The neural basis of task-switching in working memory: Effects of performance and aging

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We studied the performance of young and senior subjects on a well known working memory task, the Operation Span. This is a dual-task in which subjects perform a memory task while simultaneously verifying simple equations. Positron-emission tomography scans were taken during performance. Both young and senior subjects demonstrated a cost in accuracy and latency in the Operation Span compared with performing each component task alone (math verification or memory only). Senior subjects were disproportionately impaired relative to young subjects on the dual-task. When brain activation was examined for senior subjects, we found regions in prefrontal cortex that were active in the dual-task, but not in the component tasks. Similar results were obtained for young subjects who performed relatively poorly on the dual-task; however, for young subjects who performed relatively well in the dual-task, we found no prefrontal regions that were active only in the dual-task. Results are discussed as they relate to the executive component of task switching.

Working memory (WM) is a system for the temporary storage and processing of information. A major reason why researchers are interested in this system is its connection to higher-level cognition. In many computational models of higher-level cognition that simulate planning, mental calculation, and reasoning, WM is used as a kind of "mental workspace," allowing calculations to be performed on active data structures (1, 2). In behavioral work, there are numerous demonstrations that individual variations in WM capacity, as measured by certain kinds of tasks, are correlated with individual variations in planning and reasoning (e.g., see ref. 3). Given the apparent importance of WM to thinking, it is not surprising that there has been a rush of neuroimaging studies in the last several years to explore the neural bases of WM. However, by and large the WM tasks used in neuroimaging are not the kind of tasks that correlate with measures of higher-level cognition. Thus, much of what we know about the neural bases of WM may not bear on the way in which WM is used in higher-level cognition.

A WM paradigm that is known to correlate with higher-level cognition, and that we used in our experiment, is the Operation Span (4). On every trial, a sequence of items (e.g., five) is presented, each item consisting of an equation and an unrelated word; the subject has to determine whether the equation is correct and then commit the word to memory, maintaining the words in order. Essentially, this is a dual-task paradigm, involving both math and memory processes. At the end of the trial, memory is tested by a probe that contains the words in a particular order, and subjects have to indicate whether the probe order corresponds to the input order. The microstructure of this task involves a cycle of processing and storage. The subject applies task-specific arithmetic processes to the first equation, then adds a word to WM (a task switch), then processes the second equation while maintaining the WM load (a task switch), then updates WM with the second word (a task switch), and so on. The cycle thus requires switching back and forth between task-specific processes and updating WM. This same kind of process–storage cycle seems to be involved in mental calculation (e.g., when multiplying two 2-digit numbers, first multiply the right most digits, store the partial product in WM, perform the

next arithmetic operation, etc.), and in planning (e.g., mentally make a particular chess move, store the new board configuration in WM, mentally make your opponent's move, etc.). This common cycle may be why tasks like the Operation Span correlate highly with measures of higher-level cognition.§

Subjects were imaged by positron-emission tomography (PET) while performing the Operation Span and three other tasks: a Math task that requires only evaluating the equations, a Memory task that requires only remembering the words in order, and a baseline or Control task. Contrasting the images obtained during Operation Span with those obtained during Math and Memory tasks allows us to isolate two "executive" components that may lie at the heart of the process–storage cycle: switching between tasks (evaluating equations vs. updating WM) and maintaining a WM load while performing a distracting activity.

One issue of concern is whether these executive processes recruit areas in prefrontal cortex (PFC) that are not involved in the constituent tasks of Math and Memory. Finding such PFC areas would imply that the executive processes require specific PFC regions (i.e., activation of these regions is necessary for the executive processes to be implemented). (Whether these PFC regions are also exclusively devoted to the executive processes is a related, but distinct question.). There is mixed evidence on this question of specific PFC regions for task-switching. D'Esposito et al. (5) required subjects to alternate between two (nonmemory) tasks, and found that the task-switching requirement activated the dorsolateral PFC, whereas performing either task alone did not. However, in a more recent study, Adcock et al. (6) did not find evidence for the selective recruitment of PFC in task-switching.

In one of the only prior studies that used a WM task that required a process–storage cycle, Bunge et al. (7) imaged subjects while they performed tasks similar in structure to the Operation Span. (The dual-task of Bunge et al.'s experiment required evaluating sentences and remembering the sentence-final word, whereas their other tasks required just sentence evaluation, or just memory for words.) They found no PFC area that was activated only during the dual-task. However, the Bunge et al. dual-task may not have been sufficiently demanding, because

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performance on memory and sentence evaluation was as accurate in the dual-task as when tested alone. Because our dual-task will prove more demanding, our contrast between Operation Span and the Math and Memory tasks could well reveal regions in dorsolateral PFC that are specific to task-switching and storage-during-distraction.

A second issue is how the task-switching and storage-during-distraction executive components are affected by normal aging. Accordingly, older as well as younger subjects were tested. Aging is known to disproportionately affect the PFC (e.g., see ref. 8), and some executive processes (e.g., selective attention and inhibition) are suspected to be mediated by specific PFC regions (e.g., see ref. 9). One possible experimental outcome is that the contrast between the Operation Span and the Math and Memory tasks may reveal less PFC activation for older than younger subjects, because a specific prefrontal area is needed for the executive components and this area is dysfunctional in older subjects. Alternatively, the contrast between Operation Span and the other tasks may reveal more activation for older than younger subjects, because the specificity hypothesis for executive processing is wrong and numerous PFC areas can implement executive components, with older subjects having to recruit more of these regions. Prior research on aging and WM has shown both of these patterns of results (e.g., see refs. 10 and 11).

Methods

Subjects. Twelve young volunteers (average age, 22.9; range, 18–29), and 12 senior volunteers (average age, 66.6; range, 65–72) participated after providing informed consent. In each age group, there was an even number of males and females. All subjects were right-handed.

Behavioral Procedures. Slightly different versions of the tasks were used with the young and senior subjects to equate performance and task difficulty between groups. Young subjects performed four different tasks in the scanner: Operation Span, Math, Memory, and a Control condition. In Operation Span, a trial started with a 500-msec fixation point. Then a total of five equation–word pairs were presented in sequence, each for 3 sec (with 200 msec between items), followed by a probe list of the five words presented for 4 s. By pressing one of two mouse buttons (labeled "Yes" and "No"), subjects first indicated whether each equation was correct, and later in the trial indicated whether the probe order was identical to the input order. The other three conditions were created by altering some aspects of the Operation Span. In the Math task, five equations were again presented in sequence for 3 sec each, and the words were replaced by rows of five circles and the memory probe replaced by five rows of five circles each. The purpose of presenting the circles was to keep the perceptual input roughly comparable to that in Operation Span, and subjects arbitrarily pushed one of the two response buttons to the pseudoprobe. In the Memory task, five words were presented in sequence for 3 sec each, while each equation was replaced by six squares to provide perceptual input comparable to that in Operation Span; subjects arbitrarily made one of the two responses to the squares. After the last word, a probe list of the words was presented, and subjects indicated by a button press whether the probe order matched the input order. In the Control condition, five items were presented in sequence, but now each item consisted of six squares and five circles; the last item was followed by a pseudoprobe of five rows of five circles: Subjects arbitrarily made one of two responses to the squares and the pseudoprobe. In all four tasks or conditions, there were 20 trials.

The same four tasks were performed by the senior subjects, but the tasks were modified in two ways to promote performance levels equivalent to those obtained with young subjects: (*i*) In all tasks, four, rather than five, items were presented; and (*ii*) each item was presented for 3.75 sec rather than 3 sec, and there was 250 msec rather than 200 msec between items (so that the overall time for a trial remained the same as for the young subjects). Pilot work showed that these parametric changes produced accuracy levels comparable to those obtained by young subjects on the Memory and Math tasks.

Subjects participated in each of the four conditions for four PET scans each, counterbalanced for order of presentation. Before the PET session, subjects received practice on the Operation Span, Math, and Memory tasks in a session that included five trials of each. Stimuli were presented on a Macintosh computer controlled by PSYSCOPE software (12). To indicate their decisions about the equations and memory probes, subjects used a two-button mouse, responding with either their index ("Yes") or middle ("No") finger of their right hand. In both the Operation Span and Math conditions, 50% of the equations were correct; in the Operation Span and Memory conditions, 50% of the memory probes matched the input order; when there was a mismatch, only two words had been switched in order. The equations used were based on Turner and Engle (4) and involved two components: (*i*) The multiplication or division of two integers, and (*ii*) the subtraction or addition of a third integer to the product of the first component. A fixed set of 14 concrete words, selected from LaPointe and Engle (13), was used. Half the words were one syllable, the other half three syllables.

Image Acquisition. A Siemens ECAT EXACT-47 PET (Iselin, NJ) scanner acquired data in three-dimensional mode (septa retracted), with measured attenuation but no correction for scattered events. Three-dimensional reconstruction yielded 47 contiguous slices that were 3.375 mm (center to center) apart with in-plane resolution of 10 mm at full-width half maximum. Subjects were positioned in the scanner, and head position was recorded and verified before each scan. A bolus of 10 mCi (1 Ci = 37 GBq) of [^{15}O]water was delivered intravenously over a 10-s interval as the subject began the sequence of trials. Acquisition began when the true coincidence rate exceeded half the random coincidence rate. Eight minutes separated each scan to allow the residual radiation to return to an acceptable level.

Image Analysis. A complete description of the image analysis protocol is given elsewhere (14). In brief, it consisted of the following steps: Intrasubject registration corrected motion between scans for each subject (15). Each subject's image sets then were transformed to a stereotaxic system (16). A subtraction image set then was created for each subject between the averaged images for each contrast of interest. The subtraction images were then averaged across subjects. SDs for the voxels were averaged within the brain to create a pooled estimate of variance, and a *t* statistical value was calculated for each voxel by using a pooled variance estimated correcting for multiple nonindependent comparisons (17, 18). Significant changes in cerebral blood flow were localized by using stereotaxic coordinates (and are displayed in Figs. 1 and 2 on a standard nonlinearly warped MRI for visual interpretation).

Results

Behavioral Findings. Performance was measured for the different tasks—just Math or just Memory on the one hand vs. Operation Span on the other—separately for young and senior subjects. Starting with the young subjects, accuracy in the Operation Span—83% for Math and 76% for Memory—was less than in either of the constituents—88% for Math only and 91% for Memory only. Thus, there is a cost in both math and memory accuracy from having to perform the two tasks concurrently. In the Operation Span, latency for the math constituent was 2,054 msec, whereas that for the memory constituent was 1,974 msec. When each task was performed separately, the math latency remained almost unchanged (2,023 msec), but the memory latency was faster (1,873 msec).

For the senior subjects, accuracy in Operation Span was 82% for the math constituent and 72% for the memory constituent. In
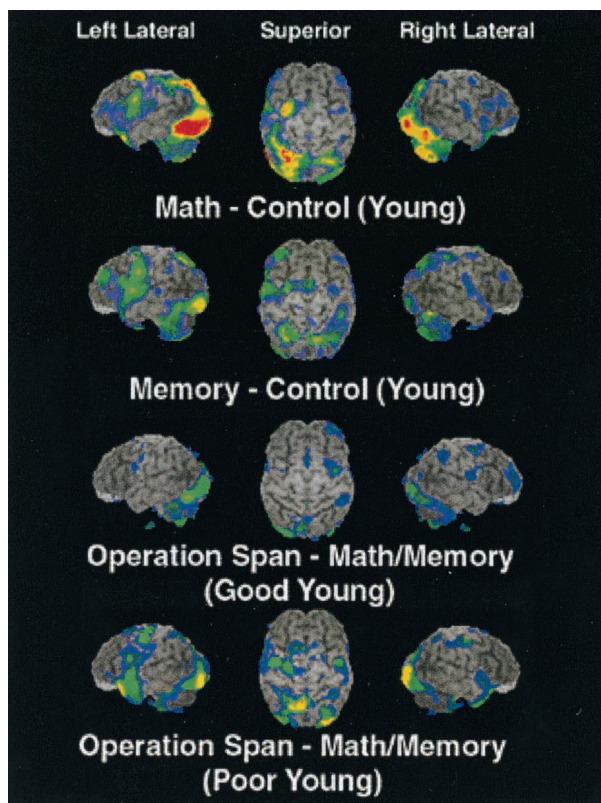
Fig. 1. PET activations for the young subjects. The first two rows correspond to the Math and memory conditions, each with the control activations subtracted for all of the young subjects. The last two rows correspond to the activations of the good-young and poor-young, respectively, with the average of the constituent tasks subtracted (math and memory). Shown in the figure are left and right lateral views, as well as a superior view. The PET activations are superimposed on a surface rendering of a brain created from a standard MRI image. The PET activations are shown as areas of increased brightness on the background MRI image, with the brightest possible areas corresponding to a *z*-score of 7.0. and the lowest activations corresponding to a *z* of 1.65.

Fig. 2. PET activations for the senior subjects (see Fig. 1 legend for details).

contrast, accuracy was 91% on the Math only and 93% on the Memory only. In terms of RT, overall senior subjects tended to be slower than their younger counterparts (but slowing is ubiquitous in age comparisons—e.g., see ref. 19). Their RT for the math and memory constituents of Operation Span was 2,522 msec and 2,017 msec, respectively. This is to be contrasted with a 2,365 msec latency to Math only and 1,762 to Memory only. Thus, like the young subjects, the seniors demonstrate a cost in accuracy and latency in the Operation Span compared with the Math and Memory tasks.

All of these claims are supported by statistical tests. Analyses of variance for math accuracy and memory accuracy show main effects of performance on the single- vs. the dual-task, but no effect of age and no interaction between task and age. (For math accuracy: $F(1,22) = 18.1$, $P < 0.003$, for the task effect; $F(1,22) = 0.06$, $P < 0.80$, for the age effect; and $F(1,22) = 0.72$, $P < 0.404$, for the interaction. For memory accuracy: $F(1,22) = 50.42$, $P < 0.001$, for the task effect; $F(1,22) = 0.062$, $P < 0.80$, for the age effect; and $F(1,22) = 1.08$, $P < 0.31$, for the interaction.) Analyses of variance of math latency and memory latency show main effects of both task and age, as well as an interaction that reflects the fact that senior subjects pay a higher cost for doing two tasks concurrently. (For math latency: $F(1,22) = 8.10$, $P < 0.009$, for the task effect; $F(1,22) = 37.61$, $P < 0.001$, for the age effect; and $F(1,22) = 3.56$, $P < 0.073$, for the interaction. For memory latency: $F(1,22) = 24.49$, $P < 0.001$, for the task effect; $F(1,22) = 0.10$, $P < 0.754$, for the age effect; $F(1,22) = 4.46$, $P < 0.046$, for the interaction.) The upshot
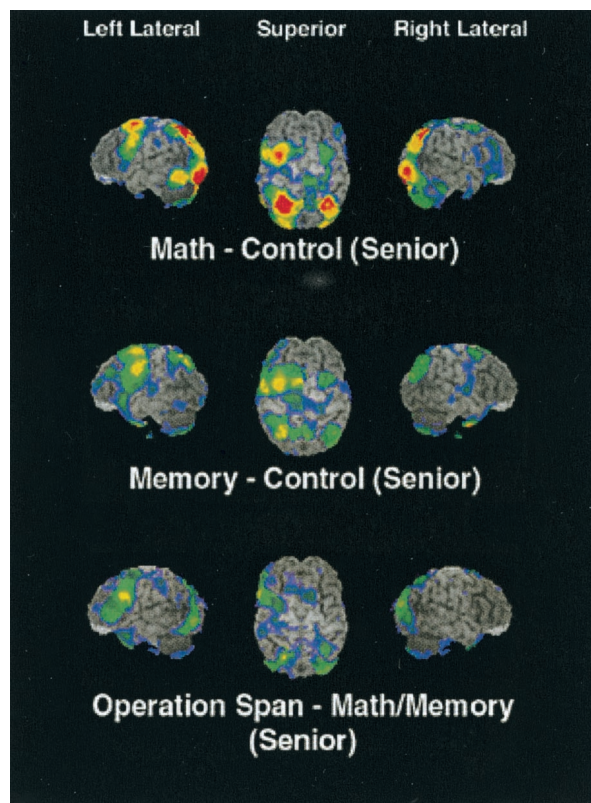
is that our version of the Operation Span is indeed more demanding than the constituent tasks [recall this was less the case in the Bunge *et al.* (7) study], and that our parametric changes were successful in equating accuracy levels for senior and young subjects.

PET Findings. Fig. 1 presents the images for the relevant subtractions for young subjects. The first two rows contain the activations for the Math and Memory tasks, relative to the Control condition. The contrast of critical interest, although, is that between Operation Span on the one hand and an average of the Math and Memory tasks on the other. Preliminary inspection of the images indicated that this critical contrast depended on performance level. Accordingly, we divided the young subjects (by a median split) into relatively good versus relatively poor performers on the basis of their memory accuracy in the Operation Span. The third row of Fig. 1 presents the critical contrast for the "good" performers, whereas the final row contains the contrast for the "poor" performers.¶ (The differences between the good and the poor performers were fewer on the Math Minus Control and Memory Minus Control contrasts.) The coordinates and significance levels of the significant activations in the four contrasts are contained in Table 1 *a–d*.

In the Math condition (Math Minus Control), the activations were primarily in posterior cortex, particularly the occipital and cerebellum cortex, although there were activations in parietal, temporal, and posterior frontal regions as well. The Memory task (Memory Minus Control) led to a pattern of activations that has been found in many tasks that tap short-term storage (see ref. 9 for a review), namely activations in posterior parietal sites and left-hemisphere posterior frontal areas that are thought to mediate

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¶On Memory accuracy, the good-young showed a 4% decline between the single- vs. dual-task. In contrast, the poor-young showed a 17% decline. This task × group interaction was significant ($P < 0.005$).

Table 1. Young: Significant activation foci

	Stereotaxic coordinates			
x	*y*	*z*	*z*-score	Brain area

a. Young: Significant activation foci in Math Minus Control

x	*y*	*z*	*z*-score	Brain area
				Left hemisphere:
−42	1	27	5.13	Premotor (area 6)
−26	−1	47	6.64	Premotor (area 6)
−46	21	−27	5.31	Anterior temporal (area 38)
−42	23	−27	5.21	Anterior temporal (area 38)
−39	−37	38	6.44	Posterior parietal (area 40)
−42	−67	−9	8.66	Visual association (area 19)
−26	−55	34	8.57	Visual association (area 19)
−28	−82	−2	6.60	Visual association (area 18)
				Right hemisphere:
35	−85	−4	6.60	Visual association (area 18)
28	−60	32	5.81	(Area 39/19)
35	−55	−20	6.72	Cerebellum
26	−62	−43	5.94	Cerebellum
				Midline:
−3	−64	−22	7.89	Cerebellum
3	−51	−16	7.01	Cerebellum

b. Young: Significant activation foci in Memory Minus Control

x	*y*	*z*	*z*-score	Brain area
				Left hemisphere:
−57	8	9	4.45	Broca's (area 44)
−21	−4	43	5.09	Premotor (area 6)
−42	−8	32	4.69	Premotor (area 6)
−35	−10	34	4.69	Premotor (area 6)
−42	−51	−11	4.4	Visual association (area 37)
−26	−53	36	6.48	Superior posterior parietal (area 7/40)
−37	−80	−7	5.16	Visual association (area 19)
				Right hemisphere:
15	−67	43	4.63	Superior parietal (area 7)
33	−55	−22	4.86	Cerebellum
				Midline:
−1	−55	−18	4.74	Cerebellum

c. Good-young: Significant activation foci in Operation Span Minus Math/Memory

x	*y*	*z*	*z*-score	Brain area
				Left hemisphere:
−42	−67	−14	4.31	Visual association (area 19)
				Midline:
−8	−60	29	4.25	Posterior cingulate (area 31)

d. Poor-young: Significant activation foci in Operation Span Minus Math/Memory

x	*y*	*z*	*z*-score	Brain area
				Left hemisphere:
−33	−82	−7	5.09	Visual association (area 18/19)
−19	−64	36	5.09	Visual association (area 19)
				Right hemisphere:
24	−85	0	5.54	Visual association (area 18)
				Midline:
−6	−55	40	6.07	Superior parietal (area 7)

verbal rehearsal. Of greatest interest are the comparisons of activations in Operation Span and the average of the constituent tasks (Math and Memory). For good-young subjects, there is no indication of activation in PFC (i.e., there is no PFC area that is activated in Operation Span but not in the constituent tasks). There are posterior activations in this critical contrast; but presumably they reflect the fact that the Math activations are not fully subtracted out, because it is an average of Math Plus Memory that is subtracted from Operation Span. The null findings about the PFC are consistent with the negative results of Bunge *et al.* (7). The critical results are different for the poor-young subjects. The contrast between Operation Span and Math Plus Memory shows extensive activations in left-hemisphere PFC (as well as in occipital cortex). Thus, for poorer performers, there are PFC areas activated in the Operation Span but not the constituent tasks.

The images for the senior subjects are presented in Fig. 2. The

coordinates and significance levels of the relevant contrasts are in Table 2 *a–c*. The Math condition again shows activations in posterior cortex, including occipital, parietal, and temporal regions, as well as in the posterior frontal cortex. This much is like the findings for the young subjects. The activations in the memory task show a similar pattern to that obtained with the young subjects, although the seniors seem to manifest more activation in the standard WM areas—posterior frontal cortex and posterior parietal cortex. In the contrast of greatest interest—that between Operation Span and the constituent tasks—the senior subjects show activation in left-hemisphere PFC.

It appears that the addition of the executive components of task-switching and storage-during-distraction recruits left-hemisphere PFC areas for some subject groups (particularly poor-young and senior performers), but not for others (good-young performers). These conclusions rest on our procedure for contrast-

Table 2. Senior: Significant activation foci

	Stereotaxic coordinates			
x	y	z	z-score	Brain area

a. Senior: Significant activation foci in Math Minus Control

x	y	z	z-score	Brain area
				Left hemisphere:
−30	1	52	6.82	Premotor (area 6)
−39	1	36	5.94	Premotor (area 6)
−51	−55	−11	4.59	Visual association (area 37)
−26	−60	36	9	Visual association (area 19)
−26	−80	18	5.64	Visual association (area 19)
−26	−82	−9	7.32	Visual association (area 18)
				Right hemisphere:
28	−58	36	7.1	Visual association/posterior parietal (area 19/39)
35	−82	−2	6.31	Visual association (area 18)
26	−58	−22	4.52	Cerebellum
				Midline:
6	−69	−22	7.23	Cerebellum
−6	8	47	4.92	Anterior cingulate (area 32)

b. Senior: Significant activation foci in Memory Minus Control

x	y	z	z-score	Brain area
				Left hemisphere:
−28	1	50	6.11	Premotor (area 6)
−39	−6	36	5.16	Premotor (area 6)
−37	−44	40	4.44	Posterior parietal (area 40)
−30	−62	36	5.51	Visual association (area 19)
				Midline:
−8	1	56	4.52	Premotor (area 6)
−8	−62	−16	4.35	Cerebellum
				Right hemisphere:
21	−37	52	4.63	Superior/posterior parietal (area 7/40)
35	−62	47	5.5	Superior parietal (area 7)
37	−78	22	4.65	Visual association (area 19)

c. Senior: Significant activation foci in Operation Span Minus Math/Memory

x	y	z	z-score	Brain area
				Left hemisphere:
−21	−62	34	4.94	Superior parietal (area 7)
−44	14	22	4.60	Broca's area (area 44)
−39	3	43	4.30	Premotor (area 6)

ing the Operation Span with its constituents, which involves taking an average of the Math and Memory activations. An alternative procedure is simply to subtract the Memory activations from those in Operation Span. This latter procedure was used by Bunge *et al.* (7). Applying this procedure to the current data changes none of the critical results—the resulting images are very similar to those in the last two rows of Fig. 1 and the last row of Fig. 2.

The patterns of results for the different groups of subjects was further supported by regions-of-interest (ROIs) analyses, where the regions were taken from PFC regions that had been activated in previous studies of verbal WM by using 2-back and 3-back tasks (14, 20). These tasks are hypothesized to involve executive processing. Table 3 *a–c* presents the relevant results for, respectively, good-young, poor-young, and senior subjects. Each panel lists the ROIs and any significant change in activation in the ROIs for four different contrasts: Math vs. Control, Memory vs. Control, Operation Span vs. Memory, and Operation Span vs. Math and Memory. Again, two kinds of activation patterns are of particular interest: (*i*) PFC regions activated in Operation Span vs. Math and Memory but not in Math or Memory alone, and (*ii*) PFC regions activated in Operation Span vs. Memory, but not in Memory alone. Each of these patterns is compatible with the hypothesis that the executive components of task-switching and storage-during-distraction are mediated by specific PFC regions.

For the good-young subjects (see Table 3*a*), consistent with the images in Fig. 1, there are no PFC regions in the left-hemisphere that conform to either of the above two patterns. There is, however, one right-hemisphere PFC region, Brodmann Area 10 (BA 10), that

conforms to the two patterns. Inspection of the images in Fig. 1, although, indicates that this region is relatively small and isolated. Turning to the results for the poor-young subjects (Table 3*b*), consistent with the images in Fig. 1, there is one relatively extensive left-hemisphere PFC region that conforms to pattern 1. This region is in the dorsolateral PFC (BA 9), an area that has been found in studies of the executive process of selectively attending to one source of information while ignoring another [e.g., ignoring irrelevant matches in Cohen *et al.* (21)]. Lastly, consider the results for the senior subjects (Table 3*c*). Consistent with the image in Fig. 2, there is one left-hemisphere region in the dorsolateral PFC (BA 9) that conforms to patterns 1 and 2, and an anterior cingulate region that conforms to pattern 2.

To further support the argument that only the senior and poor-young recruit similar left frontal regions when performing the dual-task, a comparison of peak PFC activations was made. These peaks were defined by considering the Operation Span–Math/Memory subtractions for poor-young, good-young, and seniors. Spherical ROIs, approximately 15 mm in diameter, were placed on each of the individual's scans, centered on the coordinate of peak activation. This analysis allowed us to directly contrast the activation in the PFC for (*i*) the poor-young vs. the good-young and (*ii*) the seniors vs. the poor-young. The results revealed a peak activation for the poor-young in BA 9 that was active for the senior subjects, but not for the good-young.

Discussion

The major findings are that adding to a task the executive components of task-switching and storage-during-distraction has

Table 3. Significant PFC ROIs

Stereotaxic coordinates				Percentage change in activation or deactivation as a function of task			
x	y	z	Brain area*	Math-Cntrl	Mem-Cntrl	Ospan-Mem	Ospan-Math/Mem
a: Significant PFC ROIs in the good-young performers							
			Left hemisphere				
−33	53	11	10	−3.34	—	—	—
−46	44	22	46	1.11	—	—	—
−46	19	29	9	—	2.11	—	—
−28	1	52	6	5.22	—	—	—
−46	1	36	6	—	—	—	—
−1	12	38	32	—	1.69	—	2.54
			Right hemisphere				
35	50	18	10	—	—	1.36	1.82
26	48	−11	11	—	1.91	—	—
44	30	27	9/46	3.74	2.96	—	—
30	19	4	45/47	—	—	—	—
24	1	52	6	—	3.16	—	—
b: Significant PFC ROIs in the poor-young performers							
			Left hemisphere				
−33	53	11	10	—	—	−1.71	—
−46	44	22	46	1.74	—	—	—
−46	19	29	9	—	—	—	1.80
−21	17	2	Putamen	3.34	2.64	—	—
−1	12	38	32	—	1.83	1.54	1.21
−46	1	36	6	1.71	3.06	—	—
−28	1	52	6	4.87	2.71	—	—
			Right hemisphere				
35	50	18	10	−2.34	−1.75	—	—
26	48	−11	11	—	—	—	−0.64
30	19	4	45/47	1.03	—	—	−1.58
c: Significant PFC ROIs in the senior performers							
			Left hemisphere				
−33	53	11	10	—	2.18	—	—
−46	44	22	46	—	1.52	—	—
−46	19	29	9	—	—	2.95	2.92
−1	12	38	32	2.11	—	1.56	—
−46	1	36	6	4.09	4.16	1.86	1.90
−28	1	52	6	5.34	4.48	—	—
			Right hemisphere				
24	1	52	6	2.87	2.79	—	—

*Brodmann areas are based on ref. 14.

different effects for different groups of subjects. The executive components recruit left-hemisphere, PFC areas, including the dorsolateral PFC, for poor-young performers and seniors, but not for good-young performers. Perhaps the most plausible interpretation of these results is that the executive components at issue (*i*) do not require a specific region of PFC, or even the good-young subjects would have had to activate this region in the Operation Span, and (*ii*) may require the executive process of selective attention in those subjects who find Operation Span particularly demanding (poorer young performers and older

subjects). This interpretation is in agreement with the claim by Bunge *et al.* (7) that there is no special switching area in PFC at least for cases in which switches are made between some discrete processing task and an ongoing WM task.

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