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Age-Related Differences in Movement Representation

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Repetitive movements have been used as motor activation tasks in the investigation of various neurological disorders. To determine the importance of an age-matched control group in such studies we investigated whether there are significant age-related changes in the pattern of cortical activation seen during simple repetitive movements. Sixteen right-handed healthy subjects were studied—8 young and 8 old. Functional magnetic resonance images were acquired while subjects performed a motor task or a nonmovement rest condition. Two continuous motor tasks, index finger abduction/adduction and wrist extension/flexion, were performed by each hand, paced using a metronome. The fMRI data were processed and analyzed with SPM '99. For the between-group comparisons, for each motor task, contralateral primary sensorimotor cortex and premotor cortex had significantly greater activation in the Young group and caudal supplementary motor area had significantly greater activation in the Old group. Ipsilateral sensorimotor cortex was more significantly activated in the Old group for index finger motor tasks of both hands. All noted differences in the Old group were more prominent for the index finger movement and most prominent when using the nondominant hand. In conclusion, there are significant age-related differences in the activation pattern associated with repetitive movements. This may represent compensatory recruitment of motor cortical units in the older subjects as larger differences are noted in the older group during the more difficult motor tasks, those of isolated finger movement and nondominant hand use. This study has important implications for functional imaging experiments of neurological disorders in older subjects.

INTRODUCTION

Repetitive movements have been used as fMRI motor activation tasks in the investigation of various neurological disorders and in particular in the study of stroke recovery (Weiller *et al.,* 1993; Seitz *et al.,* 1998; Sabatini *et al.,* 2000). The normal activation pattern produced by such tasks is derived from control groups that are frequently younger than the population affected by the disease (Weiller *et al.,* 1993; Cao *et al.,* 1998; Jenkins *et al.,* 2000; Marshall *et al.,* 2000). Alternatively, no normal control group is studied and the activation pattern of the unaffected hand is used for comparison (Chollet *et al.,* 1991; Seitz *et al.,* 1998). It is assumed that the neural activity associated with simple motor tasks is similar between young and elderly subjects (D'Esposito *et al.,* 1999) on the basis that simple reaction time varies minimally across age groups (Gottsdanker, 1982) and it is only on tasks of increasing complexity that age-related differences in motor performance are detected (Smith *et al.,* 1999). Performance differences in cognitive tasks between old and young subjects are associated with differences in the activation pattern on functional imaging (Grady *et al.,* 1995; Backman *et al.,* 1997). However, even when cognitive tasks are performed by the elderly at the same level of accuracy and speed as younger subjects, there are still differences in the activation pattern during task performance. These differences are believed to reflect compensatory changes required by the older subjects to perform the task at the same level (Cabeza *et al.,* 1997; Grady *et al.,* 1998; Madden *et al.,* 1999). It may be the case that even simple repetitive motor tasks that are performed by older subjects in a manner similar to that of younger subjects require a different pattern of activation in older subjects.

In this study, the presence of significant age-related differences in the pattern of cortical activation seen during repetitive hand movements was examined. As differences between groups may be noted only during certain motor tasks (Cramer *et al.,* 2001) and as the goal of this investigation is to determine the importance of an age-matched control group in studies of disease affecting the motor system, two motor tasks that would be suitable for the investigation of stroke recovery were selected: wrist extension and flexion and index finger abduction and adduction.

MATERIALS AND METHODS

Subjects

A total of 16 healthy right-handed subjects were studied. The Young group consisted of 8 subjects (4 women; mean age 26 years, range 22 to 34 years) and the Old group consisted of

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8 subjects (5 women; mean age 68 years, range 54 to 76 years). The subjects were deemed healthy following a clinical history, neurological examination, and unremarkable imaging studies including anatomical T1- and T2-weighted imaging. All subjects were consistently right-handed according to a hand preference questionnaire (Annett, 1970). Subjects were excluded if they had a history of neurological or psychiatric disease, were taking psychoactive medications, or had significant pathological findings on anatomical MRI scanning. Fine motor skill was assessed using a finger-tapping task (Peters and Durding, 1978). Maximal finger tapping rate over 20 s was recorded for each hand. Tapping rates did not significantly differ between the Old and the Young groups ($P > 0.05$). All subjects gave informed written consent and the Institutional Review Board of Beth Israel Deaconess Medical Center (Boston, MA) approved this study.

Motor Activation Tasks

The motor tasks used in the current study were developed to examine recovery of hand function following stroke. Good hand motor recovery is associated with return of wrist extension and isolated finger movement (Brunnstrom, 1966). The two motor tasks were (1) full wrist extension and flexion and (2) full index finger abduction and adduction. Full excursion for each movement was encouraged, and other digit or hand movement was restricted, by taping the hands and remaining fingers to a soft foam rubber splint. During scanning each task was performed continuously, by either the right or the left hand, for a period of 35 s, paced by a metronome at 1 Hz for each complete excursion (e.g., full abduction through full adduction). The tasks were briefly rehearsed prior to scanning. During a nonmovement rest condition the metronome continued to beat at 1 Hz. Each task was performed by the right and left hand separately. Each of these four motor blocks, right wrist extension, left wrist extension, right index finger abduction, and left index finger abduction, was repeated five times and arranged in a Latin-square design with the nonmovement rest condition (each epoch was 35 s). Verbal instructions were given in a 5-s period in between acquisitions as to the next required action. Subjects lay supine in the scanner and were asked to keep their eyes open and fixate on a spot on the scanner ceiling. During the experiment the subjects were continuously observed by an examiner who specifically monitored for both task performance (congruence of movement rate with metronome and degree of excursion) and ancillary movements (including mirror movements). We did not have to exclude any subject because of ancillary movements.

Imaging Methods

Scanning was performed on a 1.5-T Siemens Vision (Erlangen, Germany). A gradient echo T2*-weighted echo-planar MR sequence was used for fMRI with the following parameters: TE (echo time) = 50 ms, field of view 240 cm, matrix 128 × 128, voxel size 2.5 × 2.5 × 5 mm. Using a midsagittal scout image, we acquired 22 contiguous axial slices parallel to the anterior–posterior commissure plane covering the entire brain over a period of 2.2 s and repeated this acquisition every 7 s, resulting in five acquisitions per epoch. The first two acquisitions were discarded to account for T1-saturation effects and to achieve steady state of the spin system. Prior to the functional MR sequence, an anatomical data set was acquired by using a high-resolution (1 mm^3 voxel size) T1-weighted sequence. In addition, we acquired a set of axial non-EPI T2-weighted (TE = 90; TR = 3800) MR images prior to the functional data set in order to exclude any subjects with T2 hyperintense lesions.

Image Processing and Data Analysis

Image processing and statistical analysis were carried out using the SPM '99 analysis package (http://www.fil.ion.ucl.ac.uk/spm) and MATLAB (Mathworks, Natick, MA) software. The data was corrected for motion artifacts by realigning all volumes to the first volume, mean adjusted by proportional scaling, coregistered with the subject's corresponding anatomical (T1-weighted) image, normalized into standard stereotactic space (template provided by the Montreal Neurological Institute), and smoothed using an 8-mm full-width-at-half-maximum Gaussian kernel. In addition, the time series of hemodynamic responses were high-pass filtered to eliminate low-frequency components, temporarily smoothed, and adjusted for systematic differences across trials. These adjusted measures were subjected to statistical analyses. Voxels associated with motor tasks were searched for using the General Linear Model approach for the time-series data suggested by Friston and colleagues (1995). For this, we defined a design matrix comprising contrasts modeling the alternating periods of each motor task and the between-group differences for this contrast using a boxcar reference vector. Four conditions were defined: right wrist, right index finger, left wrist, and left index finger. The nonmovement rest condition was not explicitly modeled. Significant group motor task versus rest and between-group differences were determined for all four motor tasks using a fixed-effects model. The fMRI data were analyzed by looking at main effects of each movement condition (separated by age) as well as for a main effect of age for each movement condition (using a contrast level of +1 or −1 for the active conditions to be examined). Voxels were identified as significant if they passed a statistical threshold corrected for multiple comparisons ($T = 4.55$, $P < 0.05$ corrected).

RESULTS

Group Mean versus Rest Contrasts

In each comparison of motor task versus nonmovement rest condition for both the Old and the Young groups, a large cluster of significantly activated voxels was found spanning the contralateral primary sensorimotor cortex (SMC), lateral premotor cortex (PMC), and supplementary motor area (SMA) with local maxima in contralateral SMC and one or both of the motor association areas (Fig. 1). Additionally, in each comparison of motor task versus nonmovement condition, for both age groups, there was a cluster of activated voxels in the ipsilateral cerebellum. A region of the ipsilateral motor system was activated for each motor task in both

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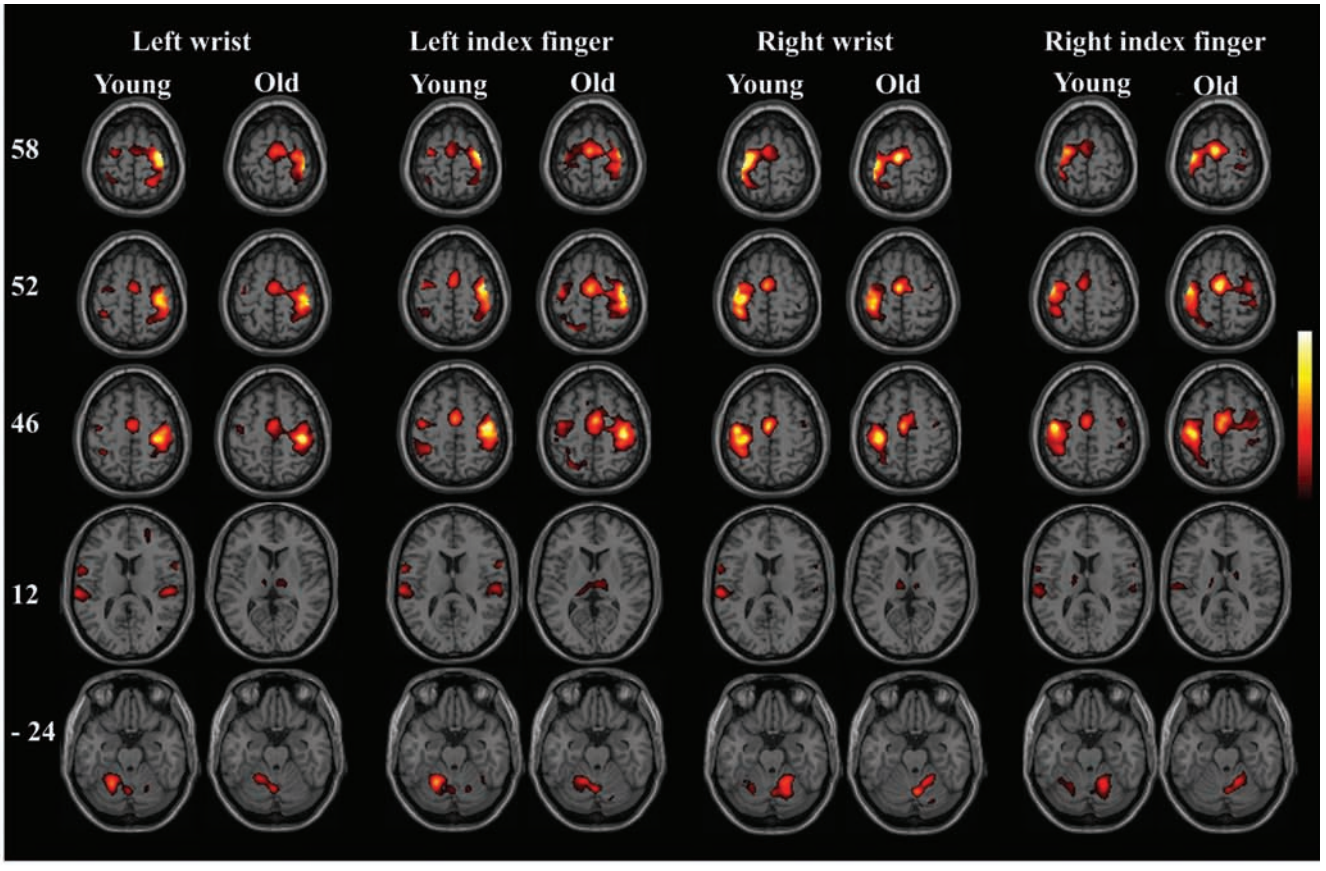

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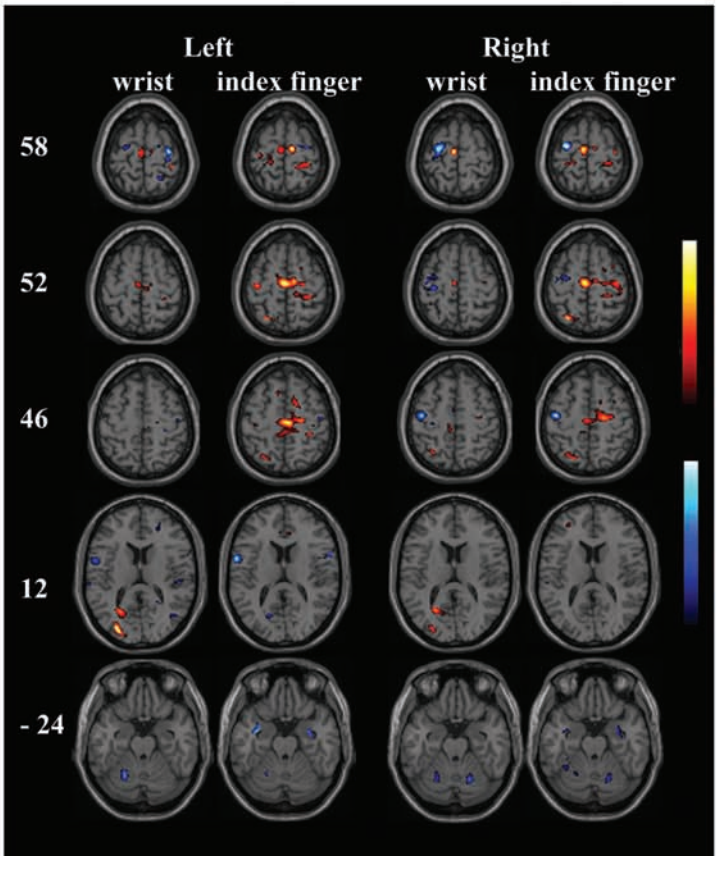

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TABLE 1

Brain Areas with Significantly Greater Activation in the Old Group

Motor task	Area activated	Cluster size (voxels)	Talairach coordinates of activation maxima			*T* level
			x	*y*	*z*	
Right wrist	SMA L	77	−4	−18	56	7.57
	Precuneus L	155	−20	−64	8	6.40
	Caudate R	52	8	6	2	5.32
	Superior occipital gyrus L	80	−24	−86	8	6.06
Right index finger	SMA L, R	862	−4, 16	−18, −20	56, 50	9.08, 7.42
	SMC R	108	22	−34	56	6.70
	Superior parietal lobule L	221	−18	−72	42	8.13
	Cuneus L	228	−16	−82	26	6.90
	Caudate R	63	12	14	0	5.86
Left wrist	Lateral occipital gyrus L	669	−24	−86	6	8.62
	Inferior frontal gyrus	325	28	22	−8	7.47
	SMA R, L	220	6, −4	−16, −20	64, 56	6.97, 6.60
Left index finger	SMA R, L	1521	8, −2	−16, −18	58, 56	8.75, 8.52
	SMC L	183	−32	−22	54	7.70
	Caudate R, L	647	4, −2	6, 8	4, 2	7.36, 7.24
	Superior parietal lobule L	131	−22	−64	52	7.16
	Superior occipital gyrus L	65	−16	−84	26	6.01
	Anterior cingulate L, R	140	−4, 4	32, 30	10, 12	6.74, 5.01
	Thalamus L	127	−14	−32	4	5.68
	Thalamus R	63	24	−30	−4	5.38

Note. Voxels (2 mm^3) showing significantly greater activation ($P < 0.05$, corrected) in the Old group compared to the Young group. Clusters are listed under each motor task in rank order of significance threshold (*T* level). SMA, supplementary motor area; PMC, premotor cortex; SMC, sensorimotor cortex; L, left; R, right.

age groups: separate maxima over the ipsilateral PMC (all tasks in both groups) or SMC (postcentral gyrus—all tasks except right wrist for both groups) or a cluster covering ipsilateral PMC and SMC (precentral gyrus—both index finger tasks in the Old group) or an area in the contralateral cerebellum (all tasks in the Young group and only left index finger in the Old group). Bilateral thalamic activation with a larger contralateral cluster was found in each task versus rest comparison in the Old group. Significant contralateral thalamic activation was found only for the right index finger and left wrist comparison in the Young group. Parietal opercular (inferior postcentral gyrus) activation was significant for all motor tasks in the Young group (contralateral for right-sided and bilateral for left-sided motor tasks) but only for the right index finger and left-sided motor tasks in the Old group. Frontal operculum (inferior frontal gyrus) was activated in the Young group for all motor tasks (contralateral for right-sided motor tasks and bilateral with larger cluster size for left-sided motor tasks).

Between-Group Contrasts

On comparison with the Young group (contrast level of −1 for main effects in each contrast), the pattern of activation in the Old group (contrast level of 1 for main effects in each contrast) was more widespread, involving both motor and nonmotor areas (Table 1). Of note, for each motor task, the Old group had T1
significantly greater activation in SMA. The cluster covering bilateral SMA varied in size between motor tasks (77 voxels for right wrist to 1521 voxels for left index finger) with the peak activation in contralateral SMA proper. In addition, the Old group had significantly greater activation than the Young group in ipsilateral SMC for both index finger tasks.

These noted activation differences had greater cluster size and higher level of significance for the index finger motor tasks and more for the left-sided (nondominant) than for the right-sided (dominant) task (Fig. 2). F2

Comparing the Young group to the Old group (Table 2), for T2
each motor task, the Young group (contrast level of 1 for main

FIG. 1. Group mean activation for each motor task versus rest for the Young group and the Old group overlaid on a standard T1 brain image in neurological view. Talairach *Z* position of selected slices is indicated on the left. Significant voxels ($P < 0.05$, corrected for multiple comparisons) are indicated on the red spectrum where in each the height threshold is $T = 4.55$.

FIG. 2. Contrast of mean activation of the Old and Young groups for each movement overlaid on a standard T1 brain image in neurological view. Talairach *Z* position of selected slices is indicated on the left. Significant voxels ($P < 0.05$, corrected for multiple comparisons) are indicated: those showing significantly greater activation for the Old group are in the red spectrum and those with significantly greater activation for the Young group in the blue spectrum where in each the height threshold is $T = 4.55$.

TABLE 2

Brain Areas with Significantly Greater Activation in the Young Group

Motor task	Area activated	Cluster size (voxels)	Talairach coordinates of activation maxima			*T* level
			x	*y*	*z*	
Right wrist	PMC L, SMC L	451	−22, −28	−16, −26	60, 54	9.75, 7.11
	Cerebellum R	144	16	−66	−24	6.84
	Cerebellum L	75	−20	−64	−22	6.01
	Cingulate L	131	−4	−8	42	6.07
Right index finger	PMC L, SMC L	267	−24, −38	−14, −16	58, 50	10.34, 9.8
	Cerebellum R	58	16	−66	−24	6.24
	Cerebellum L	136	−30	−38	−20	5.81
Left wrist	Cuneus L	407	−6	−84	16	8.92
	PMC R	100	28	−18	58	8.71
	Cerebellum L	117	−20	−62	−22	7.56
	Parietal operculum R	72	44	−26	14	6.56
	Frontal operculum L	101	−48	2	14	6.52
	PMC L	32	−20	−14	58	5.86
Left index finger	PMC R	38	42	−16	44	6.59
	Precuneus	48	−22	−58	16	6.54
	Frontal operculum L	89	−54	2	12	6.35
	Parietal operculum R	34	48	−32	6	5.27

Note. Voxels (2 mm^3) showing significantly greater activation ($P < 0.05$, corrected) in the Young group compared to the Old group. Clusters are listed under each motor task in rank order of significance threshold (*T* level). SMA, supplementary motor area; PMC, premotor cortex; SMC, sensorimotor cortex; L, left; R, right.

effects in each contrast) had significantly greater activation in contralateral SMC and PMC than the Old group (contrast level of −1 for main effects in each contrast). This activation difference had greater cluster size for right-sided tasks. In each motor task there was a maximum activation point in PMC. For right-sided tasks only, the cluster spread to SMC, where there was a second maximum activation point (Fig. 2). Significantly greater cerebellar activation was seen in the Young group in all tasks. Both right-handed tasks had significantly greater bilateral cerebellar activation in the Young group. Parietal and frontal opercular activation was greater in the Young group for both left-handed tasks.

DISCUSSION

The motor tasks used in this experiment produced a robust pattern of activation in the cortical motor system, namely contralateral primary SMC, PMC, SMA, and ipsilateral cerebellum in both the Old and the Young groups. These results are similar to previous functional imaging experiments using repetitive movements in normal healthy subjects (Roland *et al.,* 1980; Fox *et al.,* 1985; Colebatch *et al.,* 1991; Remy *et al.,* 1994). However, significant differences exist between the activation patterns produced by repetitive movements in these two groups of subjects that differed only by mean age. The Old group had significantly greater activation than the Young group in a widespread distribution involving both motor and nonmotor areas and, in particular, significantly greater activation in SMA for each motor task and ipsilateral SMC for both index finger tasks. These differences were greater, comprising a larger number of voxels of higher significance threshold, when the task was performed with the nondominant hand. The Young group had significantly greater contralateral SMC and PMC than the Old group during all motor tasks, bilateral cerebellar activation for tasks of the dominant hand, and bilateral opercular activation in tasks of the nondominant hand. These differences in activation pattern occurred despite identical motor task performance during scanning and motor testing outside the scanner, revealing no significant difference in maximal finger-tapping rates between the two groups. The differences are particularly important to note as previous functional imaging studies have assumed that repetitive movements performed similarly produce similar activation patterns across age groups and hence have omitted the use of an age-matched control group in the study of various neurological disorders (Chollet *et al.,* 1991; Weiller *et al.,* 1993; Cao *et al.,* 1998; Seitz *et al.,* 1998; Jenkins *et al.,* 2000; Marshall *et al.,* 2000; Sabatini *et al.,* 2000). This is particularly pertinent for stroke recovery as areas in which we have found significantly greater activation in an older normal group, namely SMA and ipsilateral SMC, have been associated with recovery in previous studies in which stroke subjects were not compared to age-appropriate controls (Chollet *et al.,* 1991; Weiller *et al.,* 1993; Cao *et al.,* 1998; Seitz *et al.,* 1998; Marshall *et al.,* 2000). However, other investigators have used age-appropriate controls and found similar results (Cramer *et al.,* 1997; Nelles *et al.,* 1999; Calautti *et al.,* 2001a).

It is unclear what accounts for the age-related group differences noted. Differences observed in fMRI activation during a task between two groups may be explained by differences in the hemodynamic response, the resting neural

activity, the task performance, or the task-related neural activity between the groups. Comparing a group of older subjects to younger subjects, many of these factors may contribute to the observed results.

Age-related differences in BOLD-derived signal between two groups may be attributed to differences in the hemodynamic coupling of signal change to neural activity rather than a true difference in neural activity. Using simple paradigms, investigators have noted similar significant decreases in the BOLD signal response in older subjects (Ross *et al.,* 1997; D'Esposito *et al.,* 1999; Buckner *et al.,* 2000; Hesselmann *et al.,* 2001). Although there was regional variability in the reduction in amplitude of hemodynamic response, motor cortex being less affected than visual cortex (Buckner *et al.,* 2000), in none of these experiments did altered hemodynamic coupling produce regions of increased BOLD signal in the older groups. Indeed, it is suggested that experiments, such as this one, that result in areas of increased activation in addition to areas of decreased activation in the older group probably have insignificant effects of altered hemodynamic coupling (D'Esposito *et al.,* 1999). BOLD signal differences in such studies may therefore be inferred to be due to differences in neural activity.

A difference noted between the two age groups in the degree of change in neural activity between rest and task could reflect a difference in the baseline resting activity rather than the assumed difference in task-related activity. Calautti *et al.* (2001b) used high-resolution perfusion PET to investigate the effect of age on rCBF during thumb-to-index opposition and found a significant increase in activation of the ipsilateral superior frontal cortex during right-sided opposition in the older group compared to the younger. However, the authors noted that the results of this comparison in part reflected a difference in the rCBF resting pattern between the two groups in the frontal brain regions (higher rCBF at rest in the young group) and the "deactivation" noted in this brain region in the young group during movement rather than true "overactivation" in the older group. Other studies support Calautti and coauthors' (2001b) findings of lower resting metabolic measures in the frontal cortices of older subjects (Moeller *et al.,* 1996; Petit-Taboue *et al.,* 1998) and deactivation of certain brain regions during goal-directed tasks (Shulman *et al.,* 1997; Raichle *et al.,* 2001). Unfortunately, with the technique employed in the current study, we are unable to compare the resting metabolic state of the subjects. However, when deactivation during a task was specifically examined, none of the areas of reduced BOLD signal during task versus rest in each group (results not shown) corresponded to the areas of significant overactivation in the comparator group. This suggests that deactivation upon movement, which influenced the results of Calautti and coauthors (2001b), did not contribute to the results of this study.

Differences in task-related neural activity might exist between two groups either because of actual differences in task performance or because of strategic or compensatory changes in the pattern of neural activity to produce the same performance. Observed motor task performance (rate and degree of excursion) during scanning and finger-tapping speed measured outside the scanner did not differ between the groups in this study. Age-related changes in hand coordination, strength, and fine motor performance time have been documented (Shiffman, 1992; Smith *et al.,* 1999) and such measures are particularly sensitive to increased complexity of the motor task (Smith *et al.,* 1999). Indeed the significant differences found in the Old versus Young group comparison, particularly SMA and ipsilateral SMC activation, became more prominent with the more difficult motor tasks, those that involved the nondominant hand and isolated finger movement. It is possible that a subtle difference in motor performance did exist that was more evident in the more effortful motor tasks. Altering motor performance parameters such as force, velocity, and frequency is associated with greater SMA activation but only on comparison of relatively large differences in magnitude of these motor parameters (Dettmers *et al.,* 1995; Schlaug *et al.,* 1996; Turner *et al.,* 1998). Such sizable differences in motor task performance should have been detected by the methods employed in this study; therefore we suggest the differences noted between the Old and the Young group are not explained by a performance difference alone.

If the observed significant differences in activation are not explained by performance difference then additional activation seen in either group may reflect different strategies employed to perform the task. Differences in activation in the Young group compared to the Old may reflect more effective strategies. In the Young versus Old group subtraction contralateral posterior operculum was significantly more active for both nondominant tasks. Significant activation in bilateral posterior operculum, a secondary somatosensory area (Penfield and Rasmussen, 1950), has been described during motor tasks (Colebatch *et al.,* 1991; Dettmers *et al.,* 1995). It is known that the response of neurons in this area is affected by the level of attention to the stimulating modality (Hsiao *et al.,* 1993). Such an increase in activation during selected attention is also seen using other modalities in other cortical areas (Roland, 1982). It could be speculated that the increased activation seen in the Young group in the posterior operculum represents increased attention to the task that may be necessary for nondominant movements in this group. The Young group also had increased activation in contralateral SMC on both wrist motor tasks and the right index finger. It is proposed that, in this subtraction analysis, increased activation in contralateral SMC in the Young group represents attenuated activation for this task in the Old group. As discussed below, attenuated activation in the primary areas typically associated with a task is a feature of aging that has been noted in functional imaging during cognitive tasks. In the Old group differences in activation may reflect a compensatory recruitment of cortical units required to perform the task at the same level as the Young group. Compensatory strategies have been proposed to explain age-related differences in rCBF during memory tasks (Cabeza *et al.,* 1997; Grady *et al.,* 1995, 1998; Madden *et al.,* 1999). A pattern appears consistent through these studies in which activity in cortical areas typically associated with the task performance in younger subjects is significantly less in older subjects in whom the pattern of activation becomes more

widely distributed, involving areas not activated in younger subjects. An EEG study of the effect of aging on cortical physiology found a similar shift in the task-related EEG pattern between the age groups during a simple motor task, from mainly contralateral sensorimotor high beta activity in the young group to additional ipsilateral sensorimotor and mesial frontocentral alpha band activity in the older group (Sailer *et al.,* 2000). It has been noted in functional imaging studies of cognitive aging that, in addition to the emergence of widespread areas of activation and reduction in activation in the primary area typically associated with the task, activation increases in the area homologous to this region in the opposite hemisphere (Madden *et al.,* 1999; Reuter-Lorenz *et al.,* 2000). Therefore bilateral activation in homologous areas has been proposed as a model of cognitive aging compared to the prominent laterality that is seen with these tasks in young adults (Cabeza, 2002). A similar reduction in laterality with age, with attenuation of contralateral SMC activation and increase in ipsilateral SMC activation, was evident for movement in the EEG study of Sailer *et al.* (2000) and is further elucidated in our study in which, during repetitive motor tasks, greater activity was noted in contralateral SMC in the Young group and in ipsilateral SMC and SMA in the Old group. The gradation in effort between the motor tasks employed in this study, from dominant wrist movement to nondominant index finger movement, allows us to speculate on how this influences the activation patterns seen with each motor task. First, it is of interest to note that the difference between the Young and the Old groups in contralateral SMC activation is most prominent for what would be regarded as the least effortful movement, that of dominant wrist movement, and that this difference is no longer present with the most effortful movement, that of nondominant index finger movement. One inference from this observation is that with increasing effort the Old group can now recruit contralateral SMC to the level of the Young group. This is given weight by a similar observation in encoding, in which the attenuated frontal activation typically seen in older adults was restored by supporting the task performance, suggesting that the frontal areas are underrecruited rather than absent in older adults and can be recruited with strategies to improve performance (Logan *et al.,* 2002). Similar underrecruitment with age may exist in contralateral SMC during motor tasks and may be restored during more demanding tasks. Second, it can be observed that the emergence of a distributed network in the Old group including increased activation in SMA and ipsilateral SMC is more pronounced during the more effortful motor tasks, those using the nondominant hand and involving isolated finger movement. It has been demonstrated that more complex movements in young healthy adults produce a similar pattern of greater SMA, ipsilateral SMC, and bilateral PMC activity (Rao *et al.,* 1993; Shibasaki *et al.,* 1993). These findings suggest that a hierarchical model of motor control exists, in which, with increasing demands, more of the motor network activity is required. Such a model could explain the activation differences seen in the Old group. To maintain performance, in the presence of the small changes in motor function seen in normal aging (Smith *et al.,* 1999), more regions of the motor network may be recruited. One study of cognitive aging supports this proposed association between improved performance and increased activity in the distributed network or homologous cortical area in older adults (Reuter-Lorenz *et al.,* 2001). However most have been unable to comment on the association between cognitive performance in the elderly and the distributed activation observed (Cabeza *et al.,* 1997; Grady *et al.,* 1995, 1998; Madden *et al.,* 1999), some suggesting that it may represent dysfunctional connectivity that is evident in aging (Logan *et al.,* 2002).

Regardless of whether the significant differences in activation between the groups are due to undetectable performance differences or alternative strategies employed, they have important implications for functional imaging investigation of neurological disorders. The significant activation pattern differences found in the Old group upon comparison with the Younger group in this study, in particular greater SMA and ipsilateral SMC activation, are similar to the pattern of activation that has been associated with stroke recovery (Weiller *et al.,* 1993; Seitz *et al.,* 1998). If such areas are recruited with increasing age, they may not represent neuronal plasticity following stroke as is suggested, but may simply reflect the age of the population being studied.

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