

Research Article

An Age-Related Deficit in Prefrontal Cortical Function Associated With Refreshing Information

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ABSTRACT—Older adults are slower than young adults to think of an item they just saw, that is, to engage or execute (or both) the simple reflective operation of refreshing just-activated information. In addition, they derive less long-term memory benefit from refreshing information. Using functional magnetic resonance imaging (fMRI), we found that relative to young adults, older adults showed reduced refresh-related activity in an area of dorsolateral prefrontal cortex (left middle frontal gyrus, Brodmann's Area 9), but not in other refresh-related areas. This provides strong evidence that a frontal component of the circuit that subserves this basic cognitive process is especially vulnerable to aging. Such a refresh deficit could contribute to poorer performance of older than young adults on a wide range of cognitive tasks.

Older adults typically perform more poorly than young adults on memory tests, particularly in situations in which they are intentionally trying to remember information and few cues are provided (Balota, Dolan, & Duchek, 2000; Craik & Jennings, 1992; Grady, 2000; Light, 1991). Age differences in performance are sometimes reduced when the experimenter specifies the cognitive operations that participants should perform at encoding or provides additional cues for remembering (Craik, 1986; Multhaup, 1995). Even so, age-related deficits in performance often persist (Johnson, Reeder, Raye, & Mitchell, 2002). Collectively, such findings suggest that aging is associated both with a decrease in the spontaneous recruitment of appropriate cognitive processes and with a loss of efficacy in some of these processes (Craik, 1986; Hasher & Zacks, 1979, 1988; Salthouse, 1996).

Studies of the potential neural correlates of age-related differences in cognition and memory have found positive correlations between older

adults' memory performance and their performance on standard neuropsychological tasks that are sensitive to frontal functions (Craik, Morris, Morris, & Loewen, 1990; Glisky, Polster, & Routhieaux, 1995; Henkel, Johnson, & De Leonardis, 1998; Moscovitch & Winocur, 1995). These findings, together with evidence of increased likelihood of neuropathology in prefrontal cortex (PFC) with age (Grady, 2000; Gunning-Dixon & Raz, 2000; O'Sullivan et al., 2001; Raz, 2000; West, 1996), strongly suggest that some age-related memory deficits are a consequence of changes in frontal cortex. Recent studies of cognitive changes with age using functional neuroimaging techniques have tended to show two types of findings (Cabeza, 2001a, 2001b; Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady, 2000; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Park, Polk, Mikels, Taylor, & Marshuetz, 2001; Reuter-Lorenz, 2002; Reuter-Lorenz, Marshuetz, Jonides, & Smith, 2001; Stebbins et al., 2002): Sometimes older adults show less activity than young adults, for example, in frontal regions associated with semantic processing (left Brodmann's Area, BA, 45/47), and sometimes they show relatively more activity than young adults in other regions, especially in regions contralateral to those found to be activated in young adults. This second finding suggests that less selectivity in recruitment of brain areas may be a characteristic of age-related dysfunction, or that compensatory recruitment of brain areas occurs as a positive coping response to dysfunction.

In short, it is clear that there are age-related deficits in memory performance and that there are age-related differences in brain activation patterns, including in frontal cortex. However, distinguishing between age-related changes in particular cognitive processes versus age-related changes in which processes are engaged remains a major challenge. That is, in any given situation, do older adults engage the same processes as young adults, but less efficiently? Do they engage different, or additional, processes? Or might all of these possibilities be true under different conditions? The more complex the cognitive task, the more difficult it is to distinguish among these alternatives.

We recently reported a study (Johnson et al., 2002) using a paradigm intended to engage a simple, basic cognitive function—*refreshing*

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just-activated information (Johnson, 1992). Healthy young adults and older adults read words aloud as they were presented one at a time at a 2.5-s rate on a computer screen. Sometimes a word was the same as the previous word (a *repeat* item), and sometimes a dot (●) was presented, signaling the participant to think of the last word presented and say it aloud again (a *refresh* item). Verbal response times were compared for items presented once (*read* items), repeat items, and refresh items. Participants were told (correctly) that we were interested in the time to read words and the time to think of words. This is an easy task, and young and older adults did not differ in accuracy. Compared with young adults, older adults showed the same facilitation in response times for repeated words, but they were disproportionately slower in saying the previous word on refresh trials. Furthermore, young, but not older, adults showed a long-term recognition memory benefit for refreshed items relative to single-presentation items.

A parallel event-related functional magnetic resonance imaging (fMRI) study of young adults (Raye, Johnson, Mitchell, Reeder, & Greene, 2002) used a similar paradigm but without the verbal response: Participants simply read the words silently on read and repeat trials, and on refresh trials they were cued with a dot to think of the just-previous word. Activity in an area of left middle frontal gyrus (GFm), BA 9, was significantly greater on refresh than repeat and read trials (i.e., this area showed refresh-related activation). Furthermore, activation was greater in left BA 9 for items that were subsequently recognized than for items that were subsequently missed on a long-term recognition test. Control experiments ruled out the possibility that left BA 9 activation was prompted by task switching, responding to a symbolic cue, or thinking any thought in response to a cue.

Given that there is cognitive-behavioral evidence of a refresh deficit associated with aging, and that a frontal region associated with refreshing has been identified in young adults, we predicted that older adults would show less refresh-related activation than young adults in that region (i.e., left GFm, BA 9). The present study was a test of this hypothesis.

Whether older adults show greater activity than young adults in other regions on refresh trials was also of interest. As already noted, it has been suggested that activity in additional regions in older adults reflects either a loss of selectivity in brain function or the engagement of compensatory cognitive processes (e.g., Cabeza et al., 2002; Reuter-Lorenz, 2002). Because the refresh paradigm is relatively unlikely to induce compensatory cognitive operations, activity in other regions in older adults would tend to support a loss-of-selectivity hypothesis. However, if older adults show less activation in regions engaged by young adults, and no areas of greater activation, the results would support a loss-of-efficiency hypothesis and provide strong converging evidence about the neural substrates of the refresh process.

METHOD

Participants

Participants were healthy, right-handed young ($n = 7$, 4 females; $M = 19.6$ years) and older ($n = 7$, 4 females; $M = 65.3$ years) adults. Data from 2 additional participants, 1 in each age group, were excluded because of excessive head movement. Young participants were students from Yale University (mean education = 13.9 years), and older participants were recruited from New Haven, Connecticut, and surrounding communities (mean education = 16.1 years). All participants reported being in good health, with no history of strokes, heart disease, or primary degenerative neurological disorders; none were taking psychotropic medications. The older adults scored high on the Folstein Mini-Mental State Examination ($M = 29.7$, maximum possible = 30; Folstein, Folstein, & McHugh, 1975), and there were no differences between the groups on a modified version of the verbal subtest of the Wechsler Adult Intelligence Scale–Revised (maximum possible = 30, $M_{\text{young}} = 22.8$, $M_{\text{older}} = 24.0$, $p > .50$; Wechsler, 1981). All participants were paid. The Human Investigation Committee of Yale University Medical School approved the protocol; informed consent was obtained from all participants.

Task Design

During scanning, stimuli were projected onto a screen at the foot of the scanner, which participants viewed through a mirror mounted on the head coil. Each trial was 12 s (see Fig. 1). Participants silently read a word (1,450 ms); 550 ms later, the word was followed by a repetition of the word (*repeat* trial), a new word (*read* trial), or a dot (●) that signaled participants to think of the word that preceded the dot (*refresh* trial; Raye et al., 2002). In each case, the second stimulus was presented for 1,450 ms. The second stimulus was followed 550 ms later by a series of three arrows (each on the screen for 1,400 ms and followed by a blank screen for 600 ms) and then a final blank screen (2,000 ms). Participants were told that whenever they saw a word on the screen, they were to read it silently to themselves, and when they saw a black dot, they were to think of the just-previous word. They were told that when they saw an arrow, they should push a button with their left hand if the arrow pointed left and with their right hand if it pointed right. The arrows provided an 8-s task common to all conditions to allow time for the hemodynamic response associated with reading or refreshing words, and to decrease variability among participants due to uncontrolled mental activity between trials.

Words were chosen from a pool of 160 common one- to three-syllable words (e.g., *chime*, *proposal*, *toad*). There were four runs of 30 trials each (10 per condition). In each run, read, repeat, and refresh trials were pseudorandomly intermixed, with different orders for participants within age groups and parallel orders between age groups.

Word	Delay	Same Word, New Word, or ●		<		>		>		Blank Screen
1,450 ms	550	1,450	550	1,400	600	1,400	600	1,400	600	2,000

Fig. 1. Sequence and timing (in milliseconds) of the events in a trial.

Across participants, each word occurred in each of the three conditions. About 14 min after participants exited the scanner, there was a surprise old/new recognition test consisting of 108 old words (36 from each condition) and 108 new words intermixed in a pseudorandom order. Each test word was presented for 2 s, with 1 s between words. Participants indicated with a button press whether each item was old or new.

Imaging Details

T1-weighted anatomical images were acquired for each participant using a 1.5-T SIGNA scanner (GE Medical Systems) at the Yale University School of Medicine. Functional scans were acquired with a single-shot echoplanar gradient-echo pulse sequence (TR = 2,000 ms, TE = 35 ms, flip angle = 80°, field of view = 24 cm). The 24 axial slices (resolution of 3.75 × 3.75 mm in plane, 3.8 mm between planes) were aligned with the anterior commissure-posterior commissure line. Each run began with 12 s of blank screen to allow tissue to reach steady-state magnetization and was followed by a 1-min rest interval. For each person, 240 volumes of data, 1 volume every 2 s (6 full brain scans for each trial), were collected in each condition.

fMRI Analyses

After reconstruction, time series were shifted by sinc interpolation to correct for slice acquisition times. Data were motion-corrected using a 6-parameter automated algorithm (Automated Image Registration, AIR; Woods, Cherry, & Mazziotta, 1992). A 12-parameter AIR algorithm was used to co-register participants' images to a common (young) reference brain. Data were mean-normalized across time and participants, and spatially smoothed (three-dimensional, 8-mm full-width/half-maximum Gaussian kernel).

The data were analyzed using an analysis of variance (ANOVA) with participant as a random factor (NIS software, Laboratory for Clinical Cognitive Neuroscience, University of Pittsburgh, Pittsburgh, PA, and the Neuroscience of Cognitive Control Laboratory, Princeton University, Princeton, NJ). Age (young, older), run (1–4), condition (read, repeat, refresh), and time within trial (Volume 1–6) were fixed factors. The hemodynamic response that indexes brain activity in fMRI responds slowly, rising to a peak 4 to 6 s after the critical event. Thus, we expected the fMRI signal as a function of experimental condition to peak 8 to 10 s into each trial (Volumes 4 and 5).

To identify potential age differences, we focused on Age × Condition interactions rather than main effects of age (Buckner, Snyder, Sanders, Raichle, & Morris, 2000; Mitchell, Johnson, Raye, & D'Esposito, 2000). As noted by Logan et al. (2002), significant Age × Condition interactions are evidence against alternative interpretations of group differences in terms of global age differences in properties of the hemodynamic response (e.g., D'Esposito, Zarahn, Aguirre, & Rypma, 1999). We identified brain regions in the Age × Condition × Time interaction that had a minimum of six spatially contiguous voxels each significant at $p < .01$ (Forman et al., 1995). We were also interested in examining brain regions in which refresh-related activity did not differ between the groups; these regions were identified by the Condition × Time interaction (minimum of six contiguous voxels each significant at $p < .001$). The resultant F maps were transformed to Talairach space using AFNI (Cox, 1996), and areas of activation were localized using Talairach Daemon software (Lancaster, Summerlin, Rainey, Freitas, & Fox, 1998), as well as

manually checked with the Talairach and Tournoux (1988) and Mai, Assheuer, and Paxinos (1997) atlases. Reported Talairach coordinates represent the local maximum for a region of activation.

Finally, for brain regions identified in the Age × Condition × Time and Condition × Time interactions, we conducted additional ANOVAs of the fMRI data that included subsequent accuracy on the long-term recognition test as a factor. Following our previous study (Raye et al., 2002), we analyzed those responses that were classified as fast hits (for each participant, responses faster than the mean of that individual's response times for "yes" responses to old items) or misses ("no" responses to old items). For each region of interest identified in the fMRI analyses, the mean of the percent signal change (i.e., change from Time 1) was submitted to a 2 (age) × 3 (condition) × 2 (fast hits vs. misses) ANOVA. Fast hits rather than total hits were used to minimize the impact of guessing, on the assumption that fast hits were likely to be the more confident responses to old items (e.g., see Wagner et al., 1998). This analysis examining long-term recognition accuracy provided information about which brain activations at encoding were associated with successful recognition of old items on the later memory test (Raye et al., 2002; Wagner et al., 1998).

RESULTS

Behavioral Results

Figure 2 shows corrected recognition scores (hits minus false positives). This group of older adults performed somewhat better overall than those in our previous study (Johnson et al., 2002), perhaps because they were, on average, younger ($M = 65$ years vs. 74 years), and the younger adults performed somewhat worse. In an ANOVA with age and condition as factors, there was a main effect of condition, $F(2, 24) = 9.66$, $p < .001$, and the Age × Condition interaction was not significant. However, using the read condition for each group as the baseline, planned comparisons conducted separately on each group indicated that young adults' old/new recognition was better for words that had been repeated than words that had been read once, $t(6) = 2.50$, $p < .05$, and better for words that had been refreshed than for words that had been read once, $t(6) = 3.76$, $p < .01$. Neither of these comparisons was significant for older adults ($ps > .10$). The same pattern was found for d' scores. These behavioral findings replicate those we reported previously (Johnson et al., 2002) with an n of 27 for each age group.¹

¹Our primary interest here was in investigating the process of refreshing. Clearly, there are potential memorial effects of perceptual repetition as well. Benefits from an immediate second presentation of a stimulus might arise for at least two reasons. First, compared with a single presentation, two presentations should result in a richer or more enduring perceptual representation that better supports a match at test. Second, a subsequent presentation provides an additional opportunity for reflective processes to be engaged (e.g., a chance to refresh the information, or to note that the item was repeated or that it was related to another item). This additional reflective processing should be beneficial for long-term memory (e.g., Johnson, 1992). Thus, the fact that older adults did not show a significant benefit on repeat items in long-term memory suggests either (or both) that (a) a second immediate presentation had less effect on perceptual representations for older than young adults or (b) a second presentation was less likely to result in spontaneous reflective activity for older than young adults. Our previous finding (Johnson et al., 2002) that older adults showed as much benefit as young adults from an immediate repetition on a subsequent perceptual identification test suggests that the first alternative is incorrect (although, of course, the perceptual representations resulting in perceptual priming are not necessarily the same perceptual representations that support recognition; e.g., Johnson, 1992).

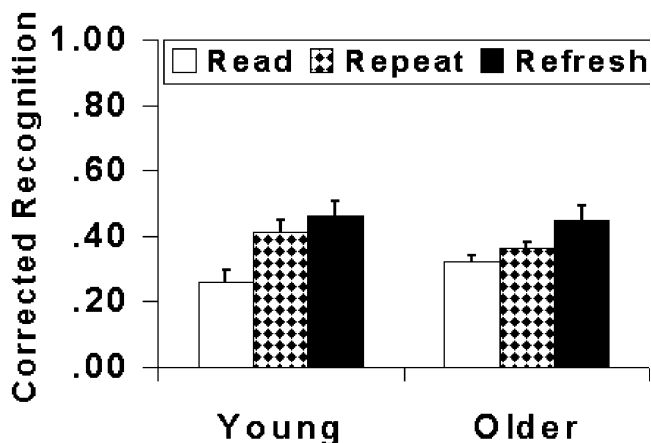


Fig. 2. Mean corrected recognition scores (proportion of hits minus proportion of false positives) on read, repeat, and refresh trials. Results are shown separately for the two age groups. Bars indicate standard error of the mean.

fMRI Results

As predicted, a region of left GFm in BA 9 showed an Age \times Condition \times Time interaction. As indicated by the time lines in Figure 3, this region showed clear refresh-related activity in young, but not older, adults. Furthermore, it is striking that the local maximum of this region was less than two voxels from the refresh-related, left-GFm maximum we identified in our earlier study (Raye et al., 2002) using a different scanner and an independent group of young adults. There were no regions showing greater refresh-related activity in older than young adults.² An additional ANOVA including subsequent long-term recognition accuracy as a factor (fast hits vs. misses) was conducted on the fMRI data from the region shown in Figure 3. The Age \times Condition \times Accuracy interaction was not significant. However, when each group was analyzed separately, for young adults, activation in this area was greater for items subsequently recognized than those missed, $F(1, 6) = 4.71$, $p < .07$, consistent with our earlier findings for young adults (Raye et al., 2002). For older adults, there was no significant difference relating activity in this region to long-term recognition accuracy ($F < 1$).

Although we found an expected age-related deficit in left-PFC activation, older adults are, in fact, able to perform the refresh task (Johnson et al., 2002). Thus, we also expected to find some evidence of refresh-related activity for older adults in PFC. As shown in Figure 4, in the original analysis there were three areas of left GFm identified as showing Condition \times Time interactions that did not significantly interact with age. Two were anterior and inferior and one was posterior to the left-GFm region shown in Figure 3 (the regions labeled A and B in Fig. 4 overlapped with the region reported in Raye et al., 2002).

For region B in Figure 4, the analysis contrasting items that were later fast hits or misses on the recognition test showed an Age \times Condition \times Accuracy interaction, $F(2, 24) = 7.70$, $p < .003$. For young adults, activity in this region was greater on refresh than read

²Only one other brain region (in right BA 6) showed a three-way interaction, but the activity for this region did not show refresh-related activity in either group.

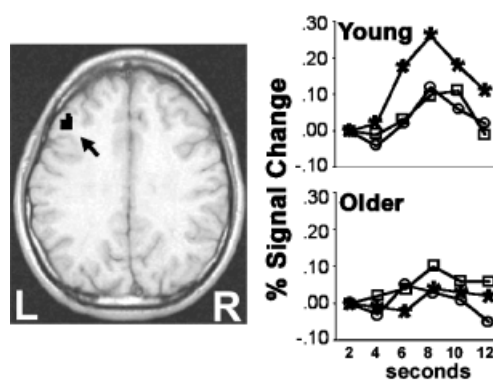


Fig. 3. Prefrontal region (left middle frontal gyrus, Brodmann's Area 9) showing an Age \times Condition \times Time interaction and corresponding time courses for young and older adults (Talairach coordinates: $x = -40$, $y = 28$, $z = 31$, maximum $F = -3.17$). Note that group-average F maps are overlaid onto a single young-adult reference brain; the left side of the image corresponds to the left side of the brain. For the time courses, the x -axis represents time within a trial (Seconds 2, 4, 6, 8, 10, and 12, corresponding to Volumes 1–6); the y -axis represents percentage change from Time 1. Asterisks show results for refresh trials, circles show results for repeat trials, and squares show results for read trials.

($p < .001$) or repeat ($p < .008$) trials for items subsequently recognized, but there were no differences among conditions for items subsequently missed. For older adults, there were no differences related to accuracy in this region. There was also an Age \times Condition \times Accuracy interaction for the more anterior left-GFm region in Figure 4 (A), $F(2, 24) = 3.70$, $p < .04$. In this case, for older adults, activity in this region was greater on refresh than read ($p < .005$) and repeat ($p < .001$) trials for remembered items, and there were no differences among conditions for items subsequently missed. For young adults, there were no differences related to accuracy in this region. There were no differences in either age group related to accuracy in region C in Figure 4.³

Firm conclusions about age-related changes in the exact frontal topography of refresh-related processing require replication and extension (e.g., studies on refreshing information other than words; e.g., Johnson, Raye, Mitchell, Greene, & Anderson, 2003). Nevertheless, it is apparent that activity in left GFm was associated with refreshing just-activated verbal information, that activity in this region was associated with long-term memory, and that older adults showed reduced activity in this region (Fig. 3).

Other areas showing refresh-related activity that did not interact with age (Condition \times Time) were as follows: left parietal cortex, BA 40,7 ($x = -34$, $y = -57$, $z = 48$); left middle temporal gyrus, BA 37 ($x = -60$, $y = -49$, $z = -6$); right middle temporal gyrus, BA 21,22 ($x = 65$, $y = -40$, $z = -1$); left superior temporal gyrus/inferior frontal gyrus, BA 38,22,47,45 ($x = -48$, $y = 14$, $z = -8$); right superior temporal gyrus/inferior temporal gyrus, BA 38/22/47 ($x = 54$, $y = 17$, $z = -8$); and a region including anterior cingulate cortex, BA

³It is interesting that Rypma, Prabhakaran, Desmond, and Gabrieli (2001) found greater activity in older than younger adults in a left BA 10 area ($x = -25$, $y = 52$, $z = 16$) near, but more medial than, the area we have identified as area A in Figure 4 ($x = -34$, $y = 50$, $z = 14$) and suggested that this activity might reflect age-related compensatory activity in the Sternberg working memory task that they investigated. One possibility is that this hypothesized compensatory activity was *refreshing*.

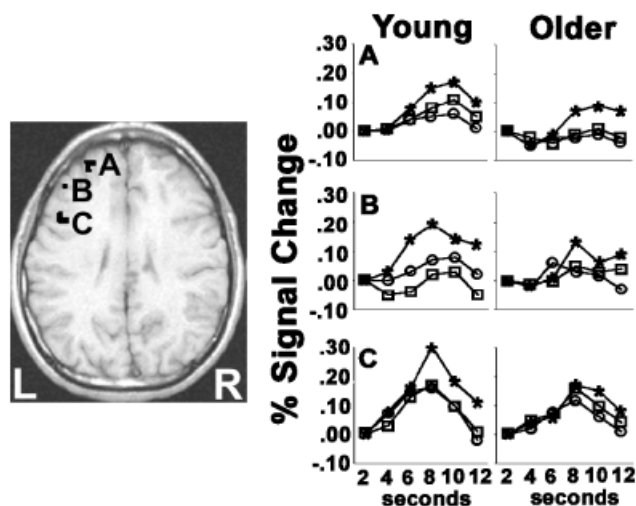


Fig. 4. Prefrontal regions showing a Condition \times Time interaction and corresponding time courses for young and older adults. An axial slice at $z = 28$ was selected to show all three regions in one illustration. The following coordinates represent the local maximum for each region: A—left superior/middle frontal gyrus, Brodmann's Area (BA) 10/9 (Talairach coordinates: $x = -34$, $y = 50$, $z = 14$, maximum $F = 5.30$); B—left middle frontal gyrus, BA 9 ($x = -41$, $y = 35$, $z = 24$, maximum $F = 3.89$); C—left middle/inferior frontal gyrus, BA 9/44 ($x = -41$, $y = 13$, $z = 33$, maximum $F = 3.67$). Note that group-average F maps are overlaid onto a single young-adult reference brain; the left side of the image corresponds to the left side of the brain. For the time courses, the x -axis represents time within a trial (Seconds 2, 4, 6, 8, 10, and 12, corresponding to Volumes 1–6); the y -axis represents percentage change from Time 1. Asterisks show results for refresh trials, circles show results for repeat trials, and squares show results for read trials.

32, and BA 8 ($x = 1$, $y = 26$, $z = 40$). None of these regions showed significant accuracy-related differences.

DISCUSSION

Our goal was to identify age-related changes in activity in the brain regions engaged when people think about a word they have just seen a half second before. The present findings implicate reduced activation in left GfM as underlying the refresh deficit in older adults reported previously (Johnson et al., 2002). To what extent this deficit reflects structural changes (e.g., cell loss, loss of white matter fibers) or metabolic changes remains to be determined. There was no evidence that other refresh-related regions were more engaged by refreshing in older than young adults, nor that older adults recruited new regions for refreshing that were not engaged by young adults. Thus, the present results suggest that it is the frontal aspect of a refresh circuit that may be disrupted by aging. Furthermore, these results indicate that for this simple component process, older adults are not recruiting new areas into the cognitive network (e.g., Grady, 2000), but are using the same network less well than young adults.

In a recent study consistent with this conclusion, Stebbins et al. (2002) found no evidence for compensatory processing when attempts were made to equate the processing of young and older adults on tasks requiring judgments about verbal items. Stebbins et al. compared the difference in young and older adults between brain activity during a semantic task (is this word abstract or concrete?) and a nonsemantic

task (is this word printed in uppercase or lowercase?). The results were consistent with previous findings in that young adults showed more activity in left BA 45/47 during the semantic than the non-semantic task, but the effect was less for older than young adults. Stebbins et al. noted that this reduction was not accompanied by an increase in right-PFC activity. Both their and our results are consistent with the possibility that increased contralateral activation in older adults relative to young adults, when observed, reflects the engagement of additional or different processes, rather than “more brain” or “different brain” for the same process.

Interestingly, Logan et al. (2002) recently reported evidence suggesting that whereas underrecruitment of a brain area may develop during the sixth decade of life, compensatory (or nonselective) recruitment may not develop until the seventh or eighth decade. The mean age of our participants was 65.3 years (range = 61–69); thus, the absence of significant compensatory activation in the present study is consistent with the findings of Logan et al. However, Stebbins et al. (2002) also did not find compensatory activity, and the mean age of their participants was 76.5. Thus, the extent to which compensatory activity is specific to particular processes or age ranges remains to be clarified.

An age-related deficit in refreshing could have profound consequences for cognitive functioning. Refreshing is one of a number of general-purpose component cognitive processes that are recruited for many different tasks (Johnson, 1992). Thus, it is likely to be a component of complex cognitive activities (e.g., working memory, long-term memory encoding and remembering, comprehension, problem solving). For example, refreshing may be a mechanism by which agendas (goals and subgoals) are kept in mind, or by which potentially relevant items of information are kept active during problem solving; refreshing may help bridge gaps across phrases in comprehending language, between a thought and an opportunity to express it in conversation, or between an intention and an action. Refreshing may not only keep active or privilege the target of refreshing, but it may also increase activity in (bias, e.g., Miller & Cohen, 2001) related representations, thus influencing the direction of thoughts. The present results illustrate the promise of using neuroimaging to help identify brain mechanisms underlying component cognitive processes (Posner, Petersen, Fox, & Raichle, 1988) and the potential for clarifying the nature of cognitive deficits associated with aging.

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