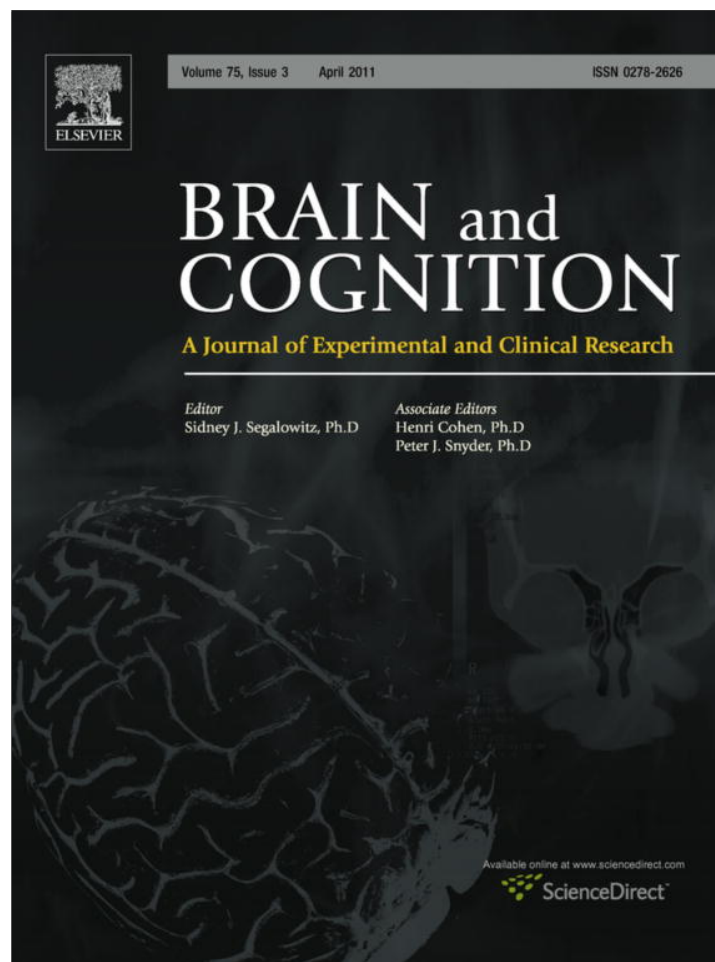


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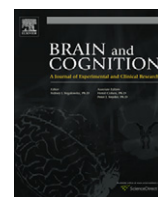
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Dual-task processing in younger and older adults: Similarities and differences revealed by fMRI

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ABSTRACT

fMRI was used to explore age differences in the neural substrate of dual-task processing. Brain activations when there was a 100 ms SOA between tasks, and task overlap was high, were contrasted with activations when there was a 1000 ms SOA, and first task processing was largely complete before the second task began. Younger adults ($M = 21$ yrs) showed activation in dorsolateral prefrontal cortex and in parietal areas as well as in ventral medial frontal cortex and sub-lobar areas. Activations in older adults ($M = 71$ yrs) did not differ significantly from younger adults except for higher activations in occipital and polar prefrontal cortex. The results were well fit by a model with two networks managing dual-task interference, a medial prefrontal network that detects changes in the stimulus situation and maps them to associated changes in the valence of response mappings and a lateral frontal–parietal network that initiates and carries out the shift from one task to the other. The additional activations in older adults as a group and the correlations of individual differences in activation with performance were consistent with recruitment within each of these networks. Alternative explanations such as hemispheric asymmetry reduction and reactive rather than proactive processing in older adults were not supported.

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1. Introduction

Carrying out more than one task at the same time is commonplace in everyday life, for example driving an automobile while conversing, either on a mobile telephone or with a passenger. Despite anecdotal claims that this can be done successfully, empirical evidence shows that under most circumstances, there is noticeable interference with both tasks. In the instance of telephoning while driving, both driving performance and conversation flow are significantly impaired (Charlton, 2009; Strayer & Drews, 2007). A very substantial body of evidence from controlled laboratory experiments confirms the validity of the findings from real world tasks (for reviews, see Pashler, 1994, 1998). Further, the difficulty in managing overlapping tasks appears to increase with advancing age (for reviews, see McDowd & Shaw, 2000; Verhaeghen, Steitz, Sliwinski, & Cerella, 2003). The existence and nature of age-related differences in dual-task management are of both theoretical interest and practical concern.

The method for studying dual-task performance that provides the most leverage in understanding interference gives two simple

tasks and systematically manipulates the onset time for the stimuli for each task. For example, in a study of simulated driving, Levy, Pashler, and Boer (2006) had participants carry out two tasks: The first task was to determine whether a brief auditory or visual stimulus had been presented once or twice; the second task was to press the brake pedal whenever the brake lights of a lead car illuminated. The SOAs between the auditory or visual stimulus and the brake light change ranged from 0 ms to 1200 ms. With single-task reaction times under 1000 ms for the auditory–visual task, this meant that there was substantial overlap between the tasks at the shortest SOAs whereas with the longest SOA the response to the first task would likely have been given before the stimulus for the second task appeared. Nevertheless, all of the processes involved in managing both tasks were present on each trial, unlike other approaches in which dual-task performance is simply compared to single-task performance. A large number of experiments using the varied-SOA procedure have been reported with very consistent results (for reviews, see Pashler, 1994, 1998). As SOA decreases (and, therefore, task overlap increases), RTs to Task 2 are slowed dramatically. RTs to Task 1 show little or no effect of SOA. This period over which the RT to Task 2 is slowed has been called the *psychological refractory period* (PRP, Vince, 1948; Welford, 1952) in analogy to the period after an initial firing when a neuron is unresponsive; the general paradigm is often called the

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PRP procedure. The overwhelming weight of the empirical evidence is consistent with *response-selection bottleneck models*.¹ These models assume that there are broadly three stages of processing, an early stage involving perceptual processing, a central stage involving response selection, and a final stage involving execution of the response. The critical assumption is that there is a bottleneck at the central processing stage, such that processes such as response selection can only be carried out for one task at a time (e.g., Lien, Ruthruff, & Johnston, 2006). Central processing of the other task must be postponed until central processing of the first task is complete. Unlike central processing, perceptual processing of the two tasks can occur largely in parallel as can execution of the responses for the two tasks (but see de Jong, 1993).

Age-related differences in cognitive function have been attributed to a reduction of executive control of cognitive processes in old age (e.g., Hull, Martin, Beier, Lane, & Hamilton, 2008). From one point of view, the PRP procedure provides an ideal vehicle to examine this hypothesis because of the need for additional executive control when the second task follows closely on the first (e.g., Erickson et al., 2005): (a) Two task sets must be maintained in working memory; (b) the order in which the two tasks are to be carried out must be prepared and then managed; (c) once processing of one task has begun, processing of the other task must be interrupted and delayed, while maintaining the results of processing already completed; (d) when processing can be returned to the second task, there must be a fast switch of attention back to that task and reinstatement of the processing; and (e) responses must be programmed and executed for two incompatible tasks. Any of these executive operations would be a plausible locus for age-related differences. In contrast to claims that the PRP procedure requires active, executive control, there is also a second and very different view point. In this point of view the behavioral slowing is simply due to passive queuing as the second task waits for necessary resources to become available (Jiang, Saxe, & Kanwisher, 2004; Marois, Larson, Chun, & Shima, 2006). In this view, the slowing is due not to increased executive demands but simply to postponement. If this point of view is correct, we might not expect any greater effect of task overlap in older adults than in younger adults, other than what would be expected from normal age-related slowing of all processes (e.g., Hartley, 2006; Salthouse & Miles, 2002).

Earlier studies of age differences in dual-task performance used procedures with little control over the relative onset of processing in the two tasks (e.g., McDowd & Craik, 1988). More recent age group comparisons have adopted variants of the PRP procedure with controlled onset of two simple tasks. The results for older adults, as for younger adults, have been well fit by response-selection bottleneck models. Allen, Smith, Vires-Collins, and Sperry (1998) concluded that interference in central stage response selection between the two tasks was greater in older than in younger adults. Glass et al. (2000) and Hartley and Little (1999), however, concluded that after general slowing was taken into account, the age differences were small, and could be localized to greater difficulty at input and to a slowed central process of the “unlocking” of

processing in the second task. Consistent with Glass et al., Hein and Schubert (2004) concluded that older adults were more sensitive to interference in input modalities. Maquestiaux, Hartley, and Bertsch (2004) also implicated greater difficulty in the switching of central processing when they found that highly trained older adults—but not younger adults—were aided by shifting to tasks that were comparable but with simpler response selection rules. Hartley and Maquestiaux (2007) concluded that central operations were equivalent in younger and older adults, but that older adults showed greater output interference. Hartley (2001) showed that much of the age difference in switching between two different tasks could be eliminated by removing output interference. Thus there are indications of age-related differences at all three phases: input processes, central processes, and output processes.

Neuroimaging is very promising as a way to put constraints on theories of dual-task interference (Jiang et al., 2004). Marois and Ivanoff (2005) reviewed a number of approaches that have been used, among them comparing dual-task performance to that of the two tasks done singly and comparison of dual-task performance with high task overlap to that with low task overlap. As they note, each approach has strengths and limitations.

Despite the variety of approaches that have been taken to neuroimaging of dual-task performance and although there are differences from study to study, the areas of activation have been relatively consistent (see Marois & Ivanoff, 2005, for a meta-analysis). Activations have been reliably found in lateral prefrontal cortex (Brodmann's Areas—BAs—9, 44, 45, 46), supplementary motor areas (BAs 6, 8), and parietal areas (BAs 7, 40). Activations have frequently been observed in the anterior cingulate cortex (BAs 24, 32), posterior areas such as cuneus (BAs 18, 19), orbital frontal cortex and anterior insula (BA 47), polar prefrontal cortex (BA 10), temporal areas (BA 37), and subcortical structures such as cerebellum, the basal ganglia, and the thalamus. Activations in these regions have been obtained in the left hemisphere, in the right hemisphere, and bilaterally.

Although different researchers describe it somewhat differently, a consensus model has emerged of how these areas might be involved in executive control of dual-task processing. In this view, the lateral prefrontal cortex is optimized for rapid, adaptive, amodal control (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Dosenbach et al., 2006, 2007; Marois et al., 2006) and is involved in the fast adaptation of response sets and the coordination of selection-for-action in situations with interfering information (Collette et al., 2005; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999; Schubert & Szameitat, 2003; Szameitat, Schubert, Müller, & Von Cramon, 2002). Medial areas, including anterior cingulate, are optimized for stable set maintenance, maintaining and monitoring associations between actions and their outcomes and the implementation of task sets particularly in situations of conflict (Dosenbach et al., 2006, 2008; Fleck, Daselaar, Dobbins, & Cabeza, 2006; MacDonald, Cohen, Stenger, & Carter, 2000; Rowe, Hughes, Eckstein, & Owen, 2008). The lateral and medial prefrontal areas interact to exercise top-down control, biasing signals to parietal areas that load, transmit, or implement the required task-set parameters (Dosenbach et al., 2006, 2008; MacDonald et al., 2000; Sigman & DeHaene, 2006). The parietal areas can also operate to feed information forward for stimulus-driven bottom-up shifts of attention.

Other studies have found little or no evidence for recruitment of executive areas in the dual-task situation beyond those activated in the single-task situation (Adcock, Constable, Gore, & Goldman-Rakic, 2000; Bunge, Klingberg, Jacobsen, & Gabrieli, 2000; Erickson et al., 2005; Jiang et al., 2004; also see Sigman & DeHaene, 2008). These studies are consistent with the passive-queuing model in which the processes carried out at short SOAs are no different from those carried out at long SOAs. Rather than active monitoring and management of processes in the two tasks, a delay is simply

¹ It has been argued that the central response-selection bottleneck is strategic and not obligatory (Meyer & Kieras, 1997a, 1997b), however the evidence for this comes from highly practiced individuals, using a very constrained set of stimuli and with 0 ms SOA (Hazeltine, Teague, & Ivry, 2002; Schumacher et al., 2001; see Meyer and Kieras (1999) and Meyer, Kieras, Schumacher, Fencsik, and Glass (2001), for lists of possibly necessary conditions). Miller, Ulrich, and Rolke (2009) have demonstrated that, even if parallel processing of two tasks were possible, serial processing would still produce the optimal outcome under a wide range of circumstances and, indeed, whether strategic or not, the bottleneck—evidenced by dual-task interference—is almost always present with non-zero SOAs. We will not attempt to resolve here the issue of whether the bottleneck is structural and immutable or strategic and malleable.

injected into the processing stream as Task 2 is passively queued until Task 1 central processing is completed.

Only one neuroimaging study has examined dual-task interference in older adults. Erickson et al. (2007b) presented older adults with two tasks simultaneously, to determine the color (yellow or green) of one stimulus and to determine the letter identity (B or C) of another. They did not report results of whole-brain analyses comparing dual and single tasks, but rather focused selectively on two regions of interest that showed significant change from before to after five dual-task training sessions, ventrolateral PFC and dorsolateral PFC. When we compared their results for older adults with those previously published for younger adults (Erickson et al., 2007a), it suggested to us that brain activations prior to training were greater in younger adults than in older adults in left ventrolateral PFC but were greater in older adults than in younger adults in dorsolateral PFC bilaterally. It is difficult to draw conclusions from this study about age differences in the neurobiological substrate of dual-task interference both because the information provided is relatively limited and because the procedure compared dual-task conditions with single-task conditions, rather than comparing short and long SOAs within the dual-task situation as is done in the PRP procedure. The present study examined age differences in dual-task interference using contrasts of activations at short (100 ms) and long (1000 ms) SOAs and using whole-brain analyses rather than predetermined regions of interest.

Absent previous findings, what age differences can we expect to find in brain activations in the PRP procedure? The literature provides three alternative schemas. Cabeza (2002) summarized a number of studies showing that areas of activation in older adults were similar to those in younger adults, but with a more bilateral pattern of activity. Because the evidence was limited, he restricted the generalization—a schema that he termed hemispheric asymmetry reduction in older adults or HAROLD—to the prefrontal cortex, but speculated that it might apply more generally. Reuter-Lorenz and Lustig (2005) concluded that these patterns were also observed in more recent studies. Although HAROLD is an empirical generalization, it has led to a number of theoretical conjectures. The asymmetry reduction can be seen either as *underactivation* or *overactivation* in older relative to younger adults. Reuter-Lorenz and Lustig describe hypotheses about underactivation as postulating impairments in cortical areas (e.g., differential age effects in the right hemisphere, Dolcos, Rice, & Cabeza, 2002) or in cortical–cortical connections (e.g., the age-related breakdown of white matter structural integrity, Ardekani, Kumar, Bartzokis, & Sinha, 2007; Bartzokis et al., 2004). Reuter-Lorenz and Lustig describe hypotheses that attribute overactivation either to compensatory or to incidental recruitment resulting from age-related impairment. Young adults show patterns of recruitment with increasing task demands (e.g., Braver et al., 1997), and older adults may attempt to compensate for greater difficulty by recruiting other areas of the cortex at lower levels of task demands. Alternatively, the overactivations may be nonselective (e.g., Logan, Sanders, Snyder, Morris, & Buckner, 2002) or may be the result of age-related failures of inhibitory connections (Cabeza, 2002). In these cases, the overactivation could be epiphenomenal or could be interfering. Reuter-Lorenz (Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Lustig, 2005) argue that the evidence is best explained by a schema somewhat broader than HAROLD, compensation-related utilization of neural circuits (CRUN) in older adults, the CRUN hypothesis or CRUNCH.

A very different schema to explain age differences in brain activation and cognitive processing has been proposed by Braver, Gray, and Burgess (2007). They propose dual mechanisms of cognitive control. When the management of task demands can be planned in advance and when resources are adequate, they argue that *proactive* control is likely to occur. Proactive control involves (a) the

active maintenance of context information in PFC, allowing it to bias processing in other systems, (b) the augmenting of PFC functions through rapid bindings of representations in the medial temporal lobe, and (c) performance monitoring in the ACC. When proactive control is not possible or too costly, *reactive* processing is invoked which is engaged only as needed on a just-in-time basis, rather than consistently and in advance of critical events. Braver et al. hypothesize that older adults, with processing limitations, are likely to resort to reactive processing in situations that elicit proactive processing from young adults. They predict that this shift will lead either to activations of brain regions not typically activated in younger adults or to different patterns of activation in the same areas activated in younger adults, decreasing in conditions most dependent on control and increasing when control is less possible. In support, they cite evidence of their own from a continuous performance task in which a long delay led to an increase in left PFC activation in younger adults, but a decrease in older adults, as well as a finding by Jonides et al. (2000) that resistance to interference in a Sternberg task in younger adults resulted in an activation in left PFC not seen in older adults. Velanova, Lustig, Jacoby, and Buckner (2006) offered a similar hypothesis that older adults shift to less taxing strategies than those used by younger adults.

1.1. Predictions

The theoretical notions we have reviewed lead to three quite different sets of predictions. First, (a) if we found activations consistent with reduced asymmetry or compensatory recruitment in older adults (i.e., consistent with the HAROLD generalization and CRUNCH hypothesis), (b) if dual-task processing is characterized by greater executive processing demands, and (c) if older adults are subject to impaired executive processing, we could expect to see more bilateral activations in lateral prefrontal cortex and in anterior cingulate and medial frontal cortex in older adults. We might also expect more bilateral activations in parietal cortex and extrastriate areas as well as subcortical areas. Second, if older adults adopt more reactive processing in the PRP procedure, following the notions of Braver et al. (2007) we would expect to see a reduction or elimination of lateral PFC and ACC and medial FC activation, in sharp contrast to the HAROLD or CRUNCH predictions. We might also expect to see increased activity in more posterior areas and in subcortical areas concerned with rapid switching of attention such as basal ganglia. Third and last, if dual-task processing simply reflects passive queuing of processes, we would expect to find few if any age differences in activation, once normalized for overall level of activity.

2. Method

2.1. Participants

Twelve older adults (7 female) age range: 65–77 years; $M = 70.67$) were recruited through the University of Michigan Institute of Gerontology and through newspaper advertisements. The 12 younger adults (6 female, age range: 19–25 years, $M = 21.00$) were recruited through University of Michigan subject pools and through newspaper advertisements. All participants were right-handed, free of positive neurological histories, and had normal or corrected-to-normal vision. The two age groups had similar median education levels (younger: 15 years; older: 16 years). All participants gave informed consent. Participants completed two sessions, one in which they were familiarized with the MR scanner and its operation and were given practice with the tasks and another in which they completed the experimental tasks in the scanner. They were told that there would be a payment of

\$100 for participation plus a bonus payment of up to \$20 for rapid responses with few errors. In fact, all participants were paid \$120. The University of Michigan and the Scripps College Institutional Review Boards approved the study.

2.2. Tasks

2.2.1. Single color-task trials

A black fixation cross appeared centered on a gray background at the beginning of each color single-task trial. After 300 ms, the color of the cross was changed from black to either red or green. After 1000 ms, the stimulus was removed. Responses were accepted from the onset of the color for 1500 ms. The instructions were to identify the color as quickly and accurately as possible by making a finger movement with the left hand. Movements were detected by microswitches embedded in the fingers of a glove-like device worn by the participant. Green was indicated by a movement of the left index finger; red, by a movement of the left second finger.

2.2.2. Single letter-task trials

A black fixation cross appeared, centered on a gray background at the beginning of each letter single-task trial. After 300 ms, the cross was replaced by the letter “C” or “D”. After 1000 ms, the stimulus was removed. Responses were accepted from the onset of the letter for 1500 ms. Responses were made by movement of the right index finger (for “C”) and the right second finger (for “D”).

2.2.3. Dual-task trials

Each dual-task trial began with a black fixation cross. After 300 ms, the color of the cross changed to red or green. Then, after an SOA of either 100 ms or 1000 ms, the cross was replaced by the letter, C or D, with the color remaining red or green as it had been. The stimulus was removed after 1000 ms. Responses, made as in the single tasks, were accepted for 2000 ms after the onset of each stimulus aspect.

2.3. Design

Prior to the scanning run, participants completed four sets of trials each comprising five dual-task trials, then five single-task color trials, then five more dual-task trials, then five single-task letter trials, for a total of 40 dual-task trials and 40 single-task trials in each of the four runs. The dual-task sections were an unpredictable mixture of short- and long-SOA dual trials. Each of two scanning runs had six sections each comprising five dual-task trials at 100 ms SOA followed by five dual-task trials at 1000 ms SOA, for a total of 60 dual-task trials in each run. Participants were instructed that both tasks would occur on each trial; the SOA was not mentioned. A 30-s resting baseline period in which a white cross appeared on a black background occurred before the first section, and after the third and sixth sections.

2.4. Image acquisition and pre-processing

MRI images were acquired using a 3T GE Signa scanner equipped with the standard quadrature headcoil (General Electric, Milwaukee, WI). Head movement was minimized using foam padding and a cloth restraint strapped across participants' foreheads. Experimental tasks were presented using E-Prime software (Psychology Software Tools, Inc.) and the IFIS 9.0 system with a 10-button response unit (MRI Devices Corp.).

Functional T2*-weighted BOLD images were acquired using a spiral sequence of 15 contiguous axial 5 mm slices (TR = 1000 ms, TE = 30 ms, flip angle = 90°, field of view (FOV) = 24 cm). Two structural images were also acquired: a T1-weighted gradient echo

(GRE) image was acquired using the same FOV and slices as the functional scans (TR = 300, TE = 6.8, flip angle = 65°); a high-resolution spoiled GRASS (Gradient Recalled Acquisition in Steady State; SPGR) image was also acquired (TR = 6.4, TE = 1.5, TI = 600, flip angle = 15°, FOV = 24 cm, 2.5 mm slice thickness). The T1 GRE images were acquired before the functional runs, and SPGR images were acquired after.

Functional images were corrected for slice acquisition timing differences using a local, 17-point sinc interpolation program (Oppenheim, Schafer, & Buck, 1999) and corrected for head movement using the realignment routines in the Automated Image Registration (AIR) package (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998). Subsequent pre-processing and analysis was done using SPM99 and SPM5 (Wellcome Department of Cognitive Neurology, London). Individual SPGR images were corrected for signal inhomogeneity (Glover and Kristoff, http://www-psych.stanford.edu/~kalina/SPM99/Tools/vol_homocor.html) and then co-registered to the corresponding T1 GRE images. SPGR images were then normalized to the SPM99 T1 template, which is in Montreal Neurological Institute (MNI) space, and those normalization parameters were applied to the T2* (functional) images. After spatial normalization, T2* images were smoothed using a 6-mm FWHM Gaussian filter. All of the analyses included a temporal high-pass filter (100 s) and each image was scaled to have a global mean intensity of 100.

2.5. Image analysis

All analyses were performed using the General Linear Model implemented in SPM99 and SPM5, with separate regressors and intercepts for each run. Epochs which were the length of each task block were convolved with a canonical hemodynamic response function (HRF). Contrast images for each participant were subjected to a random-effects analysis. The threshold for significance for individual voxels was set at 0.001. Monte Carlo simulation with Alpha Sim (Ward, 2000) was employed to select the minimum cluster size as 14 voxels in order to ensure that the false positive detection rate for the entire image was no more than 0.05. Anatomical location of activations was accomplished using xjView (Cui, 2007).

3. Results

3.1. Behavioral results

ANOVA was carried out on the median reaction times (RTs) to Task 2 (letter) on trials with correct responses to both the color task and the letter task as a function of the age group (younger or older) and the SOA (100 ms and 1000 ms). Medians were used rather than trimming to reduce the effect of outliers. There was a significant effect of age, $F(1, 22) = 19.58$, $p < .001$, $\eta_p^2 = .46$,² with older adults slower on average ($M = 969$ ms, $SE = 46$ ms) than younger adults ($M = 674$ ms, $SE = 48$ ms). There was also a significant SOA effect, $F(1, 22) = 47.99$, $p < .001$, $\eta_p^2 = .68$. The interaction of age group and SOA was not significant, $F(1, 22) = 2.03$, $p = .17$, $\eta_p^2 = .08$, with an average PRP effect ($RT_{100} - RT_{1000}$) of 296 ms ($SD = 123$ ms) for younger adults and 150 ms ($SD = 207$ ms) for older adults, a nonsignificant difference, $t(22) = 1.91$. ANOVA on the RTs to Task 1 (color) showed only a significant effect of age group, $F(1, 22) = 11.53$, $p = .002$, $\eta_p^2 = .33$, with older adults ($M = 940$ ms, $SE = 60$ ms) slower

² Partial Eta-squared (η_p^2) is calculated in all of the analyses reported here as $SS_{EFFECT}/(SS_{EFFECT} + SS_{ERROR(EFFECT)})$.

than younger adults ($M = 646$ ms, $SE = 63$ ms). Descriptive statistics are provided in Table 1.

3.2. Neuroimaging results

The locations of peak activations for significant clusters in young adults are reproduced in Table 2. Those for older adults are given in Table 3. For the younger adults there were clusters of activation in ventral medial areas (including basal ganglia, anterior cingulate cortex, and subgenual and orbital frontal cortex), in left sensorimotor cortex and right cerebellum, in right lateral prefrontal cortex, in the right temporal lobe, and in left superior parietal. There were areas of deactivation (or greater activity at long than at short SOAs) in the left inferior and middle occipital cortex (BA 19), in left middle and superior orbital frontal cortex (BA 10, 47), and in right medial supplementary motor area (BA 6). Activations and deactivations are shown graphically in Figs. 1 and 2. Whole brain analysis of older adults showed a much more limited pattern of activations, with peaks in the basal ganglia, left occipital cortex, and left orbital frontal cortex. Because there are significant methodological difficulties in application of fMRI to older adults such as age-related atrophy and change in brain morphology (Samanez-Larkin & D'Esposito, 2008), it seemed likely that activations in the older adults may have been substantial, but still may not have met the standard for significance. Consequently, we

Table 1
Mean reaction times (ms) as a function of age group, task, and SOA. (Standard Errors are in Parentheses.)

	Task	SOA		PRP ^a
		100 ms	1000 ms	
Younger adults	Task 1 (color)	643 (41)	649 (69)	272 (32)
	Task 2 (letter)	809 (51)	538 (33)	
Older adults	Task 1 (color)	956 (83)	925 (66)	179 (57)
	Task 2 (letter)	1059 (74)	880 (47)	

^a Psychological refractory period (PRP) is the difference in Task 2 Reaction Time between 100 ms SOA and 1000 ms SOA.

Table 2
Peak activations for younger adults: Locations (using Automated Anatomical Labels, AAL, Tzourio-Mazoyer et al., 2002), cluster sizes, locations (MNI coordinates), and peak Z scores showing greater activation with short (100 ms) SOA than with long (1000 ms) SOA.

AAL location	Cluster size	x	y	z	Z
<i>SOA₁₀₀ > SOA₁₀₀₀</i>					
Putamen_R	33	19	14	-10	4.67
Hypothalamus		0	-4	-10	3.98
Caudate_L		-11	30	-5	3.81
Postcentral_L	48	-38	-30	65	4.45
Postcentral_L		-41	-22	50	4.24
Postcentral_L		-41	-34	45	3.54
Cerebellum_4_5_R	21	19	-52	-25	4.39
Temporal_Inf_R	14	41	-11	-45	4.33
Temporal_Inf_R		49	-4	-40	3.90
Frontal_Mid_R	14	52	26	40	3.70
Frontal_Inf_Oper_R		52	19	25	3.34
Parietal_Sup_L	14	-22	-55	65	4.00
Cingulum_Ant_R	46	11	30	-5	3.64
Caudate_R		11	19	-5	3.55
Frontal_Inf_Orb_R		22	30	-10	3.44
<i>SOA₁₀₀₀ > SOA₁₀₀</i>					
Frontal_Sup_Orb_L	15	-30	45	-5	3.76
Frontal_Sup_Orb_L		-19	56	-5	3.47
Occ_Mid_L	23	-38	-90	-5	3.69
Occ_Inf_L		-41	-79	-5	3.66
Occ_Mid_L		-45	-94	-10	3.52

Table 3
Peak Activations for Older Adults ($SOA_{100} > SOA_{1000}$): Locations (using Automated Anatomical Labels, AAL, Tzourio-Mazoyer et al., 2002), cluster sizes, locations (MNI coordinates), and peak Z scores showing greater activation with short (100 ms) SOA than with long (1000 ms) SOA.

AAL location	Cluster size	x	y	z	Z
<i>SOA₁₀₀ > SOA₁₀₀₀</i>					
Occ_Sup_R	34	8	-98	20	4.31
Cuneus_R		22	-94	10	3.06
Caudate_L	14	-15	26	-5	3.72
Caudate_R		4	15	0	3.04
Sup_Occ_L	17	-19	-90	5	3.65
Mid_Occ_L		-26	-94	15	3.11
Caudate_R	15	11	26	-10	3.49
Rectus_L	16	-4	38	-15	3.48
Frontal_Mid_Orb_L		0	30	-10	3.22

directly compared the short SOA – long SOA contrasts for the two age groups. There were only four significant differences, consistent with the interpretation that patterns of activations in the two groups were substantially similar (see Fig. 3). Activation was significantly higher in older adults than in younger adults in right anterior prefrontal cortex (BA 10, $X = 21$, $Y = 66$, $Z = 10$) and the middle occipital gyri on the left (BA 39, $X = -42$, $Y = -79$, $Z = 10$) and right (BA 19, $X = 42$, $Y = -88$, $Z = 10$) and the right cuneus (BA 19, $X = 7$, $Y = -92$, $Z = 24$).

3.3. Behavioral performance and activation in regions of interest

To explore the relationships between dual-task interference represented in RTs and parameter values reflecting cortical activations, we defined as regions of interest the clusters of significant activation in the younger adult scans (listed in the preceding paragraph) as well as those identified in the contrast of older and younger adults (also listed in the preceding paragraph) and we extracted the individual parameter values for each participant in each of those clusters. We calculated the PRP effect, $RT_{100} - RT_{1000}$, as a measure of interference. The correlations between activations and the PRP effect were moderate in size but none reached conventional significance ($\alpha = .05$). In younger adults, Herath, Klingberg, Young, Amunts, and Roland (2001) reported a correlation of 0.84 ($R^2 = 0.70$) between activation in right lateral prefrontal cortex and PRP; Jiang et al. (2004) reported a correlation of -0.37 . We found a correlation of 0.30 in our sample. In the older adults, we found a positive correlation ($r = 0.34$) between activation in the ventral medial cluster and PRP, and negative correlations between PRP and activations in right lateral prefrontal cortex ($r = -0.25$), left superior parietal ($r = -0.32$), and right polar prefrontal cortex ($r = -0.49$). These correlations should be treated with caution. The sample sizes were very small. Also there was restriction of range for the activations, particularly in younger adults (for whom the standard deviations were 0.49 of those in the older adults on average).

4. Discussion

We will first discuss the neuroimaging results common to younger and older adults before returning to a discussion of the age differences.

4.1. Activations ($SOA_{100} > SOA_{1000}$)

4.1.1. Lateral frontal and posterior activations

The common activations—that is areas that were significant in younger adults and not significantly different in older adults than

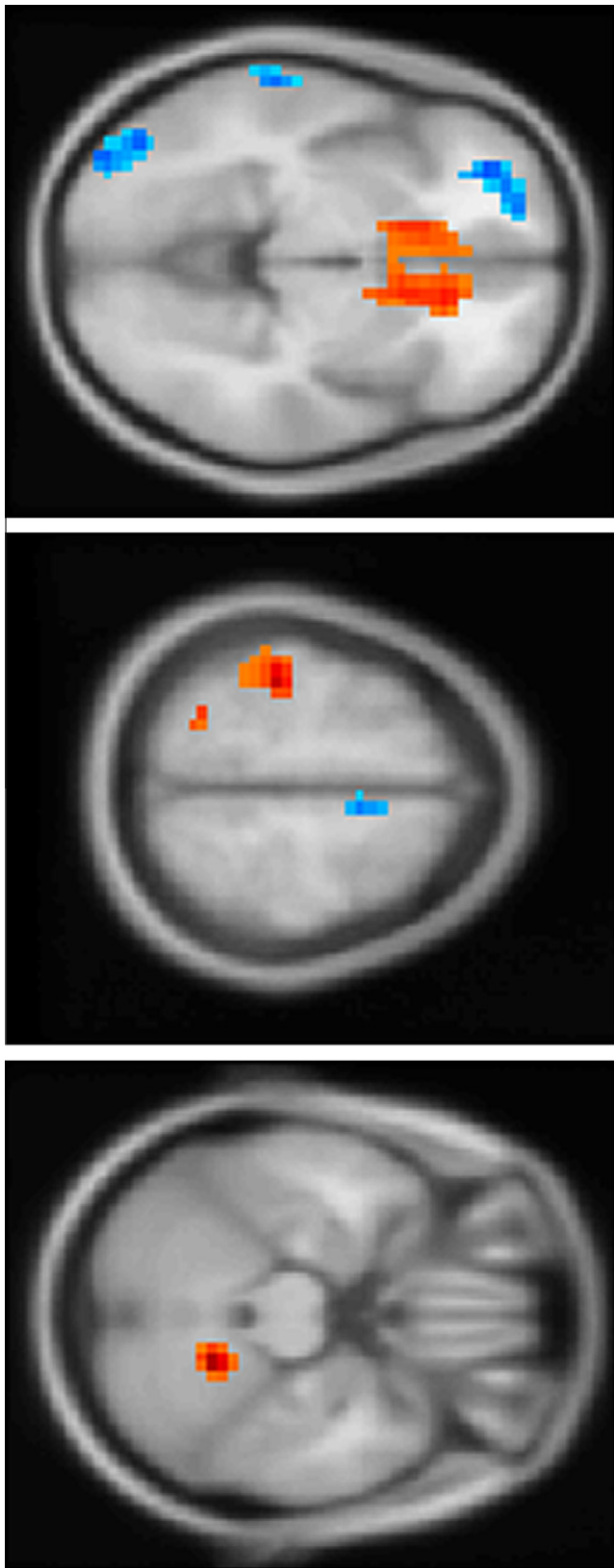


Fig. 1. Clusters of significant activations ($SOA_{100} > SOA_{1000}$, red) and deactivations ($SOA_{1000} > SOA_{100}$, blue) from younger adults. *Top.* Bilateral inferior medial (basal ganglia, anterior cingulate, subgenual and orbital cortex), $z = -5$. *Middle.* Left sensory and motor areas, $z = 60$. *Bottom.* Right cerebellum, $z = -25$.

in younger adults—were largely consistent with earlier findings, implicating a network that includes lateral prefrontal areas

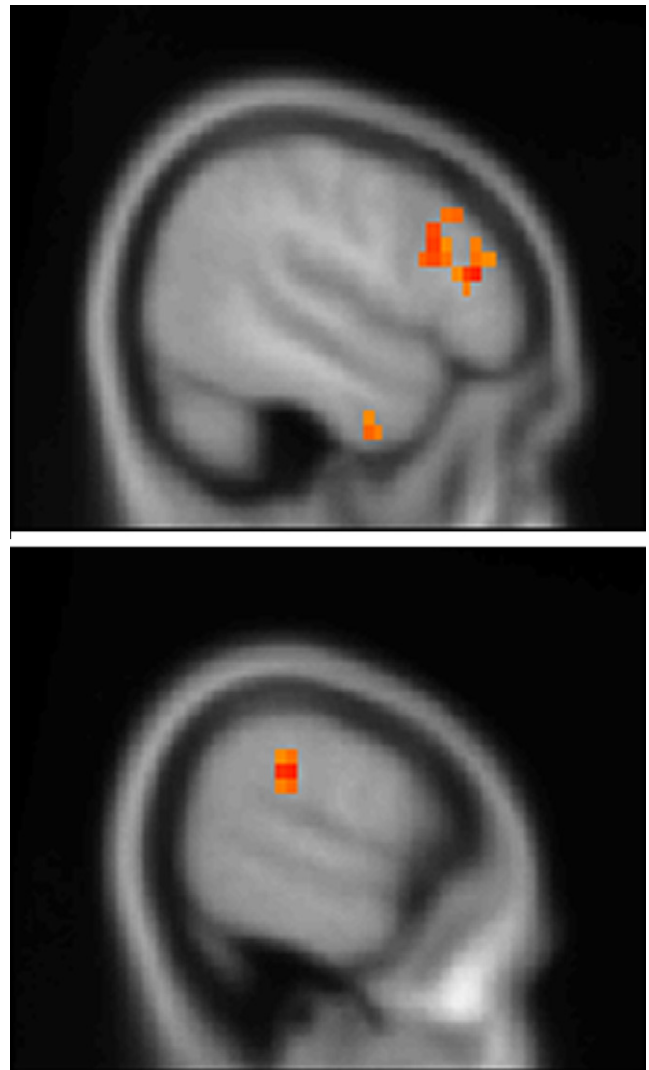


Fig. 2. Clusters of significant activations ($SOA_{100} > SOA_{1000}$, red) from younger adults. *Top.* Right dorsolateral prefrontal cortex and inferior temporal cortex, $x = 43$. *Bottom.* Left parietal cortex, $x = -60$.

responsible for the executive processes necessary to manage two tasks (Schubert & Szameitat, 2003) and extrastriate and parietal areas involved with shifting attention (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990; Corbetta, Shulman, Miezin, & Petersen, 1995; Schubert & Szameitat, 2003). In the designs most comparable to ours, Herath et al. (2001) and Jiang et al. (2004) found results resembling ours, with greater brain activation in right inferior frontal gyrus with short SOAs than with long SOAs. Marois et al. (2006) found no differences between an SOA of 175 ms and 875 ms.

The correlations between differential activation in the short versus long SOA and the differential slowing of the second task RTs should provide strong guidance about the functioning of different components of the system for detecting and managing task overlap. Positive correlations, indicating that high interference is accompanied by high activation, should be the signature of areas involved in detecting the rapid change of task sets. Negative correlations, indicating that high activation accompanies low interference, should be the signature of areas involved in managing the temporary storage of information and the rapid switch in sets. There was a moderate negative correlation of polar prefrontal activation and interference for older adults, consistent with a role for this area in managing potential interference. For right lateral

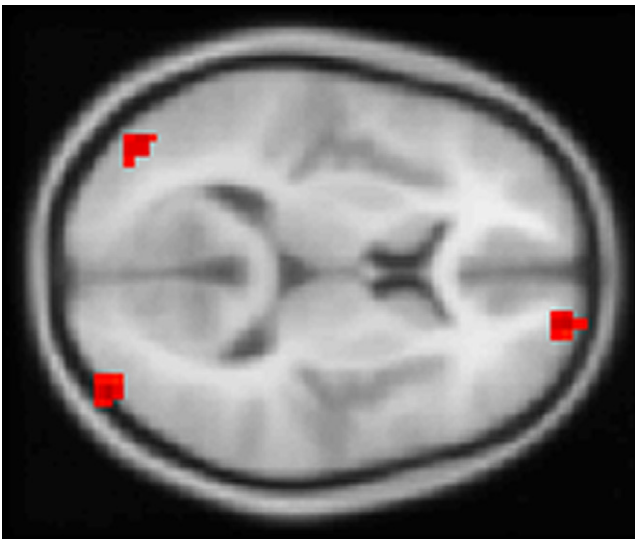


Fig. 3. Clusters with activation significantly higher for older adults than for younger adults, $z = 10$.

prefrontal cortex the picture is confused. The correlation for younger adults was positive as was that found by Herath et al. (2001), although smaller. The correlation for older for older adults was negative and similar in magnitude to that found by Jiang et al. (2004). Given the inconsistencies both across studies and within the present study as well as the small sample sizes in all of the studies, it seems premature to speculate about the implications of the correlations.

4.1.2. Medial and sub-lobar activations

We did not find activations in more dorsal medial areas including dorsal anterior cingulate and medial frontal cortex that have been reported on occasion (Dreher & Grafman, 2003; Erickson et al., 2005). Instead we found activity in more ventral medial areas—pre- and subgenual areas of anterior cingulate and orbital frontal cortex—and extensive activation in sub-lobar areas including the striatum. Activations such as these have been reported (e.g., Erickson et al.; Schubert & Szameitat, 2003; Stelzel, Schumacher, Schubert, & D'Esposito, 2006; Szameitat et al., 2002), but have received less attention than dorsal medial activations.

How might these ventral medial areas be involved in managing dual tasks? The more ventral areas in which we found activations may have been overlooked because they have been associated with emotion. In a comprehensive meta-analysis of emotion-related coactivations, Kober et al. (2008) found that pregenual and rostro-dorsal anterior cingulate cortex as well as the striatum, orbital frontal cortex, the frontal operculum, and anterior insula contributed to interrelated systems that were hypothesized to play a role in the generation and regulation of emotion and in the valuation of stimuli in general and rewards in particular. It is likely that these systems play a role in the evaluation of both internal and external affective input and the integration of that information into motivational states with associated goals. It is also the case however that activity in these areas has also been associated with cognitive operations (Bush, Luu, & Posner, 2000; Summerfield et al., 2006; Wager, Jonides, Smith, & Nichols, 2005). Other meta-analyses have linked these areas, particularly the anterior portion of the insula, to tasks that require executive control of attention (Nee, Wager, & Jonides, 2007; Wager, Reading, & Jonides, 2004; Wager & Smith, 2003) leading to speculation that this area is involved in goal formulation and reformulation, linking general motivational tenden-

cies with specific action plans (Wager & Barrett, 2004). Dosenbach has also described a network for adaptive, executive control that involves cingulate and polar frontal areas and that is distinguishable from the network involving lateral prefrontal cortex and parietal areas (Dosenbach et al., 2006, 2007, 2008). Thus the same cortical regions have been implicated in both emotional and cognitive, executive processing.

Although cognition and emotion are often conceived as independent systems, we suggest an alternative view, which is that the processing of any self-relevant event is accompanied by affective experience (Wager & Barrett, 2004), labeled *core affect* (Russell & Barrett, 1999). In any experiment, certain events are assigned by the instructions to be self-relevant, arbitrarily and temporarily, and thus carry affective valence for the duration of the experiment. The activation of this network in dual-task processing with a short SOA likely involves recognizing and managing the rapid change in valences as the stimuli for the two tasks arrive in rapid succession.

4.1.3. Sensorimotor and cerebellar activations

We also found brain activation in left sensorimotor areas and right cerebellum. This may be related to the second response, which was given with the fingers of the right hand. Finger movement responses have been found to produce activation in the contralateral sensorimotor and motor regions as well as ipsilateral cerebellum (e.g., Goerres, Samuel, Jenkins, & Brooks, 1998; Jancke, Specht, Mirzazade, & Peters, 1999; Mattay et al., 1998). It is the case, however, that activation related to both responses would have been detected for both short and long SOA thus the contrast would have removed activation that simply reflected the motor response to the second task with the right hand. It may be, however, that areas related to motor programming and execution are additionally activated when the results of processing related to the second task must be maintained while central processing in the first task is completed. A plausible hypothesis is that the processing that is held up by the bottleneck could be thought of as being maintained in this motor-cerebellar network. For a response-selection bottleneck model, this hypothesis implies, in turn, that the processing held at the bottleneck involves the selection of the motor response rather than simply an abstract response category. In retrospect, in order to determine whether these motor activations were related to dual-task demands or simply artifactual, it would have been desirable to model the motor responses without the processing demands. Unfortunately, we did not do this.

4.2. Deactivations ($SOA_{1000} > SOA_{100}$)

The deactivations, or more correctly selective activations with a long rather than short SOA, that we observed in occipital cortex can likely be attributed to the sudden onset of the letter after the processing of the color was complete or nearly complete. We speculate that the most informative part of the letter for discriminating C from D was to the right of fixation, projecting to the left side of the retina and the left visual cortex. The activations in left orbital frontal cortex and dorsal medial supplementary motor areas are in regions that have been implicated in task shifts (Nee et al., 2007). We speculate that activations in these areas may reflect activation of a task set when demands to manage two sets both competing for processing resources are absent, as is the case with a long SOA.

4.3. A model of dual-task processing

All of the operations that must be carried out with a long SOA must also be carried out with a short SOA: maintaining both sets

of response mapping rules and processing the stimuli, mapping them onto responses, and executing those responses for both tasks. As a result, a passive-queuing explanation of dual-task processing would predict that no additional cortical areas would be recruited by a short SOA. We found substantial recruitment and so our results are compatible with explanations that assume additional executive demands at short SOAs. On any trial, an individual must maintain top-down preparation for either a long SOA (low interference) sequence or a short SOA (high interference) sequence. Whether the shift between tasks is rapid or not must be signaled bottom-up. Our hypothesis is that the stimuli and their linked actions are made self-relevant, and therefore affectively charged, by the instructions. The affect-related ventral medial network senses the arrival of the second stimulus and an associated shift in valence is activated. This information is communicated to the lateral prefrontal–parietal network that maintains and manages the abstract representations of the goal sets. The interaction of these two networks initiates processes in sensorimotor cortex and cerebellum that maintain information about the second stimulus (including results of partial processing) until the processing of the first task is sufficiently complete. At that time, parietal areas that actually execute the shift of attention from one task to the other are activated. On long-SOA trials, instead of overlapping tasks with different valences, one task is completed before the second task arrives. The greater activations in visual cortex and goal-maintenance areas of orbital frontal cortex at long SOAs (seen as deactivations in Fig. 2) may reflect this less-pressured shift. The shift in motor programs itself with a long SOA may be reflected in the activations in the medial dorsal supplementary motor area.

There are two important questions to be addressed. First, why did we find ventral medial activations whereas others had found more dorsal activations? The studies that have reported medial activations in ACC and pre-SMA/SMA have all used the approach of contrasting dual-task with single-task situations (e.g., Erickson et al., 2005; Koechlin et al., 1999; Schubert & Szameitat, 2003; Stelzel, Schumacher, Schubert, & D'Esposito, 2006; Szameitat et al., 2002). It is possible that when the necessity of a particular shift can be anticipated on each trial, a more top-down control may be exercised, and this may involve more dorsal medial structures. Nevertheless, Erickson et al. (2005) used an event-related design in which single-task and dual-task trials were randomly intermixed. It would not be possible to plan for a regular shift in this design. However, the onsets of the two tasks were simultaneous (0 ms SOA). With simultaneous onset, the order of processing is determined by the individual and could be controlled top-down whereas with a delayed onset, processing is primarily controlled by the order of appearance of the stimuli and may be more bottom-up driven (see also Sigman & DeHaene, 2008). Our hypothesis is that the ventral medial network is activated when the shift between tasks is more reactive and that the dorsal medial network is activated when the shift is more prepared. Using resting-state functional connectivity methods, Dosenbach et al. (2008) concluded that anterior prefrontal cortex along with anterior insula and frontal opercular cortex and dorsal medial anterior cingulate and medial superior frontal cortex formed a distinguishable fronto-opercular network for top-down control, responsible for stable set control. The frontal opercular network (a) was distinguishable from a second, fronto-parietal network involving lateral prefrontal cortex and parietal areas, (b) was responsible for rapid adaptive control of the operative set, and (c) communicated indirectly with the fronto-parietal network via the cerebellum. In this view, the dorsal and ventral regions for detecting and responding to changes in the stimulus state are different components of the same underlying network.

The second question to be addressed is why we found several areas more activated at a short SOA than at a long SOA, suggestive

of additional executive demands, whereas earlier studies with similar approaches found no difference (Marois et al., 2006) or differences only in the right inferior frontal gyrus (Herath et al., 2001; Jiang et al., 2004), suggestive to Jiang et al. of passive queuing of the second task rather than activation of executive functions. It cannot simply be scanner sensitivity. Although Herath et al. used a 1.5 T scanner, Jiang et al. and Marois et al. used 3 T scanners as did we. It is unlikely to be task complexity. Although Herath et al. used simple reaction time tasks, Jiang et al. and Marois et al. used complex reaction time tasks involving colors and either shapes or letters, comparable to ours. The question remains unresolved.

4.4. Age differences in activations and an extension of the model

The behavioral evidence for dual-task interference—the slowing of Task 2 RTs at the short SOA—was statistically equivalent in younger and older adults. Nevertheless, the older adults had significant additional activations in right polar prefrontal cortex and, bilaterally, in occipital cortex. We made three different predictions about age differences in cortical activations: (a) compensatory recruitment in older adults of areas of frontal cortex involved in executive processing, (b) reduced frontal activation due to more reactive processing, or (c) little or no age difference because dual-task processing largely involves passive queuing. The results are most consistent with the compensatory recruitment schema. We relaxed the criteria for significance to $p = .005$ (from .001) and for cluster size to 10 (from 14) and found that each of the occipital areas in which older adults showed significantly greater activation either overlapped or was directly adjacent to an area of activation in younger adults, suggestive of compensatory recruitment of nearby regions of cortex. The activation in right polar prefrontal cortex, however, was unique to older adults. Several studies have concluded that anterior prefrontal cortex maintains task and context information (Braver, Reynolds, & Donaldson, 2003; Dosenbach et al., 2006; Koechlin et al., 1999; Sakai & Passingham, 2003, 2006). The correlations between the PRP effect and activations, while they must be interpreted with caution, suggest that older adults vary in the extent of recruitment. Following the resting-state functional connectivity analyses of Dosenbach et al. (2008) we can speculate from the correlations we observed that the older adults who selectively recruited the lateral frontal–parietal and cingulo-polar prefrontal network in order to manage the current goal set of Task 1 and the pending goal set of Task 2 avoided an increase in dual-task interference.

Our results are not, however, consistent with the HAROLD schema of compensatory recruitment. There were lateralized activations in right lateral prefrontal cortex, in left sensorimotor cortex and right cerebellum, and left parietal cortex in younger adults. No significant increase in activation in homologous contralateral areas was observed when older adults and younger adults were contrasted. One possibility is that HAROLD was largely (but not completely) derived from neuroimaging studies of episodic or semantic memory (Cabeza, 2002). Colcombe, Kramer, Erickson, and Scalf (2005) have suggested that recruitment of prefrontal cortex regions may depend on whether the additional cortical processing brought to bear can play a complementary role in task performance. It is possible that other areas of prefrontal cortex can play a compensatory role in memory tasks, but not in other tasks. To explore this possibility, we reviewed studies in which the task was not explicitly memory, for example the flanker task (Colcombe et al., 2005), the Stroop task (Langenecker, Nielson, & Rao, 2004), and visual search (Madden, Whiting, Provenzale, & Huettel, 2004). We found evidence for HAROLD-type recruitment of prefrontal regions by older adults in most of these studies (Colcombe et al., 2005; DiGirolamo et al., 2001; Langenecker,

Briceno, Hamid, & Nielson, 2007; Langenecker et al., 2004; Lee et al., 2006; Riecker et al., 2006; Townsend, Adamo, & Haist, 2006) but not all (Madden et al., 2004; Milham et al., 2002; Thomsen et al., 2004). The activations we observed in anterior frontal cortex were in an area already implicated in a top-down control network engaged in dual-task processing. This converges on the conclusion that this is a specific compensatory recruitment in response to task demands. It is not a homologous activation indicative of reduced lateralization.

The results also appear inconsistent with the schema that assumes that older adults will respond reactively to demands that younger adults handle proactively (Braver et al., 2007). This schema predicted different activations in younger and older adults. However, the model we offer for both younger and older adults views task shifts in the dual-task situation as largely reactive. If processing is already reactive for younger adults, it might be difficult to detect any strategic age differences. The additional activation in older adults is in anterior prefrontal cortex, which we presume to be part of the network that reactively assesses stimulus changes and associates them with changes in the valence attached to response mappings, so the additional frontal activation is not inconsistent with more reactive processing in older adults. We did not find any overall significant age-related reduction in activity in the lateral prefrontal and parietal cortex, presumed to underlie the proactive maintenance of response mappings for both task sets and for engineering the shift between them. Nevertheless, we did find that older adults with greater activation in those areas showed less behavioral interference. In this view, older adults who adopt a more proactive processing strategy are more successful.

One possibility that must be considered is that the older adults tested were anomalous. The PRP effect in RTs was equivalent in the older and younger adults, whereas most studies have found a larger PRP in older adults, suggesting that this might simply be a particularly able sample of older adults. Nevertheless, the age differences that have been observed have not been large and have not always been significant. For example, Hartley and Little (1999) in seven experiments using samples from the same populations, failed to find significant age differences in the PRP effect in two of those experiments. A more likely possibility is that our procedures led to an underestimation of the PRP effect for older adults. With mean Task 1 RTs over 900 ms, Task 2 central processing would have been delayed on a substantial fraction of trials even with a 1000 ms SOA.

Our results are consistent with the interpretation that overlapping tasks elicit active, executive operations as well as, rather than only, passive, stimulus-driven operations. Our results further suggest that the neural substrates responsible for managing dual-tasks are largely similar in younger and older adults, involving a medial prefrontal network that detects changes in the stimulus situation and maps them to associated changes in the valence of response mappings and a lateral frontal–parietal network that initiates and carries out the shift from one task to the other. Among older adults, there appears to be recruitment of a polar prefrontal area responsible for top-down management of task goals. We found correlational evidence suggesting that individual differences in the activation of this region may be related to more successful reduction in dual-task interference. It is important, however, to end with a caveat. We caution that our speculations range beyond the limits of generalizability of our single, small study. We offer them as guides to hypothesis generation for future work by ourselves and others.

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