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Switching attention and resolving interference: fMRI measures of executive functions

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Abstract

Is there a single executive process or are there multiple executive processes that work together towards the same goal in some task? In these experiments, we use counter switching and response inhibition tasks to examine the neural underpinnings of two cognitive processes that have often been identified as potential executive processes: the switching of attention between tasks, and the resolution of interference between competing task responses. Using functional magnetic resonance imaging (fMRI), for both event-related and blocked design tasks, we find evidence for common neural areas across both tasks in bilateral parietal cortex (BA 40), left dorsolateral prefrontal cortex (DLPFC; BA 9), premotor cortex (BA 6) and medial frontal cortex (BA 6/32). However, we also find areas preferentially involved in the switching of attention between mental counts (BA 7, BA 18) and the inhibition of a prepotent motor response (BA 6, BA 10), respectively. These findings provide evidence for the separability of cognitive processes underlying executive control.

Keywords: Executive function; Switching; Response inhibition; Interference; Attention

1. Introduction

Executive processes are responsible for controlling and coordinating the execution of goal-directed behavior [29]. In this paper, we are concerned with two situations in which such processes play a role. One is when there are multiple task goals, and attention must be shifted back and forth between the tasks based on the current task goal. The other is when there are two competing alternatives in some task, and the interference between the two must be resolved so that attention can be paid to one instead of the other. There is general agreement that both of these frequently discussed examples recruit executive processing (see [2,31,38,42]). However, there is also a good deal of theoretical debate about the nature of executive processing. This debate has focused on the issue of whether there is there a single "central executive" process mediated by a single brain system, or there are multiple such processes, each different from the others in function and brain mechanism.

Several prominent theories of working memory and attention have promoted a singular view of executive function. According to this view, executive function can be conceptualized in terms of a unitary mechanism responsible for the allocation of attention to specific ongoing processes. An example of this view is Norman and Shallice's [36] model of attentional control, which proposes that a unitary "supervisory attentional system" biases the activation of task schemas, favoring one over the others via inhibition or enhancement of activation values. Similarly, the framework for working memory introduced by Baddeley [1] proposed that it is a single "central executive" that manipulates the contents of a set of storage and rehearsal buffers in the service of some ongoing task. This singular view can be readily applied to the two situations that concern us here, as one might propose that both attention-shifting and response inhibition require only the allocation of attention; it is the allocation of attention to one task that inhibits the previously or currently irrelevant task.

By contrast, one can conceive of executive functions as a set of processes that are distinct from one another but that nonetheless work together in order to meet a particular common goal. In the task examples mentioned earlier, one might postulate one mechanism that allocates attention, another that coordinates the shifting of attention and information-flow between two tasks, and yet a different

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mechanism that resolves interference between the two tasks by inhibiting attention to the irrelevant one [40].

The behavioral literature on the issue of whether there are multiple or dissociable executive processes has led to mixed conclusions. Rogers and Monsell [39] demonstrated that the time taken to switch attention between two different tasks was disproportionately increased when interfering information was present, suggesting that the processes of attention-switching and interference-resolution interact with each other, and are not independent [44]. However, using a confirmatory factor analysis, Miyake et al. [35] concluded that the latent constructs of attention-shifting and interference resolution were only modestly related to one another, proposing that these processes may in fact be separable. Thus, the behavioral data suggest that attention-switching and interference resolution may share some common mechanisms, but may involve separable mechanisms as well.

If one assumes that different cognitive mechanisms are likely to be implemented in different brain systems, physiological data may provide information on the number and nature of executive functions. Whether tasks that involve each putative process activate different brain networks may provide insight into whether the processes are truly different, or whether they are simply competing conceptualizations of the same process.

Previous research using functional magnetic resonance imaging (fMRI) has examined processes of attention-switching and interference resolution in separate experiments using different tasks. In attention-switching paradigms, activation has been reported in dorsolateral prefrontal cortex (DLPFC) and posterior parietal areas in particular, although it is clear that these regions are part of a larger distributed neural network [15,17,25,43]. With regard to tasks that require interference resolution such as the Stroop and Go/No-Go tasks, fMRI studies have shown activation in inferior and dorsolateral PFC, as well as anterior cingulate, again as part of a larger network of areas [10,18,22,26,28,30,32,33,41,45].

In the current experiments, we used fMRI to determine if there are common or distinct areas of neural activation for the processes of attention-switching and interference resolution. We use a switching task similar to that used by Garavan and colleagues [16,17] in which participants viewed a sequence of two stimulus types and were required to maintain internal counts for each type of stimulus. The task was constructed so that on successive trials, attention either remained on the previous count or switched to the other count. To study interference resolution, we used a task in which responses to the two stimulus types were either compatible with the stimuli, or required participants to inhibit the dominant compatible response and execute an incompatible one. In the first experiment we report, both tasks were combined in a single rapid event-related paradigm; in the second experiment, participants performed each task separately in a blocked design.

2. General methods

2.1. Participants

Fourteen undergraduate students ranging in age from 18 to 25 were recruited using advertisements in the university newspaper for Experiment 1. For Experiment 2, another 14 undergraduate students were recruited in the same manner. All participants were screened (using a self-report inventory) for neurological or psychiatric diagnoses as well as drug or alcohol abuse. They read and completed informed consent forms approved by the Institutional Review Board of the University of Michigan and were compensated approximately US$ 45 for their participation (inclusive of performance bonuses for speed and accuracy).

2.2. Acquisition and pre-processing

Images were acquired using a 3T whole body MRI scanner (General Electric, Milwaukee, WI), equipped with the standard quadrature headcoil. Functional T2* BOLD images were acquired with a spiral sequence using 15 contiguous axial 5 mm slices (TR = 1000 ms, TE = 30 ms, flip angle = 60°, field of view (FOV) = 24 cm). A T1-weighted gradient echo (GRE) anatomical image was also acquired using the same FOV and slices as the functional scans (TR = 300, TE = 6.8, flip angle = 65°). In addition, a high-resolution set of anatomical images was acquired using spoiled gradient recalled acquisition in steady state (GRASS; SPGR) imaging (TR = 6.4 ms, TE = 1.5 ms, TI = 600, flip angle = 15°, FOV = 24 cm, 2.5 mm slice thickness). The T1 GRE images were acquired at the start of the scanning session, and the SPGR images were acquired at the end of the scanning session. Experimental tasks were presented using E-Prime (Beta 5.0 Version) software (Psychology Software Tools Inc.) and the IFIS 9.0 system (MRI Devices, Corp.), using a 10-button response unit for response collection. Head movement was minimized using both foam padding as well as a restraint strapped across participants' foreheads. Images were corrected for slice acquisition timing differences using a local, 17-point sinc interpolation program [37]. Head movement was corrected using the realignment routines in the automated image registration (AIR) package [48]. Subsequent processing and analysis was done using SPM99 (Wellcome Department of Cognitive Neurology, London). SPGR images were corrected for signal inhomogeneity (Kristoff and Glover, http://www-psych.stanford.edu/~kalina/SPM99/Tools/vol_homocor.html), and then co-registered to the T1 images. SPGR images were normalized to the SPM99 T1 template, which is in Montreal Neurological Institute (MNI) space, and the same normalization parameters were applied to the T2* (functional) images. After spatial normalization, T2* images were smoothed using an 8 mm FWHM Gaussian filter. All of the analyses included a temporal high-pass filter and each image was scaled to have a global mean intensity of 100.

2.3. Image analysis

All analyses were performed using the General Linear Model implemented in SPM99, with separate regressors and intercepts for each run. For Experiment 1, event onset times for the four combinations of *counter switch*/*counter nonswitch* × *compatible*/*incompatible* response were convolved with a standard hemodynamic response function (HRF). For Experiment 2, epochs of the length of each task block were convolved with the HRF. Statistical models were fit for each participant and two contrasts of interest were estimated: switch − nonswitch and incompatible − compatible in Experiment 1, and High-Switch − Low-Switch and incompatible − compatible in Experiment 2. Contrast images for each participant were subjected to a random-effects analysis, and all statistical results were thresholded using a false discovery rate (FDR) correction for multiple comparisons of 0.05 [20]. The FDR correction ensures that on average no more than 5% of activated voxels for each contrast are expected to be false positive results. The critical *t*-values under FDR were 3.41 and 3.09 for switching and inhibition respectively in Experiment 1, and 3.35 and 3.35 in Experiment 2. Peak coordinates in MNI space were converted into Talairach coordinates using a transform developed by Matthew Brett (http://www.mrccbu.cam.ac.uk/umaging/mnispace.html) in order to report activations in Brodmann areas using the Talairach and Tournoux atlas [46] as implemented by the Talairach Daemon (http://ric.uthscsa.edu/projects/talairachdaemon.html); both MNI and Talairach coordinates are reported in the data tables.

3. Experiment 1

3.1. Procedure

In this task, participants were presented with a sequence of centrally positioned arrows that pointed left or right. One of their tasks was to keep track of the numbers of left-facing and right-facing arrows in each block of 8–11 arrows. Participants were instructed to update the counts for both arrows silently after each arrow was presented, rehearsing first the count for the left arrow and then that for the right arrow, then making a motor response which initiated the display of the next arrow. Trials on which successive arrows pointed in different directions and required a switch in the counter to be updated were considered "switch" trials, and trials on which successive arrows pointed in the same direction were considered "nonswitch" trials. At the end of each block of arrows, they were asked to make a positive or negative decision about a probe that showed either a right or left arrow together with a possible count (see Fig. 1). If the participant's mental count agreed with the number displayed for that arrow, he/she was instructed to respond with a keypress with the left index finger; if the count was judged to be incorrect, a keypress with the right index finger was required.

An instruction screen showing either the word "SAME" or "OPPOSITE" preceded each block of arrows. This determined the type of motor response required after participants completed counting each arrow. If the instruction was "SAME", participants made responses compatible with the direction in which the arrow pointed (e.g. left index-finger

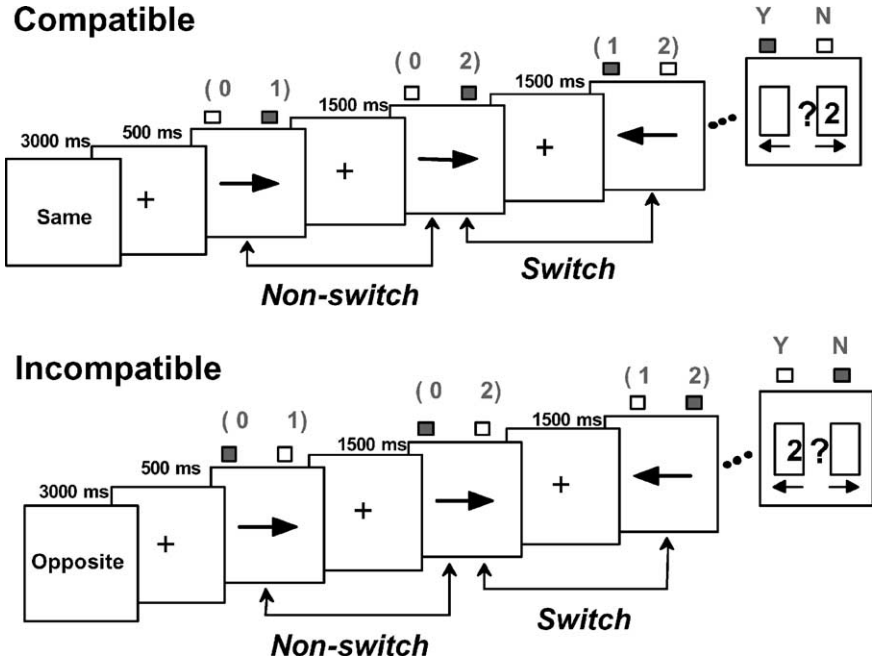

Fig. 1. Schematic of task design used in Experiment 1. Numbers in parentheses indicate the correct count after each trial, which participants are instructed to rehearse silently. Grey boxes indicate the correct motor response (left or right) on each trial, including the probe trial.

response to a left-pointing arrow). If the instruction was "OPPOSITE", the assignment of responses to arrows was reversed so that the responses were incompatible with the directions of the arrows. Participants performed alternating blocks of compatible and incompatible responses, separated by probe displays (see Fig. 1).

In this experiment, each arrow was preceded by a central fixation cross of 500 ms in duration, and remained on the display until the participant made a response. The order of presentation of the arrows was determined by a genetic algorithm that minimized the estimation error of the BOLD response for both the switching contrast and the compatibility contrast [47]; there were approximately equal proportions of switch and nonswitch trials, as well as left and right arrows.

Every fourth block, participants performed a baseline control task. In these blocks, participants first saw the instruction "press both keys when you see the bar", then saw a series of bars in the middle of the screen, of equal length and thickness to the stalks of the arrows presented in the task blocks. Participants were asked to press with both index fingers as quickly as possible each time a bar appeared. Each bar was preceded by a fixation cross of randomly varying duration (800 or 1400 ms) and remained on the screen until a response was made.

In this experiment, there were six imaging runs of 420 s each. Participants completed as many alternating compatible and incompatible (and baseline) blocks as possible in each run. They were informed that they would be provided with bonuses for both speed and accuracy.

3.1.1. Practice

Participants in this experiment were given 16 blocks of practice on the experimental task (8 blocks compatible, 8 blocks incompatible) and 2 blocks of practice on the baseline control task the day before the scans. Additionally, they were given two blocks of practice on the experimental task and one block of practice on the baseline control task immediately before being placed in the scanner.

3.2. Behavioral results

Participants were faster at responding on nonswitch trials than switch trials with average median reaction times (RT) of 612 ms for nonswitches and 1001 ms for switches, $F(1, 13) = 40.8$, $P < 0.05$ as assessed via a two-way ANOVA (factors were switching and incompatibility). Participants were also faster on compatible trials than incompatible trials: 743 ms on compatible trials and 870 ms on incompatible trials $F(1, 13) = 44$, $P < 0.05$. The interaction between switching and compatibility was also significant, $F(1, 13) = 8.48$, $P < 0.05$; specifically, it took more time to complete a switch if an incompatible response was required. (In previous behavioral research using this same paradigm, we have found that a reliable interaction between

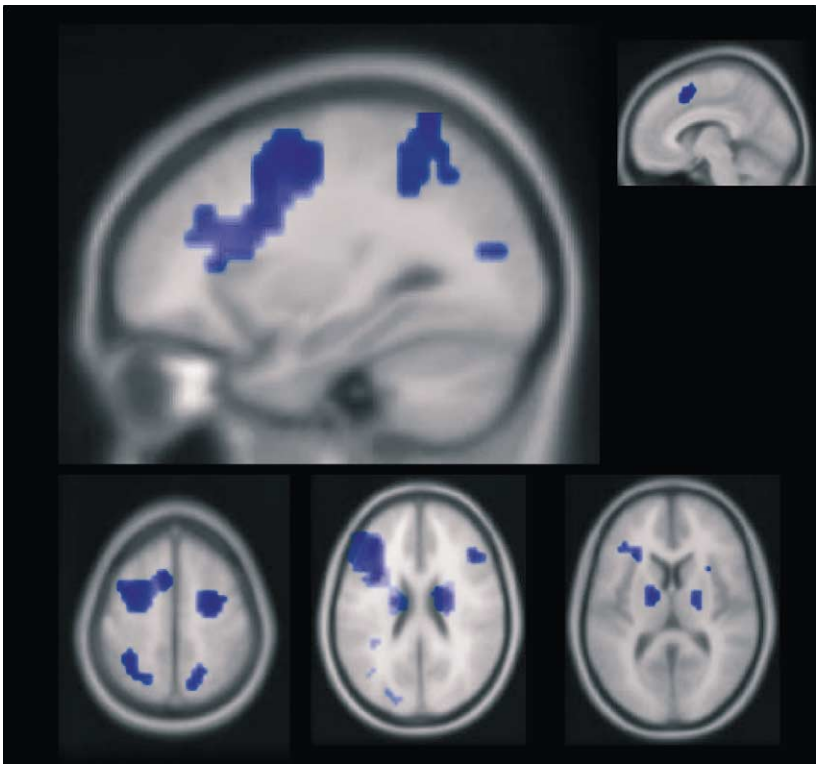

Fig. 2. Significant areas of activation in the switch–nonswitch contrast in Experiment 1. Note the upper right of the figure contains an inset with a medial sagittal slice to display activation in the medial frontal cortex.

Table 1
Areas of activation in the event-related counter-switches in Section 3

Region	Brodmann area		MNI coordinates			Talaraich coordinates			Z score
			x	y	z	x	y	z	
Parietal	7	R	15	−64	55	15	−59	54	4.04
		L	−22	−64	50	−22	−60	49	3.52
	40	R	34	−45	35	34	−42	34	3.63
		L	−34	−49	55	−34	−45	53	3.99
Premotor	6	R	26	−8	60	26	−5	56	4.29
		L	−34	0	55	−34	3	51	4.50
Dorsolateral	9/46	R	45	26	25	45	26	22	3.85
		L	−38	30	30	−38	30	26	4.96
Extrastriate	19	L	−26	−82	15	−26	−79	18	3.44
Inferior frontal	13	R	34	19	5	34	19	4	3.28
		L	−26	26	10	−26	26	8	3.03
Medial frontal	8/32	L	−8	15	50	−8	17	45	4.89
Caudate/putamen		R	19	−8	20	19	−7	19	4.11
Thalamus		L	−15	−8	15	−15	−7	14	3.86

the two factors dissipates with modest practice: [24]). Participants were highly accurate in responding to the arrows, with an average accuracy of 98%, which did not vary across different trial types.

The average accuracy on the yes/no probe trials for the counts was 94%, and there was no difference in accuracy across compatible ("SAME") and incompatible ("OPPOSITE") blocks $t(13) = 0.07$, $P = 0.95$.

3.3. Imaging results and discussion

3.3.1. Counter-switching contrast

Whole-brain analysis revealed activation in the bilateral DLPFC (BA 9/46), premotor cortex (BA 6), parietal cortex (BA 7/40), inferior frontal gyrus (BA 13), left medial frontal cortex (BA 8/32), extrastriate cortex (BA 19) and thalamus, and right caudate (see Fig. 2 and Table 1).

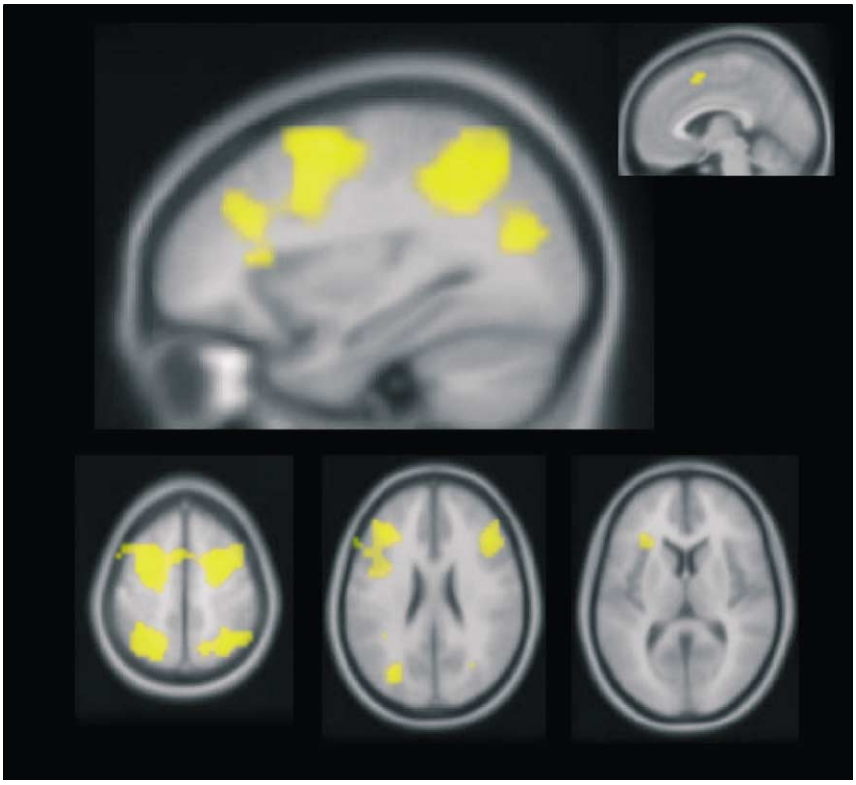

Fig. 3. Significant areas of activation in the incompatible − compatible contrast in Experiment 1. The upper right of this contains an inset with a medial sagittal slice to display activation in the medial frontal cortex.

Table 2
Areas of activation in the event-related incompatible responses in Section 3

Region	Brodmann area		MNI coordinates			Talaraich coordinates			Z score
			x	y	z	x	y	z	
Parietal	7	R	11	−68	45	11	−64	45	3.84
	40	R	38	−56	50	38	−52	49	3.91
		L	−38	−41	45	−38	−38	43	4.14
Premotor	6	R	26	0	55	26	3	51	5.04
		L	−30	4	55	−30	6	50	4.54
Dorsolateral	9/46	R	56	22	40	55	23	36	3.77
		L	−49	26	40	−49	27	35	4.17
Extrastriate	19	L	−34	−75	20	−34	−72	22	3.63
Inferior frontal	45	L	−30	26	10	−30	26	8	3.23
Medial frontal	32	R	15	19	35	15	20	31	3.48
		L	−8	11	50	−8	13	45	3.83

3.3.2. *Response compatibility contrast*

For this contrast, activation was observed in bilateral DLPFC (BA 9/46), premotor cortex (BA 6), parietal cortex (BA 7/40), medial frontal cortex (BA 32), and left inferior frontal gyrus (BA 45) and extrastriate cortex (BA 19; see Fig. 3 and Table 2).

The results from this experiment show that there is a great deal of overlap in the areas that are recruited to perform the two tasks of attention-switching and interference resolution. In particular, there appears to be similar activation in the bilateral dorsolateral, premotor and parietal areas, as well as possibly medial frontal cortex, inferior frontal gyrus and extrastriate cortex. However, it seems plausible that some of the parietal and premotor activation observed on both trial types may be attributed to eye movements, which we did not measure in this experiment. The eyes may have moved in response to the presentation of the arrows (even though they were centrally located, they nonetheless extended left and right of center), and eye movements may not have been uniform on switch versus no-switch trials, or on incompatible versus compatible trials. If there were such eye movements, these may have resulted in brain activation in parietal and frontal eye fields (PEFs and FEFs, respectively). Experiment 2 addresses this possibility.

4. Experiment 2

Because the areas activated in Experiment 1 appeared close to FEFs and PEFs, a concern with the imaging data was that both experimental tasks might involve more overt or intended eye movements than their controls, and that mechanisms controlling these eye movements might produce activations that would interfere with the interpretation of the activations due to executive processes [11,34]. To rule out this possibility, a saccade-control task was included in Experiment 2.

In addition, in Experiment 2 the counter-switching and stimulus-response compatibility (SRC) tasks were executed entirely separately from one another. That is, the counter-switching task had no response compatibility component and the stimulus-response compatibility task had no counter-switching component. This was done to replicate and extend the findings of Experiment 1 using a blocked experimental design where there was no potential for an interaction between switching and incompatibility to influence the results. All subjects performed the SRC task before the counter-switching task.

4.1. *Procedure*

4.1.1. *Counter-switching task*

This task was almost identical to that of the previous experiment—participants were shown a series of left- and right-pointing arrows in random order and asked to keep a running count of the number of arrows of each type in each block. They were instructed to rehearse the count silently for both arrows after each arrow was presented, rehearsing the count for the left and then that for the right. However, instead of responding compatibly or incompatibly to the arrows, they responded to each arrow with both left and right index fingers; they did not have to make a response based on the direction the arrow was pointing. Additionally, instead of a yes/no probe trial at the end of each block, participants had to indicate their exact count for either (unpredictably) the left arrows or the right arrows. On the probe trial, the words “how many” appeared along with either a left- or a right-pointing arrow and participants responded by pressing 1 of 10 buttons (counts of 1–10 of that type of arrow; see Fig. 4).

There were two types of blocks in this task, a “High-Switch” block in which on average 70% of the trials in each block were switch trials, and a “Low-Switch” block in which on average only 20% of the trials in each block were switch trials. In both blocks, each arrow was preceded by a central fixation cross-appearing for 440 ms. As in Experiment 1, the duration of each arrow trial depended on the participants’ reaction time; however, the duration of each

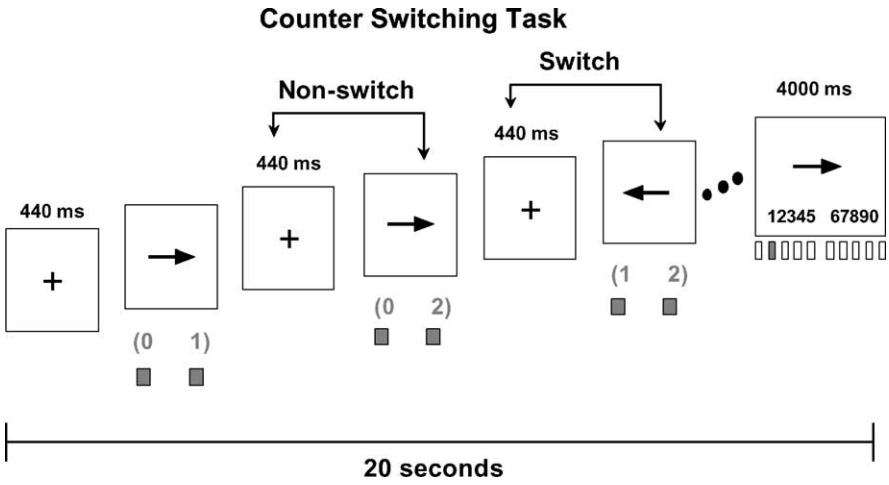

Fig. 4. Schematic of task design for counter-switching task in Experiment 2. Numbers in parentheses indicated the correct count after each trial, and grey boxes indicate the correct motor response on each trial; both fingers on each trial and 1 of 10 on the probe trial.

block was constant at 20 s (16 s of arrow trials followed by a 4 s probe). This constraint resulted in a different number of arrows in each block for each participant. All participants completed two runs of 360 s each.

4.1.2. Stimulus-response compatibility task

Again, participants were shown blocks of randomly ordered left- and right-pointing arrows, each preceded by the instruction, "SAME" or "OPPOSITE" indicating compatible or incompatible responses (see Fig. 5). In this task, each 18-second block consisted of 11 arrows, which were presented for 1000 ms each, separated with fixation crosses of 440 ms. Each participant completed two runs of 256 s each.

4.1.3. Saccade-control task

As a control for possible confounding eye movements, a saccade-task was included in which participants were asked to direct their gaze to the location of fixation crosses on the screen; no manual responses were required. Each 18 s task block consisted of 11 fixation crosses, each presented for 440 ms and separated by a 1000 ms central fixation cross. The crosses could appear in one of eight random locations on the screen. Blocks of saccade-trials alternated with 18 s

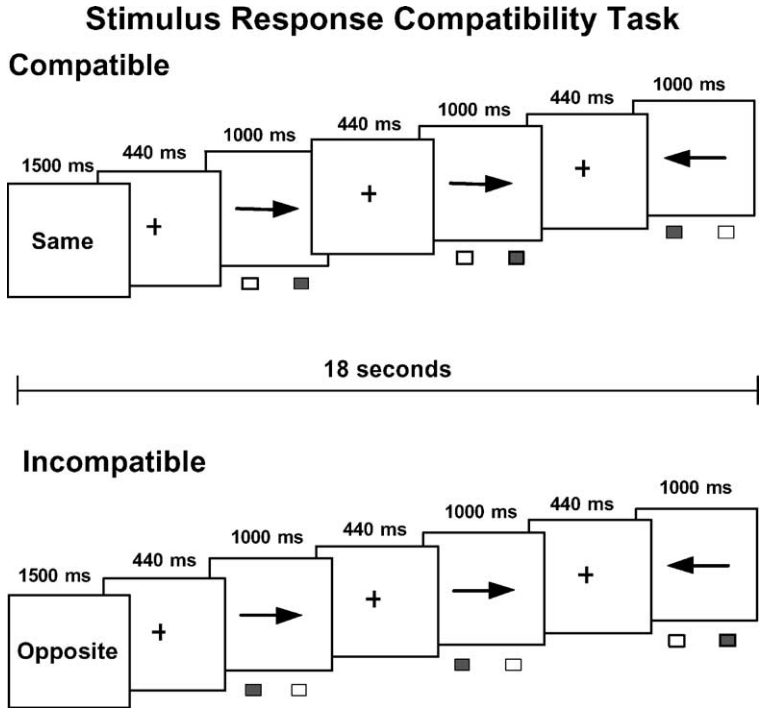

Fig. 5. Schematic of task design for stimulus-response compatibility task in Experiment 2. Grey boxes indicate the correct motor response on each trial.

Table 3
Areas of activation in the blocked counter-switching task in Section 4

Region	Brodmann area		MNI coordinates			Talaraich coordinates			Z score
			x	y	z	x	y	z	
Parietal	7	L	−15	−56	55	−15	−52	53	3.78
	40	L	−45	−41	50	−45	−37	48	4.28
Dorsolateral	9	L	−41	8	30	−41	9	27	4.82
Extrastriate	18	R	11	−60	0	11	−58	3	5.32
		L	−11	−64	0	−11	−62	3	4.94
Medial frontal	6		0	11	50	0	13	45	3.68
Thalamus		R	11	30	−5	11	−29	−3	3.90
		L	−15	−26	−10	−15	−26	−7	2.97

baseline control periods, in which participants gazed at a single central fixation cross. Each participant completed one run of 256 s.

4.1.4. Practice

For each task in this experiment, participants were given instructions via intercom while they were in the scanner, and then given two blocks of practice on that task.

4.2. Behavioral results

4.2.1. Counter-switching task

Participants were faster at responding on nonswitch trials than switch trials (average median reaction times (RT) = 754 and 1139 ms, respectively), $F(1, 13) = 48$, $P < 0.05$ (two-way ANOVA, block-type and trial-type as factors); this was also reflected in faster response times during Low-Switch blocks compared to High-Switch blocks (RTs = 918 and 975 ms, respectively), $F(1, 13) = 13$, $P < 0.05$. The interaction was also significant, $F(1, 13) = 7.9$, $P < 0.05$, and appears to be driven by the difference in RT for nonswitch trials in the two blocks. In Low-Switch blocks, the average median RT for nonswitches was 709 ms, whereas the average median nonswitch RT in the High-Switch blocks was 798 ms, $t(13) = 5.6$, $P < 0.05$. By comparison, the RTs for switches in the Low-Switch and High-Switch blocks was 1126 and 1150 ms, respectively, $t(13) = 1.1$, $P = 0.3$. Thus, the switch cost (switch RT–nonswitch RT) was greater during Low-Switch blocks than High-Switch blocks, $t(13) = -2.8$, $P < 0.05$ (RTs of 418 and 352 ms, respectively). This result suggests that subjects were being somewhat conservative in their updating of counts on nonswitch trials in the High-Switch blocks, a set-level effect of the block variable.

The average probe accuracy on the task was 95.2% using a lenient criterion (within ±1 of the correct answer), and 82.2% using a strict criterion (correct answer only).

4.2.2. Stimulus-response compatibility task

Overall, participants were faster at responding on the compatible blocks “SAME” than the incompatible blocks “OPPOSITE”. The average median RT in the compatible condition was 373 ms, and the average in the incompatible condition was 405 ms, $t(13) = 6.9$, $P < 0.05$. However, participants did not differ on their response accuracy for the two types of blocks, $t(13) = -0.46$, $P = 0.65$ (compatible block mean = 97.8%, incompatible block mean = 97.4%).

4.3. Imaging results and discussion

Data from the saccade-control task were analyzed first, at the FDR corrected threshold of $P < 0.05$. Voxels activated in the saccade task were then excluded from further analysis.[1]

Areas active at the corrected threshold of $P < 0.05$ for the counter switching and SRC tasks are shown in Tables 3 and 4, respectively. Results from Experiment 2 are depicted in Fig. 6; in addition, areas of activation from the saccade-control task (i.e. voxels that were not included in the analysis) are displayed in the bottom row. The areas of activation appeared to be similar to those observed in Experiment 1. As a method of confirming that the areas observed in Experiment 2 were the same as those observed in Experiment 1, the areas of activation in Experiment 2 for both the counter-switching task and the SRC task were used as regions of interest (ROIs) for Experiment 1. This ROI analysis (thresholded at FDR $P < 0.05$) confirmed that the areas of activation observed in the two experiments did indeed overlap.

4.3.1. Categorization of areas of activation

Once the areas of activation in each task had been identified, we categorized the areas of activation observed in the

[1] To be confident that our thresholding criterion did not result in a meaningful type II error in determining areas related to eye movements, we lowered the threshold for analyzing the saccade task substantially to $P < 0.05$ (uncorrected). Using this mask, voxels still remained in the stimulus response compatibility (SRC) task in the premotor and parietal regions. In addition, a paired t-test revealed more lateral parietal and premotor activation in the saccade task than in the SRC task, and more medial parietal and premotor activation in the SRC task than in the saccade task. Thus, we feel that using the remaining voxels in these area are not merely an artifact of thresholding.

Table 4
Areas of activation in the blocked stimulus-response compatibility task in Section 4

Region	Brodmann area		MNI coordinates			Talaraich coordinates			Z score
			x	y	z	x	y	z	
Parietal	7	R	22	−52	60	22	−48	58	4.10
		L	−22	−49	60	−22	−45	58	3.66
	40	R	26	−45	50	26	−41	48	4.21
		L	−38	−38	40	−38	−35	39	4.10
Premotor	6	R	30	0	50	30	2	46	4.55
		L	−19	0	50	−19	2	46	4.21
Frontopolar	10	R	22	49	10	22	48	7	3.21
		L	−26	49	15	−26	48	11	2.91
Medial frontal	32	L	−8	11	50	−8	13	45	4.03
Caudate		R	15	−15	25	15	−13	24	3.31
		L	−11	−4	25	−11	−3	23	3.93
Thalamus		L	−11	−19	20	−11	−17	19	3.35

switching and compatibility contrasts as common to both switching and compatibility, or preferentially associated with one of these two variables. We created an ROI mask consisting of all the active voxels in both the switching and compatibility contrasts, and determined which voxels within this network were active in each of the two tasks—again using a FDR correction of $P < 0.05$, but correcting for the number of comparisons within the mask. This more lenient criterion thus reduced the likelihood of missing any common areas that may have been active at a sub-threshold level when using a whole-brain analysis. We then looked at voxels that exceeded the corrected threshold

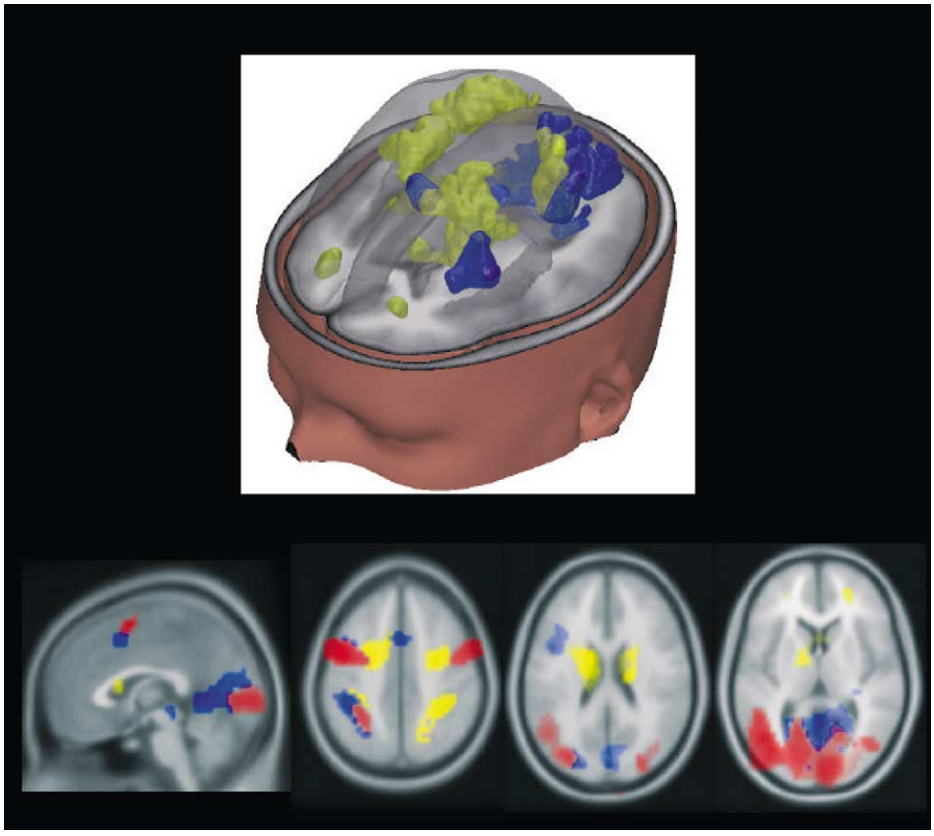

Fig. 6. Significant areas of activation in the High Switch – Low Switch contrast (blue) in the counter-switching task and incompatible – compatible contrast (yellow) in the stimulus-response compatibility task of Experiment 2, not including voxels active in the saccade task (top). The same contrasts (bottom) in addition to the areas (bottom) active in the saccade-control task (red).

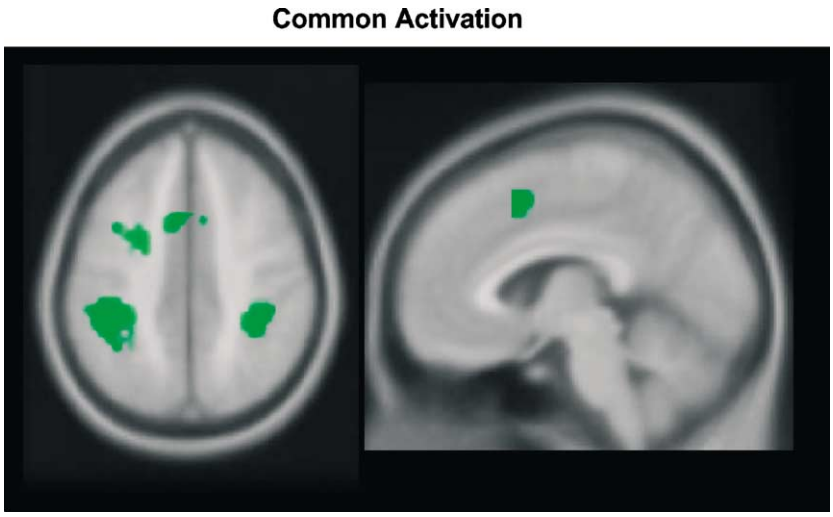

Fig. 7. Areas of common activation across counter switching and stimulus - response inhibition tasks (switch–nonswitch and incompatible − compatible) in Experiment 2 (High Switch – Low Switch and incompatible − compatible).

Table 5
Common areas of activation across switching and inhibition in Section 4

Region	Brodmann area		MNI coordinates			Talaraich coordinates		
			x	*y*	*z*	*x*	*y*	*z*
Dorsolateral	9	L	−34	5	37	−34	7	34
Parietal	40	R	32	−41	47	32	−38	46
		L	−36	−41	47	−36	−38	45
Medial frontal	6/32	L	0	10	49	0	12	45

Table 6
Areas where switching activation is greater than inhibition activation in Section 4

Region	Brodmann area		MNI coordinates			Talaraich coordinates			*Z* score
			x	*y*	*z*	*x*	*y*	*z*	
Parietal	7	L	−8	−64	55	−8	−59	54	3.07
Extrastriate	18	L	−11	−64	0	−11	−62	3	4.85
	19	R	22	64	0	22	−69	3	3.99
		L	−26	−86	25	−26	−82	27	4.57

within this ROI mask in both of the two contrasts. Common areas of activation for both tasks were bilateral superior parietal cortex (BA 40), left DLPFC (BA 9), medial frontal cortex (BA 6/32; Fig. 7; Table 5).

In order to determine areas of activation that were preferentially active in each task, a paired *t*-test was conducted between the contrast images of the two tasks, also within the ROI mask, corrected at $P < 0.05$ (FDR) for the number of

Table 7
Areas where inhibition activation is greater than switching activation in Section 4

Region	Brodmann area		MNI coordinates			Talaraich coordinates			*Z* score
			x	*y*	*z*	*x*	*y*	*z*	
Premotor	6	R	19	−8	60	19	−5	56	3.81
Parietal	7	R	15	−56	60	15	−51	58	3.77
Frontopolar	10	R	22	52	10	22	51	7	2.98
Caudate/putamen		R	8	11	10	8	11	9	3.32
		L	−15	4	10	−15	4	9	3.77

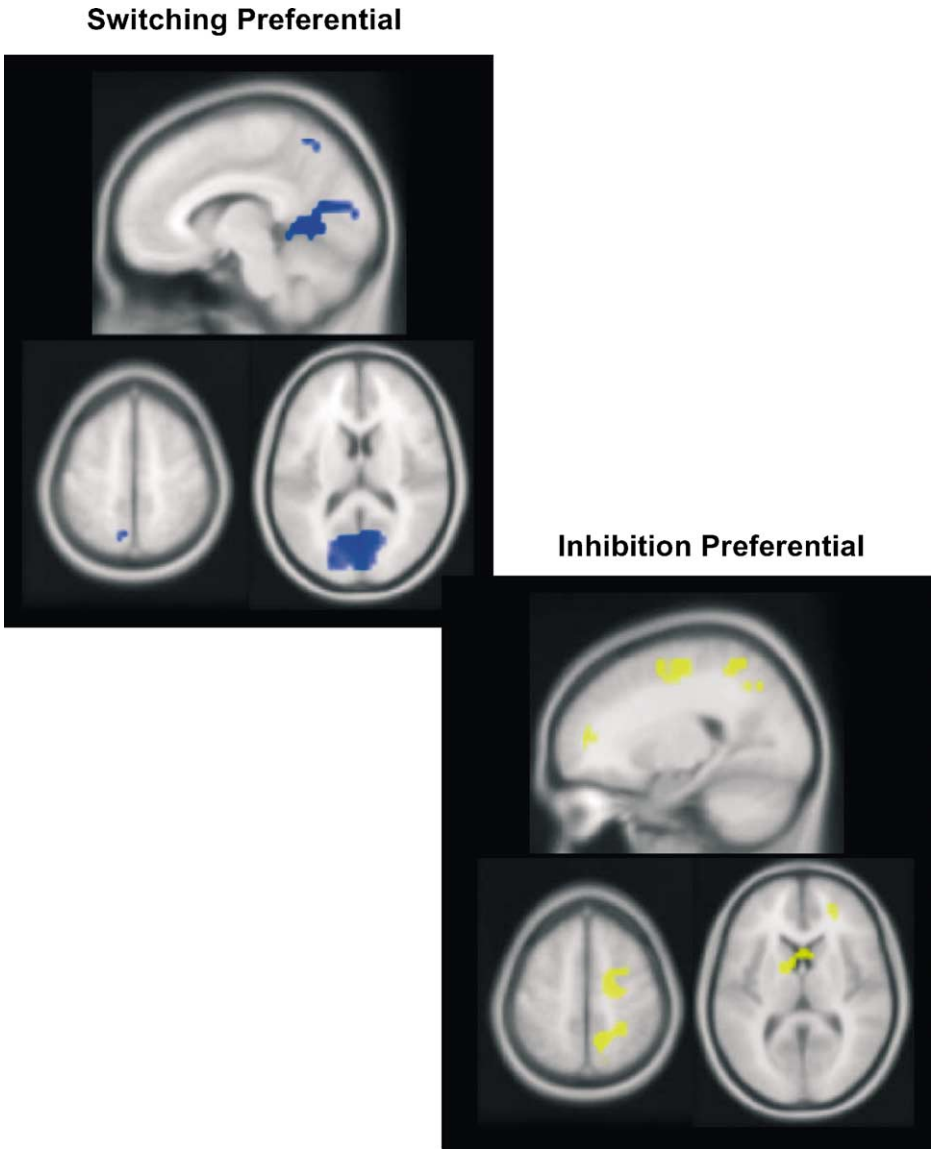

Fig. 8. Areas of preferential activation in Experiment 2 for the High Switch – Low Switch contrast (blue) and areas of preferential activation for the incompatible – compatible contrast (yellow).

voxels in the mask. Using paired *t*-tests, we found that the counter-switching task yielded significantly greater activation in bilateral extrastriate cortex (BA 18/19), and left posterior superior parietal cortex (BA 7; Fig. 8, left, Table 6). Areas of activation that were preferentially associated with response incompatibility were right parietal cortex (BA 7), premotor cortex (BA 6), frontopolar cortex (BA 10) and bilateral caudate/putamen (Fig. 8, Table 7). Note that while all of these areas are significantly more active in one task than the other, some may also be active in both tasks.

5. General discussion

The purpose of these experiments was to determine if common neural areas underlie the processes of attention-switching and interference resolution. Both of these processes are critically related to the ability to manipulate and control information in working memory, or what is often termed executive function. The results from the event-related analysis of Experiment 1, and the block design analysis of Experiment 2 showed similar areas of activation, providing a replication of findings in two different groups of subjects (see Figs. 2, 3 and 6). However, because the data from Experiment 1 may well have included areas of activation involved in eye movements, most of our discussion will be limited to Experiment 2. Given the concordance of activation across the two experiments, it is likely that analyses of common and preferential activation in Experiment 1 would yield similar results to those observed for Experiment 2.

The areas of overlapping activation between the two tasks suggest that there is indeed some commonality between the

two tasks in question. One interpretation of the pattern of activations is that activation in superior parietal cortex may mediate the process of selective attention [8,9,12] whereas DLPFC maintains and updates/manipulates the contents of working memory (e.g. the current arrow-count, or the current response-mapping rule) [3,6,13,21,23]. Additionally the anterior cingulate in the medial frontal cortex may detect or respond to conflict that arises from a competing dominant response (e.g. updating the previous counter, or responding compatibly to the arrow) [5,19,22,32]. While this is only one possible interpretation of the imaging results reported here, it is consistent with other findings reported in the literature.

Also of interest are areas of activation that are greater in one task than another. There were several areas of activation that were significantly more active in the counter-switching task than the response compatibility task. These areas were bilateral extrastriate cortex, and left posterior superior parietal cortex. This particular region of posterior superior parietal cortex has been previously implicated in attention-switching [15], while the extrastriate activation may be a result of the use of mental imagery to represent the counters (see [4,14,27], for evidence of the involvement of occipital cortex in mediating visual imagery). Supporting this hypothesis are the reports of most subjects who stated that their representations of the counters had a spatial quality to them (i.e. the counter for the left arrows represented on the left-hand side of space and the counter for the right arrows on the right-hand side of space). Conversely, areas significantly more active in the response compatibility task were the right superior parietal cortex (anterior to those observed for counter switching), premotor cortex, and frontopolar cortex. The areas in premotor and parietal cortex may be involved with motor response inhibition and response representation or selection, respectively; that is, inhibition of the incorrect prepotent response and representation or selection of the less automatic correct response [11,33,41] while the frontopolar area (BA 10), also observed by Garavan et al. [18] in a variant of the AX-CPT task and Braver et al. [6] in a variant of the n-back task, may be involved in the maintenance and monitoring of a sub-goal (i.e. “left arrow, right finger; right arrow, left finger”) before the correct response can be made [7].

It is important to remember that the frontal and parietal activations observed in Experiment 2 are not a result of saccade-related activity; saccade-related activations were removed from the analyses of switching and compatibility activation. In fact, the eye-movement results that we found are remarkably similar to those found by Merriam, et al. [34] who compared incompatible eye movements to both compatible eye movements and visually guided saccades. They found that the areas involved in incompatible eye movements lay rostral to the FEFs and rostral (and lateral) to the PEFs. Connolly, et al. [11] also showed that anti-pointing and anti-saccades result in more anterior frontal activation and more anterior and lateral parietal activation than pro-pointing or saccades. As further support for the notion that the parietal and frontal cortex activation observed in our tasks are not merely the result of eye movements, a post hoc *t*-test of activation in our compatibility and saccade tasks confirmed that rostral and medial frontal areas and rostral parietal areas were significantly more active in the compatibility than the saccade tasks.

These interpretations of the neuroimaging results, like those of most neuroimaging studies, rely on certain assumptions and are subject to certain limitations. As mentioned earlier, it is an implicit assumption that different neural activations reflect different cognitive processes. Similarly, it is also assumed that a single neural activation reflects a single cognitive process. These assumptions follow in the tradition of classical neuropsychology, and provide at least a good starting point for trying to understand the relationship between brain and cognitive function.

Under these assumptions, when given findings of greater activation in a target task-type (e.g. incompatible responding) over a control task-type (e.g. compatible responding), there can be several different interpretations of these results: (1) the neural area observed reflects a new cognitive process and corresponding neural area in the target task that is not recruited in the in the control task. (2) The neural area observed reflects a cognitive process that is recruited in both the target and control tasks, possibly for a longer duration in the target task. (3) The cognitive processes of interest in both tasks are the same, and the activation differences we observe are due to increases in processes not of interest (e.g. perceptual processing) in the target task. There is no reason to believe that changes in task such as the ones we instigated would lead to changes in perceptual or response processes alone, so we shall lay this third possibility aside. The second possibility might predict that greater reaction times costs would be correlated with greater activation. In the switching task, there is a marginally significant negative correlation in DLPFC ($r = -0.48$, $P = 0.08$); all other correlations ranged from -0.19 to 0.30. In the response compatibility task, there is a positive correlation in left frontopolar cortex ($r = 0.62$, $P = 0.02$); all other correlations ranged between -0.02 and 0.42 (note that due to the range and variability of each of these measures we may not obtain correlations even if there is a relationship between time and activation). The fact that there are both negative and positive relationships between time and activation suggest that the active regions reported may indeed be involved in the executive processes of interest and not merely due to a longer duration of the same process.

So, what do these commonalities and differences between tasks tell us about executive processes? Our conclusion is that there is, indeed, a common cognitive mechanism involved in the allocation of attention, controlled by superior parietal cortex, in both the counter switching and response compatibility tasks. This common mechanism of selective attention controls the allocation of attention—whether to an internal representation or to an external stimulus. However, attentional allocation alone cannot account for the

execution of both switching and interference-resolution processes. There are also separable mechanisms that mediate the switching of attention and the inhibition of a prepotent motor response. For the counters, this may involve the actual switching of attention from one counter to another, and may be controlled by a region in superior parietal cortex posterior to that involved in selective attention. For the stimulus-response mapping, it may involve the maintenance of a task sub-goal, controlled by frontopolar cortex, as well as motor programming and response selection operations regulated by premotor and parietal areas that allow one to inhibit a prepotent motor response and select an alternative response. Imaging data from the current study and previous behavioral research point to the same conclusion. In order to accomplish a task that requires "executive function", there is not one unitary process that is implemented. Instead, common selective attention processes are initiated, but the actual manipulation of attended information is carried out by different neural areas that implement different cognitive functions such as the switching of attention and resolution of interference. Understanding how these cognitive processes interact to implement executive control is a central challenge for future cognitive research.

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