General and task-specific frontal lobe recruitment in older adults during executive processes: A fMRI investigation of task-switching

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Performance deteriorates when subjects must shift between two different tasks relative to performing either task separately. This switching cost is thought to result from executive processes that are not inherent to the component operations of either task when performed alone. Medial and dorsolateral frontal cortices are theorized to subserve these executive processes. Here we show that larger areas of activation were seen in dorsolateral and medial frontal cortex in both younger and older adults during switching than repeating conditions, confirming the role of these frontal brain regions in executive processes. Younger subjects activated these medial and dorsolateral frontal cortices only when switching between tasks; in contrast, older subjects recruited similar frontal regions while performing the tasks in isolation as well as alternating between them. Older adults recruit medial and dorsolateral frontal areas, and the processes computed by these areas, even when no such demands are intrinsic to the current task conditions. This neural recruitment may be useful in offsetting the declines in cognitive function associated with ageing. *NeuroReport* 12:2065–2071 © 2001 Lippincott Williams & Wilkins.

Key words: Ageing; Frontal lobe function; Neuroimaging

INTRODUCTION

As human and non-human animals grow older, there is a decline in cognitive efficiency, in speed of processing and in performance free of error [1,2]. Atrophy in cortical structures, decay in cerebral vascular integrity, decreases in neurotransmitter perfusion [3] and reductions in metabolic activity [4,5] accompany these cognitive deficits. However, these changes are neither general to all cognitive tasks nor uniform across all brain regions. Disproportionate cognitive deficits are seen in tasks that require manipulating information in working memory, alternating between goal-states, solving conflict between stimulus-response mapping, or resolving interference in rule application; in short, tasks that require executive processes [1,2,6]. Likewise, the neuroanatomical and neurochemical degeneration is more pronounced in the dorsolateral and medial frontal areas than in any other regions of the brain [7,8]. These regions of the frontal cortex are thought to subserve the cognitive operations that underlie executive processes [9–11].

Interest in the executive control of cognitive processes has been reflected in the recent growth of models of cognition, which reserve an important role for executive processes in the completion of goal-directed behaviour [11–13]. There has been a recent resurgence into the empirical examination of executive control processes in human behaviour to further our understanding of the successful control of cognitive processes [14,15]. This interest has been particularly intense in understanding the declines in executive function that occur as we age [1,6,16,17].

In a recent review of the literature on the neuroanatomy, neurophysiology and neuropsychology of aging West [2] concluded that strong evidence exists for the frontal lobe hypothesis of cognitive aging. This hypothesis suggests that older adults are disproportionately disadvantaged on tasks that rely heavily on cognitive processes (e.g. executive control) that are supported by the frontal and prefrontal lobes of the brain. Disproportionate atrophy and metabolic dysfunction in frontal areas in the aging human brain are consistent with numerous reports of large and robust age-related deficits in the performance of tasks that are dependent on executive processes. One such task that relies heavily on executive processes is task switching

[6,15,16]. When subjects are required to switch between two tasks, there is an increase in both reaction time and the numbers of errors that subjects make relative to performing either task in isolation. This cost in performance is thought to result from processes that are not inherent to the operations of either task [6,15]. Rather, the switching cost is thought to result from the recruitment of executive processes to deal with the conflict resulting from multiple task sets, the inhibition of the inappropriate set, and the maintenance of multiple task rules. Medial and dorsolateral frontal cortices in particular have been theorized to subserve executive processes [9,11].

In the present study, we investigated cognitive performance in two simple numerical judgment tasks (a digit value task and a digit numerosity task) in younger and older adults. We compared blocks of trials that randomly alternated between the two tasks (switching condition) to repeated performance of each single task (non-switching condition). We manipulated the relative amount of executive processes in each condition while keeping constant the cognitive operations used to perform each individual task [1,6,15,18]. We examined brain activation in this blocked-design fMRI study to determine the relative amount of frontal lobe activity in both age groups, when subjects had to recruit executive processing to accomplish the alternation of goals and rule sets in the switching condition.

We compared the switching condition against performing each task individually. We also compared both switching and non-switching conditions against a low-level baseline of simple fixation. This latter comparison was used to determine the processes common to both cognitive conditions and for comparisons across the two age groups. Direct comparisons of the functional images between the two age groups are susceptible to neuroanatomical atrophy in older adults that may influence image processing and localization of function. In addition, cerebrovascular differences may influence both the hemodynamic response lag and the percent of signal change in the fMRI response ([19], c.f. [20]). Hence, using a low-level baseline task allowed a comparison of the relative significant changes in blood flow and size of neural areas recruited between the two groups corrected for any inherent morphological or vascular differences.

Our goal in this study was to determine how, if at all, the disproportionate behavioral costs, and structural and metabolic deficits in medial and dorsolateral frontal lobes would manifest as functional deficits as measured by human neuroimaging during a task requiring executive processes.

MATERIALS AND METHODS

Participants: Eight younger (ages 20–30, mean 25) and eight older adults (ages 63–75, mean 69) participated in the study. All subjects were tested for near and far acuity and self-reported health. Both groups possessed acuity of at least 20/40 corrected as well as comparable health scores, $F < 1$ in both cases. We also tested each group on the Kaufman K-bit IQ test and found no significant differences between the groups with older (mean $\pm$ s.d. 133 ± 11) and younger subjects (110 ± 5) scoring equally well, with $F < 1$.

The experiment was conducted with the understanding and consent of each subject. The University Institutional Review Board (IRB) approved the conduct of the experiment.

Task and design: All subjects participated in a practice phase outside of the magnet, and then a test phase during which the fMRI and behavioral data were acquired. The practice phase consisted of 40 trials of practice for each task singularly, and then 60 trials of the switching condition with 20 switch trials and 40 non-switch trials. On each trial, a colored box appeared for 150 ms and the color of the box signified the task to be performed. A string of one through nine digits then appeared for 2850 ms and all of digits were the same value between 1 and 9 (e.g. 7777). Subjects were instructed, based on the color of the box, to determine whether the value of each digit was greater than or less than 5 (digit value task) or whether the number of digits presented were greater than or less than 5 (digit numerosity task). Neither the number of digits nor the value of the digits could be five. In the non-switching condition, subjects were told ahead of time the task they were going to perform (numerosity or value), and the same color cue appeared on each trial. In the switching condition, tasks would switch randomly every second or third trial, on average. In fixation blocks, subjects were instructed to maintain fixation on a cross centered in the screen.

The test phase followed the same procedure as the practice phase. Using a block design, we acquired functional brain images during three separate blocks. The first and third blocks consisted of five 60 s periods (three switching and two non-switching) of task performance interspersed with six 30 s periods of fixation. The order of the non-switching tasks was counterbalanced across runs and subjects. This alternation of switching and non-switching conditions in the same run allowed for direct comparisons of the two conditions as well as comparisons with the simple baseline (fixation) condition. The second block consisted of a similar procedure with four 60 s periods of the non-switching condition, and five 30 s periods of fixation. Again, task order was counterbalanced across subjects and runs.

While the cognitive processes needed to process the digits in the switching and non-switching conditions are identical; the switching condition necessitated a change from one task set to another. The switching condition also challenged working memory (as subjects had to retain the appropriate rules of the two tasks) and may have been more arousing than the non-switching condition [15], but these differences are indicative of executive control processes. Hence, we changed the relative amount of executive processing required in the different conditions while keeping the judgment constant across blocks.

fMRI image processing: Multislice images of the human brain were acquired in a block design using a 1.5 T GE Signa scanner equipped for echo-planar imaging (EPI). For the experimental runs, a total of 360 EPI images were acquired (TR = 1517 ms, TE = 40 ms, flip angle = 90°), each consisting of 15 contiguous slices (thickness 7 mm, in-plane resolution 3.75 mm), parallel to the anterior commisure-posterior commisure line. High-resolution 3D anatomical images (T1-weighted 3D spoiled gradient echo images)

were collected for each participant as well as 15 T1-weighted images of the echoplaner slices. The head coil was fitted with a bite bar to minimize head motion and stimuli were presented on a goggle system designed by Magnetic Resonance Technologies.

The first six volumes of each run were discarded to allow the MR signal to reach a steady state. Prior to statistical tests, images in the data series were intensity normalized, convoluted with a Gaussian kernel (FWHM = 10.5 mm, kernel size = 7×7), temporally denoised using a 1D-wavelet transform (visu-shrink, number of levels = 4) and linearly detrended (parameter estimates based upon images in the fixation phases only). The Kolmorgorov-Smirnov (KS) statistical test was used to generate statistical maps for each block. A 4.8 s hemodynamic lag was assumed for each voxel in each condition. The switching blocks were compared to the non-switching blocks to produce difference images that depict the degrees to which a particular region of the brain was more or less active as the task requirement change across trials. Probability values from the KS test were converted to Z-scores and were then transformed to a common stereotaxic space [21] and areas of activation were averaged across each age group for each condition. MedX V3.0 was used to conduct image processing and statistical analyses. Z-score maps of significant activation were generated using a statistical threshold of >1.96. To test the validity of this threshold, we averaged the fixation condition in each run and compared them across conditions. If our threshold was valid, this comparison should yield no significant activation; and indeed, no significant activation was found.

To test the size of areas of activation across age groups, regions of interest (ROI) in the frontal lobes were defined as a set of spherical volumes in Talairach space (radius = 3 voxels). Each ROI centered on a peak level of significant activation produced by a group average of the statistical maps. These ROIs were then linked to each subject's individual activation map and a percentage of significantly active voxels within each ROI was computed for each subject per condition thereby assessing the spatial extent of activation within the frontal lobes across age groups.

RESULTS

Behavioral data: Overall, older subjects were significantly slower to respond than younger subjects ($F(1,13) = 12.28$, $p < 0.004$). Importantly, both groups were significantly slower on both digit value and digit numerosity judgments when switching between these two tasks (933 ± 196) than when performing either task in isolation (708 ± 131; $F(1,14) = 68.28$, $p < 0.0001$. Finally, as Fig. 1 shows, older subjects had a trend for larger switch costs than the younger subjects ($F(1,14) = 2.93$, $p = 0.11$); this result is consistent with our previous work showing significantly larger switch costs in older adults than younger adults [6,22].

Older subjects made significantly more errors ($7 \pm 5\%$) than younger subjects ($3 \pm 2\%$; $F(1,13) = 4.82$, $p < 0.05$). Both groups of subjects made significantly more errors during the switching condition ($6 \pm 4\%$) than the non-switching condition ($3 \pm 4\%$; $F(1,14) = 10.16$, $p < 0.008$). However, there was no interaction of age and condition ($F(1,14) = 1.78$, $p = 0.22$).

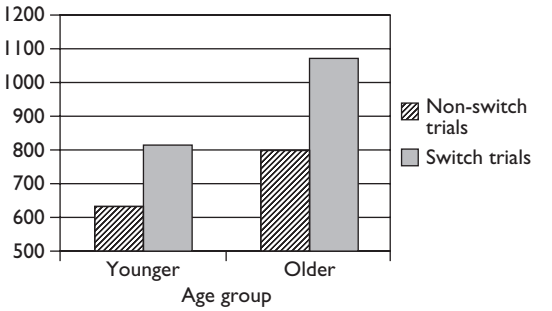

Fig. 1. Mean reaction time for switching and non-switching trials by age group.

fMRI data: Younger subjects showed significantly greater activation (Table 1) in dorsolateral prefrontal cortex (Brodmann's areas 44, 45, 46, and 47) and medial frontal cortex (Brodmann's area 24, 32 and 6) during the switching condition relative to the non-switching condition (KS test, $p < 0.001$). These data are consistent with the role of the dorsolateral prefrontal cortex (DLPFC) and medial frontal cortex (MFC) subserving executive processes in task switching [23–26]. The older subjects, however, showed no significant activation in DLPFC or MFC in the switching condition relative to the non-switching condition (Table 1). This latter result is difficult to interpret in isolation (but see [23]); hence we next asked what neural areas were active in each of the experimental conditions relative to the baseline of simple fixation.

As Table 2 shows, both younger and older subjects significantly activated the DLPFC (BA 44, 45, 46, and 47) as well as the MFC (BA 6 and 32) in the switching condition relative to fixation (KS test, $p < 0.005$). As expected [23–26], when task switching was required, both younger and older subjects activated DLPFC and MFC (Table 2), confirming the role of these areas in tasks that require executive processes. The younger subjects showed no significant activation in either DLPFC or MFC in the non-switching condition relative to a simple fixation baseline (Table 3). In contrast, the older subjects significantly activated DLPFC (BA 45, 47) and MFC (BA 6 and 32) in the non-switching condition as they did in the switching condition (KS test, $p < 0.005$). In addition, activation that approached significance was also seen in other areas in both DLPFC (BA 44 and 46) and MFC (BA 24) in the non-switching condition. Hence, the lack of significant activation in the comparison of switching *vs* non-switching condition is best explained by the activation during the non-switching condition of DLPFC and MFC (Table 3), not by a lack of activation of these areas in the switching condition. That is, the older subjects seemed to recruit similar neural tissue during the switching and non-switching conditions (Table 2, Table 3); hence, a comparison between these two conditions in the older adults resulted in no significant differences. Unlike the younger subjects, older adults recruited DLPFC and MFC in both the switching and the non-switching condition. This latter condition was a well-practiced task that required little executive processes and showed no recruitment of DLPFC and MFC in younger adults.

We next compared the size of frontal lobe recruitment

Table 1. Switch *vs* non-switch in older and younger subjects.

Lobe	Brodmann's Area	Hemisphere	x	y	z	Z-Score	x	y	z	Z-Score
OLDER SUBJECTS										
Frontal	None									
Occipital	None									
Parietal	None									
Temporal	None									
YOUNGER SUBJECTS										
Frontal	BA 10	Bilateral	−20	68	0	3.04	46	52	−2	3.78
	BA 10/46	Bilateral	−48	38	12	2.69	36	56	12	2.62
	BA 11	Right					34	48	−18	2.98
	BA 4/6	Left	−30	−12	54	2.62				
	BA 4	Left	−32	−38	58	3.43				
	BA 44	Right					52	12	8	3.03
	BA 45	Bilateral	−48	24	12	2.54	46	20	10	3.16
	BA 45/46	Bilateral	−36	48	8	2.70	46	26	24	3.09
	BA 45/47	Bilateral	−30	28	6	2.73	56	14	−2	3.08
	BA 46	Bilateral	−44	32	24	2.92	48	34	24	3.41
	BA 47	Left	−34	26	2	2.79				
	BA 5	Bilateral	−20	−40	68	2.59	2	−42	56	2.97
	BA 5/7	Right					10	−56	64	3.48
	BA 6 (Medial)	Bilateral	−2	12	46	2.59	4	12	54	3.31
	BA 6	Bilateral	−28	10	44	3.11	38	0	54	2.80
	BA 8 (Medial)	Left	−2	16	48	3.36				
	BA 8	Bilateral	−46	12	34	4.30	30	16	52	2.66
	BA 9	Bilateral	−40	16	32	4.08	48	14	28	3.47
	BA 9/46	Left	−38	28	28	2.63				
	BA 24	Right					4	−16	42	3.16
	BA 6/24	Right					0	−16	42	3.22
	BA 32	Bilateral	0	26	44	3.34	21	0	42	2.67
	BA 30	Left	−16	−54	−4	2.52				
	BA 31	Bilateral	−24	−64	16	2.60	8	−42	42	2.58
	BA 23/31	Right					18	−26	26	2.28
Occipital	BA 17	Bilateral	−12	−96	0	2.84	12	−82	6	2.80
	BA 17/18	Bilateral	−2	−82	8	2.78	18	−92	6	2.81
	BA 18	Bilateral	−30	−84	14	3.12	30	−78	14	3.19
	BA 18/19	Bilateral	−36	−74	4	3.38	2	−94	26	3.11
	BA 19	Bilateral	−18	−90	22	2.96	18	−60	−6	3.33
	BA 19/37	Left	−34	−72	8	3.58				
Parietal	BA 7	Bilateral	−2	−62	50	3.95	26	−70	48	3.59
	BA 7/40	Bilateral	−40	−42	44	3.77	44	−42	48	2.89
	BA 40	Bilateral	−48	−34	48	3.17	44	−42	42	3.57
	BA 39/40	Left	−42	−60	30	2.62				
	BA 1	Left	−44	−22	38	2.17				
	BA 2	Left	−52	−24	50	2.84				
	BA 3	Left	−36	−30	56	3.12				
Temporal	BA 20/21	Right					46	−8	−2	2.16
	BA 21/37	Right					28	−44	−2	2.55
	BA 22	Right					54	−56	22	2.23
	BA 37	Bilateral	−44	−68	−2	3.96	44	−62	−2	3.60
	Hippocampus	Left	−30	−38	0	2.35				
Sub-Lobar	Caudate	Left	−28	−38	6	2.39				
	Insula	Right					40	12	4	2.72
	Pulvinar	Right					12	−30	4	2.50

during the switching and non-switching conditions (relative to simple fixation) across the two age groups (Table 4). The percentage of voxels significantly active in a ROI was computed for each subject during each condition. The percent of significantly active voxels was then used in a repeated measure analysis of variance to determine whether the size of the activation (when compared to simple fixation) was greater in the switching condition than the non-switching and if this recruitment significantly differed between the two age groups. The switching condition produced significantly larger areas of activation in both DLPFC (BAs 45, 46) and MFC (BAs 24, 32 and 6) than the non-switching condition in the older and younger subjects ($F(1,7) = 9.02$, p lt] 0.02). Further, older subjects recruited significantly greater areas of MFC (BA 6, 32) and DLPFC (BA 45, 46) than the younger adults in both the switching ($F(1,14) = 8.57$, $p < 0.01$) and non-switching conditions ($F(1,14) = 14.64$, $p < 0.001$).

The older adults activated significantly larger areas in both the DLPFC (BA areas 44, 45, 46) and MFC (BA areas 24, 32, 6) than the younger adults ($F(1,14) = 14.94$, $p < 0.002$). These results suggest that older subjects recruit

Table 2. Switch *vs* fixation in older and younger subjects.

Lobe	Brodmann's area	Hemisphere	x	y	z	Z-Score	x	y	z	Z-score
OLDER SUBJECTS										
Frontal	BA 10	Bilateral	−28	52	12	2.56	44	50	4	2.92
	BA 11	Bilateral	−32	50	−14	2.85	32	42	−16	3.13
	BA 32	Bilateral	−2	18	46	3.66	8	26	30	2.37
	BA 4	Left	−38	−12	54	4.39				
	BA 44/45	Left	−48	18	12	3.20				
	BA 45	Bilateral	−34	28	0	2.14	40	28	2	2.73
	BA 45/46	Right					48	28	22	3.98
	BA 45/47	Right					56	20	0	4.39
	BA 46	Right					48	34	14	4.31
	BA 47	Bilateral	−40	42	−10	2.25	46	30	−14	3.07
	BA 6 (Medial)	Left	−2	6	56	3.87				
	BA 6	Bilateral	−34	−10	58	4.52	30	14	46	2.74
	BA 8 (Medial)	Left	−2	22	44	4.20				
	BA 8	Right					38	30	38	2.43
	BA 9	Right					40	30	36	2.50
	BA 9/44	Bilateral	−40	12	32	4.86	48	18	28	4.63
	BA 9/45	Left	−44	28	20	3.53				
	BA 9/46	Right					48	40	−10	2.54
Occipital	BA 17/18	Bilateral	−16	−84	0	6.84	4	−86	0	5.41
	BA 18/19	Bilateral	−30	−76	−4	6.93	20	−72	−2	7.05
	BA 19	Bilateral	−38	−66	−8	6.86	34	−78	26	3.79
	BA 19/37	Right					30	−68	−6	7.77
	BA 37	Right					34	−52	−10	5.82
Parietal	BA 40	Bilateral	−38	−34	42	4.44	34	−48	42	4.06
	BA 7	Bilateral	−26	−54	52	4.53	20	−68	58	3.20
	BA 5	Right					36	−40	62	2.43
Temporal	BA 20	Right					44	−14	−16	3.31
	BA 21	Bilateral	−64	−34	−2	2.12	60	−20	−6	3.61
	BA 22	Left	−60	−40	4	2.82				
Sub-Lobar	Caudate	Left	−12	−4	16	2.50				
	Globus Pallidus	Right					14	2	2	2.58
	Putamen	Left	−30	−10	2	2.45				
	Thalamus	Right					14	0	12	2.97
	Medial Dorsal Nucleus	Left	−8	−16	12	3.02				
YOUNGER SUBJECTS										
Frontal	BA 10	Bilateral	−26	68	−2	3.56	44	54	−4	4.88
	BA 10/11	Left	−32	64	−4	2.95				
	BA 11	Right					4	74	−14	2.24
	BA 4/6	Left	−54	−16	34	2.49				
	BA 44	Bilateral	−40	12	32	5.26	46	14	30	5.29
	BA 45	Bilateral	−38	22	2	2.54	52	18	4	3.13
	BA 45/46	Left	−30	28	4	2.66				
	BA 46	Right					50	38	24	4.64
	BA 6	Bilateral	−24	10	48	2.73	28	8	50	3.10
	BA 8 (Medial)	Bilateral	−2	16	48	3.48	4	24	44	4.09
	BA 9	Left	−44	30	32	4.47				
	BA 9/44	Right					52	18	36	5.05
	BA 9/46	Left	−44	36	24	4.16				
Occipital	BA 17/18	Bilateral	−16	−92	6	7.41	16	−92	12	6.87
	BA 18	Bilateral	−20	−92	14	7.24	14	−90	6	8.62
	BA 18/19	Bilateral	−18	−84	0	8.30	24	−74	0	8.48
Parietal	BA 7	Bilateral	−2	−70	62	2.59	38	−46	54	3.80
	BA 7/40	Bilateral	−28	−62	42	4.83	32	−62	44	4.51
Temporal	BA 21/37	Left	−46	−48	0	2.17				
	BA 37	Bilateral	−58	−56	−8	2.35	44	−62	0	5.07

more neural tissue in general than younger subjects to perform the same task and similar executive functions [25,27–29]).

DISCUSSION

As both groups practiced each task in isolation and in a switching condition prior to beginning the fMRI session, the possibility of a switch in task sets was highly salient for the older subjects (as older adults were aware of their difficulty in performing task-switching). It is likely that older subjects engaged similar cognitive processes (e.g. continually retrieving the algorithms necessary to perform the task) in both switching and non-switching conditions. To ensure that they applied the correct rules and task set

Table 3. Non-switch *vs* fixation in older and younger subjects.

Lobe	Brodmann's area	Hemisphere	x	y	z	Z-Score	x	y	z	Z-score
OLDER SUBJECTS										
Frontal	BA 10	Right					32	66	−8	2.71
	BA 10/11	Right					34	62	−10	2.24
	BA 11	Right					34	52	−16	2.38
	BA 32	Bilateral	−4	22	44	3.32	2	20	44	3.18
	BA 4	Left	−40	−12	56	3.49				
	BA 45	Bilateral	−42	26	22	2.44	56	24	0	4.06
	BA 47	Right					48	32	−14	2.86
	BA 6 (Medial)	Left	−4	6	58	3.03				
	BA 6	Left	−36	−8	58	3.65				
	BA 9	Left	−42	14	34	3.24				
	BA 9/44	Right					48	18	28	3.72
Occipital	BA 17	Right					16	−88	8	6.15
	BA 17/18	Bilateral	−16	−84	0	6.76	18	−76	−2	5.19
	BA 18	Bilateral	−32	−86	12	5.97	24	−88	20	4.63
	BA 18/19	Right					28	−86	−2	5.11
	BA 19	Right					32	−70	−4	6.52
Parietal	BA 2	Left	−48	−20	44	2.09				
	BA 2/40	Bilateral	−48	−26	42	2.22	50	−28	48	2.55
	BA 40	Bilateral	−32	−42	56	2.79	64	−24	26	2.68
	BA 7	Bilateral	−26	−54	52	2.81	2	−76	48	3.78
	BA 7/39	Right					50	−62	30	2.19
	BA 7/40	Right					32	−50	40	2.56
Temporal	BA 20	Bilateral	−38	−16	−18	2.49				
	BA 20/21	Bilateral	−44	−8	−16	2.41	60	−42	−10	3.45
	BA 21	Right					56	−12	−12	4.46
	BA 21/22	Left	−56	−40	−4	3.53				
	BA 21/37	Right					62	−46	2	3.72
	BA 37	Bilateral	−40	−62	−8	5.86	50	−64	0	4.97
Sub-Lobar	Thalamus	Right					0	−26	10	3.23
YOUNGER SUBJECTS										
Frontal	BA 10	Bilateral	−36	60	−4	2.67	34	62	−4	2.20
	BA 8	Right					44	12	30	2.49
	BA 8/9	Right					52	20	38	2.36
Occipital	BA 17/18	Bilateral	−18	−88	4	6.29	12	−88	6	6.58
	BA 18	Bilateral	−36	−72	−8	5.10	24	−78	0	6.36
	BA 19	Bilateral	−36	−78	−6	4.95	42	−86	20	2.27
Parietal	BA 2	Left	−48	−26	56	2.55				

Table 4. Percentage of active voxels in region of interest.

	OLDER SUBJECTS	YOUNGER SUBJECTS
Medial frontal		
Switch	0.65 (0.24)	0.40 (0.25)
Non-switch	0.56 (0.27)	0.11 (0.21)
Lateral frontal		
Switch	0.54 (0.15)	0.32 (0.16)
Non-switch	0.32 (0.24)	0.04 (0.03)

for the current task, older subjects may have engaged executive computations even in the non-switching condition [30]. Recent behavioural evidence suggests that following a task switching condition, older adults continue to show costs in non-switch conditions for extended periods [16]. Nevertheless, during the switching condition, the size of activation in the DLPFC and MFC was significantly greater than the non-switching condition for the older adults. Additionally, the older adults recruited more neural tissue in DLPFC and MFC than the younger adults did under the same task conditions. These results suggest that the cognitive processes recruited during the switching condition (and non-switching condition) are more extensive, require additional computations, and are more dependent on executive function for older than younger adults [22,25,27–29].

Both younger and older subjects recruit DLPFC and MFC during the switching condition demonstrating the importance of these frontal regions in executive processes [9,18]. Recent evidence suggests [23–25,31] that task switching preferentially engages DLPFC and MFC as well as areas in the parietal cortex. Indeed, both age groups significantly activated these regions during the switching condition.

Finally, older subjects recruited similar regions in DLPFC and MFC in the non-switching condition as they had activated in the switching condition. This result suggests that comparable, but not identical, cognitive processes to the switching condition are required for older adults to perform properly in the non-switching condition. As we grow older, we may rely on executive processes and the neural areas that subserve these computations even in

tasks that do not inherently require them [25,27–29,32]. Successful application of current rules and task set requirements under conditions of previous conflict [16,30] may obligate more effortful processes and more executive computations as the human brain ages or in poor task performers [25,33]. As degradation occurs in the aging human brain, both sensory input and cognitive efficiency deteriorate [34,35]. As a result of the cognitive and sensory degradation, older subjects may recruit MFC and DLPFC and the executive computations that these areas perform [25,27–29,32] to ensure successful performance and task efficiency.

CONCLUSION

Our data suggest that older adults compensate for decreased cognitive abilities by recruiting a variety of frontal lobe structures, even in tasks that appear not to require them for younger adults. Such a compensatory process may serve to reduce age-related decrements in performance and ensure successful task completion.

REFERENCES

1. Salthouse TA, Fristoe N, McGuthry KE and Hambrick DZ. *Psychol Aging* **13**, 445–461 (1998).
2. West RL. *Psychol Bull* **120**, 272–292 (1996).
3. Raz N. In: Craik FIM and Salthouse TA, eds. *Handbook of Aging and Cognition*. Mahwah, NJ: Erlbaum; 2000, pp. 1–90.
4. Shaw T, Mortel K, Meyer J et al. *Neurology* **34**, 855–862 (1984).
5. Azari N, Rapport S, Salerno J et al. *Brain Res* **552**, 279–290 (1992).
6. Kramer AF, Hahn S and Gopher D. *Acta Psychol* **101**, 339–378 (1999).
7. Coffey CE, Wilkinson WE, Parashos IA et al. *Neurology* **42**, 527–536 (1992).
8. Kemper TL. In: Albert MA and Knoepfel EJE. *Clinical Neurology of Aging*. New York: Oxford University Press; 1994, pp. 3–67.
9. D'Esposito M, Detre JA, Alsop DC et al. *Nature* **378**, 279–281 (1995).
10. Duncan J, Emslie H and Williams P. *Cogn Psychol* **30**, 257–303 (1996).
11. Posner MI and DiGirolamo GJ. In: Parasuraman R, ed. *The Attentive Brain*. Cambridge, MA: MIT Press; 1998, pp. 401–423.
12. Meyer DE, Glass JM, Mueller ST et al. *Eur J Cogn Psychol* **13**, 123–164 (2001).
13. Meiran N and Gotler A. *Eur J Cogn Psychol* **13**, 165–186 (2001).
14. Allport DA, Styles E and Hsieh S. In: Umiltà C and Moscovitch M, eds. *Attention and performance XV: Conscious and Nonconscious Information Processing* Cambridge, MA: MIT Press; 1994, pp. 421–452.
15. Rogers RD and Monsell S. *J Exp Psychol Gen* **124**, 207–231 (1995).
16. Mayr U and Liebscher T. *Eur J Cogn Psychol* **13**, 47–69 (2001).
17. West R. *Eur J Cogn Psychol* **13**, 91–105 (2001).
18. Kramer AF, Larish JL, Weber TA and Bardell L. In: Gopher D and Koriat A, eds.*Attention and Performance XVII*, (in press).
19. D'Esposito M, Zarahn E, Aguirre GK and Rypma B. *Neuroimage* **10**, 6–14 (1999).
20. Johnson SC, Saykin AJ, Baxter LC et al. *Neuroimage* **11**, 179–187 (2000).
21. Talairach J and Tournoux DP. *Co-planar Stereotaxic Atlas of the Human Brain* New York: Thieme, 1988.
22. Kramer AF, Hahn S, Cohen N et al. *Nature* **400**, 418–419 (1999).
23. Dove A, Pollmann S, Schubert T et al. *Cogn Brain Res* **9**, 103–109 (2000).
24. Sohn M-H, Ursu S, Anderson JR et al. *Proc Natl Acad Sci* **97**, 13448–13453 (2000).
25. Smith EE, Geva A, Jonides J et al. *Proc Natl Acad Sci* **98**, 2095–2100 (2001).
26. Rogers RD, Sahakian BJ, Hodges JR et al. *Brain* **121**, 815–842 (1998).
27. Reuter-Lorenz PA, Stanczak L and Miller AC. *Psychol Sci* **10**, 494–500 (1998).
28. Reuter-Lorenz PA, Marshuetz C, Jonides J et al. *Eur J Cogn Psychol* **13**, 257–278 (2001).
29. Reuter-Lorenz PA, Jonides J, Smith EE et al. *J Cogn Neurosci* **12**, 174–187 (2000).
30. Allport A and Wylie G. In: Humpreys GW, Duncan J and Treisman A, eds. *Attention, Space and Action*. Oxford: Oxford University Press; 1999, pp. 273–296.
31. Kimberg DY, Aguirre GK and D'Esposito M. *Cogn Brain Res* **10**, 189–196 (2000).
32. Jonides J, Marshuetz C, Smith EE et al. *J Cogn Neurosci* **12**, 188–196 (2000).
33. Grady CL, McIntosh AR, Bookstein F et al. *Neuroimage* **8**, 409–425 (1998).
34. Baltes PB and Lindenberger U. *Psychol Aging* **12**, 12–21 (1997).
35. Salthouse TA. *Dev Rev* **8**, 238–272 (1988).

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