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The Implications of Cortical Recruitment and Brain Morphology for Individual Differences in Inhibitory Function in Aging Humans

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The authors assessed individual differences in cortical recruitment, brain morphology, and inhibitory task performance. Similar to previous studies, older adults tended toward bilateral activity during task performance more than younger adults. However, better performing older adults showed less bilateral activity than poorer performers, contrary to the idea that additional activity is universally compensatory. A review of the results and of extant literature suggests that compensatory activity in prefrontal cortex may only be effective if the additional cortical processors brought to bear on the task can play a complementary role in task performance. Morphological analyses revealed that frontal white matter tracts differed as a function of performance in older adults, suggesting that hemispheric connectivity might impact both patterns of recruitment and cognitive performance.

Keywords: aging, attention, neuroimaging, inhibition, executive control

Advancing age has a number of deleterious effects on human brain structure and function. Older adults, on average, tend to show decreased efficacy on encoding and retrieval of information, choice reaction time (RT), inhibitory processing, and a broad range of cognitive tasks (see Park, Polk, Mikels, Taylor, & Marshuetz, 2001, for review). Declines in cognition tend to be greatest on executive control tasks, such as inhibitory functioning, scheduling, planning, task switching, and so forth, which are thought to be largely subserved by the frontal lobes of the brain (e.g., West, 1995). Perhaps not surprisingly, age-related decline in brain volume of aging humans is often disproportionately large in the frontal and prefrontal regions of cortex (see Raz, 2000; Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003). These observations are consistent with theories of cognitive aging that focus on frontal and prefrontal cortical decline as the major source of age-related disruptions in cognitive performance (see Kramer, Humphrey, Larish, Logan, & Strayer, 1994; Moscovich & Winocur, 1995; West, 1995).

However, in both human and nonhuman subjects, there is a great deal of intracohort variability in task performance; some older individuals show performance that is in the range of normal younger individuals, and others of the same cohort fall entirely out of the range of normal younger adults, even in the absence of obvious pathology (e.g., Gallagher, Burwell, & Burchinal, 1993; Morse, 1993). What, in terms of cortical recruitment and underlying brain structure, is it that allows some individuals to maintain a relatively high level of cognitive performance, whereas others fall substantially behind? Several recent studies have made progress in identifying structural and functional correlates of aging and individual differences in cognitive performance. However, an understanding of the consequences of changes in cortical recruitment patterns or morphological changes associated with aging is far from complete, and the implications of even the most basic observations in this area remain debated. In an attempt to move toward a clearer understanding of these issues, we present the results of an integrated analysis of the apparent impact of patterns of cortical recruitment and differences in brain structure on cognitive performance within an older adult cohort. After comparing and contrasting our findings with those from source memory (e.g., Cabeza, Anderson, Locantore, & McIntosh, 2002) and working memory (e.g., Reuter-Lorenz et al., 2001, 2000) paradigms, we suggest, in contrast to notions of cortical reorganization and functional dedifferentiation, that compensatory activity in prefrontal cortex (PFC) is only likely to be effective if the additional cortical processors brought to bear on the task are known to play a complementary role in task performance and that an evaluation of both function and structure in relation to performance in aging individuals will likely be fruitful.

Aging and Functional Neuroimaging

Perhaps the most common observation in neuroimaging studies of aging is that older adults tend to recruit not only similar regions of cortex as younger adults but also additional regions of cortex, often in the contralateral (opposite) hemisphere. For example, although younger adults tend to recruit the left PFC during encoding tasks, older adults often show additional recruitment in the similar regions of the right hemisphere (Anderson et al., 2000; Backman et al., 1997; Logan, Sanders, Snyder, Morris, & Buckner, 2002; see Cabeza, 2001, 2002; Cabeza et al., 2002, for reviews of similar findings in working memory and inhibitory tasks). Cabeza

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(2002) formalized this general observation as hemispheric asymmetry reduction in older adults (HAROLD).

Some authors have suggested that the HAROLD pattern of cortical activity reflects compensation for age-related losses in neuronal function, in which older adults utilize nonstandard regions of cortex to assist less efficient regions of cortex, much in the same way that stroke or lesion patients are able to compensate for specific structural damage in one hemisphere by recruiting similar regions in the contralateral hemisphere. This possibility was initially suggested by Reuter-Lorenz et al. (Reuter-Lorenz et al., 2000; Reuter-Lorenz, Stanczak, & Miller, 1999) and has been subsequently elaborated on by others (e.g., Cabeza, 2001, 2002; Cabeza et al., 2002; Dolcos, Rice, & Cabeza, 2002). For example, Cabeza et al. (2002) found that older adults who performed well on a source memory task (in which they were required to identify whether stimuli were presented in a visual or auditory mode) demonstrated a great deal of recruitment in both the left and right anterior prefrontal regions. However, both younger adults and poor-performing older adults demonstrated selective activity only in the right anterior prefrontal cortex in response to source memory demands. This, they argue, suggests that good performers were able to compensate for age-related losses in neural processing by a sort of "plastic reorganization of neurocognitive networks" (p. 1394) in response to aging-related cortical deficiencies, similar to the atypical recruitment seen in stroke or lesion patients, in which a region in the contralateral hemisphere subsumes the functionality of the damaged region (e.g., Brion, Demeurisse, & Capon, 1989; Buckner, Corbetta, Schatz, Raichle, & Petersen, 1996; Oyahama et al., 1996). Cabeza et al. also argued that the additional recruitment seen in the good-performing older adult might reflect invocation of additional control processes in memory rather than a melding of the functionality of one hemisphere into the other. Much like Cabeza et al. (2002), Reuter-Lorenz et al. (2000) found that older adults performing a verbal working memory task showed left PFC activation (as did the young) as well as additional recruitment in the right PFC. This right-lateralized activity was associated with faster responding in older adults, suggesting that the additional recruitment was beneficial for task performance in older participants. Subsequent studies have suggested that this additional right hemisphere recruitment could serve to compensate for reduced verbal control activity in the left hemisphere (see Jonides, Marshuetz, Smith, Reuter-Lorenz, & Koppe, 2000; Reuter-Lorenz et al., 2001). Such findings are consistent with the idea that the additional recruitment of these cortical areas was compensatory in nature for older adults.

Others have suggested that the recruitment of additional cortical areas is a marker of decline, unrelated to cognitive task performance, or even a detrimental outcome of declining integrity in the white matter structures that connect the frontal hemispheres or of reduced neurotransmitter levels (Li & Lindenberg, 1999; Logan et al., 2002; O'Sullivan et al., 2001). Along these lines, Logan et al. (2002) also observed a high degree of bilateral recruitment in older adults performing an encoding task. However, they found that encouraging a deeper encoding strategy in older adults improved task performance and increased activity in the standard regions but had no effect on the nonstandard regions of cortex recruited during task performance. Thus, they argue, the contralateral recruitment seen in older adults likely reflects an inability to efficiently select cortical processors appropriate for the task at hand, perhaps owing to a basic communication failure between the frontal lobes of the brain (see Logan et al., 2002). Further, Nielson, Langenecker, and Garavan (2002) found that both young and older adults showed significant activation of the right PFC during a go/no-go task, and older adults showed additional recruitment in the left PFC. However, in contrast to the source memory and verbal working memory data reviewed previously, the additional activation exhibited by older adults was negatively correlated with task performance (see also Langenecker & Nielson, 2003, for a replication of these findings). Using the same logic applied to findings from verbal and source memory paradigms, this suggests that the additional left hemisphere recruitment was detrimental to inhibitory task performance in older adults. However, to avoid misrepresenting the position of Nielson et al., it should be noted that the authors argued that, despite the apparent conflict with the patterns of data in working and source memory paradigms, the additional recruitment seen in their poor-performing older adults was still compensatory in nature, given that the participants who performed most poorly needed this additional activation to perform the task.

Aging and Structural Neuroimaging

In vivo studies of the aging human brain have revealed that cortical volume decreases with age and more so in the frontal and prefrontal regions than in motor or visual areas (Raz, 2000; Resnick et al., 2003). Moreover, several studies have linked morphological features of the aged brain, such as reduced gray matter volume or white matter integrity with cognitive performance in aged individuals. For example, Gunning-Dixon and Raz (2003), using a hand-tracing technique with high-resolution magnetic resonance imaging (MRI) scans, found that both lower prefrontal gray matter volume and greater levels of prefrontal white matter lesions (white matter hyperintensities) were related to poorer performance in the Wisconsin Card Sorting Task and a composite of working memory performance. Similarly, O'Sullivan et al. (2001), using a technique that yields measures of white matter structural integrity (diffusion tensor imaging), found that the anterior white matter tracts (a) declined with age and (b) were correlated with behavioral performance on a task of executive control (Trails B) within the older cohort. Such findings are highly consistent with studies that suggest that late-myelinating structures may be more susceptible to age-related decline (e.g., Bartzokis et al., 2004), indicating that at least some portion of age-related decline in executive functioning might be related to gray matter volumetric decline as well as impaired interhemispheric communication.

Aging, Morphological Changes, Functional Recruitment, and Cognitive Performance

Given the well-known relationship between advancing age and morphological changes in the brain (e.g., Raz, 2000; Resnick et al., 2003), as well as the impact of these factors on cognitive performance (Gunning-Dixon & Raz, 2003; O'Sullivan et al., 2001; Raz, 2000), it is not surprising that changes in brain structure are also cited as a potential cause of age-related changes in patterns of cortical recruitment associated with aging (e.g., Cabeza et al., 2002; Dolcos et al., 2002; Logan et al., 2002; Reuter-Lorenz et al.,

1999, 2000). Indeed, as mentioned previously, some have argued that the recruitment of additional cortical areas results from declines in specific cortical processing units and that additional recruitment in areas of the contralateral hemisphere is invoked to facilitate these processes (see Cabeza et al., 2002; Dolcos et al., 2002). Similarly, notions of detrimental nonselective recruitment have made reference to age-related declines in anterior white matter, in which reduced white matter integrity results in impaired interhemispheric communication and a failure to select appropriate cortical processors, which in turn leads to impaired cognition (e.g., O'Sullivan et al., 2001) and additional cortical recruitment (Logan et al., 2002). Clearly, a full understanding of the impact of aging on neurocognition will go far beyond issues of brain structure and cortical recruitment, likely including assessments of genotypic variability and neurotransmitter levels as well as measures of general health, to name a few. However, to our knowledge, no studies have concurrently examined the effects of brain structure, cortical recruitment, and cognitive performance of participants within an aged cohort.

In this article, we focus on the relationship between individual differences in performance of one subset of executive functions (inhibitory processing), levels of cortical recruitment, and brain structure within the frontal lobes. We used an inhibitory task as our main behavioral outcome measure in older and younger adults for two primary reasons. First, deterioration in inhibitory processes is thought to play a central role in age-related losses in many cognitive functions. Age-related declines in inhibition are implicated in declines in memory (e.g., Hasher & Zacks, 1988; Persad, Abeles, Zacks, & Denburg, 2002), task set shifting (Kramer, Hahn & Gopher, 1999; Kray, Li, & Lindenberger, 2002), and increased semantic interference (Stroop; Houx, Jolles, & Vreling, 1993; Panek, Rush, & Slade, 1984). Inhibitory processes are also largely thought to be instantiated in the prefrontal cortices, which, in light of their disproportionate deterioration in aged individuals, have figured prominently in theories of cognitive aging (Kramer et al., 1994; Moscovich & Winocur, 1995; West, 1995). Second, despite the traditional import assigned to inhibitory functioning in cognitive aging, relatively few neuroimaging studies of older adults have focused on tasks of inhibitory functioning per se but rather have tended to rely on tasks of episodic (e.g., Backman et al., 1997; Madden et al., 1999) working memory (e.g., Reuter-Lorenz et al., 2000; Rypma & D'Esposito, 2001). See Park et al. (2001) and Cabeza (2001, 2002) for reviews. Moreover, in those neuroimaging studies that have examined inhibitory functioning in older adults (e.g., Jonides et al., 2000; Langenecker, Nielson, & Rao, 2004; Milham et al., 2002), very little has been made of the relationship between cortical recruitment and individual differences in performance during inhibitory tasks (but see Langenecker & Nielson, 2003; Nielson et al., 2002). Certainly, the effects of age on cognition are by no means unitary, and the exploration of individual differences in inhibitory functioning both within and between age cohorts seems warranted.

We asked 40 older and 20 younger adults to perform a modified version of the flanker paradigm (Botvinick, Nystrom, Fissel, Carter, & Cohen, 1999) while scanned in a slow event-related functional MRI (fMRI) protocol. Participants were asked to identify the orientation of a central arrow cue that was flanked by arrows that were in either a congruent (e.g., <<<<<) or incongruent (e.g., >><>>) orientation. To generate a correct response during incongruent trials, participants must inhibit the response indicated by the incongruent flanking cues in favor of that indicated by the central cue. We first identified regions of the frontal cortex recruited during incongruent trials in older and younger adults. We then directly compared levels of PFC recruitment in relatively well- and poor-performing older adults to identify patterns of activity associated with successful task performance.

In addition, as mentioned previously, the relationships between cortical decline, underrecruitment, contralateral cortical recruitment, and cognitive performance remain unclear. To address this issue, we examined high-resolution structural images of our participants using an optimized voxel-based morphometric (VBM) technique (see Good et al., 2001). Specifically, we assessed these images for differences between good- and poor-performing older adults in gray matter density in the regions of PFC invoked during inhibitory task performance, as identified by means of fMRI. These data allow us to examine the relationship between gray matter deterioration in our older adults, individual differences in cognitive performance, and patterns of cortical recruitment. Finally, to examine the possibility that white matter deteriorations play a significant role in inhibitory task performance and/or contralateral recruitment, we examined the density of frontal white matter tracts in our participants and related these to individual differences in inhibitory task performance within the older cohort.

Although other regions of cortex are clearly involved in attentional and inhibitory control, we limited the scope of our analyses to the frontal lobes of the brain. This was done largely for clarity of exposition and because of the traditional import that has been assigned to frontal lobe function in models of cognitive aging and implicit in many human studies of neurocognitive aging.

Method

Participants

Twenty (11 men and 9 women) younger (M = 23.5 years; range = 19–28) and 40 (22 men and 18 women) older (M = 67.5 years; range = 52–87) adults participated in this study. All participants were right-handed, healthy adults and were prescreened for neurologic disease as well as for appropriateness for testing in an MRI environment. Older participants who scored below 27 on the Mini-Mental State Examination (Folstein, Folstein, & McHugh, 1975) were excluded. All participants were administered a preliminary visual acuity screening calibrated for a viewing distance of 18 in. (45.72 cm), which matched the functional viewing distance used for presentation of task stimuli. Those whose vision was poorer than 20/30 were provided with appropriate corrective lenses to achieve visual acuity of at least 20/30. All participants provided written informed consent before participating in the study. The University of Illinois Human Subjects Board and the Carle Hospital Foundation Medical Review Committee approved all procedures related to this study. See Table 1 for the sample demographics of our older participants. Note that the cognitive demographic variables were not collected for younger adults. However, given that our primary comparisons are between good- and poor-performing older adults, this should not obfuscate the main results in any way.

Procedures

Cognitive testing and fMRI parameters. Participants performed a flanker task in which they were asked to respond to a central arrow cue

Table 1
Demographic and Psychometric Data for Older Adults, Split by Performance Group

Variable	Good (n = 20)[a]	Poor (n = 20)[b]	t[c]
Sex			—
Male	10	12	
Female	10	8	
Age (*M*)	67.56	67.37	0.08
Education (*M* years)	16.30	16.54	−0.24
K-BIT	119.50	112.44	2.49*
Digit-Span Forward	9.00	8.20	0.92
Digit-Span Backward	8.10	5.95	2.62*
Box	48.20	42.86	1.26
Digit–Symbol	48.20	39.27	1.46

Note. Asterisks denote variables that are significantly different for good and poor performers at $p < .05$. K-BIT = the composite score on the Kaufman Brief Intelligence Test (Kaufman & Kaufman, 1990); Digit-Span Forward = the number of random digits that each individual could retain and repeat in the order in which they were presented (e.g., "1,2,3,4" required the response "1,2,3,4"); Digit-Span Backward = the number of digits that each individual could retain and repeat in the reverse order of which they were presented (e.g., "1,2,3,4" required the response "4,3,2,1") and is thought to tap aspects of working memory related to the online manipulation of information. Box and Digit–Symbol are standard measures of basic psychomotor speed.
[a] Data for those older adults who showed relatively good inhibitory functioning on the flanker task. [b] Data for older adults who showed relatively poor inhibitory function on the flanker task. [c] Results of a two-tailed Student's t test comparing the good and poor performers on the variables in each row.

embedded in an array of five arrows that pointed to either the left or the right. In half of the trials, the flanking arrows point in the same direction as the central cue (e.g., <<<<<), and in the other half the flanking arrows point in the opposite direction (e.g., >>><>). Participants held a four-button response pad during the task and were asked to press the leftmost button with their left thumb if the central arrow pointed to the left and the rightmost button with their right thumb if the central arrow pointed to the right. Each participant was given a practice block of 20 trials, in which stimuli were presented for 2 s with an interstimulus interval (ISI) of 5 s. Participants were required to achieve a minimum accuracy rate of 80% in the practice block before proceeding. Those who did not reach criterion during the first practice block repeated the practice block until criterion was reached. All but 2 participants reached criterion in the first practice block; the 2 participants who failed to meet criterion in the first block reached criterion in the second practice block.

Each participant subsequently underwent six successive 5-min blocks in which they were presented with 17 trials, during which stimuli were presented for 2 s, with a fixed 14-s ISI, during which they viewed a fixation cross. All responses were required to be made during the 2-s stimulus presentation interval. Trials were first-order counterbalanced such that congruent and incongruent trials followed each other equally often. To achieve the first-order counterbalancing, the blocks were constructed with an initial dummy trial that was either congruent or incongruent followed by eight congruent and eight incongruent trials. The initial dummy trial was discarded from analyses and modeled separately from other trials in the fMRI data. The type of dummy trial presented was counterbalanced such that an equal number of each trial type was presented across the six blocks for each participant. While performing the task, participants were scanned with an echo planar imaging (EPI) protocol (20 slices, 5-mm thick, 3.75 × 3.75 mm in-plane resolution, flip angle = 90, TR = 2,000 ms) in a 1.5 Tesla GE Signa clinical magnetic resonance imager.

Behavioral analyses. The primary behavioral outcome was computed as the percent increase in RT to incongruent stimuli over and above the average RT to congruent stimuli ([(incongruent – congruent)/congruent] * 100). The percent increase measure was derived to reflect interference unbiased by differences in base RT. Only correct responses were included in the outcome measure. We performed a median split based on the percent increase measure to identify relatively good- and poor-performing older adults in the sample, once base RT was factored out.

Functional MRI data processing and analyses. To avoid potential biases in spatial registration due to structural differences in younger and older adults (Bookstein, 2001), we initially created a study-specific template for spatial registration by (a) warping each participant's high-resolution structural scan to stereotaxic space (Montreal Neurological Institute, Montreal, Quebec, Canada), (b) creating an average of these registered images, and (c) smoothing the average image with an 8-mm (full width at half maximum [FWHM]) Gaussian kernel (see Good et al., 2001). All subsequent spatial registrations were made to this study-specific template.

Primary fMRI data analysis was conducted with a statistical parametric mapping approach under SPM99. The data for each participant were corrected for slice-time asynchrony, realigned to a common image, spatially registered to the study-specific template, and spatially smoothed with a 7-mm (FWHM) three-dimensional Gaussian kernel. The resulting time series at each voxel was modeled against an expected time series derived by convolving the onset of each event type (congruent and incongruent) with a double-gamma function, representing the expected time course of the hemodynamic response function (HRF). Given that the basic temporal and amplitude characteristics of the HRF do not change significantly with advancing age (D'Esposito, Zarahan, Aguirre, & Rypma, 1999), even into the ninth decade of life (Brodtman, Puce, Syngeniotis, Darby, & Donnan, 2003), and that in no case in our fMRI analyses did we see a lack of recruitment in our older adults (see Results section), the use of a single canonical HRF for all participants seems justified.

The resulting parameter estimates for the incongruent trials (vs. baseline) for each participant were entered into a second-level analysis, in which intersubject variability was treated as error. These parameter estimates were tested in a series of contrasts within an analysis of variance (ANOVA), in which the activation associated with young adults, older adults, and high- and low-performing older adults was identified. We initially identified regions of frontal cortex (defined as tissue anterior to the central sulcus in stereotaxic space) that were active during incongruent trials (vs. baseline), collapsing across group membership, under the null hypothesis that the groups do not differ. Regions of interest (ROI) for our

subsequent analyses were created by thresholding the resulting statistical maps with a minimum familywise error rate of $p < .05$ ($Z > 4.1$; Nichols & Hayaska, 2003) and a minimum contiguous voxel threshold of $n > 50$. In other words, to meet requirements for statistical significance in these analyses, a voxel had to reach a minimal Z score of 4.1 and be contained in a cluster that had at least 50 voxels in direct contact with each other. These regions were then used as a priori masks to guide further hypothesis-driven analyses, in which we directly compared the cortical activity of good-performing older, poor-performing older, and younger adults in a set of pairwise comparisons within our ANOVA. One set of hypothesis-driven analyses evaluated the relationship between group differences in gray matter decline, cortical recruitment, and behavioral performance within the older cohort. Specifically, we reexamined our fMRI data for differences in cortical recruitment between good- and poor-performing older adults, constrained by the ROIs identified in the initial assessments of task-related cortical activity, using a reduced threshold appropriate for ROI analyses ($p < .01$).

Assessment of brain structure. In addition to EPI images, we collected a high-resolution T1-weighted three-dimensional structural scan for each participant using a spoiled gradient sequence (240 × 240 cm field of view; 124 1.5-mm-thick slices, with a 1.3 × 1.3-mm in-plane resolution). These images were analyzed using VBM (see Good et al., 2001). For each participant, these images were initially registered into stereotaxic space, defined by the study-specific template (as discussed earlier), and then segmented into three separate three-dimensional maps representing the probability that each voxel contained cerebrospinal fluid (CSF) and gray and white matter. In short, the segmentation procedure uses a mixture model that identifies voxel intensities matching particular tissue types in the brain. On the basis of the distribution of voxel intensities in the image, the procedure then assigns a probabilistic value that each voxel, given its intensity, derived from either CSF or gray or white matter. We then smoothed these images with a 12-mm FWHM Gaussian kernel and created an average probability map for gray, white, and CSF maps for each group. These average maps were then used to seed a second-level segmentation, in which the average probability maps were used to provide a priori knowledge of the spatial distribution of each tissue type and thus refine the segmentation of structural images. See Ashburner and Friston (2000) for details on this procedure.

The images that resulted from the segmentation procedure described previously were smoothed with a 12-mm FWHM Gaussian kernel. These volumes were then compared for groupwise differences in gray and white matter density as planned contrasts within two separate one-way ANOVAs, one for gray matter and one for white matter, under SPM99. The images were analyzed in two stages. We initially examined these images for differences in gray and white matter density between age groups. In these analyses, we interrogated the frontal lobes (defined as any tissue anterior to the central sulcus in stereotaxic space) for groupwise differences in cortical density using a minimum entry criterion of $p < .01$ and a contiguous voxel threshold of $n > 50$. Clusters surviving a corrected probability threshold of $p < .01$ are reported.

In a second hypothesis-driven approach, we examined these data for differences in cortical gray matter density between good- and poor-performing older adults, constrained to those regions identified as active by older adults in the fMRI analyses. This allowed us to evaluate whether regional differences in gray matter could explain groupwise differences in either cortical recruitment (i.e., underrecruitment or contralateral recruitment) or behavioral performance. To examine the differences between white matter changes and age, another a priori ROI was created from a standard binary map of white matter tissues in stereotaxic (MNI) space, provided with the FMRIB Software Library (FMRIB, Oxford, United Kingdom). From this map, we manually removed all white matter posterior to the central sulcus and applied the remaining anterior white matter map as a mask to include all frontal white matters. Voxels falling within these ROIs were interrogated for groupwise differences in cortical density. Again, only voxels that reached a statistical threshold of $p < .01$ and were contained in a cluster that had at least 50 contiguous voxels entered the hypothesis-driven analyses. Finally, we investigated the role of structural variation in the gray and white matters in predicting task performance both between and within age groups. We regressed the mean density values from the same ROIs used in our hypothesis-driven VBM analyses against the proportional interference RT scores both across the entire sample and within the older and younger age groups separately.

Results

Behavioral Data

Flanker task performance. Errors were very low (2.2%) and did not reliably vary as a function of age or performance group, with average error rates of 2.3%, 2.5%, and 1.8% for good-performing older, poor-performing older, and younger participants, respectively. Error trials were removed from all subsequent analyses of RT and modeled separately in the neuroimaging data. Older adults were reliably slower than younger adults to respond to both congruent, $t(57) = 4.29$, $p < .001$, and incongruent, $t(57) = 4.84$, $p < .001$, trials. More important to note, they were proportionally disrupted to a greater extent by incongruent trials than were younger adults, $t(57) = 3.18$, $p < .003$. However, as can be seen in Table 2, a comparison of the good-performing and poor-performing older adults, identified by a median split of older adult data based on the proportional interference scores, shows that the better half of the older adult population performed proportionally as well as the younger adults, $t(57) < 1$, *ns*, but the poor-performing older adults are nearly twice as disrupted, $t(57) = 8.44$, $p < .001$. It is important to note that this effect results from an increased difficulty in processing the incongruent trials, because the RT to congruent trials was not reliably different for good- and poor-performing older adults, $t(57) < 1$, *ns*. In fact, across the

Table 2
Reaction Times to Congruent and Incongruent Trials by Age and Performance Groups

	Congruent		Incongruent		% Interference	
Variable	*M*	*SE*	*M*	*SE*	*M*	*SE*
Poor older	650.5	26.0	869.7	38.5	33.4	1.7
Good older	633.3	16.3	740.2	18.3	17.1	1.2
Young	530.1	18.9	624.4	22.6	17.8	1.0

Note. Mean reaction times (RTs) to congruent and incongruent stimuli, and the percentage of cost in RT to resolve an incongruent stimulus {[(incRT − conRT)/conRT]* 100}.

sample of older adults, there was no reliable correlation between RT to congruent trials and proportional interference scores (r = .16, *ns*). As such, it is clear that differences in inhibitory performance, behaviorally and in the cortical recruitment data presented later, result from a difficulty in processing incongruent items and not from a simple main effect of slowed RT.

Older adult demographic outcomes, split by performance group. When we examine the demographic variables of the older adults assigned to the good and poor performance groups, we find that they are highly similar in terms of age, sex, education, and psychomotor speed (see Table 1). The older adults in the good and poor performance groups do differ, however, on the Kaufman Brief Intelligence Test (Kaufman & Kaufman, 1990), and the Digit-Span Backward task. This is perhaps not surprising, given that working memory falls into the general category of executive tasks (Duncan & Owen, 2000), and deficits on this task are thought to reflect poor inhibitory functioning (e.g., Hasher & Zacks, 1988). However, these groups did not differ in their performance of the Digit-Span Forward task, which is a more straightforward assessment of short-term verbal memory and is less susceptible to failures of inhibitory functioning (e.g., Hamm & Hasher, 1992; Hartman & Hasher, 1991).

Cortical Recruitment

Young adults. Consistent with previous findings of inhibitory task performance in flanker (Botvinick et al., 1999) and go/no-go (Nielson et al., 2002) tasks, younger adults demonstrated robust activity in the right middle frontal gyrus (MFG) as well as bilateral activity in the anterior cingulate cortex (ACC) and supplementary motor area (SMA) in response to incongruent trials. See Figure 1a and Table 3.

Older adults. Much like younger adults, older adults demonstrated significant activity in the right MFG, bilateral ACC, and SMA. However, consistent with several previous studies, older adults also demonstrated activity in the contralateral (left) hemisphere of MFG in response to incongruent trials. More important to note, however, older adults, on average, tend to activate both left

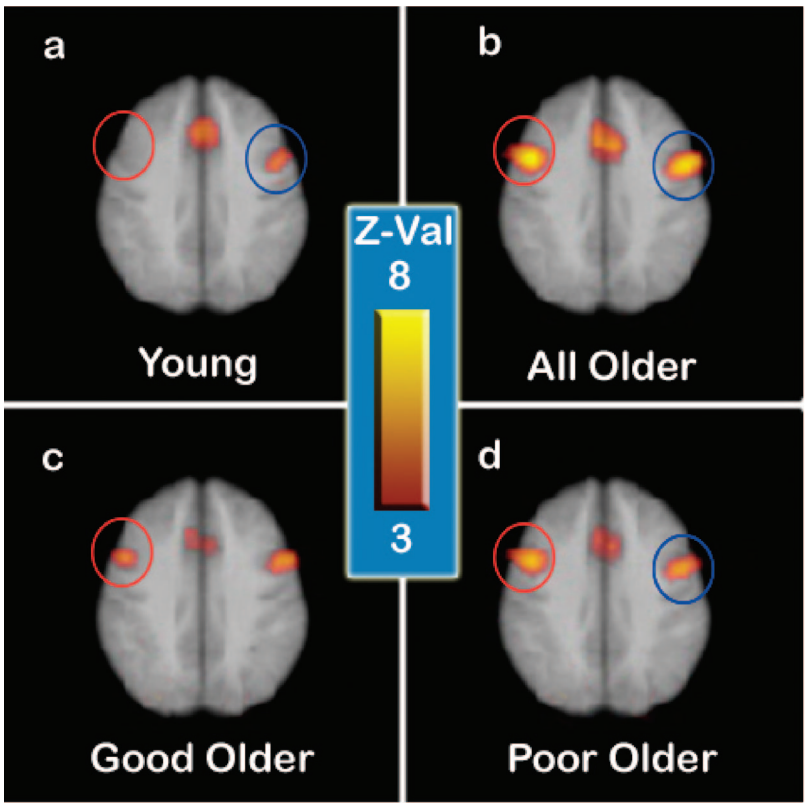

Figure 1. Regions of frontal cortex significantly activated in response to incongruent flanker trials (e.g.,<<><<), in which participants must inhibit the incorrect response indicated by the flanking cues in favor of that indicated by the central cue. Young adults (a) show right lateralized prefrontal gyrus (PFG) activity, primarily in the middle frontal gyrus (MFG), as well as bilateral medial activity in the dorsal anterior cingulate cortex (ACC) and supplementary motor area (SMA). Collapsed across performance groups, older adults (b) show significant activity in both left and right MFG as well as activity in the ACC and SMA. Both good-performing (c) and poor-performing (d) older adults show similar patterns of activity, but a direct comparison of the good- and poor-performing older adults shows that the latter exhibit significantly greater activity in the left MFG. See also Table 3. Images are presented in neurological convention and rendered with a minimum voxelwise entry of $Z > 3$ for display purposes.

Table 3
Frontal Clusters Active on Incongruent Trials for Young Adults and Good- and Poor-Performing Older Adults and Groupwise Comparisons in Activation

Group	Region	Cluster size	Peak *Z*	X (mm)	Y (mm)	Z (mm)
		Whole-brain analyses				
Young	RMFG (6/8)	391	5.53	45	6	40
	ACC/SMA (24/32)	179	5.88	4	6	45
All older	RMFG (6/8)	516	7.61	50	6	30
	LMFG (9/44)	719	7.57	−48	6	35
	ACC/SMA (24/32)	248	8.12	4	8	50
Good older	RMFG (6/8)	646	6.28	46	6	36
	LMFG (9/44)	263	5.52	−49	11	38
	ACC/SMA (32/6)	106	6.62	8	4	50
Poor older	RMFG (6/8)	349	5.28	50	6	36
	LMFG (9/44)	1,080	7.73	−50	8	30
	ACC/SMA (24/32)	157	6.73	−4	10	44
		Region of interest				
Old > young	RMFG/IFG (6/8)	258	5.26	55	8	30
	LMFG (9/44)	291	5.65	−48	7	41
	ACC/SMA (32/6)	231	4.87	4	10	50
Young > old[a] poor > good good > poor[a]	IMFG (9/44)	315	3.15	−37	10	40

Note. Prefrontal cortex recruitment to incongruent trials by age and performance group. *Z* value denotes the cluster's peak *Z* score, and the location of the peak is reported in X, Y, and Z coordinates in stereotaxic space. All clusters in the whole-brain analyses had a corrected cluster probability of $p < .0001$. All clusters in the region of interest analysis had a corrected cluster probability of $p < .005$. RMFG = right middle frontal gyrus; ACC = anterior cingulate cortex; SMA = supplementary motor area; LMFG = left middle frontal gyrus.
[a] No voxels survived threshold.

and right MFG to a significantly greater intensity than do younger adults, suggesting that (a) older adults do not demonstrate underrecruitment in right MFG during inhibitional tasks, and (b) older adults, on average, do show significantly greater contralateral activity in left MFG. See Figure 2b and Table 3.

Good- versus poor-performing older adults. When the older adults were split into relatively good and poor performance groups on the basis of their behavioral performance (i.e., percent increase in RT for incongruent in comparison to congruent trials), we found that both good- and poor-performing older adults activate similar regions of MFG, ACC, and SMA. However, a direct comparison of the cortical activity for good and poor performers reveals that the relatively good performers show significantly less contralateral recruitment in the left MFG than do poor performers. See Figure 1c and 1d and Table 3.

To ensure that our results truly reflect increased cortical recruitment in response to the increased inhibitory demands of the incongruent stimuli, we performed an additional set of confirmatory analyses. Specifically, we compared levels of cortical recruitment to incongruent and congruent stimuli within each participant (i.e., incongruent > congruent) to assess the cortical recruitment that could be attributable to the incongruent stimuli over and above that attributable to the congruent stimuli alone. We then constructed a 10-mm sphere around the peak voxel for each of the clusters reported to be activated by older adults in Table 3. We then interrogated these three regions for group differences in cortical activity attributable to incongruent stimuli beyond that elicited in response to congruent stimuli (i.e., a Group × Trial Type interaction). Similar to the data reported in Figure 1 and Table 3, poor-performing older adults showed significantly greater cortical activity than good-performing older adults in this contrast in the left MFG ROI (peak $Z = 4.1$, small-volume corrected $p < .001$). Additionally, however, poor-performing older adults showed a significantly greater level of activity than in the right MFG than good-performing older adults (peak $Z = 3.01$, corrected $p < .05$), although this difference was much less robust than the comparison in the left MFG ROI, confirming our assumptions that increased recruitment in the MFG was due to the increased attentional demands imposed by the incongruent flanking stimuli. Finally, no significant differences emerged between good- and poor-performing older adults in the ACC–SMA ROI.

Brain Structure

Younger versus older adults. Consistent with previous cross-cohort examinations of gray matter (e.g., Raz, 2000; Resnick et al., 2003), older adults show significant reductions in the amount of gray matter in the frontal and prefrontal lobes, with the largest peaks in MFG, the superior frontal gyrus (SFG), and throughout the medial wall of the brain (SMA, ACC), including those regions implicated in inhibitional task performance by our fMRI analyses. Additionally, older adults demonstrate significant deterioration of the frontal white matter tracts compared with their younger counterparts. See Figure 2 and Table 4.

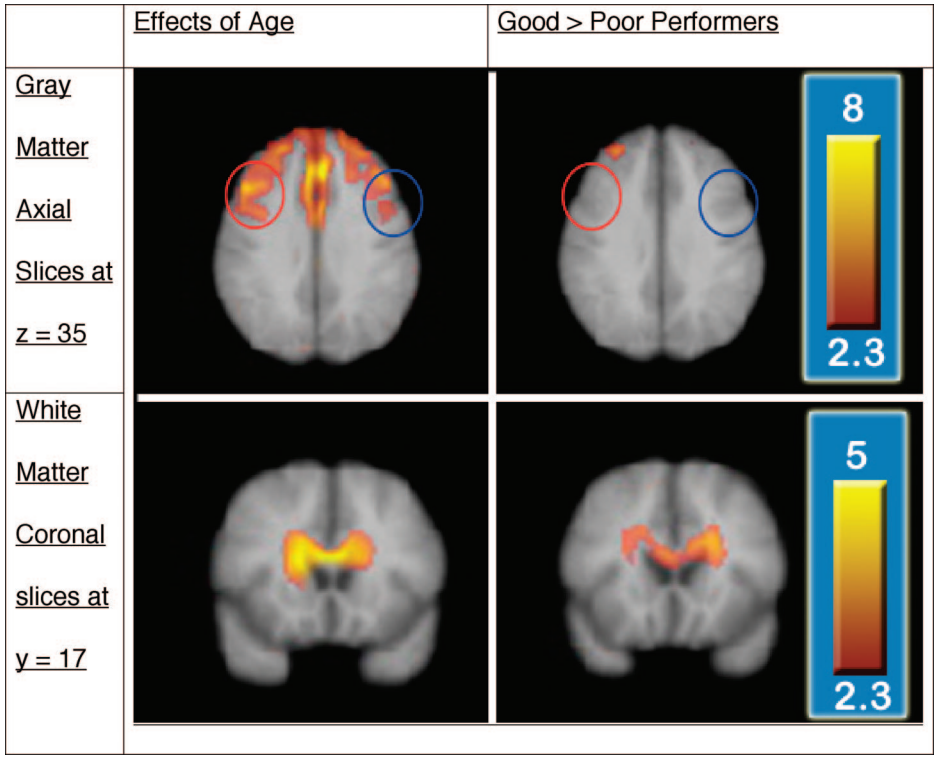

Figure 2. Differences in density of gray and white matter of the frontal lobes, as measured by voxel-based morphometry, as a function of age and performance groups. In contrast to the effects of age, no differences were detected in gray matter density as a function of performance group in regions of cortex involved in task performance, even when the statistical threshold for detecting such an effect was relaxed to an uncorrected $p < .05$ threshold. See Table 4. However, a robust effect of density in the white matter tracts was seen both as a function of age and, more importantly, as a function of performance group. Images are presented in neurological convention and rendered with a minimum voxel entry criterion of $Z > 2.33$ for display purposes.

Good- versus poor-performing older adults. We initially compared the gray matter densities of relatively good- and poor-performing older adults, masked within those regions of cortex that showed significant activation by older adults in response to incongruent trials in the fMRI analyses. On the basis of the cross-cohort comparison presented earlier and the potential role of gray matter decline in contralateral recruitment and age-related decline in cognitive performance, we might

Table 4
Regional VBM Analyses

Variable	ROI	Cluster size	*p* corrected	Peak *Z*
	Gray matter analyses			
Effects of age	Left MFG	924	.0001	6.67
	Right MFG	1,003	.0001	5.07
Good > poor[a]				
Poor > good[a]				
	White matter analyses			
Effects of age	Frontal white matter	1,220	.0001	4.92
Good > poor	Frontal white matter	854	.0001	3.60
Poor > good[a]	Frontal white matter			

Note. VBM = voxel-based morphometric technique; MFG = middle frontal gyrus; ROI = region of interest.
[a] No voxels survived threshold.

expect to find that good performers would possess greater gray matter density in these regions than poor performers. However, this was not the case. Even at a minimal $p < .05$ entry threshold and an uncorrected cluster probability of $p < .05$, no differences were found in gray matter density between good- and poor-performing older adults. These findings are consistent with data from animal models suggesting that gray matter decline may be associated with age-related decline in performance, but it has little or no bearing on performance variability within an aged cohort (Rapp & Gallagher, 1996). However, they are inconsistent with the notion that deterioration of cortical gray matter within task-specific cortical processors, at least with the level of precision available with VBM, contributes to contralateral recruitment during flanker task performance. (See Table 4.)

When directly comparing the gray matter of relatively good- and poor-performing older adults unconstrained by ROIs, we found that two clusters of prefrontal gray matter in a left-lateralized portion of the anterior superior frontal gyrus show significantly greater concentrations of gray matter in good- than poor-performing older adults. However, these regions are not spatially coincident with the regions implicated in inhibitory task performance by our fMRI analyses. Thus, it does not appear that we simply lack statistical power to detect groupwise differences in cortical density at an uncorrected level but rather that any differences in cortical gray matter density are unrelated to the regions recruited during task performance. See Figure 2 and Table 4.

In contrast to the findings from the gray matter data presented earlier, robust differences in white matter density emerged as a function of performance. Within the frontal white matter ROI, good-performing older adults showed significantly greater concentrations of white matter than did poor-performing older adults, with a corrected cluster probability of $p < .001$, and surviving voxels spanning the majority of the anterior white matter tract. When these analyses were repeated unconstrained by the a priori ROIs, the same basic findings were replicated, with greater white matter concentrations in the anterior white matter tracts for good compared with poor performers. No regions were identified in which poor performers had greater white matter density than good performers. (See Figure 2 and Table 4.)

Discussion

Cortical Recruitment in Older Adults

Consistent with most known investigations of frontal cortical recruitment and cognitive task performance (see Cabeza, 2002, for review), our older adults exhibited significantly greater bilateral recruitment of frontal cortex during task performance than did younger adults. However, in contrast to examinations of source and verbal working memory performance in older adults, we find that poor-, rather than good-, performing older adults show significantly greater PFC recruitment in the contralateral hemisphere when asked to inhibit incongruent flanking cues. Although our findings stand in contradiction to verbal source and working memory paradigms, they are highly consistent with data from Nielson et al. (2002; Langenecker & Nielson, 2003), who found that contralateral recruitment in a go/no-go task was associated with poorer performance in older adults. The contradictory nature of findings from verbal source and working memory findings and from our flanker task and Nielson et al.'s go/no-go task suggests an interesting distinction in the implications of hemispheric asymmetry in cortical recruitment for verbal memory and inhibitory functioning in older adults.

To understand the potential explanations for the opposing patterns of data, it may be useful to consider these findings within the context of the roles that various prefrontal cortical regions are thought to play in neurocognitive control. Generally, control processes in the posterior regions of PFC tend to be left lateralized for verbal materials and right lateralized for nonverbal materials (see Buckner, 2003, for review). Additionally, the right hemisphere is thought to play a role in monitoring the output from left hemisphere verbal control processes (Henson, Shallice, & Dolan, 1999; Rugg, Fletcher, Chua, & Dolan, 1999; Rugg, Henson, & Robb, 2003), may help to select among competing alternative representations in working memory (Banich et al., 2000; Milham et al., 2001), and has been shown to be sensitive to differences in retrieval strategy (Wagner, Desmond, Glover, & Gabrielli, 1998). Thus, one might reasonably argue that failures of control processes in the left hemisphere during a verbal memory task might be compensated by heightened postretrieval monitoring in the right hemisphere (e.g., in Cabeza et al., 2002; Reuter-Lorenz et al., 2000), whether implemented intentionally or not (see Reuter-Lorenz et al., 2001, for a similar account). However, when processing information that is less likely to be amenable to verbal control (e.g., our <<>>< flanker stimuli), invocation of additional verbal control processes is unlikely to be helpful and might be expected to impede task performance, as our data indicate. Under this view, one would predict that the recruitment of additional cortical areas during task performance would not be universally beneficial in nature but intimately dependent upon the potential for these additional regions to play a complementary role in task performance. Certainly, even a cursory comparison of the patterns of data acquired in our paradigm and go/no-go paradigms (Langenecker & Nielson, 2003; Nielson et al., 2002) with those seen in source and verbal working memory paradigms is consistent with such a prediction.

Examining this notion further, we can find additional support within existing data that relates patterns of cortical recruitment to working memory performance in older adults. Recall the Reuter-Lorenz et al. (2000) study, in which contralateral recruitment in older adults was significantly correlated with faster responding in a verbal working memory paradigm. In a second experiment, older adults were asked to perform a spatial working memory paradigm, in which three dots were presented at varying points along four imaginary circles at varying eccentricity from a central fixation. The dots were removed, and after a brief interval participants were presented with a cue at a location on one of the circles and asked whether one of the stimulus dots had occupied that position. They found (as expected and consistent with the verbal–spatial distinction in PFC control processes) that younger adults recruited right PFC during performance of the spatial working memory task. Older adults also showed significant activation of the contralateral (left) hemisphere. However, in contrast to their verbal working memory experiment, there was no improvement in performance associated with additional recruitment of the contralateral (left) hemisphere. In this case, in which verbal control processes were

not likely to efficiently complement spatial memory, recruitment of these regions was not apparently compensatory.

Thus far, we have taken the position that additional cortical recruitment is not universally compensatory in nature. Instead, in order for additional cortical recruitment to provide a benefit to older adults' cognitive performance, the regions recruited must serve a complementary role in task performance. This view can be separated from at least one incarnation of the general compensation view, which suggests that the individual cortical regions thought to support task performance become less differentiated, with one hemisphere partially taking over the function of another, much as in the plastic reorganization seen in stroke or lesion recovery. If such a view were correct, we should have seen that increased recruitment in the left hemisphere during flanker task performance was beneficial to task performance. However, in both our flanker data and in the go/no-go paradigm (e.g., Langenecker & Nielson, 2003; Nielson et al., 2002), left hemisphere recruitment was associated with poorer performance in older adults. It should be noted that Cabeza et al. (2002) have been careful to suggest that both plastic reorganization and complementary function accounts for their compensatory view, thus leaving both options open. We argue, however, that our data, extant findings from inhibitory paradigms, and comparisons between the spatial and verbal working memory domains are much more consistent with the idea that the functional properties of the individual cortical processors in PFC remain intact but are efficient in compensating for impaired performance only to the degree that the functions that they subserve are likely to play a complementary role in task performance.

Structural Data, Inhibitory Performance, and Cortical Recruitment

Although the VBM comparisons between young and older adults showed both a decrease in cortical gray matter with age and a decrease in inhibitory performance in older adults, no relationship was found between cortical gray matter density and cognitive performance among the older adults, even when the statistical threshold for detecting such a difference was relaxed to a minimal level. These data are consistent with animal data suggesting that decreased cellular density within the gray matter of aged rats does not necessarily predict intracohort variations in performance (e.g., Rapp & Gallagher, 1996). Our findings are also inconsistent with the idea that declines in specific cortical processors are related to additional recruitment in the contralateral hemisphere, given that poor-performing older adults showed a significantly greater level of cortical recruitment in the left hemisphere than good-performing older adults but did not differ in the gray matter densities of these regions. Rather, these data, particularly when considered in conjunction with the results of the white matter analyses (discussed later), are more consistent with theories that suggest that the additional recruitment of nonspecialized regions of cortex reflects a basic failure to select task-appropriate cortical processors (e.g., Li & Lindenberger, 1999; Logan et al., 2002), perhaps because of an effective disconnection between the hemispheres of the frontal lobes (e.g., O'Sullivan et al., 2001), a failure of dopaminergic gain control in the dorsal PFC (Braver & Barch, 2002), or even from adopting an inefficient strategy to deal with the incongruent flanking stimuli.

It should be noted that our gray matter findings are inconsistent with studies of the relationship between hand-tracing measures of gray matter volume in PFC and cognitive task performance in aging individuals. For example, Gunning-Dixon and Raz (2003) found that declines in gray matter PFC volume predicted age-related impairments on both a working memory composite score and the Wisconsin Card Sorting Task. Several possibilities exist for this difference. One potential explanation, and also a caveat for our gray matter findings, is that VBM, although clearly able to detect the age-related variation in gray matter between younger and older adults, may not be sufficiently sensitive to detect the more subtle differences in gray matter that might contribute to cognitive performance differences in the older adults. This may be particularly true in regions of cortex that are highly variable in morphology from individual to individual, as is the case with the human frontal cortex. However, the fact that we did not find any trend, even at minimal statistical thresholds, for differences in the gray matter of good- and poor-performing older adults might at least partially obviate such a concern. Additionally, it is not yet completely clear to which cellular properties VBM is sensitive (e.g., cell volume, cell density, dendritic arborization, local vascularization). As such, it could also be the case that hand tracing and VBM methods are differentially sensitive to some aspects of age-related decline in gray matter (see also Tisserand et al., 2002). Finally, it is also possible that more molar measures of cognitive performance, such as a composite working memory score, or the Wisconsin Card Sort Test used in Gunning-Dixon and Raz, are more sensitive to changes moderated by differences in gray matter than our modified flanker task. Future research that relates VBM outcomes to histological measures seems both useful and highly warranted, as does closer examination of the relationship between cognitive functioning in older adults and measures of gray matter volume derived from hand-tracing and VBM methodologies.

Much as in the gray matter data, we found that older adults showed significantly reduced density of the frontal white matter tracts compared with young adults, suggesting significant deterioration in the tissues that allow effective communication between the frontal lobes. However, unlike the gray matter findings reported previously, we found a robust relationship between structural differences in the frontal white matter tracts and individual differences in inhibitory task performance within the older adults. These data are highly consistent with previous findings that frontal white matter integrity is significantly related to impaired executive functioning in older adults (e.g., Gunning-Dixon & Raz, 2003; O'Sullivan et al., 2001) and suggestions that impaired interhemispheric communication contributes to bilateral cortical recruitment by means of an inability to select the proper cortical processors for the task at hand (e.g., Li & Lindenberger, 1999; Logan et al., 2002). However, we should note that, unlike frontal gray matter, the frontal white matters tend to show a somewhat more homogeneous spatial distribution, particularly in the anterior tracts, which might enhance our ability to detect subtle changes in these tissues. As such, some caution is suggested in interpreting the highly disparate gray and white matter findings. In addition, of course, the same caveats regarding our current lack of knowledge about the specificity of the cellular changes that underlie differences detected by VBM in regard to gray matter might also be applied to white matter findings. However, with those caveats in mind, our

data suggest a greater role of individual structural variation in white matter in the efficiency of inhibitory performance than does structural variation in gray matter.

Although we focused on individual differences in gray and white matter structures, it could be that declines in multiple systems—for example, gray (Gunning-Dixon & Raz, 2003) and white (Gunning-Dixon & Raz, 2003; O'Sullivan et al., 2001) matter integrity, dopamine (Braver & Barch, 2002; Li & Lindenberger, 1999), gamma-aminobutyric acid (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000), sex hormone levels (e.g., Moffat et al., 2004), genotypic variability (e.g., Diamond, Briand, Fossella, & Ghelbach, 2004), and gene expression (e.g., Romanczyk et al., 2002)—contribute individually and interactively to effect neurocognitive declines in older adults. Similarly, individual differences in system-specific declines may shape specific changes in neurocognitive functioning, and each may have different implications for aspects of neurocognitive decline. For example, in our rather straightforward flanker task, participants were required to respond to the stimuli very quickly, and they did so, on average, in less than 1 s. In this task, we found that gray matter and white matter were differentially associated with task performance within the older adults. Thus, in the case of the flanker task, rapid interhemispheric communication (by means of intact frontal white matter tracts) may be more important in task performance than subtle differences in the density of the local gray matter–processing units. However, in the case of a task that requires more complex and sustained processing, as in the Wisconsin Card Sorting Task (e.g., Gunning-Dixon & Raz, 2003), the density of the local gray matter might indeed be as important in task performance as interhemispheric communication. Although speculative, this supposition is quite amenable to future investigation.

In summary, our findings suggest that the relative contributions of white matter morphology to neurocognitive decline and bilateral cortical recruitment are substantially more robust than those that result from gray matter decline. As such, impaired interhemispheric communication may play a more significant role than the structure of the local gray matter in individual differences in inhibitory performance, at least in our flanker task, and with all of the caveats regarding the VBM method in mind. Our findings, and those already present in the neurocognitive aging literature, are also generally consistent with the idea that the recruitment of additional cortical processors is not universally compensatory in nature. Instead, we suggest the possibility that specific cortical processors do not undergo a plastic reorganization to share functionality with other regions. Although the recruitment of additional cortical processors can be beneficial to function in many cases, such recruitment is only likely to be of benefit to aging individuals if the additional regions brought to bear on the task already subserve a function that can play a complementary role in task performance. Future investigations that directly compare and contrast the implications of complementary and noncomplementary cortical recruitment patterns, along with contemporaneous assessments of cortical morphology with respect to task demands, will likely prove highly fruitful.

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New Editors Appointed, 2007–2012

The Publications and Communications (P&C) Board of the American Psychological Association announces the appointment of three new editors for 6-year terms beginning in 2007. As of January 1, 2006, manuscripts should be directed as follows:

- *Journal of Experimental Psychology: Learning, Memory, and Cognition* (www.apa.org/journals/xlm.html), **Randi C. Martin, PhD,** Department of Psychology, MS-25, Rice University, P.O. Box 1892, Houston, TX 77251.

- *Professional Psychology: Research and Practice* (www.apa.org/journals/pro.html), **Michael C. Roberts, PhD,** 2009 Dole Human Development Center, Clinical Child Psychology Program, Department of Applied Behavioral Science, Department of Psychology, 1000 Sunnyside Avenue, The University of Kansas, Lawrence, KS 66045.

- *Psychology, Public Policy, and Law* (www.apa.org/journals/law.html), **Steven Penrod, PhD,** John Jay College of Criminal Justice, 445 West 59th Street N2131, New York, NY 10019-1199.

Electronic manuscript submission. As of January 1, 2006, manuscripts should be submitted electronically through the journal's Manuscript Submission Portal (see the Web site listed above with each journal title).

Manuscript submission patterns make the precise date of completion of the 2006 volumes uncertain. Current editors, Michael E. J. Masson, PhD, Mary Beth Kenkel, PhD, and Jane Goodman-Delahunty, PhD, JD, respectively, will receive and consider manuscripts through December 31, 2005. Should 2006 volumes be completed before that date, manuscripts will be redirected to the new editors for consideration in 2007 volumes.

In addition, the P&C Board announces the appointment of **Thomas E. Joiner, PhD** (Department of Psychology, Florida State University, One University Way, Tallahassee, FL 32306-1270), as editor of the *Clinician's Research Digest* newsletter for 2007–2012.