Refreshing One of Several Active Representations: Behavioral and Functional Magnetic Resonance Imaging Differences between Young and Older Adults

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Abstract

■ We explored age-related differences in executive function during selection of a target from among active representations. *Refreshing* (thinking briefly of a just-activated representation) is an executive process that foregrounds a target relative to other active representations. In a behavioral study, participants saw one or three words, then saw a cue to refresh one of the words, saw one word again and read it, or read a new word. Increasing the number of active representations increased response times (RTs) only in the refresh condition for young adults but increased RTs equally in all conditions for older adults, suggesting that they experienced interference from activated irrelevant information during perception and reflection. Consistent with this interpretation, in a functional magnetic resonance imaging study, young adults showed two areas of left dorsolateral frontal cortex and a medial area of frontal cortex, including anterior cingulate, that were relatively more sensitive to number of active representations during refresh than read trials; for older adults these areas were equally sensitive to number of active items for refresh and read trials. Young and older adults showed activity associated with refreshing on trials requiring selection in left mid-ventral frontal cortex (an area associated with selection from active representations); older adults also showed activity in left anterior ventral frontal cortex (an area associated with controlled semantic activation). Our results support the hypothesis of an age-related decrease in ability to gate out activated but currently irrelevant information, and are consistent with a dissociation of function between left mid-ventral and left anterior ventral frontal cortex. ■

INTRODUCTION

Older adults often have the subjective experience of reduced cognitive function and evidence a range of everyday problems such as wondering why they just opened the refrigerator door, telling a story multiple times to the same person, or forgetting to take medication. They often perform more poorly than young adults on memory tests (e.g., Zacks, Hasher, & Li, 2000; Craik & Jennings, 1992; Light, 1991), particularly on source memory tasks (e.g., Mitchell, Raye, Johnson, & Greene, 2006; Jacoby, Debner, & Hay, 2001; Naveh-Benjamin, 2000; Chalfonte & Johnson, 1996), and they are more susceptible to interference in working memory (Hasher & Zacks, 1988), for example, proactive interference from prior trials (e.g., May, Hasher, & Kane, 1999). Aging is associated with less effective executive control (reflective) processes (e.g., Hasher, Lustig, & Zacks, 2007; Craik & Bialystok, 2006; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Jacoby, Bishara, Hessels, & Toth, 2005; Engle, 2002; Johnson, Reeder, Raye, & Mitchell, 2002; Milham et al.,

2002; Braver et al., 2001; Park, Polk, Mikels, Taylor, & Marshuetz, 2001; Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000; Balota et al., 1999; Hasher & Zacks, 1988). Although there is variability among investigators in how executive processes are defined and operationalized, there is general agreement that an age-related loss of speed or efficacy in any component process of executive function could disadvantage older adults in a wide range of tasks such as encoding and remembering information.

Here we examined the effects of aging on performance and brain activity associated with a basic executive process, *refreshing*—briefly thinking of a just-activated representation of a thought or percept (Johnson & Hirst, 1993; Johnson, 1992). Refreshing can serve multiple functions—a minimal maintenance function or, in the context of competing representations, a minimal selection function. In a prior behavioral study (Johnson et al., 2002), young and older adults read aloud single words as each word appeared on a screen. Some of the words were followed a half second later by a new word (read condition), some by the same word (repeat condition), and some by a black dot that was a cue for the participant to think of and say the just-seen word (refresh condition).

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Young adults were faster to respond in the repeat than in the read condition (repetition priming) and were slower to refresh a word than to read or repeat a word (refresh effect). Although older adults were slower overall, they showed equivalent repetition priming for repeated words. More important, older adults were disproportionately slower than young adults to refresh a just-seen word. Also, young adults later showed a long-term recognition memory benefit for the words they had refreshed compared to words they had read once or twice, but older adults did not, suggesting that this simple executive function is impaired in its execution and its memorial consequences in older adults. A subsequent functional magnetic resonance imaging (fMRI) study found an age-related deficit in activity associated with refreshing in a region of the left dorsolateral frontal cortex (DLFC; Johnson, Mitchell, Raye, & Greene, 2004).

In everyday situations, refreshing typically occurs in an environment of competing active representations, for example, trying to refresh a particular person's name when they are one of several people just introduced. In such situations, refreshing can give that representation an advantage over other information by foregrounding a target representation (making it the focus of attention; Cowan, 1999). In a previous fMRI study with young adults, we investigated the neural activity associated with refreshing as an act of selection by varying the number of competing representations. When cued to refresh one of several active representations (*selectively refreshing*), young adults showed increased activity in left DLFC and an area of medial frontal gyrus extending into anterior cingulate cortex (ACC) compared to when they were cued to refresh a single active representation (Johnson et al., 2005, Experiment 5). Activity in these areas is consistent with previous findings implicating them in top–down control under conditions of competition (e.g., MacDonald, Cohen, Stenger, & Carter, 2000). Johnson et al. also found activity related to selectively refreshing one of several active representations in an area of left ventrolateral frontal cortex (VLFC) that has been associated with resolving interference in a working memory task in young adults (Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998). Jonides, Marshuetz, Smith, Reuter-Lorenz, and Koeppe (2000) found that older adults showed greater behavioral evidence of interference in the same working memory task used by Jonides et al. (1998) and showed less activity than young adults in left VLFC.

Here we examined the effects of aging on performance and brain activity associated with selectively refreshing, that is, refreshing under conditions of potential competition from several active representations. Experiment 1 was a behavioral study that compared response times (RTs) of young and older adults when they refreshed a word after reading only that word or after reading three simultaneously presented words. We contrasted the refresh conditions with conditions in which,

after reading either one or three words, participants read a new word or read one of the same words again. Experiment 2 used fMRI to assess age-related differences in neural activity associated with increasing the number of active representations during refreshing or reading. If older adults have difficulty gating out irrelevant information, we would expect this to be reflected both in RTs in Experiment 1 and, in Experiment 2, age differences in activity in brain areas related to control and/or interference resolution in a context of competition.

EXPERIMENT 1: BEHAVIORAL STUDY

Methods

Participants

Participants were 24 young adults (11 women; *M* age = 20 years; range = 18–26 years) and 24 healthy, independently living older adults (16 women; *M* age = 75 years; range = 70–83 years). All gave informed consent, were tested according to an approved protocol, and were compensated for their participation.

Materials and Procedure

Each participant was seated at a computer and told that whenever they saw words on the screen, they should read them aloud as quickly but as accurately as possible; when they saw a dot, they were to think of, and say aloud, the word that had appeared in that same location on the previous screen. Stimuli were common one- to three-syllable words (e.g., *valley*, *boat*, *shampoo*). On Screen 1 of each trial, either three words were presented simultaneously in a column or a single word was presented in one of the three locations (top, middle, or bottom) for 2.25 sec. After 1 sec, Screen 2 was presented for 2.25 sec. Screen 2 showed either: a new word in one of the three possible locations (*read* condition), a word from Screen 1 in its same location (*repeat* condition), or a dot (•) in one of the three locations (*refresh* condition). When a word appeared on Screen 2 (*read* and *repeat* conditions), participants read the word aloud. A dot on Screen 2 (*refresh* condition) signaled participants to think of and say aloud the word that had appeared in that location on Screen 1. Thus, participants refreshed a word, re-read a word, or read a new word after seeing either three words (three-item conditions) or after seeing a single word (one-item conditions). The intertrial interval was 1 sec. The dependent variable was time to initiate speaking the correct word after Screen 2 onset. A voice-triggered microphone recorded participants' responses and the time to initiate speaking a word. The six trial types (read, repeat, or refresh crossed with one or three prior words) were pseudorandomly intermixed. For each participant, critical items (read, repeat, and refresh items defined by Screen 2) appeared in each of the three positions equally often across conditions.

There were 16 critical items in each condition for a total of 96 critical items.[1] Across participants in each age group, each critical word occurred in each of the conditions.

A surprise long-term recognition memory test was administered immediately after this phase. All 96 critical old words were randomly intermixed with 96 new words, and each was presented for 2 sec with a 500-msec intertrial interval. Participants identified words as old or new via button press.

Results and Discussion

Trials in which the voice key was triggered by erroneous responses or extraneous sounds (e.g., coughs, squeaking chair) were discarded ($M = 1.46\%$, 1.40% of the total critical responses for young and older adults, respectively; $p > .50$). This high level of response accuracy is not surprising because participants simply had to read words on the screen or refresh a word they had just seen a second earlier (see also Johnson et al., 2002). In addition, the lack of an age difference in response accuracy indicates that location information about the items was highly available over the short intervals used here (see also, Olson et al., 2004). For analysis of RTs, to minimize the impact of extreme scores, we also removed trials that fell below the 2.5 percentile within each group separately ($M = 4.41\%$, 5.13% of the total RTs [collapsed across initial presentation responses and critical responses for all conditions] for young and older adults, respectively, $p > .10$), and above the 97.5 percentile within each group ($M = 1.94\%$, 1.42% for young and older adults, respectively; $p > .10$). For each participant, the mean RT per condition was entered into the analysis reported below.

Response Times to Initiate Saying Critical Items

Mean RTs (Figure 1) to say the critical item were submitted to an analysis of variance (ANOVA) with age (young, older), condition (refresh, read, repeat), and number of items on Screen 1 (1, 3) as factors. Main effects of all factors were superseded by interactions. There was an Age × Condition interaction [$F(2, 92) = 9.48$, $MSE = 3085$, $p < .001$]. Subsequent analyses showed that, relative to young adults, older adults were disproportionately slow in the refresh condition compared to the read condition (mean difference [refresh − read] for young was 108 msec and for older was 175 msec, $p < .001$), replicating Johnson et al. (2002). Older adults showed less facilitation than young in the repeat compared to the read condition (mean difference young = 42 msec, older = 25 msec, $p < .05$). An Age × Number interaction [$F(1, 46) = 11.68$, $MSE = 2277$, $p < .001$], reflected a greater increase in RT as number of items on Screen 1 increased for older (111 msec) than for young (72 msec) adults, and a significant Condition × Number interaction [$F(2, 92) = 6.07$, $MSE = 2205$, $p < .005$] reflected a greater increase
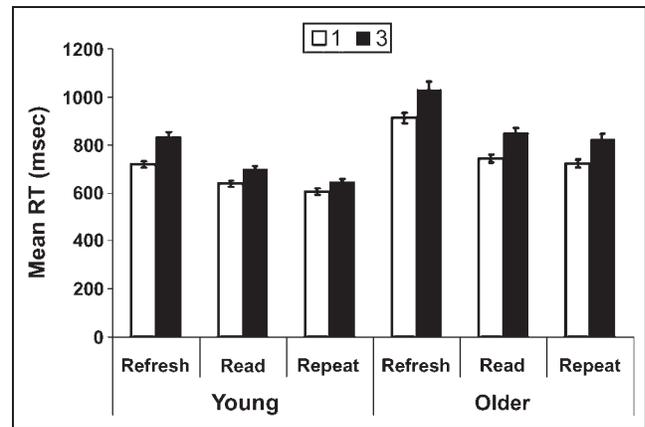

Figure 1. Mean RTs (msec) to say the critical item in Experiment 1. In the legend, 1 and 3 refer to the number of words presented on the first screen of each trial (bars are standard error of the mean).

in RT with number of items presented in the refresh condition (118 msec) compared to the read (86 msec) or repeat condition (71 msec). Because the Age × Condition × Number interaction was of particular interest and approached significance ($p = .09$), we analyzed each group separately. For young adults, the Condition × Number interaction was significant [$F(2, 46) = 11.32$, $MSE = 1572$, $p < .001$]; the increase in RT from one- to three-item trials was greater in the refresh (115 msec) than in the read (62 msec) or the repeat (40 msec) conditions. In contrast, for older adults, the increase in RTs from one- to three-item trials did not differ between conditions ($F < 1$; 120 msec, 109 msec, 102 msec for refresh, read, and repeat, respectively). This pattern suggests that older adults experienced competition from increased number of active representations in all conditions.[2]

Long-term Memory

As shown in Figure 2, corrected recognition (proportion of hits minus proportion of false alarms) was better for young ($M = 0.52$) than older ($M = 0.41$) adults [$F(1, 46) = 4.90$, $MSE = 0.17$, $p < .05$], and better for words from one-item ($M = 0.51$) than three-item ($M = 0.42$) trials [$F(1, 46) = 52.48$, $MSE = 0.01$, $p < .0001$]. The three-way interaction, Age × Condition × Number, was significant [$F(2, 92) = 3.78$, $MSE = 0.01$, $p < .05$]. For young adults, critical words in the read and repeat conditions from three-item trials were remembered less well than those from one-item trials (read, $p < .001$; repeat, $p < .05$), suggesting that they were encoded less well than single items. On the other hand, refreshed critical words from three-item trials were not disadvantaged relative to one-item trials for young adults. In short, for young adults, old/new recognition was poorest when a word was presented for the first time (read condition) after three different items had just been seen. Refreshing and, to a lesser extent, repeating one of the
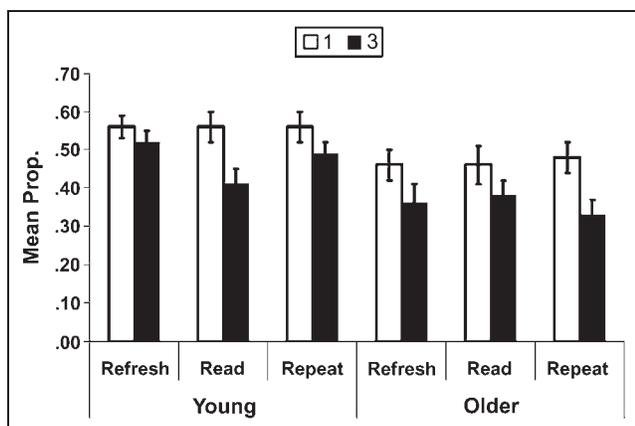
Figure 2. Corrected recognition (proportion of hits minus proportion of false alarms) for critical items in Experiment 1. In the legend, 1 and 3 refer to the number of words presented on the first screen of each trial (bars are standard error of the mean).

items helped offset the encoding disadvantage an item had from being presented in the context of other items. For older adults, critical items from three-item trials in all conditions were remembered less well than those from one-item trials. That is, neither repeating nor refreshing an item helped offset the disadvantage from processing it in the context of other active items. This pattern, such as that reported by Johnson et al. (2002), suggests that young adults derived a long-term benefit from refreshing that older adults did not.

The findings that, compared to young adults, older adults were disproportionately slower to refresh than to read or re-read (repeat) an item and did not show a benefit from refreshing on a later recognition test, are consistent with previous results indicating an age-related deficit in refreshing (Johnson et al., 2002). For young adults, compared to when one item was presented, when three items were presented, refresh RTs were slowed more than were read or repeat RTs. This is consistent with the idea that refreshing requires more cognitive control when more representations are active. Increasing the number of items presented increased older adults' RTs equally in all conditions, however, suggesting that older adults experienced interference from activated representations during perception (reading) as well as during reflection (refreshing). Consistent with this, older adults showed less repetition priming than young adults, although they frequently show no deficit in repetition priming under other conditions where potential interference from multiple active representations may be less (e.g., Johnson et al., 2002; Fleishman & Gabrieli, 1998; La Voie & Light, 1994; Howard & Wiggs, 1993). Thus, age-related deficits in resolution of interference (Hasher et al., 2007; Hasher & Zacks, 1988) appear to have an impact on perceptual (e.g., Connelly, Hasher, & Zacks, 1991) as well as reflective processes.

EXPERIMENT 2: fMRI STUDY

Given the results of Experiment 1, which suggest that older adults experience interference from recently activated representations during perceptual processing as well as reflective processing, we would expect to see neural evidence of competition on both three-item read and three-item refresh trials in older adults. In a previous fMRI study with young adults using a design similar to the current Experiment 1, Johnson et al. (2005, Experiment 5) cued participants to refresh either the single word from the previous screen or one of the three words from the previous screen; one- and three-item read trials were included for comparison. Johnson et al. found greater activity for three compared to one-item trials in the refresh but not in the read condition in an area of the medial frontal gyrus extending into the ACC, an area of the left DLFC near the intersect of the middle frontal, inferior frontal, and precentral gyrus, and an area of the left VLFC inferior frontal gyrus. These findings are consistent with other research showing, under conditions of increased competition, increases in activity in the ACC and DLFC (e.g., Zhang, Leung, & Johnson, 2003; Botvinick, Braver, Barch, Carter, & Cohen, 2001; MacDonald et al., 2000), and in the VLFC (e.g., D'Esposito, Postle, Jonides, & Smith, 1999; Jonides et al., 1998; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). The results of the current Experiment 1 suggest that when refreshing one of several active representations, older adults should show a different pattern of activity compared to young adults in some or all of these areas.

Methods

Participants

Participants were 15 right-handed young adults[3] (10 women; M age = 23 years, range = 18–26 years) and 14 healthy, independently living older adults (9 women; M age = 68 years, range = 61–81 years). Two other young participants and one older participant were excluded because of excessive head movement. All participants gave informed consent, were tested according to an approved protocol, and were compensated for their participation. Young and older participants did not differ in mean education (15.9 and 16.1 years, respectively; $p > .70$) or on an abbreviated version of the WAIS vocabulary subtest (max possible = 30; $M_{young} = 21.8$, $M_{older} = 22.9$, $p > .40$).[4]

fMRI Procedure

The stimuli and procedures were as in Experiment 1, with the following exceptions. Stimuli were projected onto a screen at the foot of the scanner, which participants viewed through a mirror mounted on the head coil. Trial event timing was adjusted to accommodate scanning parameters (see Figure 3 for the trial sequence

1 or 3 Words	Delay	New Word or ●		arrow		arrow		arrow		blank
1600 msec	400	1450 msec	550	1400 msec	600	1400 msec	600	1400 msec	600	2000 msec
scan 1		scan 2		scan 3		scan 4		scan 5		scan 6

Figure 3. Within-trial sequence of events and timing, Experiment 2.

and timing). Each trial was 12 sec long. Only read and refresh conditions were included, and participants were instructed to silently read all words that appeared on the screen and to silently refresh. The intertrial interval was 8 sec; during this time participants made left (right) keypresses in response to left (right) arrows. This provided a filled interval that was the same across conditions to accommodate the hemodynamic response. There were six runs of 32 trials each, 8 trials each of the four conditions arising from crossing read versus refresh, with one versus three items on the first screen. Trials from these four conditions were pseudorandomly intermixed, and order was varied across participants.

Imaging Details and Analyses

The experiment was run on a 1.5-T Siemens Sonata scanner at the Yale University Magnetic Resonance Research Center. T1-weighted anatomical images were acquired for each participant. Functional scans were acquired with a single-shot, echo-planar gradient-echo pulse sequence (TR = 2000 msec, TE = 35 msec, flip angle = 80°, FOV = 24). The 24 axial slices (resolution 3.75 × 3.75 mm in-plane, 3.8 mm between planes) in each volume were aligned with the AC–PC line. Each run began with 12 sec of blank screen to allow tissue to reach steady-state magnetization, and each run was followed by a 1-min rest interval. For each person, 1152 volumes of data were collected, 288 for each of the four number–condition combinations.

Data were motion-corrected using a six-parameter automated algorithm (AIR; Woods, Cherry, & Mazziotta, 1992). Motion was slightly greater in older than young adults [$t(1, 27) = 2.82$, $p < .01$], but small in absolute terms (mean distance = 0.08 mm vs. 0.05 mm for old and young, respectively). A 12-parameter AIR algorithm was used to coregister participants' images to a common (young) reference brain. Data were mean-normalized across time and participants, spatially smoothed (3-D, 8 mm full-width half-maximum Gaussian kernel), and analyzed with NeuroImaging Software (NIS; Laboratory for Clinical Cognitive Neuroscience, University of Pittsburgh, and the CSBMB, Princeton University).

A whole-brain ANOVA included participant as a random factor and age (young, older), run (1–6), condition (refresh, read), number of items on Screen 1 (1, 3), and time within trial (Scans 1–6) as fixed factors. Regions were identified that had a minimum of 6 contiguous voxels, each significant at $p < .001$ for two-way interactions or $p < .01$ for three- and four-way interactions (Forman et al., 1995). All regions of activation reported were localized anatomically using AFNI (Cox, 1996) and Talairach Daemon software (Lancaster, Summerlin, Rainey, Freitas, & Fox, 1997), and were manually checked with the Duvernoy (1999) and/or Talairach and Tournoux (1988) atlases. Planned contrasts ($p < .05$) were performed within age group, between conditions, on percent change in the bold signal from Time (scan) 1 within a trial at Times (scans) 4 and 5. The coordinates reported in Table 1 are the local maxima in each region of activation identified as showing either an Age × Condition × Number × Time, Age × Condition × Time, or Condition × Number × Time interaction that also met the following criteria for either the young adults only, the older adults only, or both: Areas showing activity associated with selectively refreshing showed a significant refresh effect (refresh > read) in the three-item condition, a significantly larger refresh effect in the three-item than in the one-item condition (or no refresh effect in the one-item condition), and Refresh 3 > Refresh 1. Areas related to refreshing, but not affected by the number of active representations, simply showed significantly greater activity in each *refresh* condition contrasted with its corresponding *read* condition. Areas related to the number of items showed only 3 > 1. Areas related to reading showed significantly greater activity in each read condition contrasted with its corresponding refresh condition.

Results and Discussion

Table 1 lists areas identified by the ANOVA and subsequent planned contrasts as described above. Figure 4A–C shows areas where there was a significant *selective refresh effect* (as defined above) for young but not older adults: left precentral gyrus, middle frontal gyrus (BA 6, 9; Figure 4A), a more lateral area of left DLFC (BA 6 [9/4/3];

Table 1. Areas of Activation, Experiment 2

Figure	Hemisphere	Anatomical Area	BA	x	y	z	F
(A) Areas Related to Selectively Refreshing in Young But Not Older Adults							
Figure 4A	L	precentral, middle frontal gyrus	6, 9	−36	3	26	3.79
Figure 4B	L	precentral, middle frontal/postcentral gyrus	6 (9/4/3)	−52	−4	39	5.27
Figure 4C	L	medial, superior frontal gyrus, anterior cingulate	6, 32/24	−2	12	51	4.63
	R	middle temporal gyrus	21	47	−32	−1	6.47
(B) Area Related to Selectively Refreshing in Both Young and Older Adults							
Figure 4D	L	inferior frontal gyrus	45	−41	22	10	4.34
(C) Areas Related to Selectively Refreshing in Older But Not Young Adults							
Figure 4E	L	inferior frontal gyrus	47	−49	22	−5	4.33
Figure 4F	L	middle temporal gyrus	21 (22)	−54	−36	2	4.68
	L	putamen/caudate nucleus	striatum	−17	12	−2	4.67
	L	putamen		−24	7	−2	5.92
	R	putamen, caudate nucleus		14	9	2	4.93
(D) Areas Related to Refreshing in Young But Not Older Adults							
	L	precentral, middle frontal gyri	6	−36	−11	43	4.70
	L	precuneus (cuneus)	7, 31, 18	−21	−76	23	4.34
(E) Areas Related to Refreshing in Older But Not Young Adults							
	L	middle temporal gyrus	21	−62	−40	−2	6.44
	R	parahippocampus/hippocampus	35, 36	28	−33	−8	3.96
(F) Areas Related to Refreshing in Both Young and Older Adults							
	R	inferior frontal, insula, superior temporal gyrus	44, 45, 13, 22	49	14	3	15.13
	L	supramarginal gyrus	40	−54	−40	30	15.56
(G) Areas Related to Reading in Both Young and Older Adults							
	L	fusiform, inferior, middle occipital, lingual gyri	18, 19, 37	−29	−84	−9	28.13
	R	inferior, middle occipital, lingual, fusiform gyri	18, 19, 37	26	−89	−5	19.89

The first column indicates a corresponding figure. Anatomical and Brodmann's areas (BA) are listed along with the Talairach coordinates and *F* value for the local maximum of each area of activation. Areas were identified in a whole-brain analysis including both young and older adults (see text for details). A lists areas associated with selectively refreshing (a significantly larger refresh effect [refresh > read] in the three-item condition contrasted with the one-item condition, and refresh 3 > refresh 1) in young but not older adults. B lists an area related to selective refreshing in both age groups. C lists areas related to selective refreshing in older adults but not young. D, E, and F list areas related respectively to refreshing (significantly greater activity in each *refresh* condition contrasted with its corresponding *read* condition) in young only, in old only, in both young and old. G lists areas related to reading (significantly greater activity in each read condition contrasted with its corresponding *refresh* condition). Effects shown in the table were significant at Times 4 and 5, except for the putamen/caudate and the parahippocampus (significant at Time 4), as well as the inferior frontal gyrus BA 47 (significant at Time 5). L = left; M = medial; R = right; BA = Brodmann's area. For each area of activation, the major anatomical regions and BA numbers are listed in descending order of size, with areas of approximately equal size indicated by a slash (parentheses indicate a small extent relative to other areas listed). Talairach coordinates (*x, y, z*) are shown for the voxel with the maximum *F* value.

Figure 4B), and medial frontal gyrus extending into ACC (BA 6, 32/24; Figure 4C). In contrast, for older adults, activity in these areas was related to the number of items presented (3 > 1). Given previous findings associating

ACC and DLFC with detection of competition and control, this pattern is consistent with our hypothesis from Experiment 1 that older adults experienced competition in the read as well as the refresh condition when more
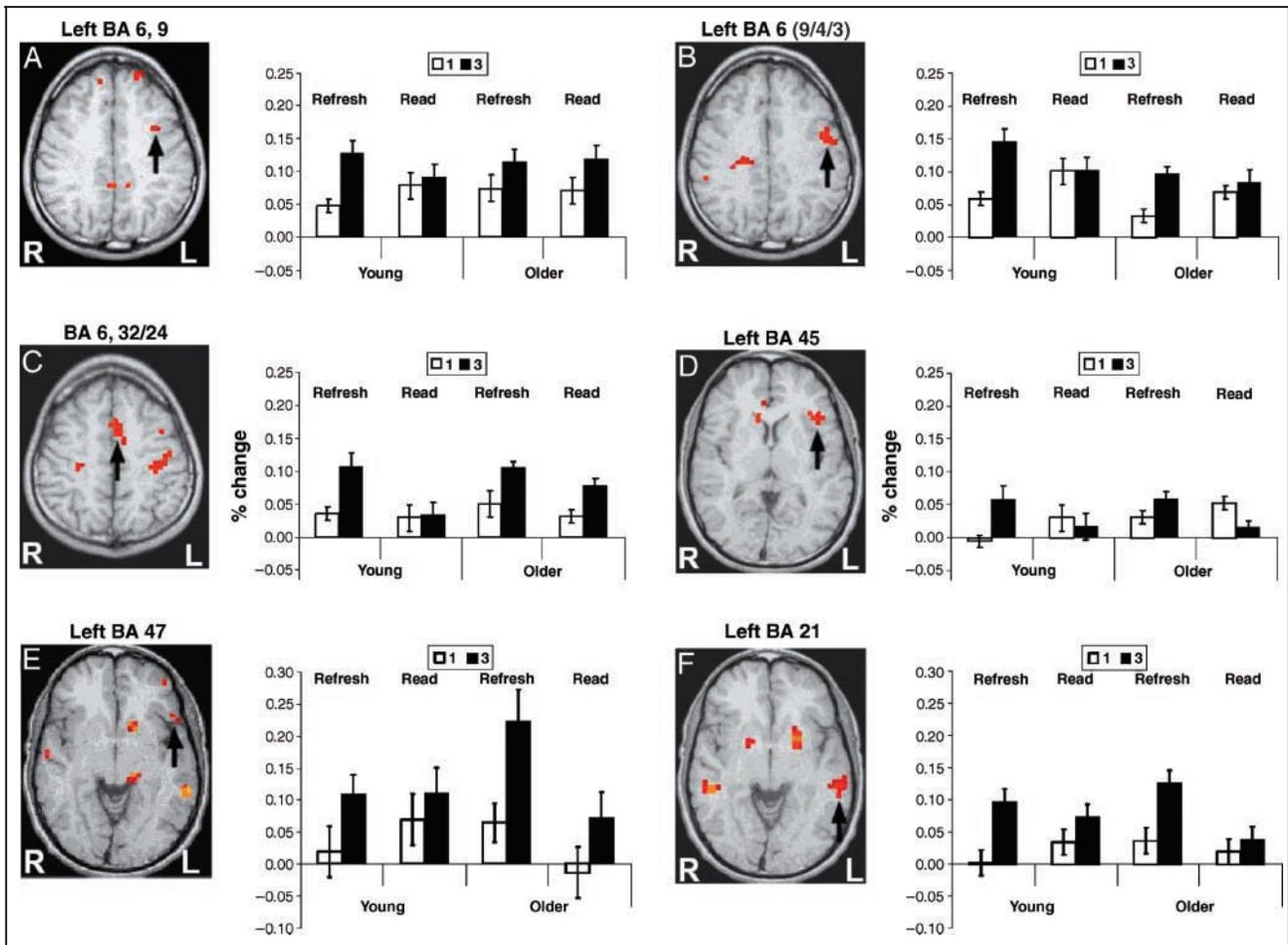
Figure 4. Experiment 2. Areas showing activity associated with selectively refreshing [refresh 3 − read 3] > [refresh 1 − read 1] in: (A–C) young but not older adults; (D) both age groups; (E–F) older but not young adults. In the legend, 1 and 3 refer to the number of words presented on the first screen of each trial (bars are standard error of the mean).

representations were active. Also, young, but not older, adults showed a selective refresh effect in right middle temporal gyrus (Table 1A).

Figure 4D shows an area of left inferior frontal gyrus (BA 45), in which both young and older adults showed a selective refresh effect. However, as can be seen in Figure 4D, the difference in activity between the three-item and one-item refresh conditions was somewhat less for older adults than for young adults ($p < .07$, one-tailed). Although only marginally significant, this pattern converges with the one reported by Jonides et al. (2000), in which both young and older adults showed activity in left BA 45 ($x = -51$, $y = 21$, $z = 11$) associated with interference among conflicting representations, but the effect was less reliable in older adults. Because the Jonides et al. task involved presenting the same items repeatedly (sometimes as targets and sometimes as distractors) over trials, whereas in our task the items were unique on each trial, the potential for interference was likely greater in their task. It would be useful to explore the relative importance of the number of active distractors versus distractor strength (e.g., familiarity) in pro-

ducing age-related differences in neural activity associated with selectively refreshing.

Figure 4E–F shows two areas where older adults showed a selective refresh effect and younger adults did not: the left inferior frontal gyrus (BA 47, Figure 4E) and left middle temporal gyrus (BA 21[22], Figure 4F). For young adults, these areas showed only an effect of number of items ($3 > 1$). Older adults also showed activity related to selectively refreshing in left and right putamen/caudate (Table 1C), whereas young adults did not.

We also identified areas related to refreshing which did not differ with the number of active representations. As shown in Table 1D, young, but not older, adults showed refresh-related activity in an area of left precentral and middle frontal gyrus (BA 6) as well as in precuneus and cuneus (BA 7, 31, 18), and, as shown in Table 1E, older, but not young, adults showed refresh-related activity in left middle temporal gyrus (BA 21) and in right parahippocampus and hippocampus (BA 35, 36).

Areas showing similar patterns of activity in young and older adults are shown in Table 1F and G. Both age

groups showed greater activity in each refresh condition relative to its corresponding read condition in an area of right inferior frontal gyrus, extending into insula and superior temporal gyrus (BA 44, 45, 13, 22) and in an area of the left parietal cortex (supramarginal gyrus, BA 40). Finally, both groups showed greater activity for reading than refreshing words bilaterally in areas that included fusiform, inferior and middle occipital, and lingual gyri (left and right BA 18, 19, 37).

Like the results of Johnson et al. (2004), which included only single-item trials, the results of Experiment 2 provide evidence of age-related disruption of function in left DLFC: Young, but not older, adults showed greater activity in refresh than read conditions. However, it is worth noting that the left DLFC areas in the present study showing age-related differences associated with refreshing (−36, −11, 43) and selectively refreshing (−36, 3, 26; −52, −4, 39) were posterior to the area (−40, 28, 31) reported in Johnson et al. (2004). As Johnson et al. (2005) noted, the specific areas of the DLFC engaged during refreshing may depend to some extent on task context, for example, single-item trials only as in Johnson et al. (2004) versus both single- and three-item trials as in the present study (see also Raye, Johnson, Mitchell, Reeder, & Greene, 2002), or type of information (e.g., words vs. objects, Johnson, Raye, Mitchell, Greene, & Anderson, 2003). The left VLFC (BA 45) showed activity associated with selectively refreshing one of several active representations in both age groups, consistent with previous results associating this area with selection (Jonides et al., 1998, 2000; D'Esposito et al., 1999; Thompson-Schill et al., 1997). The present results indicate that this area is important not only when prepotent responses must be overcome (e.g., distractors familiar from earlier trials; Jonides et al., 1998), but also when the distractors, like the target, have been seen only once just a half second earlier. Interestingly, older, but not young, adults showed activity in left BA 47 associated with trials requiring selective refreshing, suggesting that, on selective refresh trials, older adults engage additional areas of the ventrolateral frontal cortex to compensate for reduced dorsal function. This is an example of within-hemispheric compensation, in contrast to the contralateral compensation reported by Cabeza (2002) and Reuter-Lorenz (2002).

GENERAL DISCUSSION

Older adults are more susceptible to interference from irrelevant information in working memory, leading investigators to propose that many cognitive deficits in aging may result from reduced ability to gate out interfering information (e.g., Jonides et al., 2000; May et al., 1999; Hasher & Zacks, 1988). Results from the present two studies provide evidence consistent with this view.

In Experiment 1, we compared the time to read or re-read a word with the time to think of (refresh) a just-seen word immediately after seeing a display of one word or a display of three words. Relative to young adults, older adults were disproportionately slower to refresh a word than re-read a word or read a new word, providing additional behavioral evidence of the age-related refresh deficit previously reported by Johnson et al. (2002). In addition, for young adults, increasing the number of active representations increased RTs more in the refresh condition than in the repeat or read condition, but for older adults, increasing the number of active representations increased RTs equally across all conditions. This pattern suggests that older adults experience interference from active irrelevant items during relatively automatic *perceptual* processes (e.g., reading a word) as well as during more controlled *reflective* processes (e.g., refreshing a word). This interference did not prevent older participants from accurately reading or refreshing items aloud, but was reflected as a cost in their RTs. Furthermore, for young but not for older adults, refreshing offset the reduced long-term recognition memory found in read and repeat conditions for words from three-item compared to one-item trials.

Experiment 2, an fMRI study, investigated brain areas involved in refreshing in young and older adults when the number of activated representations was varied. For young adults, there was activity associated with selectively refreshing in left DLFC and in an area of medial frontal cortex extending into ACC. For older adults, activity in these areas reflected only the number of items seen. This age difference in the pattern of activation, in combination with prior results associating activity in ACC and DLFC regions with detection of competition and implementation of control (e.g., MacDonald et al., 2000), suggests that older, but not young, adults experienced competition from multiple active representations when reading a new item as well as when refreshing an item, consistent with their RT data from Experiment 1. The fact that, unlike young adults, older adults did not show greater activity in DLFC for refresh than read trials replicates and extends findings reported by Johnson et al. (2004).

It is interesting that young adults showed one region of left DLFC associated with refreshing for both one-item and three-item trials, and two other left DLFC regions associated with refreshing only for the three-item refresh trials. That is, we found that additional DLFC areas were engaged specifically for selectively refreshing rather than greater activity in the same refresh area(s). One interpretation of this pattern is that the DLFC areas engaged during refreshing depend on factors such as the amount of competition, as well as the type of information refreshed (Johnson et al., 2003, 2005). For example, some DLFC activity observed during selective refreshing may be associated with refreshing the location with the word; Johnson et al. (2005, Experiment 3) had young adults refresh location information (i.e., where a small square had appeared on the previous screen) and found an area (−44, −4, 38) near the one

shown in Figure 4B (−52, −4, 39). Another possibility is that some DLFC activity, perhaps in conjunction with VLFC (e.g., Badre & Wagner, 2002; Thompson-Schill et al., 1997), reflects a separate selection process engaged during selective refreshing.

With regard to the VLFC, the present results are particularly interesting from the perspective of the proposal by Badre, Poldrack, Pare-Blagoev, Insler, and Wagner (2005) and Badre and Wagner (2002) that the functions of left mid-VLFC (BA 45/44) and left anterior VLFC (BA 47) can be dissociated. Badre et al. propose that left mid-VLFC subserves selection of activated information in working memory (e.g., Thompson-Schill et al., 1997) and that left anterior VLFC subserves controlled access to semantic information stored in left temporal cortex (i.e., semantic memory). In the present Experiment 2, both age groups showed a selective refresh effect in left mid-VLFC (BA 45), although, as noted above, the effect of increasing the number of active representations on refresh trials was marginally greater for young than older adults. In contrast, older, but not young, adults showed activity related to selectively refreshing in left anterior VLFC (BA 47). This pattern suggests that older adults were engaged in, or attempting to engage in, more controlled semantic activation when they had to refresh under conditions of interference. Increased activity related to selective refreshing in the VLFC (BA 47) and less activity in the DLFC in older than young adults is consistent with the idea that older adults engage an additional cognitive operation (controlled semantic activation) to support or compensate for a compromised cognitive operation (refreshing). One possibility is that perceptual representations are poorer to begin with or start to decay more quickly for older adults, perhaps due to inefficient sensory processing or impaired perceptual/attentional processing (e.g., Madden, 2007). Selectively refreshing one of several degraded representations may be particularly difficult, and thus, likely to require additional process(es). This possibility suggests it would be useful to explore age-related differences in the time intervals over which different features remain available for refreshing or must be recovered via reactivation.

Other evidence suggesting that young and older adults may be refreshing somewhat different representations comes from age differences in areas that show refresh-related activity but no effect of the number of active representations. Young, but not older, adults showed refresh-related activity in the precuneus, an area associated with the representation of visual information (e.g., Johnson, Mitchell, Raye, D'Esposito, & Johnson, 2007; Raye, Johnson, Mitchell, Greene, & Johnson, 2007; Gonsalves et al., 2004). In contrast, older, but not young, adults showed refresh-related activity in left middle temporal gyrus, an area associated with activating long-term semantic information (Badre et al., 2005). This pattern suggests that refreshing involved relatively more

top–down modulation of visual information for young adults and of semantic information for older adults. Studies controlling the nature of the representation refreshed (e.g., semantic vs. perceptual feature) would help clarify whether age-related differences reflect differences in the features participants focus on or differential availability of different types of representations.

Acknowledgments

Notes

1. There were also several filler trials intermixed, including some degraded items. These fillers are not relevant to the present report and are not discussed.
2. When refresh RTs were expressed relative to read RTs ([Refresh − Read]/Read), there was a significant interaction between age and number [$F(1, 46) = 4.01$, $MSE = 0.01$, $p < .05$]: for young adults, the proportion increase in refresh RTs was greater in three-item (0.20) than one-item (0.13) trials, whereas for older adults, three-item (0.21) and one-item (0.23) conditions did not differ. This lack of a significant effect of number in proportion scores for the older adults reflects the fact that the response times in the read-3 condition increased relative to the read-1 condition more for older than for young adults. This pattern converges with the main analysis to suggest that older adults experienced more competition than young adults in the read condition.
3. These same young adults were previously reported in Johnson et al. (2005), Experiment 5.
4. Due to a clerical error, the WAIS score was missing for one older adult.

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