

# Dissociating the Roles of the Rostral Anterior Cingulate and the Lateral Prefrontal Cortices in Performing Two Tasks Simultaneously or Successively

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**A fundamental question about the nature of cognitive control is whether performing two tasks successively or simultaneously activates distinct brain regions. To investigate this question, we designed a functional magnetic resonance imaging (fMRI) study that compared task-switching and dual-task performance. The results showed that performing two tasks successively or simultaneously activated a common prefronto-parietal neural network relative to performing each task separately. More importantly, we found that the anterior cingulate and the lateral prefrontal cortices were differently activated in dual-task and task-switching situations. When performing two tasks simultaneously, as compared to performing them in succession, activation was found in the rostral anterior cingulate cortex. In contrast, switching between two tasks, relative to performing them simultaneously, activated the left lateral prefrontal cortex and the bilateral intra-parietal sulcus region. We interpret these results as indicating that the rostral anterior cingulate cortex serves to resolve conflicts between stimulus–response associations when performing two tasks simultaneously, while the lateral prefrontal cortex dynamically selects the neural pathways needed to perform a given task during task switching.**

## Introduction

Human behavior depends upon an interaction between our goals (top-down control) and our reactions to stimuli (bottom-up influences). The capacity to achieve internal goals in situations where stimuli-induced behavior needs to be overcome, referred to as cognitive control, has received a renewed interest from behavioral, neurophysiological, brain imaging and neuropsychological studies (Grafman, 1994; Shallice and Burgess, 1996; Miller, 2000; Pashler *et al.*, 2001; Corbetta and Shulman, 2002; Dreher and Berman, 2002). This ability is at the heart of any complex attentional task tested in the laboratory that requires subjects dynamically and flexibly to establish arbitrary stimulus–response associations. Different tasks in which the very same stimuli are presented can only be distinguished by the internal goals of the subjects, directed by the specific instructions of the task. Cognitive control is especially needed when taxing the capacity or computational limitations of the cognitive system, as is the case when the stimuli–response associations are rapidly changing (e.g. in task-switching situations) or when performing two tasks simultaneously (as in dual-task situations). Failure to switch flexibly between different tasks or to perform two tasks simultaneously is a characteristic feature of the disexecutive syndrome exhibited by patients with frontal lobe lesions (Norman and Shallice, 1986; Grafman, 1994; Fuster, 2001). In a classical dual-task situation, a substantial slowing of one or both tasks is usually observed. This effect, called the ‘psychological refractory period’ (PRP), becomes greater as the stimulus onset asynchrony (SOA) is reduced (Pashler, 2001). A behavioral effect that has been related to the slowing observed in dual tasks occurs when subjects perform two tasks in succession. This

effect, called a ‘task switch cost’, is an increase of response times (RTs) in the switch compared to the repeat trials (Allport *et al.*, 1994; Rogers and Monsell, 1995; Meiran, 1996). The exact causes of the PRP effect and of the switch cost remain debated (Allport and Wylie, 2000; Monsell *et al.*, 2000; Logan and Delheimer, 2001; Pashler, 2001).

An important question that arises about cognitive control is whether distinct brain regions are activated when performing two tasks simultaneously or successively. The goal of this study was to address this question by directly comparing the neural basis of performing two tasks simultaneously (dual task) or successively (task switching). Previous brain imaging studies have examined task switching or dual tasks in isolation, but did not directly compare brain activation in these two paradigms (D’Esposito *et al.*, 1995; Passingham, 1996; Goldberg *et al.*, 1998; Klingberg, 1998; Adcock *et al.*, 2000; Bunge *et al.*, 2000; Dove *et al.*, 2000; Kimberg *et al.*, 2000; Sohn *et al.*, 2000; DiGirolamo *et al.*, 2001; Rushworth *et al.*, 2001; Smith *et al.*, 2001; Dreher and Berman, 2002). Direct comparison of brain activation during dual-task and task-switching performance should allow us to examine whether dual tasks require activation of specific brain regions as compared to task switching and whether specific brain regions are required in task switching relative to dual tasks.

We designed a new dual-task paradigm that requires subjects to perform two tasks simultaneously with only one stimulus and one motor response. In this new dual task, subjects had to discriminate simultaneously whether a stimulus letter was a vowel or in upper case (or both) by pressing a right response button, and a left button otherwise. In the task-switching condition, subjects performed two letter discrimination tasks successively (vowel/consonant or upper/lower case discrimination). This allowed us to directly compare dual-task situations to task switching, by equating for stimulus presentation and the number of motor responses. In contrast, in classical dual-task paradigms, there are two successive stimuli and two separate motor responses. Because there is only one motor response required in our new dual-task design, we can exclude the interpretations, which are valid in dual-task designs with two close successive motor responses, that subjects have an intrinsic limitation in the initiation and execution of motor responses (Keele, 1973; Gottsdanker, 1980; De Jong, 1993) or adopt a specific strategy to prevent response reversals, i.e. never make response R2 before response R1 (Meyer and Kieras, 1997). For instance, the increased RT for the second task at a short SOA obtained in classic dual-task paradigms could be due to reduced task preparation because subjects have to prepare for two tasks at a short SOA, but only one task at a long SOA. Our new paradigm also maximizes the chances that two tasks are really performed simultaneously, because the use of only one stimulus should activate, in parallel, the two pathways corresponding

to the two tasks. In contrast, in classical dual-task paradigms, the two stimuli cueing the two tasks are only rarely presented simultaneously (the study of the PRP effect requiring a variable SOA), making it more likely that the two tasks are not performed simultaneously.

Two potential neurophysiological mechanisms have been proposed to explain the decrease of performance in dual tasks relative to performing each task separately and these may also be applied to task-switching performance: (i) dual tasks and/or task switching may require additional cognitive operations and activation of specific brain regions in addition to those activated by the single task performed alone, or (ii) two tasks may interfere (and thus increase RTs) if they recruit the very same population of neurons at the same time or if they activate distinct neural populations (within the same brain region) that inhibit each other mutually when activated simultaneously (Klingberg, 1998). To illustrate the first point, several previous brain imaging studies have proposed that dual tasks involve specific higher-order cognitive processes that activate specific brain regions, such as divided attention (Corbetta *et al.*, 1991) or task coordination (D'Esposito *et al.*, 1995). The second point should be especially likely if the stimuli of the two tasks belong to the same sensory modality and *a fortiori* if these stimuli are the same for the two tasks.

We hypothesize that performing two tasks simultaneously, relative to performing them in succession, should activate the anterior cingulate cortex (ACC) because: (i) when two tasks are activated simultaneously, they should create conflicts between stimuli-response associations (Barch *et al.*, 2000; Carter *et al.*, 2000) and (ii) the PRP found in dual tasks is often considered to reflect a bottleneck stage at the level of motor selection (Pashler, 1994; Pashler *et al.*, 2001), which may also involve the ACC (Badgaiyan and Posner, 1998). Conversely, we hypothesized that performing two tasks in succession, relative to performing them simultaneously, should activate a brain network including the lateral prefrontal cortex (PFC) and the intra-parietal sulcus (IPS) region. More specifically, the lateral PFC has been proposed to dynamically select the neural pathways needed to perform a given task (Tomita *et al.*, 1999; Miller, 2000; Murray *et al.*, 2000; Miller and Cohen, 2001), while the IPS region has been proposed to be involved in assembling associations that link the appropriate stimuli and responses for a given task during task-switching situations (Le *et al.*, 1998; Kimberg *et al.*, 2000; Rushworth *et al.*, 2001; Corbetta and Shulman, 2002). Thus, during task switching, the lateral PFC may provide a bias signal to the IPS region to select the appropriate stimulus-response mapping for the task at hand (Miller, 2000; Miller and Cohen, 2001).

## Materials and Methods

### Subjects

Eight subjects were recruited following procedures approved by the NINDS Institutional Review Board. All subjects (mean age = 25 years, range 20–31) were native speakers of English and strongly right-handed, as measured by the Edinburgh handedness inventory. Informed consent was obtained from each subject. One or two days before the MR session, subjects participated in a behavioral testing session during which they were trained to perform each of the tasks and were required to attain an overall accuracy score >90% to participate in the fMRI experiment. The high performance rate (>95 % correct) during scanning indicates that all the tasks were overlearned.

### Stimuli and Task Parameters

Subjects responded to visually presented single letters (vowels or

consonants, in either upper or lower case, red or green) by pressing response buttons held in each hand (Fig. 1). Each condition (24 trials each) was cued by a distinct written instruction displayed for 2 s at its beginning.

In the vowel-consonant discrimination condition, subjects had to press the right button if the letter was a vowel and the left button if the letter was a consonant. In the case-discrimination condition, subjects had to press the right button if the letter was in upper case and the left button if the letter was in lower case. For both conditions, the color of the letters was irrelevant and changed every three letters. The baseline was composed of the mean of these two discrimination tasks (i.e. the two single tasks averaged together).

In the task-switching condition, subjects had to perform one of the two discrimination tasks according to the color of the letter. Red letters indicated the vowel-consonant discrimination task and green letters indicated the case-discrimination task.

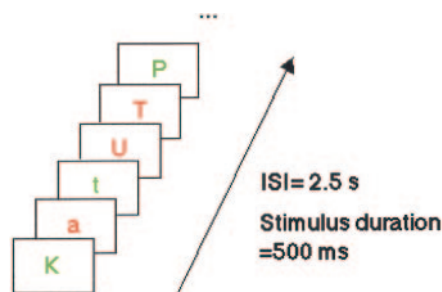
In the dual-task condition, subjects had to press the right button if the letter was a vowel or was in upper case (and if both were true) and the left button otherwise. In both the task-switching and dual-task conditions, the color of the letter changed pseudo-randomly. Note that in the dual-task condition, the color of the letter was irrelevant to performance of the task.

The letters used in the different conditions were taken from among the following set of letters (which were in upper or lower case, red or green): c, d, f, h, k, m, p, r, t, v, a, e, i, o, u, y. Both the task-switching condition and the two simple discrimination tasks used for baseline were constructed by pseudo-randomly choosing among this set of letters that were equated for the number of vowels/consonants (12 of each), of upper/lower case letters, of red/green letters (12 of each) and of left/right responses (12 of each). These constraints were violated for the dual-task condition in order to keep an equal number of left/right responses (there were more consonants than vowels and more lower case than upper case letters). In all these conditions, each stimulus appeared for 500 ms every 2.5 s.

In addition, task-switching conditions not reported in this study were also performed with a random timing ( $2.5 \pm 260$ ,  $\pm 390$ ,  $\pm 510$  ms) and in predictable order (subjects switched from one task to the other on every second trial). Thus, each run comprised eight conditions consisting of the two conditions used for baseline (vowel-consonant and case discrimination), four task-switching conditions (obtained by crossing task order and timing predictability) and two dual-task conditions (one with fixed ISI = 2.5 s and the other with pseudo-random timing of ISI =  $2.5 \pm 260$ ,  $\pm 390$ ,  $\pm 510$  ms). Only the dual-task and the task-switching conditions with fixed timing and unpredictable color change were used to allow us to make direct comparisons not susceptible to timing. Each task-switching condition alternated with one of the dual-task conditions or one of the two conditions used for baseline.

### fMRI Methods

High-resolution structural images were obtained using a standard 1.5 GE whole-body Signa scanner with an RF coil. For each subject, six time-series of 180 whole-brain images (first four images removed) were obtained with a gradient-echo, echo-planar scanning sequence ( $T_R$  3 s,  $T_E$  40 ms, flip angle 90°, FOV 24 cm, acquisition matrix  $64 \times 64$ , 22 axial slices, thickness 6 mm). Each run was pseudo-randomly ordered according to a Latin square design, so that each condition appeared only once at different serial positions within a run and that baseline; dual-task and task-switching conditions alternated. The order of runs was also counterbalanced across subjects. Using SPM96 with modified memory-mapping procedures, for each subject, the series of functional images for the six runs was realigned using a bilinear interpolation method, normalized to the Montreal Neurological Institute template, smoothed with a Gaussian filter [10 mm full width at half maximum (FWHM) kernel] and, finally, scaled across scans. Then, the data from all subjects were pooled together and statistical parametric maps were computed from local MR signals using linear multiple regression with conditions, modeled as two temporal basis functions and with runs as covariates – the fixed effect model (Friston *et al.*, 1991). Only regions formed by >10 adjacent active voxels (voxel size =  $4 \text{ mm}^3$ ) were reported ( $Z > 4.3$ ,  $P < 0.05$ , corrected for multiple comparisons).



**Figure 1.** Experimental design. Subjects responded to visually presented letters by pressing response buttons with their right or left hand. Each condition was cued by a distinct written instruction displayed at the beginning of the run. In the dual-task condition, subjects had to discriminate simultaneously whether a stimulus letter was a vowel or in upper case (or both) by pressing a right response button, and a left button otherwise. In the task-switching condition, subjects had to switch between two letter-discrimination tasks depending upon the color of the letter. If the letter was red, subjects performed a vowel–consonant discrimination task (vowel, right; consonant, left). If the letter was green, subjects performed a case discrimination task (upper case, right; lower case, left). Stimuli appeared with fixed timing in a pseudo-randomized order. In two conditions used for baseline, subjects performed each of these two vowel/consonant and upper/lower case discrimination tasks in separate blocks of trials. The baseline was the average of these two simple discrimination tasks.

## Results

### Behavioral Performance

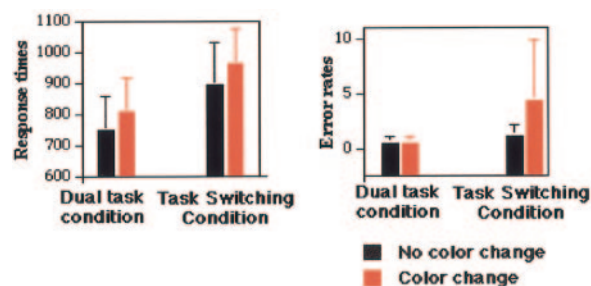
Behavioral data were analysed with a two-factor, repeated-measures analysis of variance (ANOVA) that included the two executive control conditions (task switching versus dual task) and color change (no change versus change) as factors (Fig. 2). Response times (RT) were significantly slower in the task-switching condition than in the dual-task condition [ $F(1,7) = 42.8$ ,  $P < 0.0001$ ], indicating that the switching conditions demanded cognitive processes additional to those needed for processing dual tasks. Furthermore, there was a significant increase of RTs with color change [ $F(1,7) = 16.9$ ,  $P < 0.005$ ]. No interaction between factors or main effects for error rates reached statistical significance. The absence of an RT interaction between color change and executive control conditions [ $F(1,7) = 0.8$ ,  $P = 0.38$ ], shows that the color change was significant for both the dual-task [ $F(1,7) = 15.4$ ,  $P < 0.01$ ] and the task-switching conditions [ $F(1,7) = 12.2$ ,  $P < 0.05$ ]. The mean RTs of the two tasks used for baseline were 717.5 ms (SD 100.6) for the vowel/consonant discrimination task and 656.6 ms (SD 90.15) for the case discrimination task.

To ensure that subjects maintained two tasks simultaneously in memory in the dual-task condition, we investigated whether subjects coded this condition as a single stimulus–response mapping. If the dual task was coded as only one task and not two tasks, subjects should have directly associated the lower-case consonants to a left motor response and other letters to a right button press. However, RTs were not faster for lower-case consonant letters than for other letters [ $F(1,7) = 2$ ,  $P = 0.2$ ].

### fMRI Results

#### Brain Regions Activated by the Task-switching Condition Relative to Baseline

We first identified brain regions activated by the task-switching condition relative to baseline (Fig. 3). Activation was found in the medial and superior frontal gyri bilaterally, the IPS bilaterally, the inferior temporal gyrus (ITG; BA 20/37) bilaterally, the right operculum and the left cerebellar hemisphere (Table 1).



**Figure 2.** Behavioral results. Left: mean response time (RT) averaged across subjects in the dual-task and task-switching conditions. Right: mean error rates averaged across subjects in the dual-task and task-switching conditions. Factors included executive control condition (dual task versus task switching) and color change (change versus no change). Mean response time was examined for correct response trials only.

#### Brain Regions Activated by Dual-task Performance Relative to Baseline

Secondly, we identified brain regions activated by the dual-task condition relative to baseline (Fig. 4). Activation was found in the medial and superior frontal gyri bilaterally, the pre-SMA, the ACC, the somato-motor area (BA 4), the intra-parietal sulcus bilaterally, the right ITG (BA 20/37), the occipital gyrus bilaterally (BA 18/19), the right caudate nucleus and the cerebellum (Table 1).

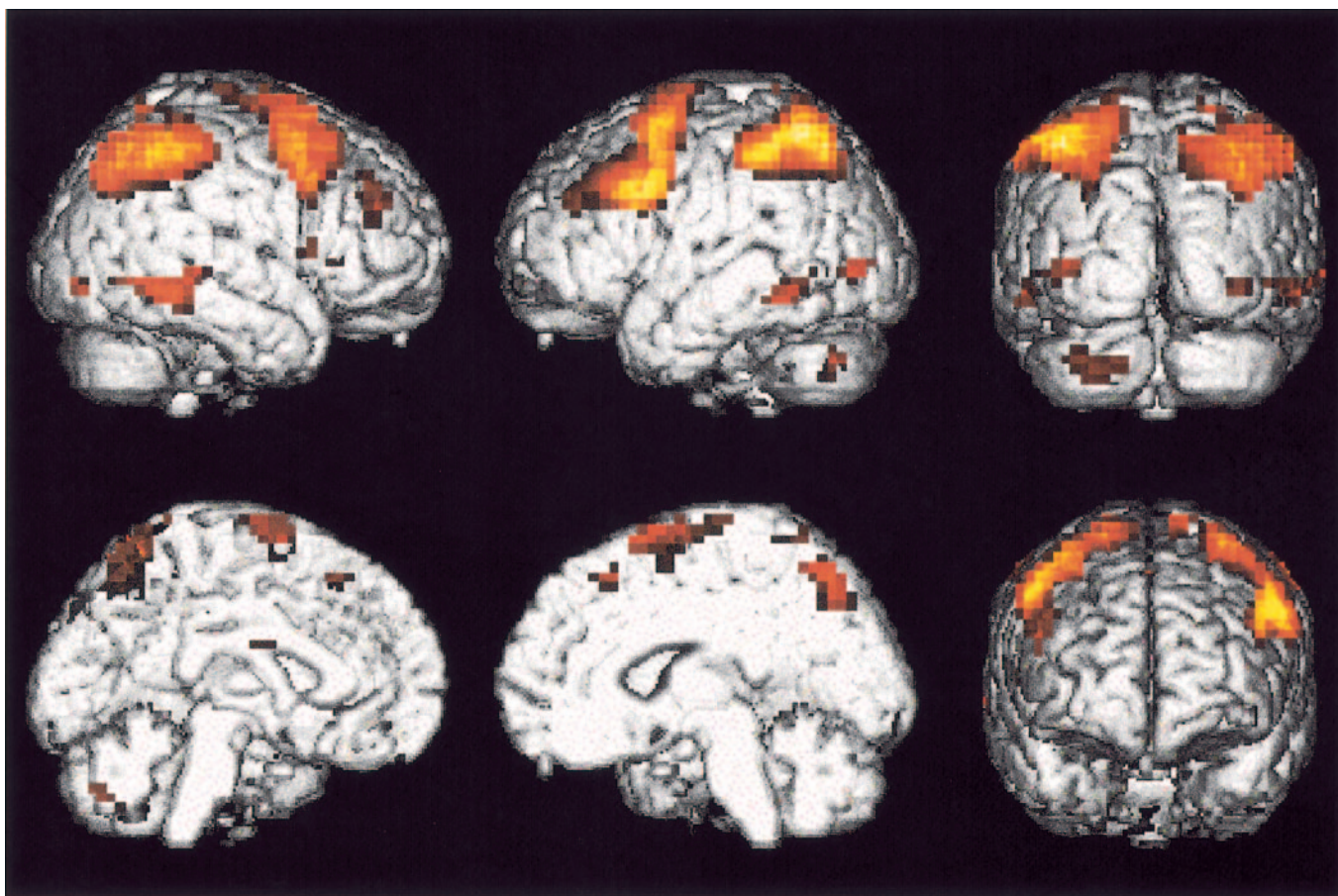
#### Brain Regions Activated by Dual-task Performance Relative to Task Switching

Thirdly, we directly compared the dual-task condition relative to the task-switching condition. This contrast mainly activated the rostral part of the anterior cingulate gyrus ( $x, y, z = 0, 36, 12$ , BA 24/32; Fig. 5, Table 1). Activation was also found in the posterior cingulate gyrus, the left middle and superior temporal gyrus (BA 21/22), the precuneus and the lateral cerebellar hemisphere bilaterally. It should be noted that what we describe as the rostral ACC encompasses part of the anterior medial PFC. As deactivation of both the ventral and dorsal parts of the anterior medial PFC has often been observed in a variety of goal-directed paradigms (Binder *et al.*, 1999; Gusnard and Raichle, 2001; Raichle *et al.*, 2001), it could be argued that the deactivation observed for task-switching relative to baseline comes from the anterior medial PFC rather than the rostral ACC (Fig. 5). However, the rostral ACC remained activated when using a more stringent threshold ( $Z = 5.6$ ,  $P < 1 \times 10^{-7}$ , corrected;  $x, y, z = 0, 52, 4$ ,  $Z$ -value = 7.45), showing that the deactivation found in task-switching relative to baseline is not only due to the anterior medial PFC.

#### Brain Regions Activated by Task Switching Relative to the Dual-task Condition

Finally, we examined brain regions activated by the task-switching condition relative to the dual-task condition (Fig. 6). Activation was found in the left medial frontal gyrus, the right inferior frontal gyrus, the fronto-polar cortex bilaterally (BA 10), the left superior parietal cortex, the intra-parietal cortex (BA 7/40) bilaterally, the left superior temporal gyrus (BA 22) and the left medial occipital gyrus (BA 18/19; Fig. 6A, Table 1). As it is difficult to interpret areas more activated by task-switching than dual task but that are also more activated by single-task than dual-task performance, we selected the brain regions engaged by task switching relative to the dual task ( $Z > 4.3$ ,  $P < 0.05$ , corrected) that were also more activated by the dual task than





**Figure 3.** Data for regions significantly activated by the task-switching condition relative to baseline (averaged of the two single tasks) were overlaid onto a 3D rendered brain. The Z-values and stereotactic coordinates for the regional maxima are listed in Table 1.

the baseline ( $P < 0.05$ ). The only brain regions surviving this inclusive mask were the IPS bilaterally ( $x, y, z = -36, -60, 56$ ,  $Z = 5.14$ ;  $x, y, z = 48, -48, 52$ ,  $Z = 5.42$  and more in the superior parietal cortex for the left hemisphere). When using a less stringent threshold ( $Z > 3.09$ ,  $P < 0.001$ , uncorrected), we found that in addition to the bilateral IPS, the left DLPFC was also activated ( $x, y, z = -52, 12, 32$ ,  $Z = 4.15$ ;  $x, y, z = -28, 8, 64$ ,  $Z = 4.06$ ; Fig. 6B).

In order to ensure the robustness of the results reported with this fixed effect model, we also performed single subjects analysis and reported the number of subjects activating the frontal regions (rostral ACC, fronto-polar cortex and lateral PFC) found in the two major contrasts. Among the eight subjects tested, six activated the rostral ACC in the contrast comparing the dual-task to the task-switching condition ( $Z > 4.3$ ,  $P < 0.05$ , corrected), while seven activated the fronto-polar cortex and the lateral PFC found when directly comparing the task-switching to the dual-task condition ( $Z > 4.3$ ,  $P < 0.05$ , corrected). In addition, none of the eight subjects showed a significant activation of the rostral ACC for task-switching relative to dual-task performance ( $Z < 1.3$ ,  $P > 0.1$ , uncorrected). Two subjects showed right lateral PFC activations for dual-task performance relative to task switching (subject 1,  $x, y, z = 44, 32, 28$ ; subject 2,  $x, y, z = 32, 40, 48$ ;  $Z > 4.3$ ,  $P < 0.05$ , corrected) and one subject showed a bilateral inferior frontal gyrus (BA 45) activation for dual-task performance relative to task switching ( $x, y, z = -52, 20, 4$  and  $x, y, z = 52, 36, 12$ ;  $Z > 4.3$ ,  $P < 0.05$ , corrected).

## Discussion

The results of our study showed that performing two tasks successively or simultaneously activated a common prefronto-parietal neural network relative to a baseline consisting of the average of two discrimination tasks performed separately (Figs 3 and 4). This shows that this network is not specific for task-switching or dual-task performance, but is more generally recruited for executive processes. Although there have been discrepancies in findings between studies, a bilateral network including the DLPFC and the IPS region has repeatedly been found in dual-task and in task-switching experiments. An early dual-task fMRI study reported a specific DLPFC and anterior cingulate cortex activation for dual tasks, relative to performing each task separately (D'Esposito *et al.*, 1995), while recent studies have failed to show additional brain activation associated with dual tasks and have instead reported an increased activity in the same brain regions as those recruited by the component tasks (Passingham, 1996; Goldberg *et al.*, 1998; Klingberg, 1998; Adcock *et al.*, 2000; Bunge *et al.*, 2000). Similarly, most event-related fMRI studies of task switching reported no specific brain region for switch trials, but simply an increased activation of a bilateral DLPFC-parietal network for switch relative to repeat trials (Dove *et al.*, 2000; Rushworth *et al.*, 2001). Block design studies that compared task switching with performing each task individually also reported activation of a bilateral prefronto-parietal network (DiGirolamo *et al.*, 2001; Smith *et al.*, 2001; Dreher *et al.*, 2002). The only discrepant result with those

**Table 1.** Foci of activations in the different statistical contrasts

Anatomical structure (Brodmann's area)	Task switching versus baseline				Dual tasks versus baseline				Task switching versus dual tasks				Dual tasks versus task switching			
	Talairach coordinates				Talairach coordinates				Talairach coordinates				Talairach coordinates			
	x	y	z	Z-value	x	y	z	Z-value	x	y	z	Z-value	x	y	z	Z-value
Frontal																
L sFG (BA 6)	−28	4	60	7.07	−24	4	56	6.58								
L iFG/mFG (BA 8/9/44)	−52	12	36	7.29	−36	24	28	6.93	−60	12	32	6.36				
					−44	16	40									
R sFG (BA 6)	36	8	60	6.58	16	8	64	6.36								
R mFG (BA 8/9/46)	48	16	40	7.16	48	44	32	7.17								
	48	44	28	5.87	44	12	40	6.99								
					44	0	44	6.97								
R iFG (BA 44/45)									60	12	8	6.55				
Pre-SMA	4	28	52	5.34	8	20	52	6.50								
Rostral ACC					12	40	−8	6.78					0	36	12	7.29
					12	28	28	6.34					4	28	20	7.05
					−8	32	4	6.52					8	56	28	6.71
					12	4	40	5.76								
ACC													−8	−48	24	4.95
Posterior cingulate																
L fronto-polar cx									−28	60	−4	5.40				
R fronto-polar cx									48	52	0	6.53				
L somato-motor area (BA 4)					−16	−20	64	4.90								
R somato-motor area (BA 4)					16	−20	68	6.08								
Parietal																
L IPS (BA 7/40)	−36	−56	52	8.16	−32	−60	44	7.45	−36	−60	56	5.14				
					−40	−44	44	7.01								
L superior parietal cx									−12	−56	68	5.55				
R IPS (BA 7/40)	36	−60	48	7.84	36	−60	40	7.30	48	−48	52	5.42				
Precuneus													−4	−68	24	5.02
Cerebellum																
L lat. cerebellar hemisphere	−24	−68	−40	6.55	−16	−60	−44	7.47					−16	−44	−20	5.49
R lat. cerebellar hemisphere	32	−72	−44	6.83									12	−44	24	5.11
Vermis					4	−68	−32	5.86								
Gyrus temporal																
L iTG (BA 20)	−48	−48	−8	5.64	−64	−28	−8	7.96								
	−32	−64	0	4.45	−36	−64	8	6.31								
L mTG (BA 21)													−64	−28	−8	6.93
R iTG (BA 37)	56	−44	−8	7.12												
L sTG (BA 22)									−60	0	−8	5.84	−60	−48	12	5.48
R sTG (BA 22)																
R operculum					40	28	0	5.15								
L m occip. gyrus (BA 18/19)					−8	−72	20	5.93	−40	−80	20	5.29				
R m occip. gyrus (BA 18/19)	36	24	4	5.08	20	−72	20	5.29								
R caudate					12	16	0	5.81								

The coordinates are given within the framework of the standardized stereotaxic brain atlas of Talairach and Tournoux (Talairach and Tournoux, 1988). All areas were significant at  $P < 0.05$  (corrected for multiple comparisons). Abbreviations: L, left; R, right; sFG, superior frontal gyrus; mFG, middle frontal gyrus; IPS, intra-parietal sulcus; INS, insula; iTG, inferior temporal gyrus; sTG, superior temporal gyrus; somatosens.cx., somatosensory cortex; occip. gyrus, occipital gyrus.

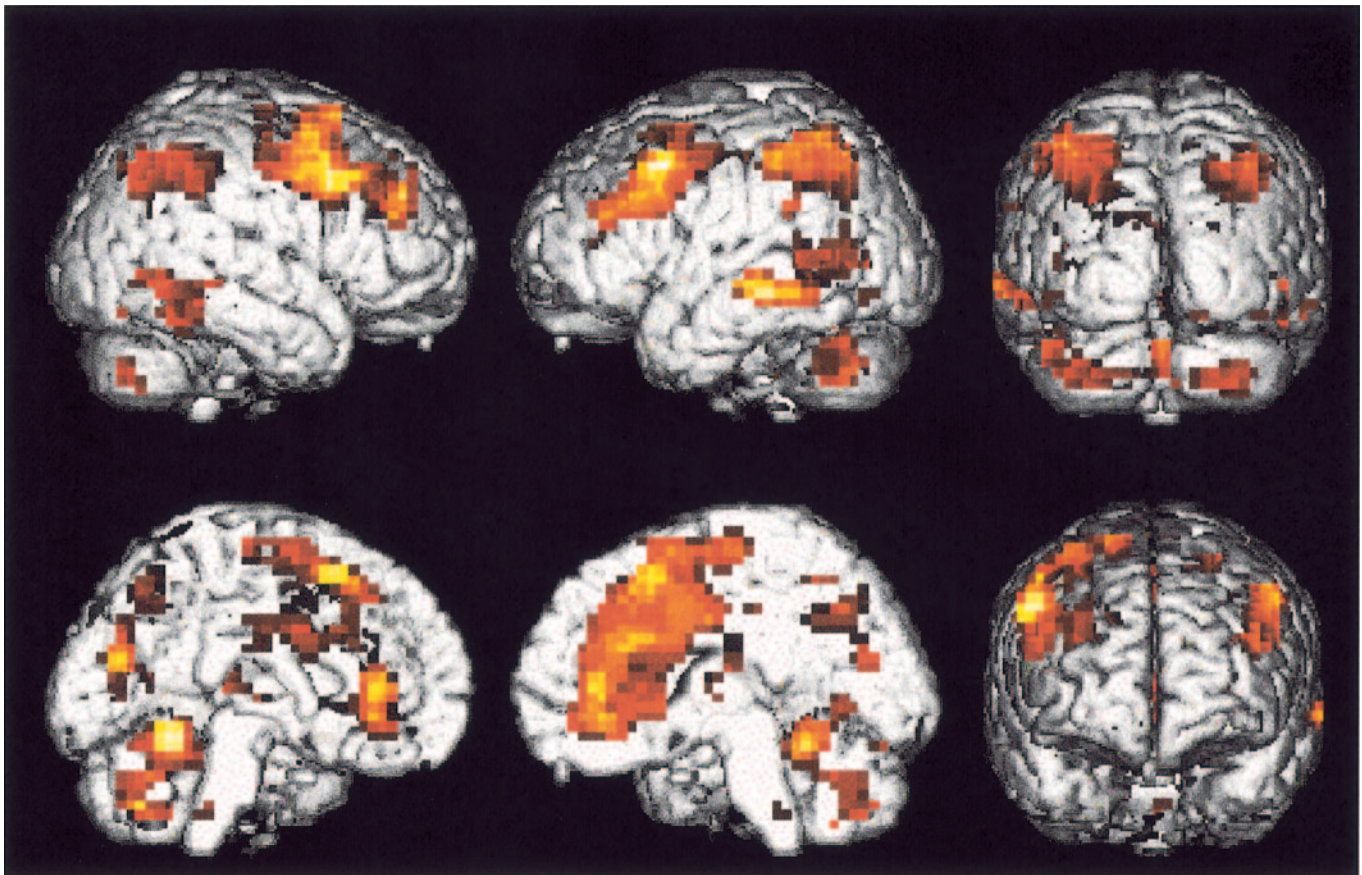
findings comes from one fMRI task-switching study that reported a superior parietal cortex activation during switching that was not part of task-related regions (Kimberg *et al.*, 2000).

Importantly, our study allowed us, unlike previous studies, directly to compare brain activation induced by distinct executive processes (task-switching versus dual-task situations). When directly comparing simultaneous and successive performance of two tasks, we found that the rostral ACC and the lateral PFC were distinctively activated by simultaneous and sequential task performance. Performing two tasks simultaneously activated the rostral anterior cingulate relative to successive performance of the two tasks (Fig. 5). Conversely, performing two tasks successively activated the left lateral PFC and the bilateral IPS region relative to performing the two tasks simultaneously (Figs. 6B). We discuss these findings in details in the next two sections.

First, it may be noted that the present study used a baseline (average of the two discrimination tasks) that is perfectly appropriate because it includes the two component tasks used in

both task switching and dual task. However, it would also have been interesting to know the direction of signal changes relative to a low-level baseline. Previous studies showed that both task-switching (DiGirolamo *et al.*, 2001) and dual-task conditions (Klingberg, 1998) activate a bilateral DLPFC–IPS network relative to such low level baselines. Thus, our data complement these studies reporting no specific brain region for dual-task and task-switching performance by directly showing that both situations activate a bilateral DLPFC–parietal network. It has also to be noted that recent studies have emphasized the importance of the choice of the baseline, both from a technical neuro-imaging perspective (Gusnard and Raichle, 2001; Newman *et al.*, 2001; Stark and Squire, 2001) and from a cognitive point of view (Allport and Wylie, 2000). In particular, it has been suggested that subjects are not fully prepared in repeat trials (Allport and Wylie, 2000), which may explain the absence of frontal activation in a task-switching study using repeat trials as a baseline (Kimberg *et al.*, 2000). *Post hoc* analysis of our data also showed that RTs in our baseline, in which subjects





**Figure 4.** Data for regions significantly activated by the dual-task condition relative to baseline were overlaid onto a 3D rendered brain. The Z-values and stereotactic coordinates for the regional maxima are listed in Table 1.

performed only one task, were faster than the repeat trials of the task-switching condition. Future event-related studies of task switching with two tasks may thus benefit from inclusion of a control baseline similar to that employed here (e.g. block of single task) in addition to a more classic baseline constituted by the average of repeat trials.

#### ***Rostral Cingulate Activation in Performing Two Tasks Simultaneously Relative to Switching Between Them***

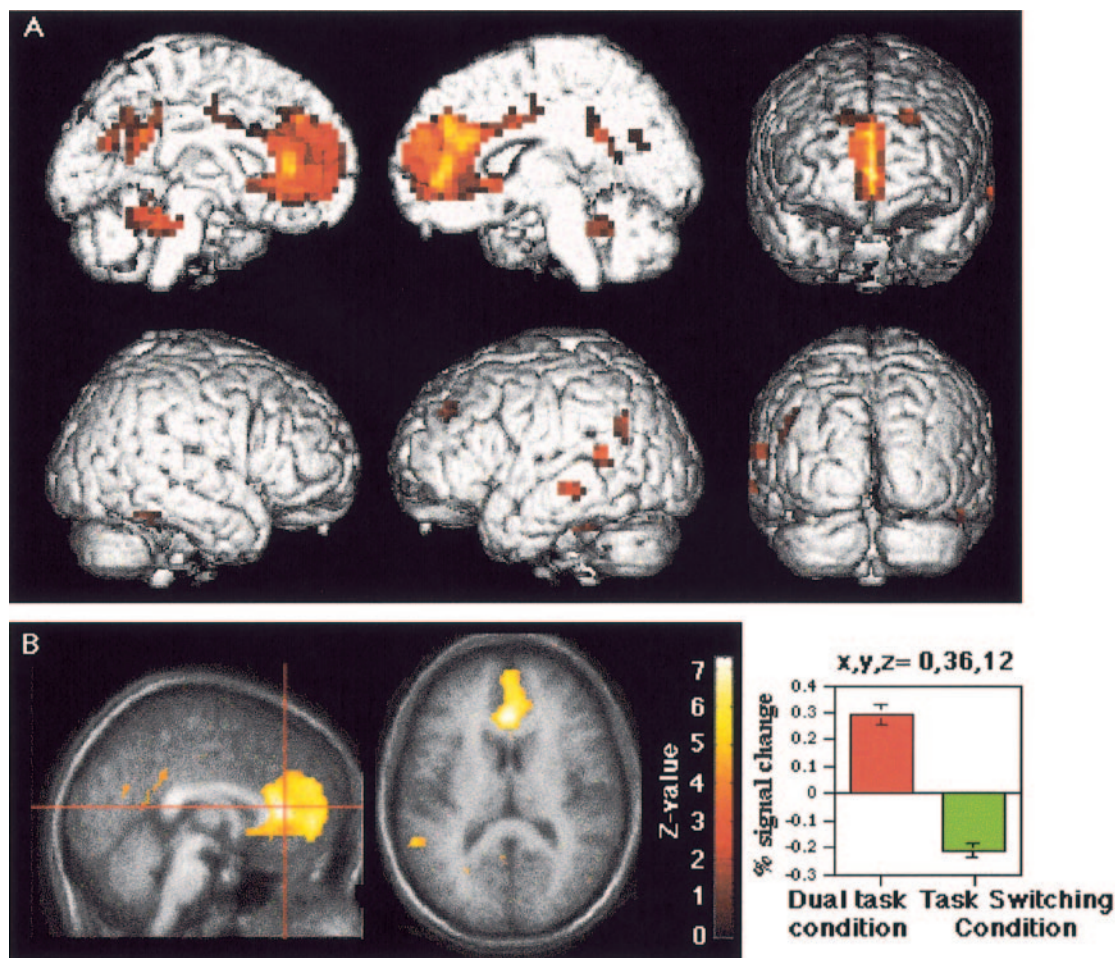
A possible interpretation of the rostral ACC activation is that it monitors the occurrence of conflict or crosstalk between different information-processing pathways (Carter *et al.*, 2000). Neural network models support the conflict-detection hypothesis and predict that the ACC should be especially involved when two or more incompatible responses are simultaneously activated (Botvinick *et al.*, 2001). An important link, suggested by our results, between the behavioral literature on dual-task performance and this conflict detection theory is that the PRP found in dual tasks is often considered to reflect a bottleneck stage at the level of motor selection (Pashler, 1994; Pashler *et al.*, 2001) and motor selection is known to activate the ACC (Badgaiyan and Posner, 1998).

In a similar fashion, tasks such as verb generation and verbal fluency that activate the ACC have been thought to do so because multiple pathways are activated simultaneously by the cue, creating crosstalk in the pathways responsible for the selection and/or production of these responses (Barch *et al.*, 2000). It is worth noting that most of the tasks reported as showing ACC activation with conflict monitoring generally

showed more activation in the dorsal ACC than in the rostral part of the ACC. In fact, a recent review showed that the rostral ACC and subcallosal portions of the ACC are more engaged in emotional behavior, while the dorsal region of the ACC is more frequently engaged by cognition (Bush *et al.*, 2000). However, this division is relative because some cognitive studies also activated the rostral ACC, while some studies on emotion activate the caudal ACC (Bush *et al.*, 2000). Our study confirms that this division is not absolute. A possible reason for the rostral ACC activation in our study may be related to the need, in the dual-task condition, to sub-vocalize in order to remember the complex instructions (upper case or vowel, or both – right button; left button otherwise). Indeed, the rostral ACC, together with the dorsal ACC, has been related to vocalization during a stimulus-response conflict task requiring speech utterance (Paus *et al.*, 1993; Paus, 2001).

The dual-task condition incorporated components of a divided attention task (e.g. processing several stimulus attributes simultaneously) and the Stroop task (i.e. inhibiting response tendency to read a colored word). Both tasks are known to activate the ACC and the DLPFC (Corbetta *et al.*, 1991). In our dual task, the subjects had both to process multiple stimulus attributes (identification of the color, particular letter and case) and to inhibit the tendency to switch task with color change. Thus, our data are consistent with a role of the ACC in these two processes and, additionally, distinguish the roles played by the ACC and the DLPFC, that are often coactivated during tasks demanding high cognitive control (Duncan and Owen, 2000; Paus, 2001). The possibility that the rostral ACC may reflect, in part, a Stroop-like





**Figure 5.** (A) Data for regions significantly activated by the dual-task condition relative to the task-switching condition were overlaid onto a 3D rendered brain. (B) Left: activation is superimposed on normalized structural MRI slices averaged across subjects ( $x, y, z = 0, 36, 12$ ). Right: percentage of signal change relative to baseline for the dual-task and task-switching conditions in the rostral anterior cingulate cortex (BA 24/32). The Z-values and stereotactic coordinates for the regional maxima are listed in Table 1.

effect, i.e. interferences due to the overlearned association between a specific color and an individual discrimination task, is supported by the observation of a behavioral color cost in the dual task. However, it should be noted that activation related to the Stroop effect is classically reported in the dorsal part of the ACC rather than in the rostral ACC (Pardo *et al.*, 1990; Carter *et al.*, 1995; Bush *et al.*, 2000). Furthermore, although none of our subjects had a total absence of behavioral cost due to color change in the dual task, half of them had a cost  $<30$  ms (while the other half had a cost  $>60$  ms), but still activated the rostral ACC in the dual task relative to the task-switching condition. This suggests that activation of this brain region is unlikely to result only from the need to suppress irrelevant rules activated by the colors.

An alternative interpretation of the rostral ACC activation is that it reflects simultaneous memory retrieval of the task rules. Indeed, an important component of the dual-task condition is that it requires subjects to retrieve two tasks simultaneously from memory, while in task switching it is necessary to retrieve each task rule successively from memory (Mayr and Kliegl, 2000). This interpretation is consistent with the current ACC theory of conflict detection, because simultaneous memory retrieval may create conflicts between stimulus and response. In our current design, simultaneous memory retrieval is possible in the dual-task condition because items belong to the same

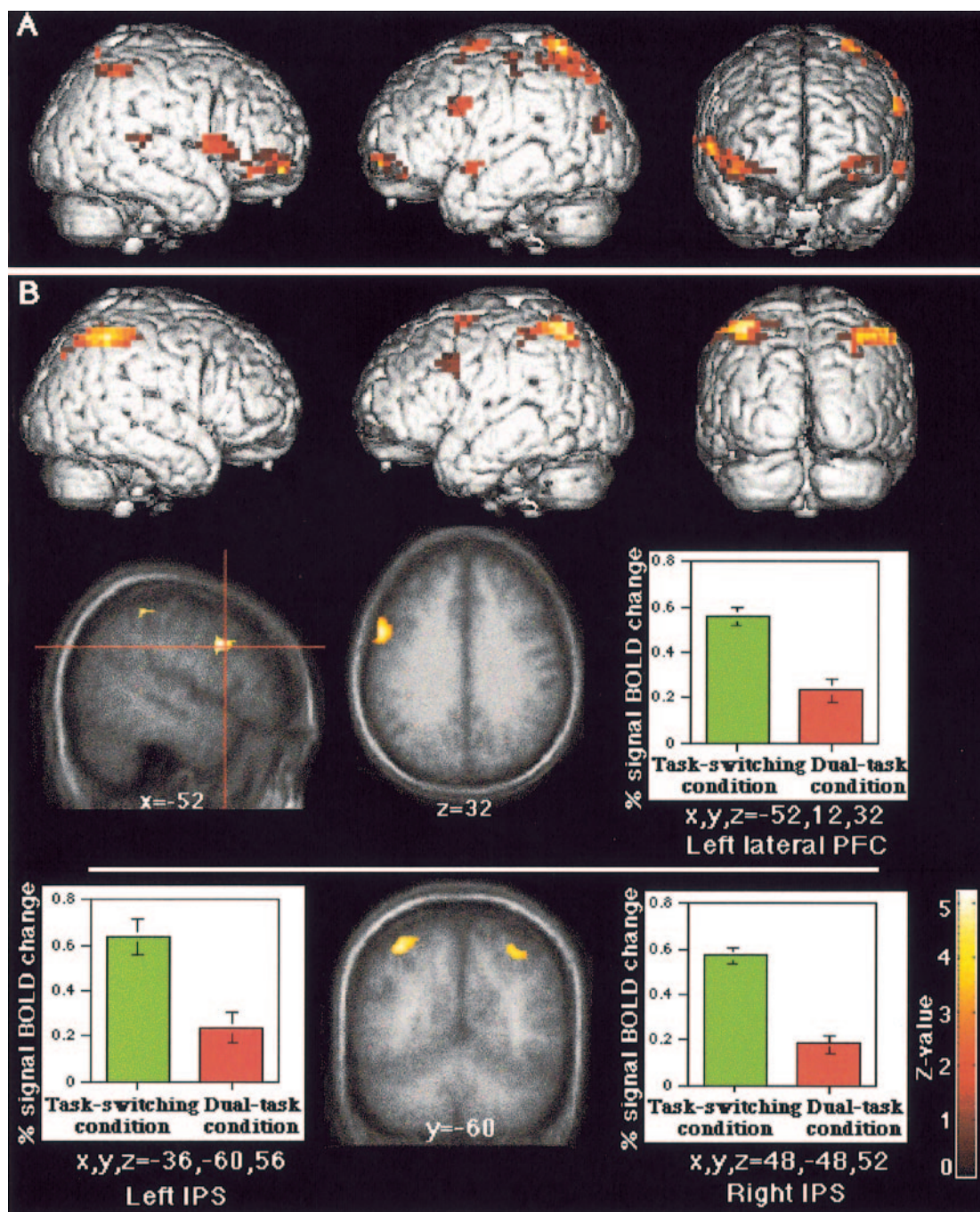
category (letters). It was previously shown that in dual-task situations, two items from the same category can be retrieved in parallel from long-term memory, whereas two items from different categories must be retrieved serially (Rohrer *et al.*, 1998; Logan and Delheimer, 2001; Navon and Miller, 2002).

The ACC activation is unlikely to reflect novelty detection (Clark *et al.*, 2000), error detection (Kiehl *et al.*, 2000), or an increase in motivation (Gehring and Willoughby, 2002). Constant unpredictability of letters' color in both the dual-task and task-switching conditions precluded a novelty effect and no more errors were made in the dual task than in the task-switching condition. Although the motivation interpretation of the ACC activation cannot be totally excluded, it is difficult to explain why more motivation should be necessary for the dual-task condition compared to the task-switching condition.

#### ***Lateral PFC and Intra-parietal Cortex Activation in Switching Between Two Tasks Relative to Performing Them Simultaneously***

When directly comparing switching between two tasks and performing them simultaneously, we found activations in the lateral PFC (right inferior frontal gyrus and left middle frontal gyrus), bilateral IPS region and bilateral fronto-polar cortex (Fig. 6A). When we further investigated which brain regions were more engaged by task switching than dual task and were





**Figure 6.** (A) Data for regions significantly activated by the task-switching relative to the dual-task condition were overlaid onto a 3D rendered brain. The Z-values and stereotactic coordinates for the regional maxima are listed in Table 1. (B). Slices showing activations in the task-switching relative to the dual-task condition, that were also activated by the dual task relative to baseline. Top: activations in the left inferior frontal gyrus ( $x, y, z = -52, 12, 32$ , BA 9/44) and bilateral IPS ( $x, y, z = -36, -60, 56$ ,  $Z = 5.14$ , BA 7;  $x, y, z = 48, -48, 52$ ,  $Z = 5.42$ , BA 7/40) are superimposed on normalized structural MRI slices averaged across subjects. Bottom: percentage of signal change relative to baseline for the task-switching and the dual-task conditions in the left lateral PFC and bilateral IPS. Error bars indicate standard error.

also more activated by the dual task relative to baseline, we found that the fronto-polar cortex and the right inferior frontal gyrus were no longer activated, while the left DLPFC and the IPS region survived this comparison (Fig. 6B). We only concentrate on the interpretation of the activations of the left DLPFC and IPS regions because it is difficult to interpret areas more activated by task-switching than dual task that are not more activated by dual task than baseline.

Behaviorally, switching between two tasks took longer than

simply maintaining two tasks simultaneously in memory. This suggests that task switching requires an additional cognitive process compared to dual task. One such process could be the dynamic selection of the neural pathways needed to perform a given task. Previous studies have suggested that this may be the specific function of the lateral PFC (Tomita *et al.*, 1999; Miller, 2000; Murray *et al.*, 2000; Miller and Cohen, 2001). Our left DLPFC activation is consistent with the view that this brain region provides a bias signal to posterior regions to select the



appropriate stimulus–response mapping for the task at hand (Rogers *et al.*, 1998; MacDonald *et al.*, 2000; Miller, 2000). A particular role of the left DLPFC in task-switching situations is also supported by a neuropsychological study that reported that patients with lesions of this brain region have greater RT switch cost than patients with right DLPFC lesions, when there were interferences between tasks (Rogers *et al.*, 1998). A recent event-related fMRI study of task switching also supported a specific role of the left fronto-lateral cortex in the selection of cue-related task rules (Brass and von Cramon, 2002). This role of the lateral PFC is coherent with known electrophysiological properties of prefrontal neuronal activities that flexibly code for the actual stimulus–response mapping (Assad *et al.*, 1998; White and Wise, 1999; Miller, 2000) and reflect learned associative relations between cues and motor responses (Watanabe, 1992; Miller, 2000).

It could be argued that the left lateral PFC activation found in task switching relative to dual task is simply due to an increase in task difficulty, because RTs were slower in the task-switching condition, although error rates were not significantly increased (Fig. 2). If this were true, subjects showing the highest activation in this brain region should have had a concomitant increase in the RT differences between task switching and dual task. This was not the case because *post hoc* analysis revealed no significant correlation between individual RTs and activation in the left PFC when comparing task switching to the dual-task condition (for each subject, the mean signal intensity was identified on the basis of peak of activation observed in the group analysis in the contrast comparing task switching to dual task and was tested for significant correlation with the corresponding RTs).

The basic operation subserved by the IPS region may either reflect associations that link the appropriate stimuli and responses for a given task (Le *et al.*, 1998; Kimberg *et al.*, 2000; Rushworth *et al.*, 2001; Corbetta and Shulman, 2002), or may reflect more specific selective attention to the color of the stimuli to identify which task to perform (since, in the dual task, selective attention to the color was not necessary). The IPS activation cannot be attributed to a task-switching function *per se*, because it was engaged by processes common to both dual task and task switching and was only more activated by task switching than dual task (Fig. 6B). This non-specific function of the IPS region during task switching is compatible with event-related studies of task switching that reported transient IPS activation not only for switch, but also for repeat trials (Le *et al.*, 1998; Dove *et al.*, 2000; Rushworth *et al.*, 2001).

The selective attention interpretation of our IPS activation found in task switching relative to dual task is in accordance with the fact that this brain region is more activated when switching between tasks (cued by colors) in an unpredictable order than in a predictable order – when tasks order is unpredictable, attention to the color of the letters is needed to know which task to perform (Dreher *et al.*, 2002) – showing that selective attention to the color does increase IPS activation. Furthermore, lateral intra-parietal neurons increase their firing rate to cue color if the tasks require constant changes of the association between cue color and motor responses (Toth and Assad, 2002). However, it is unlikely that our current IPS activation can solely be attributed to selective attention to the color of the letters. Indeed, a recent study showed that the IPS region remains activated in similar tasks to those performed here when suddenly presenting letters with no color cues to indicate which task to perform, once the task order is overlearned – these tasks being previously cued by the color of the letters (Koechlin *et al.*,

2002). Another argument against the interpretation that the IPS activation reflects only selective attention to the color of the letters is the recent finding that the posterior parietal cortex is activated when switching between verbal fluency tasks that implicate no visual component (Gurd *et al.*, 2002).

Thus, we favor the interpretation that our IPS activation reflects a more general coordinate transformation converting sensory inputs to motor outputs, consistent with several studies that have observed activation of the IPS region in a variety of tasks (Wojciulik and Kanwisher, 1999; Kanwisher and Wojciulik, 2000; Vandenberghe *et al.*, 2000; Culham and Kanwisher, 2001; Andersen and Buneo, 2002; Corbetta and Shulman, 2002; Simon *et al.*, 2002).

## Conclusion

Taken together, these results help to specify the functions served by distinct regions of the PFC and the ACC. In particular, we have seen that when two tasks are performed simultaneously relative to successively, this operation is associated with an increased activation of the rostral ACC. We interpreted this ACC activation as reflecting crosstalk in the pathways responsible for the selection and/or production of two simultaneously activated responses. In contrast, switching between two tasks, as compared to performing two tasks simultaneously, activated the left lateral PFC and the IPS region that may, respectively, reflect selection of the neural pathways needed to perform a given task and transformation of sensory inputs to motor outputs. These results indicate that when two tasks need to be performed simultaneously, as compared to successively, the ACC is involved, possibly because these two tasks recruit similar neural network populations at the same time. In contrast, when these networks are recruited successively, the ACC involvement is minimized while the demand on dynamic selection of the appropriate stimulus–response mapping is maximized.

## Notes

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