memory performance.

The load-shift model also receives support from studies by Park and others (2004) who provide evidence for broadly tuned perceptual responses in older adults. Likewise, Gazzaley and others (2005) have recently provided a dramatic demonstration of a failure by older adults to suppress unwanted perceptual information. A load-shift model specifically proposes a compensatory response to impoverished or inappropriately filtered information. Taken in this context, these prior studies of failed processing and the present work may be revealing 2 aspects of the same phenomenon; that is, failures to appropriately filter or tune incoming information may increase the burden on later processing stages (Hasher and Zacks 1988; Zacks and Hasher 1994; Reuter-Lorenz and Lustig 2005).

Thus, the load-shift model has the potential to account for a series of behavioral and functional observations and makes predictions about specific mechanisms of changed or preserved performance in nondemented aging. In this regard, it is important to note that the present data speak only to the presence of augmented late-selection processing in advanced aging. Potential earlier recruitment differences were not specifically

examined here, although they have been described previously in the context of encoding rather than retrieval (Logan and others 2002). Gutchess and others (2005) recently noted frontal activation increases in older adults relative to young adults during encoding, but showed the reverse pattern in medial temporal regions. Conceptually similar to the present work, they suggest frontal recruitment may be compensatory for decreased engagement of medial temporal regions.

An open question is the nature of age-associated changes that cause altered recruitment patterns. Executive difficulties in older adults are correlated with white matter lesions, frontostriatal atrophy, and neurotransmitter depletion (for reviews, see Buckner 2004; Raz 2005). A target for future exploration is to test the multiple predictions of a load-shift model by linking structural atrophy and other markers of disruption to the augmented frontal recruitment hypothesized here as a compensatory response.

Notes

CL and KV share lead authorship on this work. We thank Fran Miezin, Abraham Snyder, Erbil Akbudak, and Tom Conturo for support and development of the magnetic resonance imaging procedures, Mark McAvooy for invaluable assistance and support with functional data analysis, and Alex Konkel for assistance with data collection and analysis. We also thank Denise Head, Katherine O'Brien, Mark Wheeler, and Pascale Michelon for assistance with data collection. The Washington University ADRC assisted with recruitment of older adults in experiment 1. This research was supported by the Howard Hughes Medical Institute, the James S. McDonnell Foundation Program in Cognitive Neuroscience, and the National Institute on Aging (R01 AG021910, P50 AG05681, and P01 AG03991). *Conflict of Interest:* None declared.

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