

Neural Mechanisms of Transient and Sustained Cognitive Control during Task Switching

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Summary

A hybrid blocked and event-related functional magnetic resonance imaging (fMRI) study decomposed brain activity during task switching into sustained and transient components. Contrasting task-switching blocks against single-task blocks revealed sustained activation in right anterior prefrontal cortex (PFC). Contrasting task-switch trials against task-repeat and single-task trials revealed activation in left lateral PFC and left superior parietal cortex. In both sets of regions, activation dynamics were strongly modulated by trial-by-trial fluctuations in response speed. In addition, right anterior PFC activity selectively covaried with the magnitude of mixing cost (i.e., task-repeat versus single-task trial performance), and left superior parietal activity selectively covaried with the magnitude of the switching cost (i.e., task-switch versus task-repeat trial performance). These results indicate a functional double dissociation in brain regions supporting different components of cognitive control during task switching and suggest that both sustained and transient control processes mediate the behavioral performance costs of task switching.

Introduction

The ability to rapidly and flexibly adjust behavior to changing environmental demands is a defining characteristic of cognitive control and represents one of the most sophisticated capabilities of the human species. This capability is clearly demonstrated within the context of experimental paradigms that require individuals to perform two or more different tasks in an intermixed fashion (hereafter referred to as *task switching*). An important requirement for success in these paradigms is that the participant internally represents and updates task-set information about each task—i.e., the appropriate rules that govern the mapping between stimuli and responses. This internal representation and rapid updating of task-set information is critical for enabling the participant to react quickly to a switch in the task to be performed. Recently, task-switching paradigms have become an important tool of experimental psychologists and cognitive neuroscientists for investigating

the component processes of cognitive control and their realization in the brain.

Within the experimental psychology literature, it has been observed that task switching produces a dramatic decline in behavioral performance (Allport et al., 1994; Rogers and Monsell, 1995). This finding has been demonstrated in a number of ways. The original studies of task switching contrasted blocks of trials in which a single task was repeated (hereafter termed *single-task* blocks) against blocks in which multiple trials were intermixed (often times in an alternating fashion, hereafter termed *mixed-task* blocks) (Jersild, 1927; Spector and Biederman, 1976). Response times were reliably longer and error rates were higher in the mixed-task blocks. The response time effects were particularly striking, with the performance of mixed-task blocks resulting in an increased response latency of 200–300 ms or more per item (Pashler, 2000). In more recent studies, the performance costs of task switching have been isolated on a trial-by-trial basis by contrasting trials in which the task has just repeated (termed *task-repeat* trials) against those in which the task has just switched (termed *task-switch* trials; Rogers and Monsell, 1995). This type of trial-specific experimental design is more flexible, in that it allows for the examination of within-trial effects, such as the timing between different trial components (e.g., the interval between the previous response and the occurrence of the next task cue versus the interval between the task cue and target stimulus). Another benefit of the trial-specific task-switching paradigm is that it allows a more precise linkage of switch costs with processes associated with the internal reconfiguration of task-set representations. As such, trial-specific task-switching designs have received the most attention in recent experimental work.

Potentially, the most powerful type of experimental design is one that combines both a blocked and trial-specific examination of task switching. In such designs, single-task blocks are compared against mixed-task blocks, and these mixed-task blocks are further separated into task-switch and task-repeat trials. In this manner, the performance costs of task switching can be decomposed into those that are trial specific (by comparing task-switch versus task-repeat performance) and those that are not. The trial-specific effects on performance are referred to as *switching costs*. Likewise, non-trial-specific task-switching effects can be isolated by comparing performance on single-task trials against performance on task-repeat trials within mixed-task blocks. In studies that have utilized such a design, it has been observed that a large proportion of the total cost associated with rapid task switching (i.e., performing intermixed blocks) is actually due to these non-trial-specific effects, which have been termed *mixing costs* (Los, 1996; Meiran and Gotler, 2001; Pashler, 2000). Likewise, studies comparing task-switching effects in different populations have found evidence that the two effects might be functionally dissociable. For example, older adults show sizeable increases in mixing

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cost but only subtle increases in switching cost (Kray and Lindenburger, 2000; Meiran et al., 2001).

Importantly, mixing costs may be highly informative regarding the types of control processes needed to be fully successful in rapidly switching between different tasks. In particular, mixing costs might reflect sustained components of cognitive control, such as the increased active maintenance demands associated with keeping multiple task sets at a relatively high level of activation or with engaging attentional monitoring processes to increase sensitivity to environmental cues that signal task changes. In contrast, switching costs may index more transient control processes associated with task switching, such as the internal reconfiguration or updating of goals or the linking of task cues to their appropriate stimulus-response mappings. Interestingly, behavioral analyses have also suggested that cognitive control may fluctuate across task-switching trials, such that for certain switch trials, there is a minimal cost in performance, while for other switch trials the performance cost is dramatic. These analyses, first described by De Jong and colleagues (De Jong, 2000; De Jong et al., 1999), indicate that the trials associated with the fastest response times involve only minimal switching costs. In contrast, the trials with the slowest response times have a very large switching cost. As such, trial-by-trial fluctuations in the speed of response may serve as an important index for operationally identifying trials that are high versus low in cognitive control during task switching.

Within cognitive neuroscience, investigators have recently become interested in the neural mechanisms of cognitive control indexed by task-switching paradigms. A particular focus of this research has been on the role of the prefrontal cortex (PFC) and superior parietal cortex, due to the extensive animal and human neuropsychological literatures suggesting that these brain regions are centrally involved in either representing task-set or goal-related information (PFC) or in switching attentional focus (superior parietal cortex) (Miller and Cohen, 2001; Posner and Petersen, 1990). With the advent of neuroimaging and, especially, event-related methods, investigators have been able to examine the activation of these brain regions during task switching in healthy human participants. Although there have been only a handful of published neuroimaging studies of task switching to date, their findings have generally been consistent with the previous literature. Specifically, both blocked (DiGirolamo et al., 2001; Dreher et al., 2002) and event-related (Dove et al., 2000; Kimberg et al., 2000; Sohn et al., 2000) studies have identified dorsolateral PFC and/or parietal cortex activity associated with task switching. Furthermore, in the event-related studies, there has been some indication that the PFC and parietal activity is selectively increased on task-switch trials.

Blocked-design studies (in contrast to event-related designs) can identify sustained changes in activity across conditions. Thus, blocked task-switching studies are potentially informative regarding brain regions associated with sustained task-switching components. Interestingly, the two published studies using blocked designs observed activation in anterior PFC regions during task switching, in addition to dorsolateral PFC activity. In Dreher et al. (2002), anterior PFC activity was associated

with improved performance under conditions where sustained endogenous preparation for task switching could be achieved (i.e., when task switches were predictable across the block). Anterior PFC is a likely candidate brain region for showing sustained activation associated with task switching, since it has been observed to show sustained activity in other cognitive domains, such as episodic retrieval (Duzel et al., 1999). However, a fundamental limitation of block designs is that they cannot reliably decompose sustained from event-related activation (Donaldson and Buckner, 2001). Thus, in studies such as Dreher et al. (2002), it is impossible to determine whether the activation in anterior PFC truly represents a sustained control process engaged during task switching rather than a transient increase. The only way to truly identify and dissociate sustained from transient neural activation is via an experimental design that enables direct decomposition of such effects. Recently, the use of such hybrid blocked and event-related designs within functional neuroimaging has been reported (Donaldson et al., 2001). These hybrid designs employ both state-related or blocked manipulations as well as trial-type ones and enable decomposition of the two effects via multiple regression and jittering of the intertrial interval within task blocks. Such a design would be especially useful within a task-switching paradigm, based on behavioral evidence showing effects due both to block-level (single-task versus mixed-task) and trial-level (repeat-trial versus switch-trial) task-switching effects. However, to date, no such studies have been conducted.

In the current study, we addressed this gap in the literature by examining and dissociating sustained from transient cognitive control processes during task switching through the use of the hybrid blocked and event-related paradigm. Participants were asked to perform semantic classification tasks on visually presented words under two different block conditions. In both blocks, the classification task to be performed (man-made/natural or large/small judgments) was cued at the beginning of each trial (see Figure 1). In one condition, the cue, and hence the task, was the same for each trial in the block. Such blocks were classified as *single-task* blocks. In the other condition, the cues varied on a trial-by-trial basis, such that the two classification tasks were randomly intermixed throughout the block. Such blocks were classified as *mixed-task* blocks. Within each block, we decomposed activity into that which was event related (i.e., due to performance of the trial) and that which was state related (i.e., increased activity for the block relative to a resting control condition). Furthermore, in the mixed-task block we separated trials into those in which the task switched relative to the previous trial (*task-switch*) from those in which the task repeated (*task-repeat*).

We identified brain regions showing sensitivity to transient aspects of task-switching cognitive control via the event-related contrast of *task-switch* to *task-repeat*. Likewise, we identified brain regions sensitive to sustained aspects of cognitive control during task switching via the state-related contrast of *mixed-task* to *single-task*. Our goal was to determine whether such sustained and transient regions could be considered functionally selective (i.e., doubly dissociated from each other). Con-

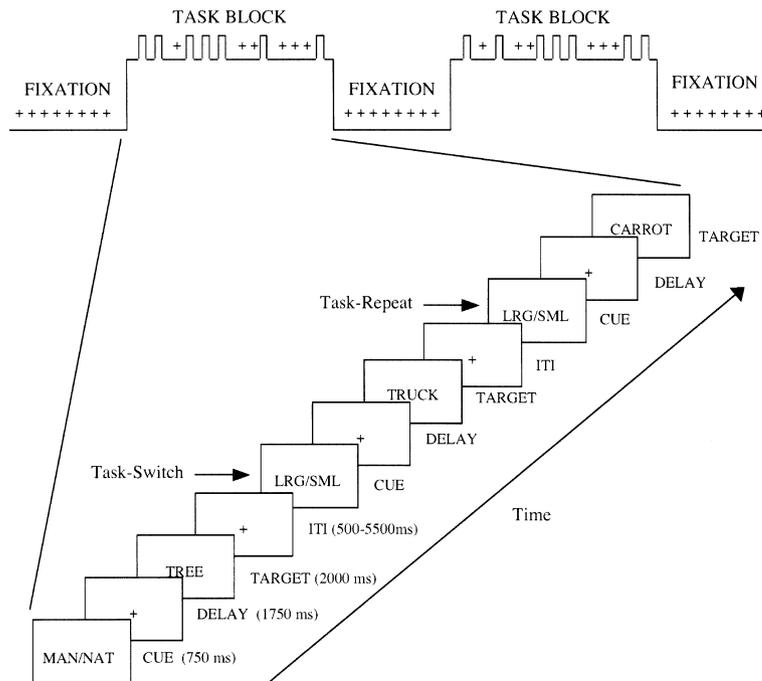


Figure 1. Task Design

State effects are estimated by comparing the sustained element of the bold signal during the task block to the blocks of fixation trials, whereas item effects are estimated by comparing the event-related response to different trial types within each task block (task-repeat versus task-switch trials in the mixed block) or different trial types across blocks (task-repeat trials in the mixed block versus trials in the single-task block). In mixed-task blocks, task cues vary randomly from trial-to-trial, producing both task-switch and task-repeat trials. In single-task blocks (data not shown), the task cue stays the same throughout the block.

sequently, we performed additional control contrasts to ensure that the identified brain regions could be selectively associated with each of these aspects of cognitive control and dissociated from related functions. In particular, we tested whether the transient regions also showed an absence of sustained effects and whether the sustained regions also showed an absence of transient effects. Based on the previous literature, our prediction was that lateral PFC and parietal cortex would be selectively sensitive to transient components of task switching and that anterior PFC would be selectively sensitive to sustained task-switching components. Finally, we sought to provide convergent information regarding the functional contribution of active brain regions to task-switching behavioral performance through an analysis examining the relationship between trial-to-trial fluctuations in response speed and brain activation dynamics. In particular, we tested the hypothesis, motivated by the work of De Jong and colleagues (De Jong, 2000, 2001), that the effects of task switching on brain activation would be different for fast and slow response trials, as these should respectively indicate periods of high versus low cognitive control.

Results

Behavioral Data

Overall, behavioral performance was high in the task, with participants averaging 94% accuracy across all conditions. We focused our analyses of behavioral performance data on both sustained and transient effects of task switching, as indexed by the mixing and switching costs, respectively. Evidence for both sustained and transient task-switching effects was present in the performance data (see Table 1). There was no mixing cost on error rates ($p > 0.1$), but there was a highly significant effect on RT [$t(12) = 3.61, p = 0.004$]. The switching

cost was equally present in RT [$t(12) = 4.05, p = 0.002$] and also marginally present for errors [$t(12) = 1.81, p < 0.1$].

We also examined the effect of response speed on task-switching RT effects. In previous work, De Jong and colleagues have found that task-switching effects were minimal in trials from the fastest portion of the RT distribution and maximal for trials from the slowest portion of the distribution (De Jong, 2000). Our analysis replicated the De Jong findings. For trials from the fastest portion of the RT distribution, there were neither significant mixing [$t(12) = 1.17, p > 0.1$] nor switching costs [$t(12) = 1.08, p > 0.1$] on estimated response latency (Table 1). In contrast, for the trials from the slowest portion of the RT distribution, there were highly significant effects for both mixing [$t(12) = 3.22, p = 0.007$] and switching costs [$t(12) = 4.03, p = 0.002$] on estimated response latency (Table 1). These results are consistent with the hypothesis that cognitive control level was maximal for the trials with the fastest responses but minimal for the trials with the slowest responses.

Neuroimaging Data

Eight regions were identified that showed a pattern of activity associated with selective involvement in either transient or sustained components of task switching. For the results discussed below, each region showed significant effects (see Experimental Procedures) in all statistical tests for sustained task-switching activity but a lack of significance in all tests for transient task-switching activity or vice versa. A summary of such results is provided in Table 2.

Sustained Regions

Three brain regions met our statistical criteria for showing selective sustained activation in response to task switching. These regions were all found in the right hemisphere and included ventral anterior cingulate cortex

Table 1. Behavioral Performance

	Single-Task	Mixed-Task		
		Task-Repeat	Task-Switch	Switch Costs
Error rate	4.5 (1.4)	5.4 (2.3)	8.4 (2.0)	3.0 (3.6)
Response time (ms)	969 (56)	1053 (82)	1129 (94)	76 (41)
Fastest bin	675 (42)	691 (61)	706 (79)	15 (31)
Slowest bin	1258 (95)	1397 (125)	1539 (134)	141 (76)

Data refer to group means with 95% confidence intervals in parentheses.

and two anterior PFC regions (Table 2, Figures 2 and 3). Activation plots confirm that these regions showed a state-related increase in activation during performance of mixed-task blocks but no state-related activation on single-task blocks (e.g., Figure 3A). Further, as constrained by the analysis procedure, the event-related response in these regions did not differentiate between task-switch and non-task-switch trials (e.g., Figure 3B). In general, the event-related response in these state regions was minimal on all trial types, indicating a preferential involvement of these brain regions in tonic rather than item-specific aspects of processing.

Transient Regions

Five brain regions met the criteria for showing selective transient activation in response to task switching. These regions were primarily located in the left hemisphere and included dorsolateral PFC, ventrolateral PFC, and superior parietal cortex (see Table 2, Figures 2, 4, and 5). Activation plots confirm that these regions showed increased event-related activity on trials during the task-switch blocks relative to trials in the pure-task blocks (e.g., Figure 4B). Moreover, the activation dynamics were different on task-switch versus task-repeat trials within the task-switch block, indicating an additional effect of task switching per se. However, the effect of

task-switch trials was often complex; for example, in the two PFC regions, activity appeared to rise and decay more quickly on task-switch trials (e.g., Figure 4B). This pattern might be indicative of different temporal dynamics of activity during task-switch trials rather than a simple increase in event-related response amplitude. We also examined the sustained effects in these regions. As expected, given their selectivity to transient influences of task switching, state-related increases in activity during mixed-task blocks were minimal or absent in these regions (e.g., Figure 4A). Instead, a general trend was present across all transient regions that single-task blocks showed greater state-related activation than mixed-task blocks (and was even statistically significant at the ROI level in the ventrolateral PFC region). This pattern was directly opposite to that observed in the right hemisphere sustained regions. As such, the pattern of effects across brain regions strongly support the notion of a double dissociation in functional response to task switching.

Brain-Behavior Relationships

We tested for converging evidence of the identified brain regions' relevance to cognitive control during task switching by examining the sensitivity of activation to trial-by-trial fluctuations in response speed. We exam-

Table 2. Regions of Interest

Brain Region	Brodman Area	X	Y	Z	Size (mm ³)	Time F(7,84)	Switch × Time F(7,84)	Block × Time F(7,84)	Mixed State vs. Fixation t(12)	Mixed vs. Single State t(12)	Block × Effect F(1,12)
Transient											
Left supplementary motor cortex	6	-16	3	63	459	5.53***	2.88**	2.80*	-1.37	-2.11	7.61*
Left superior parietal cortex	7	-28	-66	45	459	12.05***	2.58*	3.14**	-0.1	-1.59	5.94*
Left ventrolateral PFC	45/47	-40	30	0	378	7.29***	2.34*	3.00**	-2.41*	-2.27*	5.32*
Left dorsolateral PFC	44/9	-46	15	21	324	10.62***	2.22*	3.79***	0.1	-0.59	6.38*
Hippocampus	-	16	-21	-30	729	3.78***	3.14**	3.79***	-1.51	-1.75	9.19**
Sustained											
Right medial anterior prefrontal cortex	9/10	22	39	18	1161	0.83	0.47	1.51	3.57**	3.94**	9.68**
Right lateral anterior prefrontal cortex	46/10	34	48	18	648	0.95	0.33	1.33	2.99*	3.08*	6.99*
Ventral anterior cingulate cortex	24	4	27	18	837	0.96	0.98	1.53	3.22**	2.92*	8.82*

The last six columns report F statistics, t statistics, p values, and df at the level of the ROI, for each of the tests used in the conjunction procedure. The df are the same across regions and are reported with the name of the test. "Time" refers to the main effect of time in task-switch trials. "Switch × Time" refers to the comparison between task-switch and task-repeat trials. "Block × Time" refers to the comparison between trials in mixed-task and single-task blocks. "Mixed State vs. Fixation" refers to the comparison between fixation and the state effect for the mixed block. "Mixed vs. Single State" refers to the comparison between mixed-task blocks to the single-task blocks. "Block × Effect" refers to the block type (single versus mixed) × effect (transient versus sustained) interaction that tests the functional dissociation. *p < 0.05; **p < 0.010; ***p < 0.001.

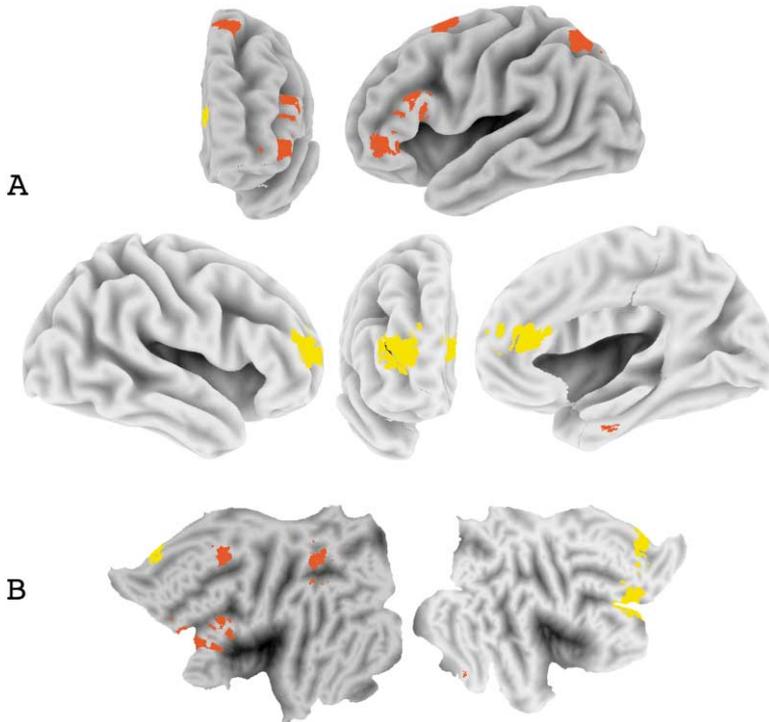


Figure 2. Transient and Sustained Brain Activity during Task Switching

(A) All identified brain regions, imposed on an inflated surface rendering. Red regions were identified via the transient analysis, whereas yellow regions were identified via the sustained analysis. (Top) Anterior and lateral views of the left hemisphere. (Bottom) Lateral, anterior, and medial views of the right hemisphere. (B) All identified brain regions, projected onto cortical flat maps for each hemisphere. Both panels were created using CARET software (Van Essen et al., 2001).

ined the relationship between activation dynamics and RT by sorting the data into ten bins arranged from fastest to slowest responses. The bin number for each trial was included as a regressor in the GLM analysis in order to estimate brain activation dynamics for the fastest and slowest trials in each of the three trial types (single-task, task-repeat, task-switch). We investigated the influence of response speed on brain activation on the identified ROIs, by estimating activation dynamics on the fastest versus slowest trials. All of the identified ROIs showed significant effects of response speed on activation dynamics, manifest as a significant effect of the response speed \times time interaction in the event-related response epoch (see Figures 3–5). In particular, in all transient regions, the peak event-related response on slow response trials was of greater amplitude but longer latency than on fast response trials.

In point of fact, the response speed effect on event-related activity was more complex than this basic finding. In particular, for the initial time points of the trial (i.e., during the period in which the task cue and delay occurred) there was greater activation in the fastest response trials across most brain regions when compared to the slowest responses. The cue period effect was most apparent in the two left lateral PFC regions (see Figures 4C and 4D) and was statistically significant in both. That is, for the time points reflecting the cue and preparatory period (scans 1 through 3, collapsed), there was significantly increased activation in the fastest response trials when compared to the slowest responses [ventrolateral PFC: $F(1,12) = 5.1$, $p < 0.05$; dorsolateral PFC: $F(1,12) = 5.7$, $p < 0.05$]. This effect, however, did not interact with trial type (both F 's < 1). Moreover, when considering the time points reflecting presentation of the target item and response period (scans 4 through

6, collapsed), the opposite pattern was found—greater activation for the slowest responses compared to the fastest [ventrolateral PFC: $F(1,12) = 37.8$, $p < 0.001$; dorsolateral PFC: $F(1,12) = 66.2$, $p < 0.001$] and no interaction with trial type (both F 's < 1).

Importantly, within the left parietal cortex, trial type did modulate the effect of response speed on event-related activation. When directly contrasting task-switch and task-repeat trials, a significant trial type \times response speed \times time interaction was found [$F(7,84) = 2.12$, $p = 0.05$; see Figures 5C and 5D]. This three-way interaction was caused by significantly increased event-related activation for task-switch trials when considering the fastest responses, but no significant differences in event-related activation across the two trial types when considering the slowest responses. In contrast, when comparing single-task and task-repeat trials, the three-way interaction was not close to significant ($F < 1$). As such, this pattern suggests that activation in left parietal cortex might be directly, and selectively, related to the *switching* cost, and the modulation of this performance cost by response speed.

It is striking that there were also significant effects of response speed in the brain regions showing sustained effects, even though these regions tended to show minimal event-related responses. An examination of response speed effects suggested that the pattern was weaker but generally of the same type observed in the transient brain regions: reduced activation in the initial time points of the trial but increased activity during the later time points of the trial for the slowest responses when compared to the fastest responses. Moreover, for the fastest responses, the activation level during the course of the trial was essentially flat (i.e., no effect of time) in the brain regions showing sustained responses,

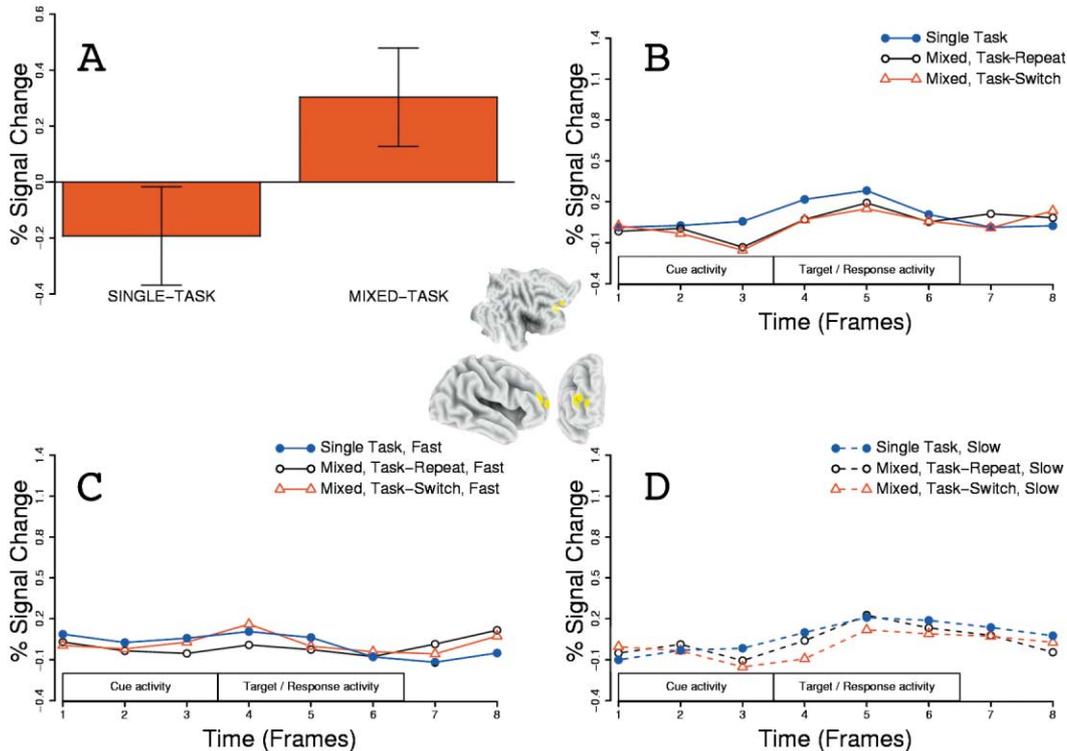


Figure 3. Right Anterior Prefrontal Cortex Activity

Region identified in the sustained analysis (center of mass: 34, 48, 18) and its corresponding effects. (A) Estimated state effects. Error bars correspond to the 95% C.I. around the difference between conditions. (B) Estimated time courses for task-repeat and task-switch trials in the mixed-task condition and trials in the single-task condition. (C) Estimated time courses for the fastest trials in each of the three conditions. (D) Estimated time courses for the slowest trials in each of the three conditions.

whereas for the slowest responses there was a significant modulation of activation amplitude during the trial epoch. Importantly, within the most anterior right PFC region, a significant trial type \times response speed \times time interaction was observed in the event-related response when comparing single-task and task-repeat trials [$F(7,84) = 2.62, p < 0.05$; see Figures 3C and 3D]. This three-way interaction was caused by significantly increased event-related activation for single-task trials when considering the fastest responses, but no significant differences in event-related activation across the two trial types when considering the slowest responses. In contrast, when comparing task-switch and task-repeat trials, the three-way interaction was not significant [$F(7,84) = 1.62, p > 0.1$]. As such, this pattern suggests that activation in right anterior PFC might be directly, and selectively, related to the *mixing* cost, and the modulation of this performance cost by response speed.

Discussion

This study provides an important contribution to the literature on cognitive control processes in task switching and their neural substrates. The cognitive demands of task switching appear to be 2-fold. Performing blocks of trials in which multiple tasks are intermixed increases the demands on cognitive control in a sustained manner. In addition, performing a trial in which the task has just

switched results in a transient increase in the demand for cognitive control. The temporal dissociability of these two types of cognitive control demands suggests the possibility that they might be mediated by different neural substrates. Our results confirm this hypothesis by demonstrating a strong double dissociation in activation of regions sensitive to transient versus sustained task-switching effects. The brain regions sensitive to transient aspects of task switching were primarily left lateralized and included ventrolateral and dorsolateral PFC and superior parietal cortex. In contrast, the brain regions sensitive to sustained aspects of task switching were wholly right lateralized and included anterior PFC. Our ability to detect the presence of such a functional double dissociation was due to our novel experimental design and analysis procedure, which isolated global or state-related effects due to performing mixed-task blocks relative to single-task blocks and separated these from effects due to task-switch versus task-repeat trials within blocks of intermixed trials.

Importantly, our results strongly converge with and extend those obtained from the behavioral literature. First, the results indicate that a significant portion of the increased demands of task switching occur as a result of the global effect of performing multiple tasks in an intermixed fashion, rather than just the very specific effects of reacting to an immediate switch in the task to be performed. We found that these global effects of task switching are present both in terms of a sustained

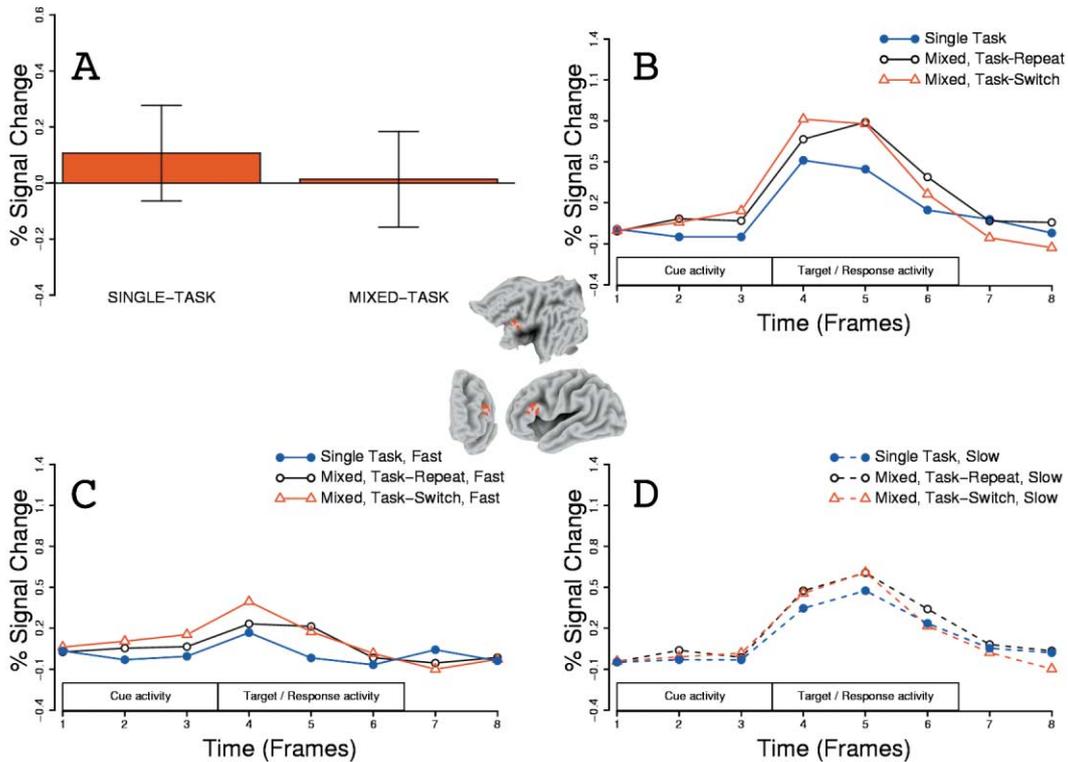


Figure 4. Left Lateral Prefrontal Cortex Activity

Region identified in the transient analysis (center of mass: $-46, 15, 21$) and its corresponding effects. (A) Estimated state effects. Error bars correspond to the 95% C.I. around the difference between conditions. (B) Estimated time courses for task-repeat and task-switch trials in the mixed-task condition and trials in the single-task condition. (C) Estimated time courses for the fastest trials in each of the three conditions. (D) Estimated time courses for the slowest trials in each of the three conditions.

increase in right anterior brain regions and also in terms of the transient activation increases in a network of left-lateralized regions that occur during non-task-switch trials (i.e., task-repeats) performed in the context of a mixed-task block. Second, our results support the idea that the level of cognitive control exerted by participants during task switching fluctuates on a trial-by-trial basis and that these effects are mediated by the fluctuating activity of discrete brain regions. Specifically, we observed that performance costs of task switching are minimal and the brain activation effects maximal for the trials having the fastest responses. This suggests that the ability to successfully meet the increased demands on cognitive control associated with task switching is dependent upon whether specific brain regions (e.g., left superior parietal cortex and right anterior PFC) can be differentially activated to a sufficient degree.

Sustained Cognitive Control during Task Switching

What particular cognitive control functions might be subserved by the brain regions showing sustained activation associated with task switching? There is a long tradition of theorizing that right anterior brain regions are critically involved in sustained attentional functions (Posner and Petersen, 1990), based primarily on lesion studies (Wilkins et al., 1987). More recently, neuroimaging studies have observed right anterior PFC activation

in tasks presenting similar cognitive demands, such as prospective memory (Burgess et al., 2001), episodic retrieval (Konishi et al., 2000; McDermott et al., 2000), subgoal processing (Braver and Bongiolatti, 2002; Koechlin et al., 1999), planning (Baker et al., 1996), and tasks with high active maintenance demands (Christoff and Gabrieli, 2000; Sakai and Passingham, 2003). In the current task-switching paradigm, the activation of anterior PFC might also reflect similar functions. For example, it is clear that the mixed-task block has a higher working memory demand than the single-task block, since the stimulus-response mappings for two different tasks have to be maintained simultaneously (versus a single mapping in the single-task blocks). The attentional control demands of the mixed-task block are also higher, since attention toward the task cue must be maintained across trials in order to be sensitive to trials in which the cue indicates a task switch. Finally, the mixed-task blocks can also be conceptualized as involving a subgoal component, since the task-set mappings have to be maintained in working memory, while attention is directed toward completing the various subgoals represented by the individual task trials themselves. Another important dimension that may be relevant is the temporal duration of information representation itself. In previous computational work, we have suggested that the posterior-anterior dimension within PFC might be organized according to the temporal duration of actively maintained representations, with the

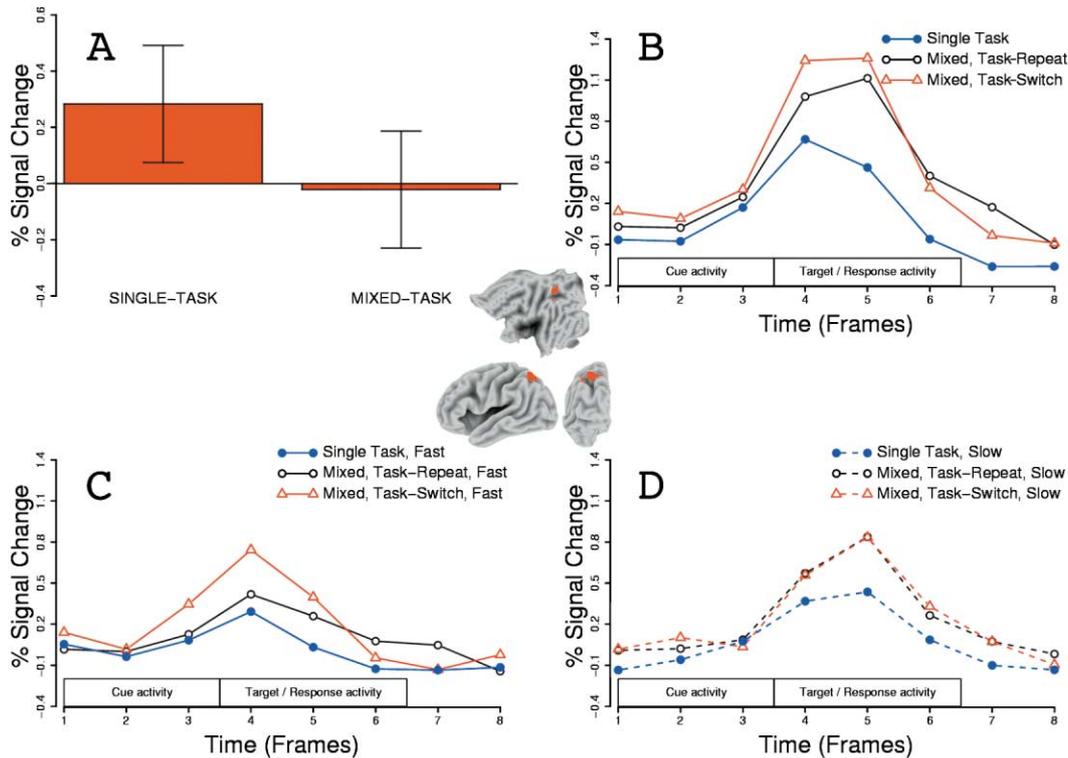


Figure 5. Left Superior Parietal Cortex Activity

Region identified in the transient analysis (center of mass: $-28, -66, 45$) and its corresponding effects. (A) Estimated state effects. Error bars correspond to the 95% C.I. around the difference between conditions. (B) Estimated time courses for task-repeat and task-switch trials in the mixed-task condition and trials in the single-task condition. (C) Estimated time courses for the fastest trials in each of the three conditions. Notice the difference in estimated time courses between task-switch and task-repeat trials. (D) Estimated time courses for the slowest trials in each of the three conditions. Notice the identical nature of the estimated time courses between task-switch and task-repeat trials.

most anterior regions being recruited under conditions where active memory needs to be sustained for long periods of time (O'Reilly et al., 2002). A previous event-related potential study has suggested that anterior PFC might be activated in a state-like manner during episodic retrieval (Duzel et al., 1999).

A notable characteristic of the activity dynamics for the sustained task-switching regions was the absence of a true event-related response during task trials. Indeed, this was a specific requirement of our identification procedure and established the dissociability of the right anterior brain regions from those showing transient task-switching effects. However, because of the tonic character of activity dynamics in these right anterior regions, an important question arises as to whether they are causally relevant to task performance. In other words, do these regions just provide a nonspecific arousal or motivational signal or, rather, something more specific? Evidence that addresses this question was found in the analyses relating brain activity to behavioral performance. We found that all three sustained regions were affected by trial-to-trial fluctuations in response speed. Specifically, during the trials with fastest responses, which were assumed to be associated with optimal cognitive control, the activation level in these regions tended to remain fairly constant across the course of the trial. In contrast, during the slowest response trials, which were assumed to index a low level

of cognitive control, there were noticeable fluctuations in the activation level during the course of the trial.

Most strikingly, in the anterior-most PFC region, the modulation of event-related activation by response speed suggests that it serves a mediational role in the size of the mixing cost on performance. In particular, for the slowest response trials, there were significant modulations in event-related activity in both single-task and task-repeat trials but no differential activation across the two conditions. In contrast, for the fastest response trials, there was no significant modulation of event-related activity on task-repeat trials but differentially increased activation during single-task trials. At first blush, this pattern seems anomalous, as the greater single-task trial activation is not consistent with the reduced control demands thought to be present during these trials. However, consider that the event-related activation occurs in addition to the level of sustained (state-related) activation. Moreover, single-task activation is generally at a lower level than that occurring during mixed-task blocks. Thus, it may be that on single-task trials with high cognitive control the level of anterior PFC activation increases somewhat relative to the overall block background. This pattern would be detected as an event-related effect. In contrast, for trials in the mixed-task block, high cognitive control might be associated with minimal modulation of activity from the overall increased level being sustained throughout the block.

Regardless of the particular interpretation given to the pattern of activation dynamics, the selective modulation of these dynamics in relationship to the mixing cost lends greater credence to the suggestion that right anterior PFC activity preferentially contributes to such costs.

Transient Cognitive Control during Task Switching

The set of primarily left-lateralized brain regions identified showing transient activation associated with task switching is consistent with the findings from previous event-related neuroimaging studies (Dove et al., 2000; Kimberg et al., 2000; Sohn et al., 2000). In particular, lateral PFC activity has been frequently associated with task switching and has been interpreted as reflecting transient cognitive control operations associated with task switching, such as endogenous task-set reconfiguration (Sohn et al., 2000). However, our results suggest a more complex interpretation, in that the peak activation in left lateral PFC was actually no greater on task-switch trials relative to task-repeat trials. In fact, this result is not really in conflict with the previous literature, since only one previous study has observed greater lateral PFC activation on task-switch trials relative to task-repeats (Dove et al., 2000), and in this study the task-switch effect was confounded with differential frequencies of task-switch versus task-repeat trials.

So, what interpretation should be given for the nature of left lateral PFC activation in our study? It seems unlikely that the activation directly reflects task-set reconfiguration, given the lack of increase specifically associated with task switching. Some insight may be gained by the response speed analysis. This analysis suggested that during initial time points of the trial (1–3), during which the task cue was being presented and processed, activation was significantly higher for the fastest response trials than for the slowest response trials. Yet this effect did not interact with the type of trial being performed (i.e., it was present on single-task and task-repeat trials as well as task-switches). In contrast, during the later time points of the trial (4–6), which were associated with target presentation and response selection, activation was significantly greater for the slowest response trials than for the fastest responses. Yet again, this pattern did not interact with trial type. Taken together, the pattern of results suggest that left lateral PFC might mediate a general role in task-set representation and response preparation that is not dependent upon having just recently switched tasks. Indeed, such a hypothesis has been put forth conceptually in previous theories of task switching (Wylie and Allport, 2000) and explicitly in computational models implementing such theories (Gilbert and Shallice, 2002). In our own recent computational work, we have suggested a similar idea, in which lateral PFC serves an important role in utilizing cue information as preparatory context for optimally responding to the upcoming probe (Reynolds and Braver, 2002). Finally, the left lateralization of PFC activation is likely to also reflect the semantic classification tasks performed during task switching. Indeed, the location of the PFC regions identified appear to closely match the anterior and posterior left inferior prefrontal cortex regions (aLIPC and pLIPC, respectively) engaged in

many previous studies requiring controlled processing of lexical/phonological or semantic information (Gold and Buckner, 2002; McDermott et al., 2003; Poldrack et al., 1999). Our data suggest that the demands of task switching—linking a task cue to a particular lexical-semantic task—represent another type of control process that may engage these LIPC regions.

The other key brain region showing transient activation associated with task switching was the left superior parietal cortex. This brain region has also been reliably observed in almost all task-switching neuroimaging studies (Dove et al., 2000; Dreher et al., 2002; Kimberg et al., 2000; Sohn et al., 2000). The activation dynamics in superior parietal cortex were somewhat different than that of the lateral PFC regions. In particular, this region showed a more specific effect of task-switch trials on activation amplitude. Yet this effect also appeared to interact with the trial-by-trial fluctuations in cognitive control highlighted by the response speed analysis. For the fastest response trials, there was a clear effect of task switching that increased event-related activation. In contrast, for the slowest response trials no such differential activation was present. Likewise, the response speed effects were only present when considering task switching specifically, since the interaction did not obtain when contrasting task-repeat and single-task trials. The selective modulation of task-switching activation by response speed suggests that left superior parietal activation might directly contribute to the magnitude of switching costs in behavioral performance. As such, our results strengthen functional interpretations regarding parietal involvement in transient reconfiguration processes that occur during task switching. Such reconfiguration processes might involve task sets but could also be more directly linked to stimulus or response related representations. In particular, Meiran has argued that response-set reconfiguration is an operation that only occurs on task-switch trials and cannot begin until after target onset (Meiran, 2000).

Our results also significantly inform more general conceptualizations of how transient task-switching effects should be evaluated. In particular, in addition to examining task-switch versus task-repeat trials, we also examined the event-related response on task-repeat trials in the context of the single-task versus mixed-task blocks. Consistent with the behavioral performance results, we found that much of the effects of task switching on brain activation were observed in task-repeat trials and not just in task-switch trials. This finding indicates that task-repeat trials within mixed-task blocks may have significantly increased cognitive control demands relative to task-repeat trials within single-task blocks and as such may not represent the best baseline state for examining the neural substrates of task-switching mechanisms. In the behavioral literature, there is some evidence for “micropractice” effects in which performance improves with the number of task-repeat trials occurring in a row (Meiran et al., 2000; Salthouse et al., 1998). Similarly, it may be the case that the increased event-related activity associated with task-repeat trials might be inversely related to the number of task-repeat trials occurring since the last task switch. Such an effect should be directly investigated in future studies.

Trial-by-Trial Fluctuations in Cognitive Control

Our analysis of response speed provided novel insights into how event-related brain activation might vary on a trial-by-trial basis during cognitive task performance. There has been a growing appreciation in the experimental psychology literature that the level of cognitive control exerted by task participants may significantly wax and wane across the course of a block of trials. In addition to the work by De Jong et al. in task switching, fluctuations in cognitive control have been noted by West and colleagues across a number of different task domains, including selective attention, prospective memory, and working memory (West, 1999; West and Alain, 2000a, 2000b). Indeed, West has suggested that the fluctuating nature of cognitive control processes may be an important characteristic of their normal dynamical operation and as such represent an important focus for investigation (West, 2001). Our own recent computational modeling work has suggested that active maintenance of task-set information in PFC is inherently probabilistic and linked to a noisy active memory updating system (Reynolds and Braver, 2002).

The current results suggest a reciprocal relationship between the behavioral indices of cognitive control and the dynamically varying activation of discrete brain regions during task switching. In particular, we found that the trials in which mixing and switching costs were high (i.e., the slowest response trials) were the ones in which there was little differentiation of brain activity across trial types. Conversely, when there were no switching or mixing costs in behavioral performance (i.e., during the fastest response trials), there was maximal differentiation of brain activation, at least in left superior parietal cortex and right anterior PFC. These findings indicate that the differential activation of discrete brain regions in response to changing task demands might serve as the mechanism by which behavioral performance is regulated and optimized to such demands. Nevertheless, the results are purely correlational and as such do not provide guidance as to whether the anterior PFC and superior parietal cortex are themselves the source of such fluctuations in cognitive control during task-switching performance or rather just reflections of fluctuations that are generated in other brain regions. Nevertheless, it is clear that our ability to uncover the dynamically covarying relationship between brain activation and behavioral performance was directly tied to the use of an analysis procedure that exploits such sources of covariance. The current results highlight the utility of dynamic analyses relating brain activity to behavior and point to their increased utilization in future cognitive neuroimaging studies.

Conclusions

The current study points to three distinct neural mechanisms of task switching. First, sustained activation of right anterior PFC during mixed-task blocks may be important for maintaining a heightened level of cognitive control over an extended period in situations requiring rapid and flexible alternation between multiple different tasks. The dynamic activation of this brain region may directly contribute to the behavioral performance costs associated with mixed-task environments. Second, lat-

eral PFC activation may reflect the internal representation and maintenance of task-set information. Dynamic fluctuations in the activation of this region may reflect variability in the utilization of available preparatory cue information. Third, superior parietal cortex activation might reflect processes associated with the online reconfiguration and updating of task-set information immediately following a switch in task. Dynamic fluctuations in superior parietal activation during task-switching performance may directly contribute to the behavioral performance costs associated with switches in task, by regulating the speed or efficiency by which task-set reconfiguration occurs.

Experimental Procedures

Participants

Thirteen right-handed participants with no evidence of neurological compromise participated in this study. Participants were eight males and five females with a mean age of 21 years (age range 19–26 years). Participants gave informed consent per guidelines set by the Washington University Medical Center Human Studies Committee and were paid \$25 for each hour of participation.

Behavioral Tasks

The experimental paradigm participants performed two semantic classification tasks under either pure-block or mixed-block conditions (see Figure 1). One classification task required a decision as to whether a visually presented word described an object that is either larger (LARGE; e.g., *truck*) or smaller (SMALL; e.g., *carrot*) than a standard computer monitor. The other task required a decision as to whether the object was manmade (e.g., *truck*) or natural (e.g., *carrot*). For both tasks, a task cue appeared prior to the target word and signaled the classification judgment to be made (LRG-SML or MAN-NAT). In the mixed-block condition, the classification task to be performed varied randomly from trial to trial. In the single-task condition, only a single task was performed during the entire block. Thus, in the single-task condition, the task cue information could be ignored. All words varied on both the MAN-NAT and LRG-SML dimensions with each possible combination presented with equal frequency (manmade/large, manmade/small, natural/large, natural/small). Thus, in mixed blocks, there were approximately equal numbers of switch-task and repeat-task trials. Moreover, the word list assigned to each task condition (single versus mixed block) was counterbalanced across participants.

The words for both conditions were presented centrally on a visual display, in 36 point Helvetica font. Words were taken from standardized lists of concrete nouns. All words were three to seven letters in length and consisted of one or two syllables. Responses to stimuli were made by pressing different buttons on a hand-held response box with either the index or middle finger of the right hand. The stimulus-response mappings were counterbalanced across participants. However, it is important to note the response overlap across tasks, in that the same button marked a particular feature in each of the two semantic dimensions (e.g., the right button could indicate that an item was manmade or large, and the left button could indicate that an item was natural or small). Such response overlap (and associated ambiguity) is considered to be an important feature of task-switching paradigms that contribute to the demands for cognitive control (Meiran, 2000). Within each trial, the timing and sequence of events was as follows. First, the task cue was presented for 750 ms, followed by a 1750 ms delay. Next, the semantic target word was presented for 2000 ms, during which responses were recorded. Participants were instructed to make a classification decision as quickly and accurately as possible following target onset and to indicate this decision with a button press. Next, a variable ITI occurred of between 500 and 5500 ms. The variability in ITI allowed for estimation of the event-related hemodynamic response on each trial, as described below (Friston et al., 1995). Each scanning run consisted of 40 trials. Two scanning runs were performed for each condition, yielding 80 single-task trials and 80 mixed-task trials.

Prior to the scanning session, participants were given instructions regarding all tasks to be performed. Participants were then given practice trials in which to perform each task. During practice trials, the experimenter answered any further questions, validated that instructions were understood, and ensured that the tasks were performed appropriately and with a reasonably high level of accuracy. The use of semantic classification tasks for the investigation of task switching departs somewhat from the previous literature (which has tended not to employ semantic tasks). The decision was motivated by an interest in the effects of task switching on episodic memory encoding. For this reason, a surprise yes/no recognition test was administered to participants following the scanner session, in order to examine memory for words presented in the scanner. The details regarding this test and behavioral results from it will be the subject of a future report.

Functional Imaging

Images were acquired on a Siemens 1.5 Tesla Vision System (Erlangen, Germany) with a standard circularly polarized head coil. A pillow and tape were used to minimize head movement. Headphones dampened scanner noise and enabled communication with participants. Both structural and functional images were acquired at each scan. High-resolution ($1.25 \times 1 \times 1$) structural images were acquired using a sagittal MP-RAGE 3D T1-weighted sequence (TR = 9.7 mm, TE = 4, flip = 12° , TI = 300 ms) (Mugler and Brookeman, 1990). Functional images were acquired using an asymmetric spin-echo echo-planar sequence (TR = 2500, TE = 50 ms, flip = 90°). Each image consisted of 18 contiguous, 7 mm thick axial slices acquired parallel to the anterior-posterior commissure plane (3.75×3.75 mm in-plane), allowing complete brain coverage at a high signal-to-noise ratio (T.E. Conturo et al., 1996, Soc. Neurosci., abstract). Participants were scanned in four separate scanning runs, with two scans each of the single-task and mixed-task conditions. For the single-task condition, one run was performed of each classification task (MAN-NAT, LRG-SML). Each run consisted of alternating cycles of task (TSK) and fixation (FIX) blocks with the following structure: FIX, TSK, FIX, TSK, FIX. The inclusion of fixation blocks was an important feature of the scanning design to enable us to conduct state-item analyses (see below). Task blocks were 140 s (20 trials) in duration. Fixation blocks (denoted by a centrally presented cross-hair) were 37.5 s in duration. Finally, the first four images in each scanning run were used to allow the scanner to reach steady state and, hence, were discarded. Each run lasted approximately 6.5 min, and a 2 min delay occurred between runs, during which time participants rested.

Visual stimuli were presented using PsyScope software (Cohen et al., 1993) running on an Apple PowerMac G4. Stimuli were projected to participants with an AmPro LCD projector (model 150) onto a screen positioned at the head end of the bore. Participants viewed the screen through a mirror attached to the head coil. A fiber-optic, light-sensitive key press interfaced with the PsyScope Button Box was used to record participants' behavioral performance.

Data Analysis

Behavioral performance data were analyzed for task-switching effects by conducting ANOVAs or t tests on accuracy and RT. Functional imaging data were preprocessed prior to statistical analysis according to the following procedures. All functional images were first temporally aligned across the brain volume, corrected for movement using a rigid-body rotation and translation correction (Friston et al., 1996; Snyder, 1996), and then registered to the participant's anatomical images (in order to correct for movement between the anatomical and function scans). The data were then scaled to achieve a whole-brain mode value (used in place of mean because of its reduced sensitivity to variation in brain margin definition) of 1000 for each scanning run (to reduce the effect of scanner drift or instability), resampled into 3 mm isotropic voxels and spatially smoothed with a 9 mm FWHM Gaussian kernel. Participants' structural images were transformed into standardized atlas space (Talairach and Tournoux, 1988) using a 12 dimensional affine transformation (Woods et al., 1992, 1998). The functional images were then

registered to the reference brain using the alignment parameters derived for the structural scans.

A general-linear model approach (Friston et al., 1995) was used to estimate parameter values for both event-related responses (item effects) and for sustained activity associated with the entire task block (state effects). State effects can be independently coded into the GLM, using an assumption of a fixed-shape response of long duration (i.e., boxcar convolved with a γ function). The logic of the GLM estimation approach is that event-related effects will be decaying back to baseline during the ITI, while state-related effects should remain relatively constant, and of increased amplitude relative to control (fixation) blocks. In recent work, this approach to GLM coding of sustained and transient responses has been validated via both simulation and empirically based methodological studies (Visscher et al., 2003). Event-related effects were analyzed by estimating values for the various time points within the hemodynamic response epoch. The duration of this epoch was taken to be 20 s (eight scanning frames). The event-related and state-related estimates for the time course data were then submitted to a group analysis using voxelwise random-effects model ANOVAs. Event-related responses can be determined in this approach by using time (i.e., scan) as a factor of interest and examining significant effects of this factor (both main effects and interactions). The primary advantage of this approach is that it makes no a priori assumptions about the particular shape of the hemodynamic response (Buckner and Braver, 1999). Given that the timing and shape of the hemodynamic response may vary across brain regions, incorrect assumptions regarding these parameters may lead to a significant loss of power in detecting event-related effects. However, for analyses directly examining effect type (state-related versus event-related) magnitude, we did estimate a single magnitude for the event-related response amplitude (since only a magnitude is available for state effects) by comparing it to an assumed hemodynamic response function via a cross-correlation coefficient (i.e., a γ function; Boynton et al., 1996).

To identify brain regions showing either sustained or transient activation during task switching, we used a conjunction approach (Price and Friston, 1997) that involved the application of multiple tests, with each set at a relatively low threshold. We have used such procedures in previous studies (Braver et al., 2001a, 2001b; Braver and Bongiolatti, 2002) and believe that they optimize the trade-off between sensitivity/power and false-positive protection (i.e., type I versus type II error). In order for a brain region to be accepted as selective for a particular effect, all voxels within the region were required to be statistically significant in all tests for that effect (described below). The analysis was set up such that any voxel meeting criteria in all statistical tests would have α protection equivalent to $p < 0.0001$ (although this value is likely to be an overestimate, given nonsphericity in the error terms in the statistical contrasts). Moreover, a region was considered significant only if it contained a cluster of eight or more contiguous voxels. The additional cluster size requirement ensured an overall imagewise false-positive rate of $p < 0.05$ (Forman et al., 1995; McAvoy et al., 2001). Finally, to increase interpretability, only positive activations (relative to fixation) were considered in all of these analyses (for event-related analyses this was determined through an average activation greater than zero over a window including scans 2 through 6).

We conducted a set of analyses designed to detect brain regions that demonstrated either sustained or transient brain activity in response to task-switching demands, as we hypothesized that such regions play differential roles in cognitive processing. Brain regions showing *selective* sensitivity to *sustained* components of task switching were identified based on the following contrasts: (1) state-related activity increased during task switching (mixed-task blocks) relative to fixation; (2) state-related activity increased during task-switching relative to single-task blocks (i.e., main effect of block type); and (3) state-related activity showed a larger increase in association with task switching (block-type effect) than did event-related activity (i.e., this contrast was tested via the block type \times effect type interaction). This last contrast ensured the presence of a functional dissociation, such that identified regions showed a significantly greater sustained than transient activity response associated with task switching. As a further contrast to ensure that only regions showing a *selective* sustained response were identified, we also

masked out any voxels showing event-related activation on task-switch trials, or any event-related effects related to task switching (single-task versus mixed-task or task-repeat versus task-switch trial differences).

To identify brain regions showing *selective* sensitivity to *transient* components of task switching, we required that (1) task-switch trials showed a significant event-related response (main effect of time on switch trials); (2) trials in task-switch blocks demonstrated a different event-related response than trials in single-task blocks (i.e., block \times time interaction); and (3) task-switch trials demonstrated a different event-related response than repeat-task trials (i.e., trial type \times time interaction); and (4) event-related activity showed a larger increase in association with task switching (block type effect) than did state-related activity (i.e., this contrast was tested via the block type \times effect type interaction). This last contrast ensured the presence of a functional dissociation (and was analogous to that conducted in the sustained analyses), such that identified regions showed a significantly greater transient than sustained activity response associated with task switching. As a further contrast to ensure that only regions showing a *selective* transient response were identified, we masked out any voxels showing significantly increased state activation in the task-switching block, relative to either fixation or the single-task block.

The above analyses were conducted to identify regions exhibiting a functional double dissociation—either a selectively sustained or selective transient increase in activity associated with task switching. However, we could have also tested for the presence of regions showing *both* sustained and transient effects of task switching. We opted not to do this, based on concerns regarding the potentially high degree of correlation between state and item regressors due to the nature of the GLM design matrix (e.g., Otten et al., 2002). Because of this high degree of imposed correlation, any regions detected to show both types of effects might be doing so merely because of the shared correlational structure between the effects rather than due to functional colocalization. This was also our motivation for masking out voxels showing any transient effects in the sustained analysis or sustained effects in the transient analysis. Nevertheless, recent simulation and empirical validation studies have found this potential concern to have little effect on the ability to independently detect sustained and transient effects (Visscher et al., 2003). Coding only transient effects into the GLM does not spuriously detect a transient response in “true” sustained regions, and vice versa. Our exploratory inspections of the data also suggest that shared correlations did not contribute much to the observed results. For example, we observed that the masking component of our contrasts had only a small effect on the results: it slightly reduced the number of active voxels in identified regions and caused separation of the two right anterior PFC regions. In all of the analyses presented below, the same basic conclusions would have been reached had we not masked out regions showing significant transient effects for the identification of sustained regions, or not masked out regions showing significant sustained effects for the identification of transient regions.

Regions identified in either the transient or sustained analyses were then transformed into ROIs by averaging across all contiguous voxels within a region. Three further analyses were then conducted. The first analysis validated that all effects tested in the voxelwise conjunction analysis were statistically significant ($p < 0.05$) at the ROI level. All regions described below met these criteria. The second analysis quantitatively estimated the size of transient and sustained effects in each ROI. The third analyses examined the relationship of trial-by-trial fluctuations in behavioral performance fluctuations on task-switching brain activation (see Brain-Behavior Relationships below). For these ROI analyses (and the graphs in Figures 3–5 displaying the results), data were expressed in terms of mean percent change in fMRI signal relative to fixation.

Brain-Behavior Relationships

Both behavioral and brain imaging data were analyzed in terms of the relationship of response speed to task-switching effects. De Jong and colleagues have used a response time binning procedure to demonstrate that the fastest response trials show minimal switch costs, whereas the slowest response trials show high costs (De

Jong, 2000; De Jong et al., 1999). We replicated this procedure by separating trials within each of the three task conditions (single-task, task-repeat, task-switch) into ten bins, sorted from fastest to slowest in 10% increments. We then used a linear regression procedure to estimate the relationship of bin number, representing speed of response, to both RT and brain activation. Although the relationship between bin and RT is not perfectly linear, the linear regression accounted for over 80% of the variance in RT. Moreover, the inclusion of higher order terms in the regression model did not affect the results, and so analyses were based on the simplest model for ease of interpretation. For the analysis of behavioral performance, we conducted statistical analyses of mixing and switch cost separately for the estimated fastest and slowest bins. For brain activation, we included bin number as a regressor term in the GLM for each trial type. Based on the regression parameters, we were able to estimate the event-related response at each identified ROI separately for the fastest and slowest bins. These estimates were then subjected to statistical analyses to examine whether response speed influenced task-switching effects on brain activation dynamics.

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References

- Allport, D.A., Styles, E.A., and Hsieh, S. (1994). Shifting intentional set: Exploring the dynamic control of tasks. In *Attention and Performance XV*, C. Umiltà and M. Moscovitch, eds. (Cambridge, MA: MIT Press), pp. 421–452.
- Baker, S.C., Rogers, R.D., Owen, A.M., Frith, C.D., Dolan, R.J., Frackowiak, R.S.J., and Robbins, T.W. (1996). Neural systems engaged by planning: A PET study of the tower of London task. *Neuropsychologia* 34, 515–526.
- Boynton, G.M., Engel, S.A., Glover, G.H., and Heeger, D.J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *J. Neurosci.* 16, 4207–4221.
- Braver, T.S., and Bongiolatti, S.R. (2002). The role of the frontopolar cortex in subgoal processing during working memory. *Neuroimage* 15, 523–536.
- Braver, T.S., Barch, D.M., Gray, J.R., Molfese, D.L., and Snyder, A. (2001a). Anterior cingulate cortex and response conflict: Effects of frequency, inhibition, and errors. *Cereb. Cortex* 11, 825–836.
- Braver, T.S., Barch, D.M., Kelley, W.M., Buckner, R.L., Cohen, N.J., Meizin, F.M., Snyder, A.Z., Ollinger, J.M., Akbudak, E., Conturo, T.E., and Petersen, S.E. (2001b). Direct comparison of prefrontal cortex regions engaged by working and long-term memory tasks. *Neuroimage* 14, 48–59.
- Buckner, R.L., and Braver, T.S. (1999). Event-related functional MRI. In *Functional MRI*, P. Bandettini and C. Moonen, eds. (Germany: Springer-Verlag), pp. 441–452.
- Burgess, P.W., Quayle, A., and Frith, C.D. (2001). Brain regions involved in prospective memory as determined by positron emission tomography. *Neuropsychologia* 39, 545–555.
- Christoff, K., and Gabrieli, J.D.E. (2000). The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology* 28, 168–186.
- Cohen, J.D., MacWhinney, B., Flatt, M.R., and Provost, J. (1993).

- PsyScope: A new graphic interactive environment for designing psychology experiments. *Behav. Res. Methods Instrum. Comput.* 25, 257–271.
- De Jong, R. (2000). An intention-activation account of residual switch costs. In *Control of Cognitive Processes: Attention and Performance XVII*, S. Monsell and J. Driver, eds. (Cambridge: The MIT Press), pp. 357–376.
- De Jong, R. (2001). Adult age differences in goal activation and goal maintenance. *Eur. J. Cogn. Psychol.* 13, 71–89.
- De Jong, R., Berendsen, E., and Cools, R. (1999). Goal neglect and inhibitory limitations: Dissociable causes of interference effects in conflict situations. *Acta Psychol. (Amst.)* 101, 379–394.
- DiGirolamo, G.J., Kramer, A.F., Barad, V., Cepeda, N.J., Weissman, D.H., Milham, M.P., Wszalek, T.M., Cohen, N.J., Banich, M.T., Webb, A., et al. (2001). General and task-specific frontal lobe recruitment in older adults during executive processes: A fMRI investigation of task-switching. *Neuroreport* 12, 2065–2071.
- Donaldson, D.L., and Buckner, R.L. (2001). Effective paradigm design. In *Functional MRI*, P. Jezzard, ed. (Oxford: Oxford University Press), pp. 177–193.
- Donaldson, D.L., Petersen, S.E., Ollinger, J.M., and Buckner, R.L. (2001). Dissociating item and state components of recognition memory using fMRI. *Neuroimage* 13, 129–142.
- Dove, A., Pollmann, S., Schubert, T., Wiggins, C.J., and von Cramon, D.Y. (2000). Prefrontal cortex activation in task switching: An event-related fMRI study. *Cogn. Brain Res.* 9, 103–109.
- Dreher, J.-C., Koechlin, E., Ali, S.O., and Grafman, J. (2002). The roles of timing and task order during task switching. *Neuroimage* 17, 95–109.
- Duzel, E., Cabeza, R., Picton, T.W., Yonelinas, A.P., Scheich, H., Heinze, H.-J., and Tulving, E. (1999). Task-related and item-related brain processes of memory retrieval. *Proc. Natl. Acad. Sci. USA* 96, 1794–1799.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., and Noll, D.C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magn. Reson. Med.* 33, 636–647.
- Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.-P., Frith, C.D., and Frackowiak, R.S.J. (1995). Statistical parametric mapping in functional imaging: A general linear approach. *Hum. Brain Mapp.* 2, 189–210.
- Friston, K.J., Williams, S., Howard, R., Frackowiak, R.S.J., and Turner, R. (1996). Movement-related effects in fMRI time-series. *Magn. Reson. Med.* 35, 346–355.
- Gilbert, S.J., and Shallice, T. (2002). Task switching: a PDP model. *Cognit. Psychol.* 44, 297–337.
- Gold, B.T., and Buckner, R.L. (2002). Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron* 35, 803–812.
- Jersild, A.T. (1927). Mental set and shift. *Archives of Psychology* 89.
- Kimberg, D.Y., Aguirre, G.K., and D'Esposito, M. (2000). Modulation of task-related neural activity in task-switching: an fMRI. *Cogn. Brain Res.* 10, 189–196.
- Koechlin, E., Basso, G., Pietrini, P., Panzer, S., and Grafman, J. (1999). The role of the anterior prefrontal cortex in human cognition. *Nature* 399, 148–151.
- Konishi, S., Wheeler, M.E., Donaldson, D.L., and Buckner, R.L. (2000). Neural correlates of episodic retrieval success. *Neuroimage* 12, 276–286.
- Kray, J., and Lindenburger, U. (2000). Adult age differences in task-switching. *Psychol. Aging* 15, 126–147.
- Los, S.A. (1996). On the origin of mixing costs: Exploring information processing in pure and mixed blocks of trials. *Acta Psychol. (Amst.)* 94, 145–188.
- McAvoy, M.P., Ollinger, J.M., and Buckner, R.L. (2001). Cluster size thresholds for assessment of significant activation in fMRI. *Neuroimage* 13, S198.
- McDermott, K.B., Jones, T.C., Petersen, S.E., Lageman, S.K., and Roediger, H.L., III. (2000). Retrieval success is accompanied by enhanced activation in anterior prefrontal cortex during recognition memory: An event related MRI study. *J. Cogn. Neurosci.* 12, 965–976.
- McDermott, K.B., Petersen, S.E., Watson, J.M., and Ojemann, J.G. (2003). A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. *Neuropsychologia* 41, 293–303.
- Meiran, N. (2000). Modeling cognitive control in task-switching. *Psychol. Res.* 63, 234–249.
- Meiran, N., and Gotler, A. (2001). Modelling cognitive control in task switching and ageing. *Eur. J. Cogn. Psychol.* 13, 165–186.
- Meiran, N., Chorev, Z., and Sapir, A. (2000). Component processes in task switching. *Cognit. Psychol.* 41, 211–253.
- Meiran, N., Gotler, A., and Perlman, A. (2001). Old age is associated with a pattern of relatively intact and relatively impaired task-set switching abilities. *J. Gerontol. B Psychol. Sci. Soc. Sci.* 56B, P88–P102.
- Miller, E.K., and Cohen, J.D. (2001). An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* 21, 167–202.
- Mugler, J.P.I., and Brookeman, J.R. (1990). Three-dimensional magnetization-prepared rapid gradient-echo imaging (3D MP-RAGE). *Magn. Reson. Med.* 15, 152–157.
- O'Reilly, R.C., Noelle, D.C., Braver, T.S., and Cohen, J.D. (2002). Prefrontal cortex and dynamic categorization tasks: Representational organization and neuromodulatory control. *Cereb. Cortex* 12, 246–257.
- Ottens, L.J., Henson, R.N.A., and Rugg, M.D. (2002). State-related and item-related neural correlates of successful memory encoding. *Nat. Neurosci.* 5, 1339–1344.
- Pashler, H. (2000). Task switching and multitask performance. In *Control of Cognitive Processes, Volume XVIII*, S. Monsell and J. Driver, eds. (Cambridge, MA: MIT Press), pp. 277–308.
- Poldrack, R.A., Wagner, A.D., Prull, M.W., Desmond, J.E., Glover, G.H., and Gabrieli, J.D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage* 10, 15–35.
- Posner, M.I., and Petersen, S.E. (1990). The attention system of the human brain. *Annu. Rev. Neurosci.* 13, 25–42.
- Price, C.J., and Friston, K.J. (1997). Cognitive conjunction: A new approach to brain activation experiments. *Neuroimage* 5, 261–270.
- Reynolds, J.R., and Braver, T.S. (2002). Computational and neural mechanisms of task-switching. Paper presented at the Cognitive Neuroscience Society, San Francisco, CA.
- Rogers, R.D., and Monsell, S. (1995). Costs of a predictable switch between simple cognitive tasks. *J. Exp. Psychol. Gen.* 124, 207–231.
- Sakai, K., and Passingham, R.E. (2003). Prefrontal interactions reflect future task operations. *Nat. Neurosci.* 6, 75–81.
- Salthouse, T.A., Fristoe, N., McGuthry, K.E., and Hambrick, D.Z. (1998). Relation of task-switching to speed, age, and fluid intelligence. *Psychol. Aging* 13, 445–461.
- Snyder, A.Z. (1996). Difference image versus ratio image error function forms in PET-PET realignment. In *Quantification of Brain Function Using PET*, D. Bailer and T. Jones, eds. (San Diego: Academic Press), pp. 131–137.
- Sohn, M., Ursu, S., Anderson, J.R., Stenger, V.A., and Carter, C. (2000). The role of prefrontal cortex and posterior parietal cortex in task switching. *Proc. Natl. Acad. Sci. USA* 97, 13448–13453.
- Spector, A., and Biederman, I. (1976). Mental set and shift revisited. *Am. J. Psychol.* 89, 669–679.
- Talairach, J., and Tournoux, P. (1988). *Co-Planar Stereotaxic Atlas of the Human Brain* (New York: Thieme).
- Van Essen, D.C., Drury, H.A., Dickson, J., Harwell, J., Hanlon, D., and Anderson, C.H. (2001). An integrated software suite for surface-based analyses of cerebral cortex. *J. Am. Med. Inform. Assoc.* 8, 443–459.
- Visscher, K.M., Miezin, F.M., Kelly, J.E., Buckner, R.L., Donaldson, D.L., McAvoy, M.P., Bhalodia, V.M., and Petersen, S.E. (2003). Mixed

block/event-related designs separate transient and sustained activity in fMRI. *Neuroimage*, in press.

West, R. (1999). Visual distraction, working memory, and aging. *Mem. Cognit.* 27, 1064–1072.

West, R. (2001). The transient nature of executive control processes in younger and older adults. *Eur. J. Cogn. Psychol.* 13, 91–105.

West, R., and Alain, C. (2000a). Effects of task context and fluctuations of attention on neural activity supporting performance of the Stroop task. *Brain Res.* 873, 102–111.

West, R., and Alain, C. (2000b). Evidence for the transient nature of a neural system supporting goal-directed action. *Cereb. Cortex* 10, 748–752.

Wilkins, A.J., Shallice, T., and McCarthy, R. (1987). Frontal lesions and sustained attention. *Neuropsychologia* 25, 359–365.

Woods, R.P., Cherry, S.R., and Mazziotta, J.C. (1992). Rapid automated algorithm for aligning and reslicing PET images. *J. Comput. Assist. Tomogr.* 16, 620–633.

Woods, R.P., Grafton, S.T., Holmes, C.J., Cherry, S.R., and Mazziotta, J.C. (1998). Automated image registration: I. general methods and intrasubject, intramodality validation. *J. Comput. Assist. Tomogr.* 22, 139–152.

Wylie, G., and Allport, A. (2000). Task Switching and the measurement of switch costs. *Psychol. Res.* 63, 212–233.