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Attentional Control in the Aging Brain: Insights from an fMRI Study of the Stroop Task

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Several recent studies of aging and cognition have attributed decreases in the efficiency of working memory processes to possible declines in attentional control, the mechanism(s) by which the brain attempts to limit its processing to that of task-relevant information. Here we used fMRI measures of neural activity during performance of the color–word Stroop task to compare the neural substrates of attentional control in younger (ages: 21–27 years old) and older participants (ages: 60–75 years old) during conditions of both increased competition (incongruent and congruent neutral) and increased conflict (incongruent and congruent neutral). We found evidence of age-related decreases in the responsiveness of structures thought to support attentional control (e.g., dorsolateral prefrontal and parietal cortices), suggesting possible impairments in the implementation of attentional control in older participants. Consistent with this notion, older participants exhibited more extensive activation of ventral visual processing regions (i.e., temporal cortex) and anterior inferior prefrontal cortices, reflecting a decreased ability to inhibit the processing of task-irrelevant information. Also, the anterior cingulate cortex, a region involved in evaluatory processes at the level of response (e.g., detecting potential for error), showed age-related increases in its sensitivity to the presence of competing color information. These findings are discussed in terms of newly emerging models of attentional control in the human brain. © 2002 Elsevier Science (USA)

Key Words: aging; fMRI; attentional control; stroop; competition; conflict; anterior cingulate; prefrontal cortex; parietal cortex.

INTRODUCTION

While researchers have a tendency to discuss attention and working memory in isolation of one another, advances in our understanding of cognitive neuroscience have made it clear that they are mutually dependent functions, sharing many of the same neural substrates (e.g., dorsolateral prefrontal cortex) (e.g., Baddeley, 1986; Cohen & Servan-Schreiber, 1992; Posner & Dehaene, 1994; Taylor et al., 1997; Wagner, 1999; Banich et al., 2000a, 2000b; MacDonald et al., 2000). For instance,

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working memory maintains representations of current task demands. Such representations are crucial to attentional processes responsible for selecting task-relevant representations and actions. Likewise, selective attention acts to limit the contents of working memory to task-relevant representations and actions. Furthermore, it can aid in prioritizing the contents of working memory. The interdependence of these and other cognitive functions (e.g., long-term memory) presents a major challenge to understanding the etiology of cognitive deficits associated with age (i.e., >60 years) (Salthouse, 1996). For example, researchers interested in understanding age-related declines in working memory performance must determine whether they are due to impairment of processes specific to working memory function (e.g., storage and maintenance of representations active within working memory) as opposed to impairment of related processes, such as aspects of attentional function (e.g., selection of the representations that gain access to, or are operated upon within, working memory).

In fact, recent studies suggest that age-related declines in working memory function are related to decreases in the effectiveness of selection processes. More specifically, with age (i.e., 60–75 years), working memory processes become increasingly susceptible to disruption by task-irrelevant information (West, 1999a, May et al., 1999). For example, West (1999a) found that when older adults attempted to retain the location of a target stimulus in working memory, the presence of a visual distractor impaired performance more than in younger adults. He concluded that age-related decreases in the ability to inhibit irrelevant information reduce the speed with which older adults can encode information in working memory. In another study of the impact of aging on working memory, May et al. (1999) found that age-related increases in susceptibility to proactive interference appear to be more influenced by changes in attentional mechanisms rather than decreases in the storage capacity of working memory. May et al. (1995) had a similar interpretation for age-related decreases in negative priming, arguing that increases in inhibition failures appeared to be more related to decreases in the efficiency of attentional than episodic retrieval mechanisms (but see Kieley & Hartley, 1997; Kramer et al., 1994). Decreases in the ability to discriminate between relevant and irrelevant information have also been noted in aging studies of off-target verbosity in natural speech (Gold, Andres, Arbuckle, & Schwartz, 1988).

Several researchers have suggested that the increased ability of irrelevant information to disrupt working memory processes can be attributed to an age-related decline in inhibitory function. For example, Hasher and Zacks (1988) have argued that there is a decline in the aging brain’s ability to prevent the entrance of irrelevant information into working memory, to suppress irrelevant and nongoal oriented representations active within working memory, and to inhibit inappropriate responses (for alternative findings and views related to Hasher and Zack’s theory, see Burke, 1997, & McDowd, 1997).

Current models of attention (e.g., Posner & Dehaene, 1994; Carter et al., 1995; Banich et al., 2000a, 2000b; MacDonald et al., 2000) posit that attentional control is responsible for inhibitory functions such as those described by Hasher and Zacks (1988). It is generally agreed that a distributed network of structures within the brain, including anterior cingulate cortex, prefrontal cortex, parietal cortex, extrastriate cortex, superior colliculus, thalamus, and the basal ganglia, supports attentional function. Under attentionally demanding conditions, top-down control or coordination of activity within the network of structures responsible for selection is required to enable complex goal-oriented behaviors (referred to as attentional control). For example, neural activity within processing systems containing task-relevant information needs to be amplified, whereas that of processing systems containing irrelevant and potentially interfering information must be decreased. With regard to working memory, such modulations act to dampen the activation of task-irrelevant representations capable of gaining access to working memory, as they could otherwise impair performance by needlessly taxing working memory's storage and maintenance processes. Concomitant with these modulations, attention operates on working memory processes, biasing the selection and manipulation of task-relevant representations over that of task-irrelevant representations.

Here we consider the nature of age-related changes within the attentional network that may compromise the effectiveness of attentional control. Current models of attentional control (e.g., Banich et al., 2000a, 2000b; MacDonald et al., 2000) suggest that dorsolateral prefrontal cortex (BA 9 and BA 46) maintains an attentional set by modulating activity within posterior processing systems and facilitating selection of task-relevant representations within working memory. Interestingly, structural studies of the aging brain indicate that prefrontal cortices experience the highest degree of age-related atrophy (Raz et al., 1997; Raz, 2000). Furthermore, functional neuroimaging studies have found age-related alterations in patterns of activity observed within prefrontal cortex during working memory, encoding, and attentional tasks, often showing less activity in older than younger adults (for a review, see Cabeza et al., 2000). All of these findings suggest that aging may compromise the effectiveness with which prefrontal cortex can act to impose an attentional set.

Of course it is important to note that other structures, such as parietal cortex, may work in association with prefrontal cortex to impose such an attentional set (Banich et al., 2000b). Various studies have implicated parietal cortex in attentional control, often focusing on its involvement in visual selection, orienting of attention, shifting of attention, and stimulus-to-response mappings (e.g., Corbetta et al., 1993; Coull and Nobre, 1998; Corbetta et al., 1998; Wojciulik and Kanwisher, 1999; Banich et al., 2000b; review by Cabeza and Nyberg, 2000). Across many of these studies, parietal and prefrontal activity co-occurs (Cabeza and Nyberg, 2000). Several researchers have also demonstrated the existence of both structural and functional connectivity between prefrontal and parietal cortex (Cavada & Goldman-Rakic, 1989; Neal et al., 1990; Morecraft et al., 1993; Cabeza et al., 1997), suggesting a possible interdependence of these regions in implementing an attentional set. As such, age-related changes in parietal function may also underlie decreases in the brain's ability to implement attentional control.

An alternative, but not necessarily mutually exclusive possibility, is that difficulties may arise in mechanisms responsible for evaluating the need for attentional control rather than in those responsible for implementing attentional control once the need for it has been detected. Recent models of attentional control (Banich et al., 2000; Carter et al., 2000; MacDonald et al., 2000; Botvinick et al., 1999) have emphasized the involvement of anterior cingulate in such evaluatory processes (for alternative interpretations of cingulate activity, see Posner & DiGirolamo, 1998). More specifically, these models argue that anterior cingulate cortex monitors for the presence of conditions that can lead to erroneous responses (i.e., response conflict).

Another way in which attentional control might be compromised in older adults is that the structures supporting attentional control may remain relatively unaffected (e.g., prefrontal cortex, parietal cortex, and anterior cingulate cortex), but the functional connectivity and interactions between regions within the attentional network may decrease. Age-related changes in the functional connectivity of prefrontal cortex with other regions of the brain have been noted. For example, in a study of encoding and recall processes, Cabeza et al. (1997) found a decrease in the functional connectivity between prefrontal cortex and parietal cortex. Also, several neuroimaging studies of aging have noted decreases in the extent of activation in occipital cortex, often appearing as if there was a trade-off between activity in occipital cortex and temporal or parietal cortex (Grady et al., 1994; Madden et al., 1997). Such trade-offs may reflect the presence of compensatory mechanisms.

In order to examine age-related changes in the neural substrates of attentional control we made use of the Stroop task because it is a powerful yet simple task (Pardo et al., 1990; Bench et al., 1993; George et al., 1994; Taylor et al., 1994; Bush et al., 1998; Peterson et al., 1999; Banich et al., 2000b; MacDonald et al., 2000). In this task, participants are asked to identify the ink color in which a word is printed while ignoring the word's identity. Although seemingly uncomplicated, the word itself is a potentially strong source of interference to color naming. Engagement of systems dedicated to processing words (e.g., orthography to phonology and orthography to semantics) is relatively automatic, requiring little or no attention (MacLeod, 1991). Thus, representations (e.g., semantic or phonological representations) arising from the word processing systems can compete for processing resources with those required to perform the task (i.e., those arising from color processing systems).

The competition for resources between the word and color processing systems is markedly heightened when the word names a color, as there are now two distinct sources of color information. In this case, each processing system (i.e. word processing system and color processing system) can cause activation of not only the semantic and phonological representations associated with a particular color, but associated responses as well (e.g., a button press in a manual version of the Stroop). The ability of color words to impair color identification when incongruent with the ink color and facilitate color identification when congruent provides clear evidence that the inadvertent contribution of outputs from the word processing system influence task performance.

While it is clear that incongruent-word trials require a higher degree of attentional selection than neutral-word trials, the relative attentional requirements of congruent-word trials are less obvious. Congruent-word trials are typically associated with an improvement in task performance (relative to neutral-word trials), termed ‘‘facilitation’’. This result may lead to the conclusion that congruent-word trials engender decreased attentional requirements relative to both neutral- and incongruent-word trials, as the word's identity appears to be aiding in identification of its ink color. However, this idea is based on the assumption that the participant is not fully complying with task instructions, allowing task performance to be highly influenced by a task-irrelevant source of information (i.e., the word's identity) that is supposed to be ignored (task instructions: ‘‘identify the ink color in which the word is printed while ignoring its name or identity’’). The degree to which such an assumption is valid depends on the experimental design employed. Designs that block congruent-word trials together such that they occur one after another (e.g., 12 congruent-word trials occur in a row) reward rather than penalize participants for attending to the irrelevant color–word. Such a design can lead to the development of a strategy that bases task performance on task-irrelevant information introduced by the word's identity, rather than its ink color. In contrast, designs that intermix congruent color–words with neutral words or incongruent color–words discourage and penalize the development of such strategies (Carter et al., 1995; Posner & DiGirolamo, 1998; MacLeod & MacDonald, 2000). If a participant attempts to base performance on the irrelevant information associated with the word's identity in order to facilitate performance on congruent trials, they will inadvertently impair the efficiency of processing on incongruent-word and neutral-word trial types. Thus, in an intermixed design, participants are encouraged to maintain proper task performance, attempting to base task performance on the word's ink color while ignoring its identity on all trials, regardless of trial type.

Several authors have suggested that when proper task performance is maintained, congruent color–word trials have increased attentional requirements relative to neutral word trials (Carter et al., 1995; Posner & DiGirolamo, 1998). It is important to realize that even though the word's identity facilitates performance on congruent trials, proper task performance requires that task execution be based on the word's ink color, not the word's identity, which provides a competing source of color information. Hence, congruent and incongruent color words are similar in that they both contain a second source of color information (the word's identity), which can *compete* with the task-relevant color information (the word's ink color). In contrast, neutral words (e.g., ''LOT'') contain only one source of color information (the word's ink color), as the word's identity is unrelated to color. Thus, in the case of color-related words, either congruent or incongruent, increased attentional control is required to ensure that task performance is based on the correct source of color information—the word's ink color rather than the word's identity. In support of this notion, a PET study by Carter et al. (1995) found similarities in the patterns of activity noted for congruent and incongruent color–word blocks when compared against neutral-word blocks.

Incongruent color–word trials have additional attentional demands (relative to congruent color–word trials), as the word's identity *conflicts* with the word's ink color. Such a *conflict* is lacking on both neutral and congruent trials (see Carter et al., 1995; Posner & DiGirolamo, 1998, for similar explanations). Hence, in a Stroop task containing incongruent, congruent, and neutral trials, there are two distinct ways in which attentional control must be implemented. One is associated with distinguishing between two *competing* sources of color information (as occurs on congruent and incongruent trials), and the other is associated with dealing with a *conflicting* source of color information (as occurs on incongruent trials).

Previous studies of the Stroop task have found evidence of age-related changes in the effectiveness of attentional control (Brink & McDowd, 1999; West, 1999b; Comalli, Wapner, & Werner, 1962; Dustman & Bradford, 1984; Panek, Rush, & Slade, 1984; Hartley, 1993; Spieler, Balota, & Faust, 1996), though not all studies support this conclusion (Kramer et al., 1994; Verhaeghen, 1998, 1999). More specifically, the majority of studies find age-related increases in the magnitude of both interference (incongruent–neutral) and facilitation effects (neutral–congruent). Such increases have been considered indicative of decreases in the effectiveness of attentional control, as inadvertent contributions of the task-irrelevant representations and/or actions to task performance associated with color words increase.

In the present study, we used functional magnetic resonance imaging (fMRI) and the Stroop task to examine age-related changes in the neural substrates of attentional control. We included blocks of incongruent trials, blocks of congruent trials, and blocks of neutral trials so that we could differentiate between neural activity associated with the presence of a competing source of color information (as contained in incongruent and congruent color words as compared to neutral words) and that associated with the presence of a conflicting source of information (as only occurs for incongruent words). In order to prevent the adoption of strategies during the congruent blocks that would interfere with task instructions (e.g., basing the response on the word's identity rather than its color), neutral trials were included in both congruent and incongruent blocks (50:50 mix) (see Carter et al., 1995, for a more extensive explanation of the rationale for this approach). We included two groups of participants in our study: young adults (ages 21 to 27) and older adults (ages 60 to 75). While a significant body of literature already exists with respect to regions involved in attentional control during performance of the Stroop task in young adults (Pardo et al., 1990; Bench et al., 1993; George et al., 1994; Taylor et al., 1994; Bush et al., 1998; Peterson et al., 1999; Banich et al., 2000b; MacDonald et al., 2000; Milham et al., 2001), we felt that variability in findings across studies necessitated our inclusion of a young group, as much of this variability can probably be attributed to differences in the experimental designs and analytical techniques employed across studies.

In our analyses we attempted to distinguish between those regions involved in attentional selection due to the presence of a competing source of color information (which occurs for all color words regardless of their congruency) and regions involved in attentional selection due to the presence of a conflicting source of color information. In order to accomplish this, our fMRI data analyses made use of a multiple-regression model in which the following regressors were included: (1) a regressor to identify regions that are activated by the mere presence of a competing source of color information, regardless of congruency (*competition regressor*) (i.e., active for congruent and incongruent blocks, but not neutral); and (2) a regressor to identify regions that are only active when a conflicting source of color information is present (*conflict regressor*) (i.e., active for incongruent, but neither congruent nor incongruent).

It is important to note that such an analytical approach allows us to determine the extent to which congruent and incongruent trials are similar with respect to the demands they place on the attentional network. If a region is solely activated by the presence of conflicting color information (i.e., active for incongruent blocks, but not for congruent or neutral blocks), then only the beta coefficient for the conflict regressor should be significant. Conversely, if a region is activated by the mere presences of competing color information, regardless of its congruency (i.e., active for incongruent and congruent blocks, but not for neutral blocks), then the beta coefficient for the competition regressor should be significant. It is important to note that the competition regressor does not represent a summation of activity across incongruent and congruent blocks. Rather, activity for the competition regressor indicates that the MR signal increases during incongruent blocks, returns to baseline during neutral blocks, and increases once again during congruent blocks. One other notable possibility is that a region can be active for both congruent and incongruent trials, but more so for incongruent. In this case, significant beta coefficient's should be noted for both regressors (competition and conflict).

Given the growing body of evidence for age-related changes in the structure and function of prefrontal cortex and associated regions (i.e., parietal cortex), we expected that changes in dorsolateral prefrontal cortex function and related parietal areas underlie age-related decreases in the effectiveness of attentional control. We expected that decreases in the effectiveness of regions responsible for implementing attentional control would result in increased activity in regions involved in evaluatory processes and other regions that are modulated by top-down attentional control. More specifically, we expected that decreases in the effectiveness of attentional control in older participants would result in increased activity within regions involved in evaluatory processes, such as anterior cingulate cortex. We also expected that decreases in the effectiveness of attentional control would be reflected by increased activation in other brain regions. To the degree that processing of the word's identity (task-irrelevant information) cannot be effectively suppressed, we expected to observe more extensive activation of ventral processing regions (i.e., extrastriate and temporal cortex) due to a deeper processing of the word's identity (task-irrelevant information). Furthermore, to the degree that the contents of working memory cannot be as effectively selected, we expected to observe greater activity in regions involved in storage processes within working memory (i.e., ventrolateral prefrontal cortex) (Petrides and colleagues, e.g., Owen et al., 1996; see Wagner et al., 1999, for a review of theories of prefrontal differentiation with respect to working memory function).

METHODS

Participants

Our study included two groups of right-handed, native English-speakers recruited from the Champaign–Urbana community: (1) 10 older (7 male and 3 female) participants ranging in age from 60 to 75 years old (mean = 68) and (2) 12 young (7 male and 5 female) participants ranging in age from 21 to 27 years of age (mean = 23). All participants were screened to ensure that they had no history of neurological damage or color-blindness and gave informed consent prior to participation. The older adults were further screened for medication use, recent surgical procedures, and psychiatric illness and were exempted from participation if they reported taking blood pressure medication or having had surgical procedures in the head/neck area.

Stimuli and Design

The stimuli were programmed using Mel V2.0 and presented using an IBM PC-compatible computer. Our task made use of the following three ink colors: red, orange, and green. The following three trial types were included in our experiment: (1) *incongruent trials,* in which the word named a color incongruent with the ink color in which it was printed (e.g., the word ‘‘RED’’ in green ink); (2) *congruent trials,* in which the word named the ink color in which it was printed (e.g., the word ‘‘RED’’ printed in red ink); and (3) *neutral trials,* in which the word was unrelated to color (e.g., the word ‘‘LOT’’ in red ink). The neutral words were matched with the color words for word frequency and length.

We made use of a blocked fMRI design, in which neutral blocks were alternated with incongruent and congruent blocks (i.e., neutral-incongruent-neutral-congruent) such that participants were presented a total of four incongruent and four congruent blocks. Neutral trials were intermixed in congruent and incongruent blocks (50:50 mix) to prevent the development of word reading strategies in the congruent blocks. Each block consisted of 18 trials, presented at a rate of one trial every 2 s. Each trial consisted of a 300 ms fixation cross followed by a 1200-ms presentation of the stimulus (colored word) and 500 ms intertrial interval. The order of incongruent and congruent block types was counterbalanced across participants to control for order effects.

Procedure

Participants were instructed to identify the ink color in which each word appeared (i.e., green, red, orange) while ignoring the word’s identity. A three-button response pad was used for the acquisition of participant responses.

Participants were placed in a 1.5-T GE Signa scanner equipped for echo-planar imaging (EPI). Head position was stabilized using a bite-bar attached to the head coil to minimize motion during the session. Older participants who were unable to use a bite-bar due to dental problems wore a cap that was secured to the table to minimize head motion. The visual stimuli were presented using a goggle system by Magnetic Resonance Technologies. A total of 410 gradient T1 weighted EPI images were acquired for each participant (TR = 1517 ms, TE = 40 ms, flip angle = 90°), each consisting of 15 contiguous slices (3.75 × 3.75 × 7.0 mm) parallel to the AC–PC line.

Image Processing

The first six volumes of each run were discarded to allow the MR signal to reach steady state. Functional data for each participant was then convolved using a 3D Gaussian kernel (FWHM = 8 mm × 8 mm × 8 mm, kernel width = 7 × 7 mm), temporally denoised using an ID-wavelet transform (visushrink, number of levels = 4), intensity normalized, and linearly detrended. Finally, the time series data were converted from signal units into percentage change (reference = first neutral block). MedX3.2 was used for image processing and statistical analysis.

Regression Analyses

Regression analyses were performed on the time series data for each participant. The following two regressors and two covariates were included in the regression model: (1) *competition regressor,* the presence of a competing source of color information (i.e. increased activity for *both* congruent and incongruent blocks, but not neutral blocks); and (2) *conflict regressor,* the presence of a competing source of color information that conflicts with task relevant color information (i.e., increased activity for incongruent blocks but *not* for congruent or neutral blocks); (3) a regressor for the presence of practice effects in the last two cycles for the competition regressor; and (4) a regressor for the presence of practice effects in the last two cycles for the conflict regressor. For the sake of simplicity, we limit the scope of the present article to the first two regressors.

For each group, probability maps were converted to Z-score maps, warped into a common stereotaxic space (Talairach & Tournox, 1988) and averaged across participants, producing a mean Z-score map for each age group for each regressor. In our prior work, we provided empirical evidence for the ability of this approach to control for false positives due to multiple comparisons (Banich et al., 2000b). Voxels with a mean Z-score exceeding 1.96 ($p < .05$) were considered active (see Kelley et al., 1998; Banich et al., 2000a, 2000b for other applications of this approach). In order to ensure that outliers are not driving estimates of significance, we required that a voxel's Z score must also exceed 1.96 in at least 50% of the participants for it to be considered active (according to the binomial distribution, for an $n =$ 10, the voxelwise probability for falsely meeting this criteria is $\sim 1 \times 10^{-5}$). The peak detection algorithm described by Mintun et al. (1989) was employed for localizing activation.

Comparing Groups

We performed direct between-group analyses as well. These between-group analyses may not be definitive, as differences between age groups may be influenced by a variety of factors such as changes in the vasculature or structure of a region, rather than neural activity (see Cabeza, 2000, or D'Esposito, 1999, for a longer discussion of this issue). Nonetheless, we thought them important to include as they could help to provide confirmatory evidence for any differences in the qualitative patterns of results between the two age groups.

We made use of a two-step approach in comparing data between groups. First, we attempted to identify commonalities and differences in the patterns of activity observed for the two groups. In order to accomplish this, we measured the distances between each of the peaks (in Talairach space; Talairach & Tournox, 1988) identified in regression analysis for the young and those in the elderly. If a peak in one group was within 10 mm of a peak in the other group, the two peaks were considered to be equivalent (areas of *common* activation). Previous work in our lab established this criterion to be reliable for identifying common areas of activation between groups, especially given that we are using the same acquisition and image processing techniques for both groups. Peaks that occur in one group, but have no equivalent in the other, were considered to be a site of *unique* activation.

In the second step, at each pair of common peaks, we used an independent sample t test to statistically compare young participant's parameter estimates (β coefficient) for each regressor (competition, conflict) with those of the older participants (referred to as the *direct between-group comparison*). Rather than just comparing values at the peak voxels, we used spheres (radius = 2 voxels, or 4 mm) centered about each peak in an effort to reduce the possible impact of noise. Between-group comparisons were made for unique peaks as well.

RESULTS

For both younger and older groups, we observed a pattern of results similar to prior studies of the Stroop task, with increases in the need for attentional control activating a network of structures, including anterior cingulate cortex/preSMA, middle frontal gyrus, inferior frontal gyrus, superior and inferior parietal lobules, and extrastriate cortex. Despite similarities in the basic components of the attentional network activated within each group, age-related differences were noted within regions thought to be involved in the implementation of attentional control, especially prefrontal and parietal cortices.

Prefrontal Cortex

We found age-related differences in patterns of activity within prefrontal cortex during the more attentionally demanding conditions of the Stroop task (i.e., congruent and incongruent blocks). For both groups, regression analyses indicated increased dorsolateral prefrontal cortex (DLPFC) activity for the competition regressor, indicating

TABLE 1
Areas of Activity in Prefrontal, Parietal, and Cingulate Regions Common to Younger and Older Groups

	Young					Old			
Region	BA	*X*	*Y*	*Z*	Mean *Z* score	*X*	*Y*	*Z*	Mean *Z* score
				Competition					
Left middle frontal gyrus (DLPFC)	9	−38	10	34	3.06	−34	10	36	4.19
Right middle frontal gyrus* (DLPFC)	9	44	20	28	3.46	42	14	32	2.86
		52	14	44	2.88	50	18	38	2.24
Left inferior frontal gyrus (VLPFC)	45	−56	22	4	2.20	−52	14	4	2.39
						−56	26	8	2.64
Right inferior frontal gyrus (VLPFC)	44/45	50	18	10	2.49	54	20	14	3.21
						46	24	22	2.81
Right inferior parietal lobule*	40/19	40	−56	42	2.84	34	−62	40	2.29
Left superior parietal lobule	7/40	−36	−54	52	3.04	−32	−56	46	2.64
				Conflict					
Left inferior frontal gyrus (VLPFC)	46	−48	44	8	2.13	−44	40	8	2.49
Right inferior frontal gyrus (VLPFC)	45/46	42	16	6	2.38	44	18	6	3.13
Right SMA	6	4	10	54	2.40	2	12	52	2.86
Left superior parietal lobule	7	−18	−68	56	2.52	−14	−68	54	2.17

Note. Regions in which direct comparison revealed a group difference are labeled with one of the following markers to indicate significance level: † = $p < .1$ (not considered significant), * = $p < .05$, ** = $p < .005$, *** = $p < .0005$.

Designation of DLPFC vs. VLPFC based on distinction outlined by Fletcher & Henson (2001).

that activity increased when the word's identity provided a second source of color information (i.e., during congruent and incongruent blocks, but not neutral blocks). Although a high degree of overlap was noted between active regions of DLPFC in older participants and those in younger participants (see Table 1, competition regressor), additional regions of increased activity in both left and right DLPFC were detected for younger participants (see Fig. 1 and Tables 1–3, competition regressor). Our direct between-group analyses verified this distinction, with greater activity

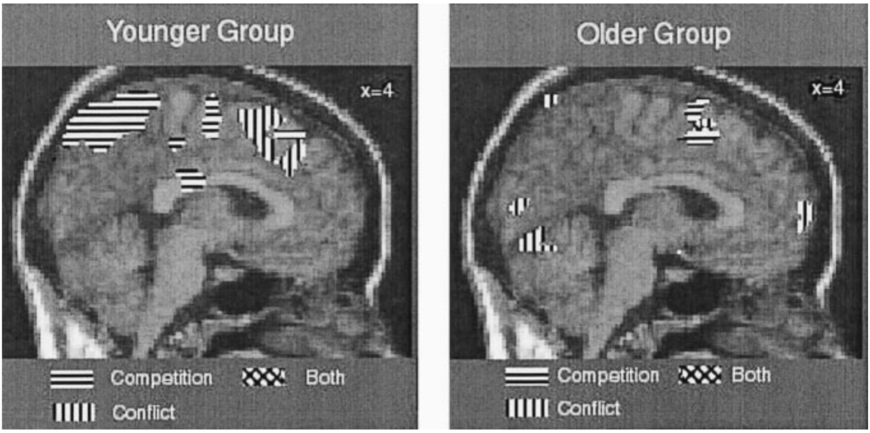

FIG. 1. More extensive dorsolateral prefrontal cortex activity was noted within younger participants than older participants in response to the need for attentional control due to the presence of competing color information.

TABLE 2
Areas of Activity in Prefrontal, Cingulate, and Parietal Cortices Specific to Younger Group

Region	BA	*X*	*Y*	*Z*	Mean *Z* score
Competition					
Left inferior frontal gyrus (VLPFC)	44	−42	22	26	3.13
Right inferior frontal gyrus* (VLPFC)	44	60	16	28	2.86
Left middle frontal gyrus* (DLPFC)	10	−28	54	10	3.34
Left middle frontal gyrus* (DLPFC)	46/9	−36	34	24	3.31
Left middle frontal gyrus (DLPFC)	6	−24	6	54	2.16
Right middle frontal gyrus*** (DLPFC)	9	40	32	32	3.57
		32	40	34	2.98
Right middle frontal gyrus* (DLPFC)	6	36	8	46	2.79
		20	34	46	2.74
Right middle frontal gyrus** (VLPFC)	10	34	54	10	3.08
		28	54	22	2.53
Midcingulate**	23	0	−20	24	3.31
	31	0	−26	42	2.47
Left precuneus*	7	−10	−58	58	2.65
Right precuneus***	7	6	−56	58	3.47
Left inferior parietal lobule	40	−58	−40	34	3.35
		−34	−46	46	3.33
Right inferior parietal lobule***	40	54	−40	26	2.49
		44	−34	50	3.35
Left superior parietal lobule*	7	−26	−66	48	3.86
Right superior parietal lobule***	7/40	38	−46	48	3.25
		8	−68	54	4.36
Conflict					
Anterior cingulate*	32	2	32	34	2.63
		4	18	40	2.62
Left middle frontal gyrus* (DLPFC)	9	−42	28	32	2.70
		−46	14	32	2.06
Left middle frontal gyrus* (DLPFC)	6	−40	4	46	2.65
Left inferior parietal lobule	40	−48	−36	50	2.07
Left superior parietal lobule*	7	−38	−46	60	2.38

Note. Regions in which direct comparison revealed a group difference are labeled with one of the following markers to indicate significance level: † = $p < .1$ (not considered significant), * = $p < .05$, ** = $p < .005$, *** = $p < .0005$.

Designation of DLPFC vs. VLPFC based on distinction outlined by Fletcher & Henson (2001).

within these regions being observed for younger participants than for older participants.

Additional active regions within DLPFC were noted for both groups for the conflict regressor, indicating that activity increased when the word's identity was a source of conflicting color information (i.e., during incongruent but neither neutral nor congruent blocks). While regions found to be active in the presence of conflict for the two groups were similar, they were not overlapping (see Tables 2 and 3). Direct between-group analyses verified the presence of unique areas of greater activity within DLPFC for the younger participants, but not those observed for the older participants. The failure of the direct comparison to support the finding of unique regions of activity within DLPFC for the older participants may suggest that increases in activity within these regions during conditions of conflict do occur in the young, but less reliably so on a within-subject basis.

Although a less extensive portion of dorsolateral prefrontal cortex appeared to be involved in mediating competition and conflict in older participants, there was greater

TABLE 3
Areas of Activity in Prefrontal, Cingulate, and Parietal Cortices Specific to Older Group

Region	BA	*X*	*Y*	*Z*	Mean *Z* score
Competition					
Left inferior frontal gyrus (VLPFC)	44/45	−42	16	8	2.29
		−30	26	10	2.81
Right inferior frontal gyrus	45	50	26	22	2.90
		28	18	4	2.12
Right inferior frontal gyrus* (VLPFC)	44	56	6	22	3.89
Right superior frontal gyrus (DLPFC)	6	4	10	60	2.34
ACC/Pre-SMA	24/32	2	8	44	2.44
		2	20	48	2.60
Left inferior parietal lobule	40	−54	−46	24	2.18
Conflict					
Left inferior frontal gyrus* (VLPFC)	47	−36	30	−14	3.32
		−48	18	−8	2.22
Right inferior frontal gyrus* (VLPFC)	47/45	40	24	−16	2.52
		56	34	4	3.25
Left middle frontal gyrus (VLPFC)	11	−20	40	−14	2.31
(DLPFC)	9	−36	20	36	2.59
Right middle frontal gyrus (DLPFC)	9	36	26	36	2.17
Left inferior parietal lobule	40	−48	−42	30	2.26
		−30	−38	54	2.46
Left Precuneus	7	−2	−56	54	2.18

Note. Regions in which direct comparison revealed a group difference are labeled with one of the following markers to indicate significance level: † = $p < .1$ (not considered significant), * = $p < .05$, ** = $p < .005$, *** = $p < .0005$.

Designation of DLPFC vs. VLPFC based on distinction outlined by Fletcher & Henson (2001).

activation of anterior inferior and ventrolateral regions of prefrontal cortex (BA 44, BA 45, and BA 47) in older than younger participants. For the competition regressor, older participants exhibited increased activity bilaterally within the anterior inferior frontal gyrus (BA 44/45) (see Table 3). However, this effect was not significant in the direct comparison between groups, suggesting that the presence of competing color information does cause increases in activity in these same areas in the young, but less reliably so on a within-subject basis. Age-related differences in the activity of these anterior inferior and ventrolateral prefrontal regions were more distinct for the conflict regressor. Increased activity was observed bilaterally in the inferior frontal gyrus (BA 47) for older but not younger participants. The direct between-groups analysis verified this distinction.

Overall, we found age-related decreases in the responsiveness of dorsolateral prefrontal cortex to an increased need for attentional control and age-related increases in the involvement of anterior inferior regions of prefrontal cortex.

Cingulate Cortex

Age-related changes were also noted in the activity of mid- and anterior cingulate cortices. While the mere presence of competing color information is enough to produce increases in anterior cingulate cortex (ACC) activity for older participants, the additional attentional demands of conflicting color information are necessary to evoke significant increases in ACC activity within younger participants (see Fig. 2). The results of our direct between-group analysis weakened this distinction, as increases in anterior cingulate activity in the older participants for the competition regressor

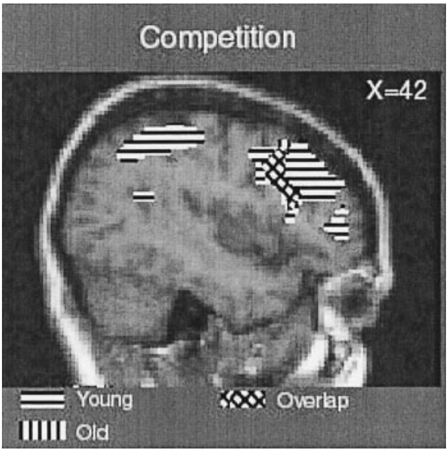

FIG. 2. For older participants, anterior cingulate cortex (ACC) showed an increased sensitivity to the presence of competing color information. While the mere presence of competing color information was enough to evoke increases in ACC activity for older participants, increases in ACC activity within the young were primarily driven by the presence of conflict.

did not differentiate from those in the young. This inconsistency between the findings of the two analyses indicates that increases in anterior cingulate activity during conditions of competition do occur in the young, but less reliably so on a within-subject basis. Of note, more consistent activations were noted in midcingulate cortex during conditions of competition for the young, but not in the old. This distinction was verified by our direct between-group comparisons.

Both groups experienced increases in activity within right SMA specific to the presence of conflicting information, while only the younger group experience increases in ACC activity specific to the presence of conflict.

We believe that changes in patterns of ACC activity reflect the heightened potential for error in older participants, produced by a decrease in the effectiveness of mechanisms responsible for implementing attentional control.

Parietal Cortex

Age-related differences in neural activity were noted throughout parietal cortex, with increases in activity associated with the presence of competing color information being far more extensive for younger participants. For both groups, regression analyses indicated increases in activity within parietal cortex for the competition regressor. While activations in the younger participants spanned precuneus cortex and the superior and inferior parietal lobules bilaterally, activations in the older participants were fewer in number, occurring only within the superior and inferior parietal lobules and tending to be more unilateral (i.e., left-sided). This distinction was verified by our direct between-group analyses. For both groups, the occurrence of conflict produced activation in the left superior parietal lobule. In the older participants, additional activations were noted in precuneus cortex.

Overall, parietal cortex appears to have a greater involvement in attentional control for younger participants than older, suggesting a greater relative reliance on the influence of anterior structures in the older participants. This may reflect differences in the ability of prefrontal regions to recruit parietal regions for task performance. Interestingly, examination of the practice covariate in the older participants revealed an increased involvement of parietal cortex in task performance with practice. An additional regression model was built to determine if increases in the difference between incongruent and neutral blocks actually reflected decreases in the neural activity associated with neutral trials. This was not the case, suggesting that this change is specific to attentional processes required by the Stroop task. It is important to note that our suggestion that older participants show a greater reliance on anterior regions does not infer that activity within anterior regions is unaffected by age (as stated earlier, DLPFC showed age-related decreases in activity). Rather, age-related decreases in responsiveness appear to be more extensive within parietal cortex (i.e., superior parietal lobule, precuneus cortex). Thus, the relative involvement of parietal regions appears to be decreased in older participants.

Extrastriate Cortex

For the competition regressor we found a diffuse region of activation for the younger group in extrastriate regions [12 peaks; median Z score $= 2.23$; between-group Direct Comparison (DC): 8 peaks: $p < .01$; 1 peak: $p < .001$; 3 peaks: $p < .0001$] that included the cuneus (e.g., -22, -88, 32; BA $= 19$; DC: $p < .0007$), lingual gyrus (e.g., 10, -74, 0; BA $= 18$; DC: $p < .01$), and middle occipital gyrus (e.g., -36, -88, 10; BA $= 18$; DC: $p < .0002$). For the older group, however, we found a much more limited region of activation in the occipital cortex (2 peaks; median Z score $= 2.59$) with peaks restricted to the fusiform gyrus (-44, -72, -12; BA $= 18/19$; DC: $p < .005$) and cuneus (-24, -70, 36; BA $= 19$; DC: $p < .005$) regions. The direct comparisons revealed that none of the peaks were common to both groups for the competition regressor.

For the conflict regressor, we observed activation in the younger group at only two peaks within the occipital cortex (median Z score $= 2.17$), occurring within the middle occipital gyrus (42, -90, 10; BA $= 18/19$; DC: $p < .01$) and cuneus (-4, -88, 34; BA $= 19$; DC: $p < .01$) gyrus. Direct comparisons revealed that these two peaks were unique to the younger group. In contrast to the younger group, activation in the older group for the conflict regressor was much more distributed throughout the occipital cortex (14 peaks; median Z score $= 2.32$, 10 peaks passed at $p < .01$; 3 peaks passed at $p < .001$; 1 peak passed at $p < .0001$) with peaks located in the lingual gyrus (e.g., 4, -78, -8; BA $= 18$; DC: $p < .01$), cuneus (e.g., -16, -86, 12; BA $= 18$, $p < .01$), fusiform gyrus (e.g., 40, -60, -10; BA $= 37$; DC: $p < .01$), and middle occipital gyrus (e.g., -46, -58, 4; BA $= 18/19$; DC: $p < .0001$). The direct comparisons revealed that all 14 peaks were unique to the older group.

Hence, while the mere presence of a competing source of color information produced greater regions of activation in occipital cortex for the younger than older adults, the presence of conflicting color information produced more extensive regions of activation in the occipital cortex for older participants.

Temporal Cortex

For the younger group, active regions noted in temporal cortex for the competition regressor were concentrated in the posterior portions of the temporal lobe (11 peaks; mean $y = -41$; median Z score $= 2.53$; between-group DC: 7 peaks: $<.01$; 2 peaks: $p < .001$; 2 peaks: $p < .0001$) around the inferior temporal gyrus (e.g., -42, -36, -16; BA $= 20$; DC: $p < .006$), middle temporal gyrus (e.g., -60, -54, 4; BA $= 21$; DC: $p < .002$), and superior temporal gyrus (e.g., 56, 12, -14; DC: $p < .0001$). For the older group, the competition regressor revealed activations within more anterior regions than the younger group (8 peaks, mean $y = -17$, median Z score $= 2.61$; 7 peaks: $p < .01$; 1 peak: $p < .0001$), located at the inferior temporal gyrus

TABLE 4
Behavioral Findings

	Younger participants Mean (*SD*)	Older participants Mean (*SD*)
Facilitation		
RT (ms)	16 (41)	26 (31)
Acc (% error)	.3 (3.1)	1.8 (4.7)
Interference		
RT (ms)	139 (93)	207 (125)
Acc (% error)	6.6 (9.8)	14.3 (11.4)

(e.g., −44, −18, −18; BA = 20; DC: $p < .003$), middle temporal gyrus (e.g., 60, −22, −10; BA = 21; DC: $p < .0001$), and superior temporal gyrus (e.g., −60, −6, 2; BA = 22; DC: $p < .008$). Direct comparisons verified this distinction between anterior and posterior regions of activation, with all peaks but one being unique. The one common region of activation determined by the direct comparisons was located in the superior temporal gyrus (−66, −32, 10, BA = 42).

For the younger group, the presence of conflicting color information resulted in one additional activation, located in the right superior temporal gyrus (68, −20, −2; BA = 21; DC: $p < .01$). Direct comparisons revealed that this peak was unique to the younger group. In contrast, for the older group there was a more diffuse network of temporal region activation (4 peaks; median Z score = 2.71, 2 peaks: $p < .01$; 1 peak: $p < .001$; 1 peak: $p < .0001$) with peaks located in the middle temporal gyrus (e.g. −52, −8, −6; BA = 21; DC: $p < .0001$) and superior temporal gyrus (e.g., −50, −50, 12; BA = 22; DC: $p < .01$). Direct comparisons revealed that all four peaks were unique to the older group.

Hence, in the case of competition and conflict for the temporal cortex, we found that activations within temporal cortex extended further in the ventral visual processing stream for older participants. This differentiation between posterior and anterior regions of activation for the younger and older groups may represent a deeper processing of the word information on the part of the older group.

Behavioral Data

For each participant we calculated reaction time (RT) and accuracy (Acc) measures of Stroop interference (incongruent–neutral) and Stroop facilitation (neutral–congruent). Both measures of accuracy and reaction time indicated a marginally significant increase [Acc: $F(1, 20) = 2.98$, $p < .10$; RT: $F(1, 20) = 2.10$, $p < .163$] in the magnitude of the interference effect in older participants (Acc: mean = 14.3%, *SD* = 11.4%; RT: mean = 207 ms, *SD* = 125) when compared to that in young participants (Acc: mean = 6.6%, *SD* = 9.8%; RT: mean = 139 ms, *SD* = 93). Nonsignificant increases in facilitation were also present in the older participants (Acc: mean = 1.8%, *SD* = 4.7%; RT: mean = 26 ms, *SD* = 31) when compared to younger participants (Acc: mean = .3%, *SD* = 3.1%; RT: mean = 16 ms, *SD* = 41). The number of participants in each group of our study is less than typically used in behavioral studies to detect differences in performance, which probably explains why some of the group differences were only marginally significant (see Table 4).

DISCUSSION

Consistent with our assertion that age-related deficits in working memory can be attributed to the impairment of attentional function, the attentionally demanding conditions of the Stroop task revealed decreased responsiveness in older participants of regions previously implicated in the support of both attentional control and working memory. In older participants, regions thought to be involved in imposing an attentional set that biases the selection of task relevant information, such as dorsolateral prefrontal and parietal cortex (Banich et al., 2000a, 2000b; Cabeza & Nyberg, 2000; MacDonald et al., 2000), were found to be less responsive to increases in the need for attentional control when irrelevant color information was present (i.e., when two competing sources of color information had to be differentiated). This loss in responsiveness suggests a decrease in the effectiveness of the structures responsible for implementing attentional control.

The presence of age-related changes in dorsolateral prefrontal function may be of particular importance to our understanding of age-related increases in the brain's susceptibility to disruption by irrelevant information. This region is thought to be involved in modulating neural activity within posterior brain regions, enhancing neural activity within those processing systems containing task-relevant information while dampening activity within those processing systems containing task-irrelevant information (Banich et al., 2000a, 2000b; Carter et al., 2000; MacDonald et al., 2000). By dampening the processing of irrelevant information early on, DLPFC is able to prevent or at least weaken the activation of associated representations (i.e., semantic and phonological) and actions. Consistent with this notion, in an fMRI study of Stroop task variants (color–word, color–object Stroop tasks) (Banich et al., 2000b), we found that when a word or object's identity is irrelevant to task performance, activations in the ventral visual processing stream are far less extensive than those observed in studies of word or object encoding (Kelley et al., 1998), terminating before reaching areas associated with recognition. Here we found that in older participants, for whom DLPFC activity appears to be compromised, activations within the ventral visual processing stream were more anterior than those noted for younger participants, reflecting more extensive processing of the word. A converging source of evidence for DLPFC's involvement in modulating the activity of posterior processing regions comes from the presence of negative correlations in our study between activity within DLPFC and various regions of extrastriate cortex previously shown to be associated with processing words (Kelley et al., 1998), such as the middle occipital gyrus ($r = -.73$).

Age-related changes in the sources of attentional control were not limited to dorsolateral prefrontal cortex. While the need for attentional control increased activity in parietal cortex for both groups, these increases were far less extensive in older participants than younger, suggesting less of a reliance on posterior regions in older participants. This decrease in the involvement of parietal cortex may be the result of decreases in the functional (Cabeza et al., 1997) or structural (Raz et al., 1997) connectivity of parietal and prefrontal regions. Interestingly, as older participants became more practiced with the task, parietal activity increased. Thus, it appears that in older participants, anterior regions may encounter greater difficulties recruiting parietal regions for task performance. However, with practice, these difficulties can be overcome.

Consistent with the predictions of several models of attentional control, age-related decreases in the brain's ability to implement attentional control impacted the activity of regions throughout the attentional network. For example, some models posit that anterior cingulate cortex is involved in evaluatory processes, such as detecting the potential for error (Carter et al., 1998; Botvinick, 2000; Carter et al., 2000; MacDonald et al., 2000) at the level of response (Milham et al., 2001). In the color–word Stroop task, during incongruent and congruent-word trials, the word's identity provides a competing source of color information on which the response can be based.

Even when the two sources of color information (ink color and word identity) lead to the activation of the identical response, selection mechanisms must ensure that the response is based on the task-relevant processing system's output to maintain proper task performance in subsequent trials. Thus, the potential for error is greatest on incongruent trials where there is a competing source of color information associated with a conflicting response, intermediate on congruent trials where there is a competing source of color information but no conflict, and least on neutral trials where there is no competing source of color information or conflict (potential for error: incongruent > congruent > neutral). If attentional control in older participants is compromised, the ability of a competing source of information to create a potential for error should increase. Consistent with this prediction, while both groups showed reliable increases in ACC activity for incongruent blocks, increases in ACC activity for congruent blocks were less reliable in the younger participants than the older.

We believe age-related increases in ACC's sensitivity to the occurrence of competition reflects a decrease in the effectiveness of attentional control in older participants. This increase in sensitivity may actually be deleterious to ACC function, as it can limit the range of activity over which cingulate operates. For example, if activity within cingulate cortex approaches a maximum level for the mere presence of competing information (i.e., congruent or incongruent vs neutral), it may be limited in its ability to differentiate between conditions of low and high conflict (congruent vs incongruent). Evidence for such a proposal comes from the finding that in older participants, there is less differentiation of ACC activity during conditions of high and low conflict than noted in younger participants.

Interestingly, while DLPFC was less active in older participants, anterior inferior prefrontal cortex (AIPFC) was more active. Some models of working memory, such as the two-stage working memory model proposed by Petrides and colleagues (e.g., Owen et al., 1996), argue that dorsolateral and ventrolateral regions of prefrontal cortex mediate different working memory processes. They posit that dorsolateral prefrontal cortex is involved in manipulation of representations in working memory (a role similar to that attributed to DLPFC in several models of attentional control). In contrast, ventrolateral prefrontal cortex is thought to be involved in the maintenance and evaluation of representations in working memory. Here we suggest that age related-changes in DLPFC compromise attentional control, decreasing the brain's ability to limit the contents of working memory and bias the selection of task-relevant representations. As such, maintenance and evaluation processes are taxed. Thus, we believe the increases in activity observed in anterior inferior prefrontal cortex may reflect the outcome of decreases in the effectiveness of attentional control, a process supported by dorsolateral prefrontal cortex.

When viewed in their entirety, our data suggest that DLPFC takes a dual approach to guiding task performance. First, as suggested by various studies of attentional function (e.g., Banich et al., 2000a, 2000b, 2000c; MacDonald et al., 2000; Milham et al., 2001), DLPFC attempts to bias the contents of working memory by modulating the neural activity of posterior processing regions, increasing that of task-relevant processing systems and decreasing that of task-irrelevant processing systems. Second, it interacts with VLPFC to select the representations within working memory on which task performance should be based. While these can be described as independent processes, the two are intimately associated. For example, as the selection of task-relevant representations within working memory becomes more difficult due to the presence of strongly activated interfering representations, DLPFC can increase its modulation of posterior processing regions in an effort to prevent further activation of interfering task-irrelevant representations while increasing that of task-relevant representations.

While it is possible that age-related decreases in the responsiveness of regions noted in neuroimaging studies of aging (e.g., DLPFC) reflect difficulties in the recruitment of neural activity or blood flow, an alternative explanation may lie in the difficulties associated with the older adults' performance of the less demanding (baseline) conditions. For example, in our study, older participants were slower than younger participants in the performance of neutral trials. It is possible that the difficulties encountered in performing the color-naming task itself may tax the brain's attentional network, reducing its dynamic range. As a result, when increases in competition or conflict occur, the brain is more limited in its response, leading to impairments in attentional control and performance. A simple way for future studies to address such a concern would be to include an extreme low-level reference condition as well, such as a resting state or fixation condition, in order to reveal changes in brain activity associated with less demanding conditions.

Summary

Our findings suggest that aging compromises the brain's ability to implement attentional control, allowing greater activation of irrelevant representations and actions capable of decreasing the efficiency of working memory processes. While the source of problems with the implementation of attentional control appears to be the decreased involvement of dorsolateral prefrontal and parietal regions, the impact of decreased control was noted throughout the brain. In particular, more extensive activation was noted within temporal cortex for older participants, indicating deeper processing of the word. In addition, greater activity was noted in ventral prefrontal cortex for older participants, reflecting the increased ability of irrelevant representations to gain access to working memory. Future studies will need to focus on explicating the causes of age-related changes in the responsiveness of prefrontal and parietal cortex to the need for attentional control.

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