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NeuroImage

www.elsevier.com/locate/ynimg NeuroImage 22 (2004) 1679–1693

Neuroimaging studies of shifting attention: a meta-analysis

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Received 15 December 2003; revised 31 March 2004; accepted 31 March 2004

This paper reports a meta-analysis of neuroimaging studies of attention shifting and executive processes in working memory. We analyzed peak activation coordinates from 31 fMRI and PET studies of five types of shifting using kernel-based methods [NeuroImage 19 (2003) 513]. Analyses collapsing across different types of shifting gave more consistent results overall than analysis within individual types, suggesting a commonality across types of shifting. These areas shared substantial, significant overlap with regions derived from kernel-based analyses of reported peaks for executive processes in working memory (WM). The results suggest that there is a common set of brain regions active in diverse executive control operations, including medial prefrontal, superior and inferior parietal, medial parietal, and premotor cortices. However, within several of these regions, different types of switching produced spatially discriminable activation foci. Precise locations of meta analysis-derived regions from both attention shifting and working memory are defined electronically and may be used as regions of interest in future studies.

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Keywords: Working memory; Parietal; Meta-analysis

Introduction

One of the most important abilities humans possess is the capacity to flexibly allocate mental resources. One prevalent model (Baddeley, 1986, 1992; Norman and Shallice, 1986) holds that currently relevant mental representations are maintained in an active state, called working memory (WM). When a particular context (a particular internal and external environmental state) calls for an action that is not highly automatized, a decision takes place that is likely to involve several processes, including (1) controlling which stimuli and actions are maintained in WM, (2) operating on or otherwise manipulating information in WM, (3) monitoring the context for changes in task requirements, (4) organizing or reordering the contents of WM, (5) shifting attention, or re-configuring perceptual and response biases as the context changes. Collectively, these operations are known as "cognitive control processes"

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Available online on ScienceDirect (www.sciencedirect.com.)

or "executive processes," and they appear to be critical in providing humans with remarkably adaptive behavioral flexibility (Miller and Cohen, 2001). Understanding what the core executive processes are and how they relate to one another has been a major challenge in cognitive psychology and cognitive neuroscience.

In this paper, we are concerned with shifting attention as a putative control process. Shifting attention has been typically discussed as a unitary construct, alternately called attention switching, task switching, or attention shifting (Corbetta et al., 1993; Smith et al., 2001). However, the concept of shifting may encompass several different operations depending on the type of information between which attention must be switched. For example, a shift in which of several attributes is relevant to a task may include changing processing biases in perceptual systems. Alternatively, if a decision rule must be applied that depends on the identity of an object (e.g., "press the left key if it is a red square"), then the relevant shift might be between sets of stimulus-response mapping rules. These shifts of perceptual and response biases, loosely referred to here as shifts in "attention," may be accomplished by separable mechanisms with identifiably different brain correlates. Alternatively, there may be a general system for controlling the biases in a range of systems. If different types of switching activate the same brain regions, this would be evidence for a unitary set of mechanisms underlying shifting. Alternatively, if different regions are specialized for different types, it would suggest that switching is not unitary, but is composed of processes that depend on the particulars of the task or the type of switching.

A second important question concerns the relationship of attention-shifting to other executive processes. Studies of individual differences in cognitive performance have shown that switching is related to other executive processes, particularly inhibition and updating of WM (Miyake et al., 2000); but it is separable as well, suggesting that switching may share some mechanisms in common with other executive processes and may not share others. Neuroimaging activations related to attention shifting and other executive processes have not been compared systematically in the brain. If switching attention and other executive operations on information in WM activate common brain areas, this would be evidence for the existence and localization of shared mechanisms.

Meta-analysis as a tool for inference

Single imaging studies are often focused on detecting activations related to a single process of interest. However, in looking

^{*}Meta-analysis image downloads are available from http://www.columbia.edu/cu/psychology/tor/.

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across studies, we can also get a picture of the range of tasks that activate a particular brain region. This information can help in interpretation of regional activations when a single process cannot be decisively excised for study (as is usually the case). In this case, examining activations over a range of studies of some process allows one to look beyond the idiosyncrasies of any individual experiment.

Apart from the benefit of meta-analysis in understanding the scope and limiting conditions for activation, meta-analysis has several other advantages. One is that imaging studies often report activations at uncorrected statistical thresholds, creating falsepositives, while at the same time power in individual imaging studies is low. Meta-analysis can help accumulate consensus across tasks that involve putatively similar processes while washing out statistical idiosyncrasies in individual studies. A second advantage is that individual studies contain no information about the spatial variability of activation locations. If a study finds partially overlapping activations between two tasks, should those tasks be said to involve the same area or different areas? For example, if one task results in slightly more dorsal activation sites, is that evidence for a dorsal/ventral segregation? The dorsal/ventral distinction must be reliable if we are to draw this conclusion from the study, but most individual studies do not provide reliability information about differences in spatial locations (but for an alternative, see, e.g., Ploghaus et al., 1999). Meta-analysis, however, allows measures of spatial error to be obtained, and one can make confidence intervals around the spatial locations of peak activations across tasks. Thus, hypotheses about spatial dissociations by task type can be directly tested.

The present study

Our meta-analysis was conducted to address three questions. What brain regions are consistently activated by shifts of attention across studies? Are some brain regions specialized for particular types of shifts of attention (e.g., shifting between locations as opposed to objects)? And finally, are the same brain areas activated by shifts of attention and other executive operations in working memory? To answer these questions, we first identified five types of attention-shift studied in the literature: shifting between *locations*, *objects*, *attributes* of objects, stimulus-response mapping *rules*, and *tasks*, as elaborated below.

To address the first question, we used peak density analysis to examine activation peaks for individual types of attention-shift, and to examine peaks across all types of attention-shifts. Peak density analysis is a nonparametric method for finding regions in which the density of reported peaks exceeds that expected by chance. This method revealed consistent sites of activation when all types of attention-shift were collapsed together, suggesting that activation patterns for different types of switching are much more similar than they are different. Across types, we identified seven distinct regions of significant activation in switching.

Within each region, we performed linear discriminant analyses (MANOVAs) to uncover differences in the spatial distribution of peaks for different types of switching. Few previous studies have reported differences among different types of switches. Rushworth et al. (2001), as one isolated example, reported spatial separation of activations for response rule and attribute-shifting within the parietal cortex. Our results, however, show that the spatial distribution of peak activations differs among switch-types in several regions, thus motivating the need for additional studies

of the spatial topography of activations due to different types of switches.

Finally, to compare switching to executive processes in working memory (WM), we performed a peak density analysis on WM tasks using a database of 60 studies compiled previously (Wager and Smith, 2003). The density analysis compared tasks requiring WM storage plus executive processing with those requiring storage alone. A task was determined to require executive processing if it required one or more of the following: (1) continuous updating of working memory, as in the n-back task (Callicott et al., 1999; Jonides et al., 1997), (2) maintenance of temporal order (Marshuetz et al., 2000; Petrides, 1991), or (3) manipulation of information in WM. Each of these requires one of the five types of executive process discussed above. Eight significant regions were identified, and those regions overlapped substantially with the regions identified in switching tasks. We used Monte Carlo simulations to test for the likelihood of obtaining overlap among the two sets of clusters by chance, and found that there was significant overlap in most regions, but that anterior PFC and DLPFC were specific to executive WM. Overall, our analyses show that different types of attention-shifting largely activate the same brain regions, and that these regions are common to executive operations in working memory.

Methods

Study selection

We analyzed 31 PET and fMRI studies of attention-switching tasks, listed by first author in Table 1. Studies were identified by searches on two versions of Medline (Medsearch and Pubmed) and PsycInfo. Studies were included if they reported whole-brain comparisons of switching tasks in comparison to a control task that contained similar perceptual and motor requirements (i.e., no passive fixation baselines), included healthy, unmedicated subjects, and reported standardized coordinates for activation foci in either Montreal Neurologic Institute (MNI) or Talairach (Talairach et al., 1988) space. However, we did not include activations related to orienting attention, a similar psychological construct recently reviewed in the literature (e.g., Corbetta et al., 2000; Hopfinger et al., 2000). We explore potential similarities and differences between shifting and orienting attention in the Discussion. As in previous meta-analyses (Phan et al., 2002; Smith and Jonides, 1999; Wager and Smith, 2003; Wager et al., 2003), we analyzed only positive switching activations, as deactivations are inconsistently reported and more difficult to interpret.

Classification of peaks into switching types

Tasks were classified into types of switches according to the following system. Tasks that contrasted shifting of spatial locations with comparable non-shift control conditions were classified as *location shifts*. Tasks in which switching involved shifting attention from one feature of an object to another (shifts of the relevant dimension of an object, e.g., from shape to color) were classified as *attribute* switches. Those tasks in which switching involved reversal of learned response mappings or reassignment of responses to stimuli, where the response sets and the stimuli themselves remained the same, were classed as *rule switches*.

Table 1 Studies included in the meta-analysis

Study	Method	Swite	ch type				Region						
		L	A	Т	R	О	MPFC	RPMC	LAIP	RAIP	LPIP	RPIP	LIT
Arrington et al., 2000	fMRI	1	0	0	0	0	1	1	0	0	0	0	0
Beauchamp et al., 2001	fMRI	1	0	0	0	0	1	2	1	0	2	1	1
Bischoff-Grethe et al., 2002	fMRI	0	1	0	0	0	4	1	2	0	0	0	0
Braver et al., 2001	fMRI	0	0	1	0	0	0	0	0	0	0	0	0
Corbetta et al., 2002	PET	1	0	0	0	0	0	1	0	1	1	1	0
Corbetta et al., 1993	fMRI	1	0	0	0	0	7	0	10	8	2	0	0
Corbetta et al., 1998	fMRI	1	0	0	0	0	1	3	0	1	0	1	0
Coull et al., 2000	fMRI	1	0	0	0	0	0	0	0	0	0	0	0
DiGirolamo et al., 2001	fMRI	0	1	1	0	0	4	3	5	2	1	1	4
Dove et al., 2000	fMRI	0	0	0	1	0	1	1	1	0	3	0	0
Fink et al., 1997	PET	0	1	0	0	0	1	0	0	0	0	0	0
Garavan et al., 2000	fMRI	0	0	0	0	1	1	1	3	1	3	0	0
Gurd et al., 2002	fMRI	0	0	0	0	1	0	0	0	0	1	1	0
Jancke et al., 2000	fMRI	0	0	1	0	0	1	0	0	0	1	1	2
	fMRI	1	0	0	0	0	4	3	3	0	0	2	0
	fMRI	0	0	1	0	1	0	0	1	1	1	1	0
LaBar et al., 1999	fMRI	1	0	0	0	0	0	0	0	0	0	0	3
Le et al., 1998	fMRI	0	1	1	0	0	0	0	0	1	3	2	0
Macaluso et al., 2001	PET	1	0	0	0	0	0	0	0	0	0	0	0
Nobre et al., 1999	PET	1	0	0	0	0	0	1	3	0	0	0	0
Omori et al., 1999	fMRI	0	0	0	1	0	0	1	0	0	1	1	2
Pollmann et al., 2000a,b	fMRI	0	1	0	0	0	0	0	0	1	0	0	0
Pollmann et al., 2000a,b	fMRI	0	0	0	1	0	1	2	0	0	1	1	0
Rushworth et al., 2002*	fMRI	0	1	0	0	0	4	0	0	0	0	0	0
Smith et al., 2001	PET	0	0	1	0	1	0	0	0	0	4	0	1
Sohn et al., 2000	fMRI	0	0	1	0	1	0	0	0	0	1	0	0
Vandenberghe et al., 2000	PET	1	0	0	0	0	0	0	0	0	0	0	1
Vandenberghe et al., 2001	fMRI	1	0	0	0	0	0	0	2	0	2	2	0
Wilkinson et al., 2001	fMRI	0	1	0	0	0	2	0	1	1	0	0	0
Wojciulik and Kanwisher 1999	fMRI	1	0	0	0	0	0	0	2	1	3	3	1
fMRI	24	9	6	6	3	4							
PET	6	4	1	1	0	1							
Total		13	7	7	3	5							

The first five columns indicate whether the task used involved each type of switch. The last seven columns indicate the number of peaks that study reported in each region identified in the density analysis. Note that some studies may have reported results in a general region (e.g., MPFC) but are not shown here because the peak coordinates were not close enough to the canonical region identified in the density analysis. *Rushworth et al. (2002) was the only study that contained multiple contrasts (an attribute switching contrast and a rule switching contrast); only the first contrast is shown in the indicator matrix, although all peaks were used in the analysis. L = location; A = attribute; T = task; R = rule; O = object switching; MPFC = Medial prefrontal cortex; RPMC = Right premotor cortex; LAIP = Left anterior intraparietal sulcus; RPIP = Right posterior intraparietal sulcus; LIT = Left inferior temporal cortex. Summary characteristics for each region are shown in Table 2.

For example, if the task was to press button A when you saw an X, and button B when you saw a Y, a rule switch would involve reversing the mappings: button B for X, and A for Y. Tasks in which the stimulus set or the relevant object only was switched were classified as object switches. Finally, tasks for which the critical contrast was either switching between response sets or switching which operations were applied to stimuli were classified as task switches. This classification differentiates task switches from simpler switches of which feature or attribute cues a response, and from the simpler re-mapping requirement of rule switching. For example, switching from making an odd/even judgment of a number to making a vowel/consonant judgment on letter-number pairs (Rogers and Monsell, 1995) entails a switch of both the relevant object and the mapping rules leading to responses, so this would be classified as a task switch. These desiderata provided a breakdown of switching into component types with clear conceptual distinctions among them. However, a task could (and many

did) involve more than one type of switch at once (see Table 2). Thus, activation peaks could have membership in multiple switching categories.

Summary of analyses

To summarize the preceding description of analyses, peak activation sites ("peaks") were analyzed in three ways. First, peaks from each type of switch, and peaks from all switch types together, were analyzed with peak density analysis to determine significant regions of consistent activation. Second, MANOVA was used to find spatial discriminants within regions for different types of switching. Third, the significant areas of activation for switching and executive function in working memory were compared, and the likelihood of overlap under the null hypothesis assessed using simulations. Before analysis, peaks reported in Talairach space were transformed to Montreal Neurologic

Institute (MNI) space using Matthew Brett's bilinear transformation (http://www.mrc-cbu.cam.ac.uk/Imaging/; no coordinate was shifted more than 10 mm).

Density analysis

Switching density analysis

This type of analysis tests a collection of peaks distributed at multiple sites throughout the brain against the null hypothesis of random distribution of peaks throughout brain tissue (gray and white matter). Both gray and white matter were included in the null hypothesis because many reported activation peaks fall within white matter near the gray/white matter boundary. This procedure avoids the somewhat arbitrary nature of defining ROIs by Brodmann's areas or some other classification (Phan et al., 2002), and our technique is similar to that employed by several other groups (Chein et al., 2002; Turkeltaub et al., 2002).

This technique also avoids the problem of outliers in cluster analysis techniques (e.g., Goutte et al., 2001). Most clustering algorithms assign all peaks to clusters and determine cluster boundaries based on the whole set of peaks; this does not take account of each peak's likelihood of being a true activation. The density analysis provides a threshold and boundaries for distinct anatomical regions; in doing so, it provides criteria for removing outliers from further analysis. We take advantage of this property in choosing peaks for discriminant analysis below. The density analysis technique has been previously described (Wager et al., 2003), but we introduce and apply several enhancements to the technique.

In the density analysis, the stereotactic (MNI) coordinates of n peaks comprise the data set for analysis. We calculated the density of reported points in each region of space by convolving the 3-D histogram of peak locations (the set of peak coordinates placed within $2 \times 2 \times 2$ mm bins or "voxels" in the brain) with a spherical smoothing kernel of radius r, and normalizing the resultant values to indicate number of peaks per square mm of tissue. Density values were compared with a null hypothesis distribution created through Monte Carlo simulations conditioned on the number of reported peaks. Thus, in the simulation, n peaks were chosen at random locations throughout gray and white matter in a standard brain (ours was based on the Montreal Neurologic Institute template Brain avg152T1.img included in SPM99; Wellcome Department of Cognitive Neurology http:// www.fil.ion.ucl.ac.uk/spm/). The density of peaks was calculated the same way as for the actual data, and the maximum density throughout the brain was saved. The process of random point selection and maximum density computation was repeated 5000 times in our simulations. In this way, we developed a distribution of the maximum density throughout the brain under the null hypothesis. Voxels with density values that reached the 95th percentile on this distribution were considered significant. Use of the distribution of maxima ensures strong control of familywise

One additional enhancement that was not included in previously published work using this method (Wager et al., 2003) is the use of a step-down test in the density analysis. The reason for using a step-down procedure is that the null hypothesis (Ho) is global; that is, it specifies no significant grouping of peaks anywhere in the brain. If Ho is false somewhere in the Brain, several peaks will be clustered in that region, but spread evenly throughout the brain in the Ho simulations, making the signi-

ficance threshold higher than it should be for other brain regions. In the step-down procedure, after significant regions are identified, two changes are made: (1) peaks falling within r mm of the significant region are excluded, and (2) significant voxels are removed from the mask of eligible brain voxels for the Ho simulation. Following these changes, the simulation is run again and a new threshold calculated. This process continues until no additional significant voxels are discovered. The switching density analyses reported here were all run using a step-down procedure, and all simulations converged in no more than two steps.

One important parameter choice in the density analysis, as in all kernel-based statistical methods, is the choice of the kernel width. We chose a kernel radius r based on the intrinsic resolution of the data. Density analysis was run on peaks for each of the five switch types for r between 5 and 40 mm, in increments of 5 mm. A radius of r=15 mm produced the maximum number of suprathreshold clusters on four of the five switch types and on the switching activations collapsed across types, as shown in Fig. 1. (solid lines), and was used in subsequent analyses. As the density analysis can potentially produce separate peaks that are very close together (e.g., separated by only one voxel), we also considered the number of contiguous clusters found after 3 mm of spatial smoothing of the density map (dashed lines). The analyses indicate that the natural spatial resolution of switching activations across studies is around 2 r, or 30 mm.

Working memory density analysis

To perform density analysis on executive functions, we used peaks reported in 60 separate studies of working memory (no studies were included in both working memory and switching analyses). The tasks either involved: (a) active maintenance of items in WM either compared to a perceptual/motor matched control condition or isolating the memory retention delay period in an event-related fMRI design (storage only), or (b) the same as

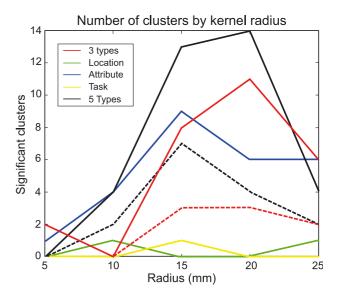


Fig. 1. Number of significant clusters found, by smoothing kernel radius (*x*-axis). The 3-types analysis collapsed across location, attribute, and task. The 5-type analysis also included object and rule switching. The dashed lines indicate the number of clusters separated by at least two voxels.

the above, but with the added demand for one of three executive processes: concurrent manipulation of items in memory, temporal order memory, or continuous updating of WM during task performance (storage + executive). To isolate activations specific to executive processing in WM, we used density analysis to compare the distribution of peaks for storage + executive with those for storage only, asking which brain regions showed significantly greater peak density for the former condition than the latter.

In the analysis, density maps were computed for executive + storage and for storage only peaks, and the density maps were subtracted to yield a difference map. The difference map was compared with a null hypothesis distribution as before. In the simulations, the same number of points as were reported in each condition were randomly distributed throughout gray and white matter voxels in the standard MNI brain, so that the comparison is not biased by the reporting of unequal numbers of peaks for each condition, and an Ho difference map was computed. The actual difference values for (executive + storage) – (storage only) were compared with the distribution of maximum Ho values over the brain, as in previous analyses.

Discriminant analysis

Each significant region in the density analysis whose voxels were located more than 2 voxels from those of another region (i.e., separate clusters after 3 mm smoothing) was analyzed for differences in the spatial distribution of peaks within the region among switch types. Peaks were included in a region's analysis if they fell within 15 mm (the density kernel radius) of a significant in-region voxel. These parameter choices ensured that very few peaks were considered part of more than one region, but in those rare cases where the region for a peak was ambiguous, it was included in both regional analyses. Within each region, five separate discriminant analyses were conducted—one for each switch type—to separate peaks for each switch type (e.g., location switching) from those of other switches (e.g., non-location). Switch class was the independent variable and x, y, and z MNI coordinates were the dependent variables in a standard MANOVA analysis, and the results of each analysis indicated whether there was an axis in 3-D space along which points in a particular switch type were separable from those in other types. Both uncorrected and corrected p values using Bonferroni for the number of switch types within each region are reported.

Monte Carlo overlap test

To provide a quantitative test of the degree of overlap between switching and executive function regions identified in the density analyses, we first calculated the number of voxels in each distinct region that were significant in both switching (collapsing across types) and executive analyses. Using a Monte Carlo technique to develop an Ho distribution, we randomly re-assigned the centers of each contiguous significant region to random coordinates within gray and white matter in the standard brain. The assignment shifted the locations of both switching and executive regions, but preserved their size and shape. Activation regions were relocated in this fashion and both total number of overlapping voxels and number of overlapping voxels for each region were calculated 5000 times. Observed overlap between sets of activations were compared with this Ho distribution.

Results

Switching density analysis

The density analysis was conducted collapsing across the five switch types and individually on peaks for each type. The results, shown in Fig. 1, display the number of significant contiguous regions at P < 0.05 (whole Brain, y-axis) for each analysis by kernel radius (x-axis). As discussed above, these results showed that a 15-mm kernel radius produced the greatest number of spatially distinct significant regions when collapsing across switch types. The number of spatially distinct significant regions on the y-axis in Fig. 1, shown by the dashed black line, is highest for radius = 15 mm. Also, collapsing across types produced more consistent grouping across studies than density analysis on any single type alone, as evidenced by the greater number of distinct regions in the combined analysis (dashed black lines in Fig. 1) than for any single switch-type analysis (dashed colored lines). This finding suggests that the consistency across switch types in regional activation patterns outweighs differences among them.

To look for regions that were significant for individual types, but not for the analysis collapsing across types, we examined the significant results for each type. No regions were unique to one type of switching. That is, no regions appeared in any of the individual analyses that were not also significant in the analysis collapsing across types.

Seven distinct significant regions were found in the analysis collapsing across switch types. The density analysis showed 13 regions (Fig. 1, solid black line), but several of these were within 2 voxels of another region and contained only one voxel. The application of 3 mm of smoothing to the results showed seven regions (Fig. 1, dashed black line) in distinct anatomical areas, and these regions were used in subsequent analyses. Descriptions of the significant regions can be found in Table 2, and slices showing their locations are shown in Fig. 2.

Notably, no regions in prefrontal cortex anterior to premotor cortex were significant: the most anterior region was right premotor cortex. The density threshold for the first step in the stepdown test was 0.011 peaks/mm³, equivalent to 15 points within the 15-mm radius. The threshold for the second step was $7.78 \times 10-4$ peaks/mm³ (11 points), and no additional regions were identified at this threshold. In an exploratory analysis, we looked for significant regions at a threshold of 7.07×10^{-5} peaks/mm³ (10 points) within the radius, corresponding to an approximate corrected P < 0.13 in the step-down test. At this threshold, four regions in frontal cortex—bilateral dorsolateral prefrontal cortex and bilateral anterior insula (at the border with inferior frontal gyrus)—emerged. Fig. 3 shows the results at a lower threshold (more than 5 peaks within the radius), and Table 2 displays summary statistics for the additional regions at the threshold of 10 peaks. These results may be useful making predictions about the location of attention switching activations in frontal cortex in future studies.

Discriminant analyses

To examine each significant cluster for differences among types of switching in the spatial distributions of peaks, we used MANOVA to find linear discriminants in (x, y, z) anatomical space that separated peaks of different types. The peaks in each region are shown on a transparent canonical brain in Fig. 3 in

Table 2 Significant regions in switching density analysis

Region	х	у	Z	Volume (mm ³)	Density (peaks)	Brodmann's areas
Significant regions of	at P <	0.05				
L occipital	-36	-82	0	424	15	BA19 (83%),
						BA18 (17%)
Medial prefrontal	-2	12	48	6952	18	BA32 (46%),
cortex						BA6 (35%),
						BA8 (17%)
L posterior IPS	-20	-66	46	2392	16	BA7 (100%)
R anterior IPS	32	-40	46	944	17	BA40 (48%),
						BA3 (29%),
						Unknown (18%
R premotor	40	2	46	920	15	BA6 (97%)
L anterior IPS	-32	-44	50	2856	17	BA40 (69%),
						BA7 (17%),
						BA3 (13%)
R posterior IPS	26	-64	50	424	15	BA7 (100%)
Additional regions a	at P <	0.13				
L dorsolateral PFC	-40	16	26	6600	11	BA9 (56%),
						BA13 (20%),
						BA46 (14%),
						BA45 (5%)
R premotor/	40	0	44	14 320	15	BA6 (67%),
dorsolateral PFC						BA9 (29%)
L anterior insula	-38	16	2	336	10	BA13 (74%),
						Unknown (24%
R anterior insula	40	16	2	1096	11	BA13 (70%),
						BA47 (18%),
						Unknown (9%)
Thalamus	2	-20	12	888	10	Tha (100%)
L temporal cortex	50	-58	6	216	10	BA39 (100%)
R occipital cortex	22	-86	4	912	10	BA17 (54%),
						BA18 (39%),
						BA19 (7%)

IPS = intraparietal sulcus; PFC = prefrontal cortex; BA = Brodmann's Area; Tha = thalamus. Coordinates are reported in mm in MNI standard space. Volume refers to the volume of the suprathreshold region, after 3 mm of smoothing was applied to combine adjacent regions. Percentage values next to BA labels indicate the percentage of suprathreshold in-region voxels classified in that BA by the Talairach Daemon (see Methods). The threshold for corrected significance was 0.0011 peaks/mm³, 15 peaks within 15 mm radius. The reduced threshold (P < 0.13) was 7.07×10 -4 peaks/mm³, 10 peaks within 15 mm radius.

axial, sagittal, and coronal views (panels A, B, and C, respectively). Peaks were considered within region if they fell within the kernel radius (15 mm) of a significant in-region voxel. Peaks for each region are color-coded in Fig. 3 with a unique color/symbol combination.

The right columns of Table 1 show the number of peaks reported for each study in each of these seven regions. Table 3 shows the results of discriminant analyses for each region. Significant MANOVA results (P < 0.05) indicate that peaks of the corresponding switch type could be spatially separated from those of other switch types. The discriminant weights give the principal axis along which the peaks are separable, and centers and intercenter distances of peaks for each class (i.e., switch type) are also reported (see Table 3 legend for additional detail).

The results show that some switch types in several regions occupy relatively distinct regions of space, raising the possibility

that spatial dissociations do exist in some areas. The most separation was found in right premotor cortex, shown in Fig. 4. Location switching peaks were lateral, posterior, and superior within this region, with a mean coordinate separated from other class centers by at least 11 mm (Table 3). Attribute peaks were located medial, anterior, and superior, but overlapped with task switching peaks. Rule switching peaks were located inferior and anterior to other peaks within the region (Fig. 4). In left anterior intra-parietal sulcus (IPS), attribute peaks were located anterior and superior to the main group, and object peaks were located inferior and posterior to other peaks (Table 3). This was not entirely consistent with results in the homologous right anterior IPS, which showed a trend toward attribute switching peaks lateral to others, and a separation of location peaks, medial and anterior to other types. In the neighboring right posterior IPS, location peaks were again medial and anterior to the other types.

Switching compared with executive processes in WM

Density analysis was performed on the WM database, comparing storage + executive processing with storage alone (Wager and Smith, 2003). Results revealed eight distinct clusters (after 3 mm of smoothing was applied to the results), described in Table 4. As expected, frontal and parietal regions showed greater frequency of activation when executive processing was required. Spatially distinct regions were found for bilateral premotor cortex (superior frontal sulcus), dorsolateral PFC, and anterior PFC. Surface renderings for switching and working memory are shown in Fig. 5. We used Monte Carlo simulations varying the spatial locations of the contiguous suprathreshold regions to quantify and assess the significance of the overlap between the two sets of results. Spatial smoothing at 3 mm FWHM was applied to each map of results before analysis. The observed overlap between the two sets was 384 voxels, with 44 expected on average by chance, P = 0.012.

Probability values for overlap between each region separately were also obtained through the simulation. Results showed significant overlap in both left and right medial prefrontal cortex (BA 32), with 32 and 111 voxels common to both switching and executive WM in each region, respectively, both P < 0.05. Table 5 shows number of overlapping voxels, coordinates for the overlap centers, expected overlap under the null hypothesis, and P values for both regions common to switching and executive WM and unique regions. Common regions were classified as those where significant regions for each process (switching and executive WM) overlapped significantly with regions for the other process. In each case, the expected value was obtained using the simulations. Larger regions are expected to have more overlap with those of the other process by chance, so they require more overlapping voxels to reach significance. Other common regions included right premotor cortex and both anterior and posterior regions in left IPS.

Unique regions were also found for each process. Left extrastriate cortex and two regions (anterior and posterior) right IPS were selective for switching (Table 5, Fig. 5). Bilateral anterior PFC and dorsolateral PFC were selective for executive WM. None of these regions contained any overlapping voxels with regions of the other process; thus, *P* values of 1 for all regions reflect that we did not observe more overlap than was expected by chance (or, in fact, any overlap at all) in any of the regions. Although these findings serve as an indication that these

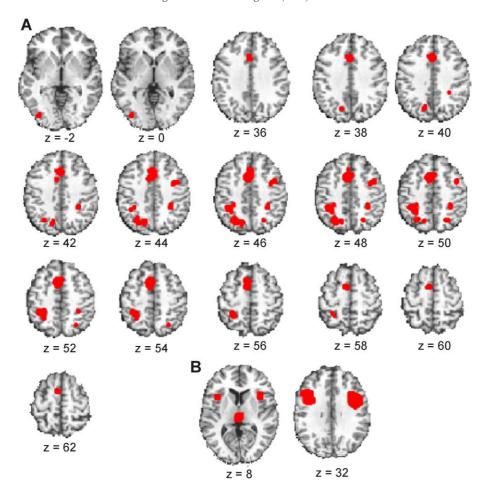


Fig. 2. (A) Significant regions of consistent activation in the meta-analysis. (B) Regions active at a lower threshold, at least 10 peaks within a 15-mm sphere.

areas are spatially distinct, they do not preclude the possibility that some regions are active in both processes, but simply did not reach the reported threshold of corrected P < 0.05 for one process. For example, bilateral DLPFC activity was observed in switching at a slightly lower threshold (Fig. 2B), suggesting that the commonalities among switching and executive WM may be greater than as suggested by Table 5.

Discussion

Overall, we found seven distinct regions in the cortex that were reliably activated across studies of attention shifting of various types. These included both posterior (parietal and occipital) regions and frontal regions, although anterior frontal regions—including DLPFC and anterior insula—were only apparent at lower statistical

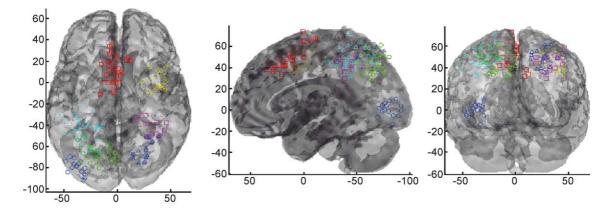


Fig. 3. Activations peaks in switching from prior studies, color- and shape-coded by associated region. Only peaks that fell within 15 mm of region boundaries are shown. Transparent brains from left to right show axial, sagittal, and coronal views. Numbers on axes indicate coordinates in mm from the anterior commissure of the standard Montreal Neurologic Institute (MNI) brain.

Table 3
Summary of discriminant analyses for switching regions

Name Peaks		MANOVA summary statistics			Discrim	inant weig	ghts	Class	Class centers (mm)			Distances between centers for each type (mm				
		λ	P	AMR	x	у	Z	X	у	Z	L	A	T	R	О	
Medial pre	efrontal co	ortex: BA	132(46%), BA	6(35%), B.	A8(17%)											
Location	14	0.85	0.190	30%	0.06	0.05	-0.03	-1	17	45	0	12	7	12	14	
Attribute	13	0.92	0.470	15%	-0.01	-0.04	0.05	-3	8	53	12	0	7	3	7	
Task	5	0.91	0.402	6%	0.06	0.13	0.16	-2	15	52	7	7	0	8	9	
Rule	4	0.95	0.661	12%	0.14	0.05	0.04	-7	9	52	12	3	8	0	10	
Object	1	Too fe	w peaks					3	7	54	14	7	9	10	0	
Right prem	notor: BA	6(95%)														
Location	11	0.55	0.0199*	15%	-0.08	0.15	-0.03	39	-4	51	0	12	11	18	20	
Attribute	4	0.46	0.0053*	5%	-0.16	0.1	0.06	29	3	54	12	0	1	22	26	
Task	3	0.69	0.102	15%	-0.11	0.1	0.07	30	3	54	11	1	0	21	25	
Rule	4	0.58	0.0291*	5%	0.04	0.1	-0.06	42	8	38	18	22	21	0	7	
Object	1		w peaks					45	4	34	20	26	25	7	0	
Left anteri	or IPS: R	440(68%	6), BA7(17%)	R43(14%	0											
Location	21	0.89	0.332	24%	-0.08	-0.01	0.1	-30	-45	48	0	10	8	6	12	
Attribute	8	0.65	0.0044*	9%	-0.04	0.07	0.13	-34	-41	56	10	0	4	15	19	
Task	6	0.86	0.214	15%	-0.05	0.03	0.12	-34	-45	55	8	4	0	12	15	
Rule	1		w peaks	1570	0.05	0.05	0.12	-32	-50	45	6	15	12	0	6	
Object	4	0.77	0.0489*	3%	0.03	0.1	0.07	-33	-56	46	12	19	15	6	0	
Right anto	rior IPS:	R 410(18	%), BA3(29%	6), Unknow	m(17%)											
Location	11	0.56	0.0383*	0), Unknow 11%	0.14	-0.04	-0.02	27	-39	44	0	14	15	_	9	
Attribute	5	0.59	0.0518+	11%	0.14	-0.04 -0.02	-0.02 -0.02	40	-39 -46	46	14	0	4	_	7	
Task	4	0.65	0.102	6%	-0.05	0.12	0	38	-50	46	15	4	0	_	7	
Rule	0		w peaks	070	-0.03	0.12	U	-	-30	-	-	_	_	0	_	
Object	2		w peaks					34	-45	45	9	7	7	_	0	
T C .	· IDC	D 47/100	9.41													
Left poster		,	· ·	220/	0.04	0.15	0.02	10		4.5	0	1.2	-	0	_	
Location	10	0.83	0.171	23%	0.04	0.15	0.02	-18	-61	45	0	13	7	8	5	
Attribute	4	0.79	0.103	7%	0.03	0.13	-0.04	-20	⁻⁷³	49	13	0	9	10	11	
Task	11	0.89	0.392	27%	0.03	0.12	0.08	-18	-68	43	7	9	0	4	4	
Rule	5	0.95	0.734	27%	-0.07	0.06	0	-14	-68	44	8	10	4	0	8	
Object	10	0.93	0.592	20%	0.07	-0.01	0.1	-21	-65	42	5	11	4	8	0	
Right poste		BA7(10														
Location	10	0.48	0.0136*	11%	-0.19	0.18	0.08	25	-61	53	0	12	8	18	4	
Attribute	3	0.71	0.172	0%	-0.17	0.14	0.07	28	-69	45	12	0	4	8	13	
Task	5	0.86	0.532	0%	-0.15	0.14	0.05	27	-67	48	8	4	0	11	10	
Rule	2	Too fe	w peaks					26	-70	38	18	8	11	0	20	
Object	2	Too fe	w peaks					29	-60	55	4	13	10	20	0	
Left inferio	or tempor	al cortex	: BA19(83%)	, BA18(179	26)											
Location	6	0.62	0.143	13%	0.25	0.09	-0.02	-42	-80	-1	0	6	7	10	16	
Attribute	4	0.74	0.324	13%	0.17	0.19	0.01	-36	-77	2	6	0	6	6	17	
Гask	7	0.76	0.359	13%	0.22	0.05	-0.09	-35	-82	0	7	6	0	7	13	
Rule	2		w peaks					-34	-80	7	10	6	7	0	20	
Object	1		w peaks					-33	-84	-13	16	17	13	20	0	

Descriptive and inferential statistics for discriminant analysis. Regions were derived from the density analysis, and MANOVA analysis was used to find axes in anatomical space (with x, y, and z MNI coordinates as dependent variables) that discriminated points of each switch type from points of other types. Coordinates reported are the mean x, y, and z coordinates in MNI space for in-region peaks of each class (i.e., switch type). Distances are Euclidean distances (in mm) between class centers. BA signifies Brodmann's area; λ = Wilk's lambda (the MANOVA test statistic); AMR = apparent misclassification rate in the discriminant analysis; L = location; A = attribute; T = task; R = rule; O = object switching.

thresholds. Parietal involvement in switching was expected based on previous research (e.g., Cutrell and Marrocco, 2002; Davidson and Marrocco, 2000), but evidence for prefrontal involvement was weaker than expected based on findings of DLPFC involvement in cognitive control (Asaad et al., 2000; Miller and Cohen, 2001; Wallis et al., 2001).

Shifting vs. orienting attention

The attention shifting tasks we review here required participants to perform one task or attend to a particular location (or object, rule, etc.) and subsequently shift to another task or location. A related paradigm is the cued attention paradigm, which requires

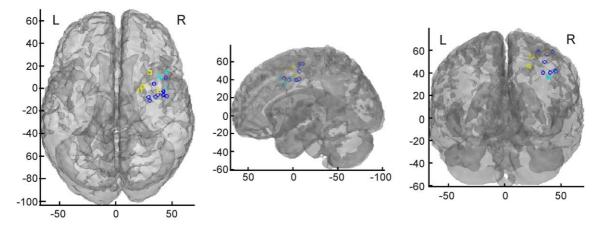


Fig. 4. Peaks in right premotor cortex for location (blue circles), attribute (yellow squares), and rule switches (cyan triangles).

participants to attend to a central cue and, based on the nature of this cue, direct their attention to a particular object or location (e.g., Posner et al., 1984). Shifting and orienting attention may be similar processes involving similar neural mechanisms, or they may require somewhat different component processes. Shifting, for example, may require participants to disengage attention in some manner from a previous task and/or resolve interference from previous stimuli or task sets (e.g., Allport et al., 1994; Mayr, 2003; Mayr and Keele, 2000; Rougier and O'Reilly, 2002). Orienting attention may not place the same demands on either selection or interference resolution mechanisms, as there is typically no competing stimulus or task set in this paradigm. Orienting attention, by contrast, may place greater demands on mechanisms of task set or stimulus encoding. In attention shifting paradigms, attention to the task is maintained continuously throughout performance. In orienting tasks, attention is diffuse or maintained on some unspecified object before the cue (the prior task, thoughts, feelings, memories?).

One kind of evidence we can use to investigate the similarities or distinctions among shifting and orienting processes is the similarity

Table 4
Significant regions for storage + executive processing vs. storage only in WM

X	у	Z	Volume	Density	Brodmann's
			(mm ³)	(peaks)	areas
34	54	- 8	1448	13	BA10 (52%),
					BA11 (48%)
-32	54	6	216	13	BA10 (100%)
42	38	28	5888	20	BA9 (43%),
					BA46 (33%),
					BA10 (24%)
-38	10	36	6112	20	BA9 (72%),
					BA6 (20%)
-4	-64	50	13 880	24	BA7 (100%)
24	10	50	12 224	30	BA6 (55%),
					BA8 (24%),
					BA32 (19%)
-38	-48	46	2840	17	BA40 (97%)
-18	8	52	3200	20	BA6 (66%),
					BA32 (20%),
					BA8 (8%),
					BA24 (7%)
	34 - 32 42 - 38 - 4 24 - 38	34 54 -32 54 42 38 -38 10 -4 -64 24 10 -38 -48 -18 8	34 54 -8 -32 54 6 42 38 28 -38 10 36 -4 -64 50 24 10 50 -38 -48 46 -18 8 52	(mm³) 34 54 -8 1448 -32 54 6 216 42 38 28 5888 -38 10 36 6112 -4 -64 50 13 880 24 10 50 12 224 -38 -48 46 2840 -18 8 52 3200	(mm³) (peaks) 34 54 -8 1448 13 -32 54 6 216 13 42 38 28 5888 20 -38 10 36 6112 20 -4 -64 50 13 880 24 24 10 50 12 224 30 -38 -48 46 2840 17 -18 8 52 3200 20

among neuroimaging activations for shifting and orienting. Two recent meta-analytic reviews have focused largely on orienting attention (Kanwisher and Wojciulik, 2000; Kastner and Ungerleider, 2000); although some shifting studies are included as well). The regions linked in these reviews to control of voluntary orienting overlap with our results in parietal and medial prefrontal cortex, and in right premotor cortex (identified as superior frontal sulcus). Evidence from human neuropsychology (Egly et al., 1994; Friedrich et al., 1998; Posner et al., 1984, 1987) and animal studies (e.g., Colby, 1991; Colby and Goldberg, 1999; Robinson et al., 1995) has implicated parietal regions in orienting attention in space. Electrical stimulation of parietal cortex appears to be sufficient to induce orienting (Cutrell and Marrocco, 2002), and infusion of the muscarinic acetylcholine antagonist muscarine into the parietal cortex delays orienting (Davidson and Marrocco, 2000). How parietal involvement in these tasks compares to its role in tasks involving attention shifting per se is an issue for further study. One theme that is emerging, however, is that the same parietal regions are involved in both spatial and nonspatial attention (Wojciulik and Kanwisher, 1999). Our results support this idea.

Unlike reviews of orienting, the current study identified bilateral anterior insula as a potentially important site for attention shifting. As studies of perceptual and response inhibition have consistently reported activations in the anterior insula and nearby ventrolateral prefrontal cortex (D'Esposito et al., 1999; Jonides et al., 1998; Rubia et al., 2001), the insula may play a selective role in the interference resolution component of attention shifting paradigms. A recent study found evidence for insula activation in both shifting and inhibition tasks in the same participants (Sylvester et al., 2003).

As in the present study of shifting attention, DLPFC activations in orienting attention have been reported rather less consistently than for parietal and premotor regions. Evidence has accumulated demonstrating that the DLPFC represents task and abstract rule information (Wallis et al., 2001)—particularly when behaviorally relevant (Rainer et al., 1998)—and abstract categories (Freedman et al., 2001), among other types of representations. One view of DLPFC function is that it represents abstract task or situational contexts that guide the selection of appropriate behaviors (Miller and Cohen, 2001). If so, then DLPFC is expected to be active on both switch and non-switch trials. One view is that as DLPFC represents tasks and rules, overall activity in DLPFC should be constant, with the pattern of neural firing changing as tasks, rules, objects, etc. are switched. Another view is that DLPFC is actively

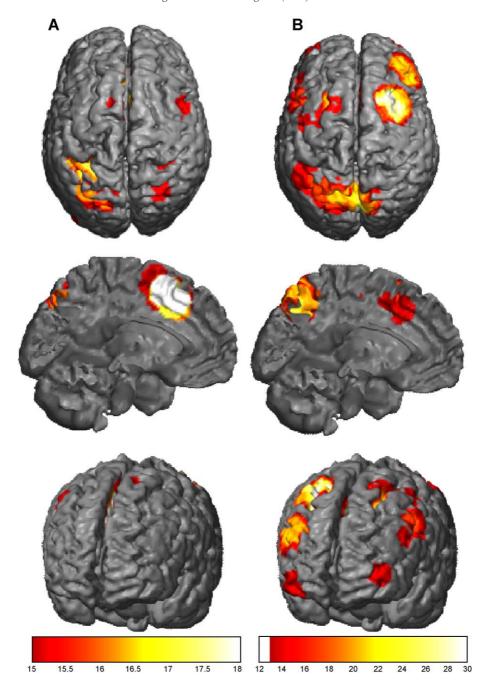


Fig. 5. Surface renderings of regions significant in switching (A) as compared to executive working memory (B). Colors represent the number of peaks falling within 15 mm of each significant voxel. The significance level is based on the probability of *n* peaks falling within a 15-mm radius by chance, given a random distribution of the total number of peaks within the brain.

involved in the switching process, and/or neural activity increases as tasks are updated, causing a mean increase in DLPFC activity during switching. Our results provide weak support for the second view. Predictions about premotor regions are less clear, but the nearby frontal eye fields seem to play an important role in mapping the space of intended actions (Wise et al., 1983).

Dissociations among types of switches

Across regions, different kinds of switching produced similar results in parietal, premotor, and medial prefrontal brain regions.

No regions were significant for one type of switching that were not significant in the general analysis across types. This finding indicates that there were no regions that responded very consistently to one type of switch, but not to others. It could have been the case that such regions existed, and were missed in the overall analysis due to inconsistency across switch types. Statistical power is an issue when comparing across studies (e.g., there were only three studies of rule switching), particularly because task and control processes differ to some degree across studies. Also, relative imprecision in the spatial localization of BOLD signal may cause additional spatial variability in peak estimates. Howev-

Table 5
Overlapping and unique regions for switching and executive function

Region	х	у	Z	Overlap volume (voxels)	Expected overlap	p	BA
L medial PFC	-10	9	50	32	3.5	0.031	32
R medial PFC	10	15	43	111	12.28	0.037	32
R premotor cortex	37	3	48	24	3.06	0.043	6
L anterior IPS	-37	-45	48	104	2.74	0.007	40
L posterior IPS	-20	-66	48	137	13.47	0.032	7
Unique to switching							
L extrastriate cortex	-36	-82	0	53	1.23	1.000	19
R anterior IPS	32	-40	46	122	2.88	1.000	40
R posterior IPS	26	-64	50	53	1.13	1.000	7
Unique to executive	WM						
R anterior PFC	34	54	-8	181	1.5	1.000	10
L anterior PFC	-32	54	6	27	0.27	1.000	10
R dorsolateral PFC	42	38	28	736	5.37	1.000	9
L dorsolateral PFC	-38	10	36	764	5.3	1.000	9

Expectations were based on average overlap in Monte Carlo simulations. All unique regions had no overlapping voxels between the two sets of regions. Voxels are $2\times2\times2$ mm volumes. Unique regions had no overlap with the other process (switching or executive WM). Dorsolateral PFC regions are listed as unique to executive WM, but showed evidence for significant activation in switching at a lower threshold.

er, given those caveats, the analysis of individual switch types uncovered no regions not also found in the analysis collapsing across switch types. In addition, the spatial locations of switch activation due to different types of switches could not be discriminated within most regions.

However, sub-regions that responded to specific types of switching appeared to be discriminable at a finer spatial resolution within right PMC and both anterior and posterior IPS. In these regions, several types of switching appeared to produce activation peaks in different areas of local space. Location switching appeared to be most clearly dissociable from other types, both in the premotor cortex and right parietal cortex. Location switching produced activations anterior and medial to other types of switches in both anterior and posterior right IPS. This result indicates that location switching may be distinct from non-spatial shifting. Because location-switching peaks were located more rostrally within each of anterior (BA 40) and posterior (BA 7) IPS, this effect may appear only if anterior and posterior parietal sites can be resolved as separate sites. One possible explanation is that separate, but overlapping, areas of parietal cortex represent different properties of objects, locations, etc. (Colby and Goldberg, 1999); another is that the frontal and parietal eye fields are specifically recruited in spatial switching but not non-spatial switching. A third possibility is that spatial and non-spatial action selection are segregated in premotor cortex, with visuospatial attention more closely linked to eye movements, and non-spatial attention most closely linked to manual motor planning. For example, makes the point that anterior premotor cortex is associated with "attention," and posterior premotor cortex is more closely associated with "intention." More detailed analysis of how eye-field activation relates to spatial and non-spatial switching is needed to distinguish among these alternatives.

One caveat to these findings is that many studies reported multiple peaks within individual regions (Table 1), and systematic differences in spatial normalization could produce differences in spatial locations larger than those expected by chance. Thus, the locations of the peaks used in the discriminant analysis are not all independent (they are repeated within study), but we report the results of the discriminant analysis because they are useful for developing predictions for future studies comparing different types of switching in the same participants.

Rushworth et al. (2001), in one of only a few previous studies comparing multiple subtypes of switching (see also Wilkinson et al., 2001), reported that response switching activations in parietal cortex (classified as rule switches according to our criteria) were located posterior and medial to visual switching (classified here as attribute switching). However, the results for each task were obtained on different participants (n = 10 and n = 10) 8 for response and visual switching tasks), and as is typical in reports of neuroimaging studies, no estimate of the spatial error in the location of activations was obtained, raising the possibility that the result is related to differences among subjects in (1) spatial normalization, (2) inter-individual variability in functional anatomy, or (3) lack of power, which may lead to reporting of a subset of truly activated voxels for each task. Even if both tasks produce identical true activation, it is likely that different voxels will reach significance in each, leading to apparent differences in activation location. Our analyses suggest that across studies, attribute shifting produces more anterior and superior activation in left anterior IPS (and more lateral activation in right anterior IPS), but that the difference is specific to shifting attributes, as opposed to all types of "visual" switching. Furthermore, rule shifting was not found to activate distinct regions of parietal cortex.

The finding that attribute shifts, but not visual shifts among objects, activate distinct regions of parietal cortex raises the question of what the psychological difference is between shifting which attribute of an object is relevant and shifting which of several objects is attended. Both have been called "task switches" in the literature, although perhaps only attribute shifts would qualify as "extradimensional" shifts (e.g., Owen et al., 1991). One difference between attribute-based and object-based shifts is suggested by studies of object storage in WM, which have shown that objects are maintained "of a piece," so that the capacity limitation in WM storage is on the number of objects rather than on the number of constituent features. Vogel et al. (2001) showed that 3-4 attributes can be maintained in WM at a time, but 3-4 objects, each with 2 attributes, can also be accurately maintained, doubling (at least) working memory capacity when features are grouped into objects. Shifting among objects thus corresponds to a shift in which of several distinct representations in WM is relevant, which may reflect activation of a distinct concept in long-term memory, as is the case in the ACT-R architecture (Anderson, 1998). Mayr and Kliegl (2000) showed that shifting takes longer when switching to a task that places high demands on long-term memory retrieval, suggesting that retrieval may be an important part of reconfiguring task set during shifting. Shifting among attributes reflects a re-prioritization of the relevance of features within multi-attribute WM representations, which may require finer-grained alteration of the nature of the representations.

In animal models of reward reversal, the re-attribution of relevance based on changes in reward feedback can be doubly dissociated from shifts among attended objects. The former has been shown to involve ventromedial PFC, and the latter has been shown to involve lateral orbital/inferior PFC (e.g., Dias et al., 1997; Roberts and Wallis, 2000). Some studies in humans support this distinction (Fellows and Farah, 2003; Owen et al., 1991). Although neither medial or lateral orbitofrontal cortex was reliably activated across shifting studies in the current analysis, insular activations may be homologous with lateral PFC/orbitofrontal activations in other primates. A common conceptual framework of types of shifting across human and animal paradigms is needed to clarify the relationships among these various results.

Development of a conceptual taxonomy of shifting processes must be paralleled in future research by a developing understanding of what regional activations mean. The latter amounts to understanding what information about psychological processes is contained in maps of regional activation. Does finding activation in face-selective parts of the fusiform gyrus in Task X mean that participants are engaging in some face-identification process during the task? Likewise, does parietal activation necessarily imply the involvement of attentional allocation processes? And, if we believe that two types of attention switching (e.g., location vs. task) involve different processes—as it seems they must—then what measures of brain activity will discriminate among those tasks?

This last question in particular must be addressed using brain-based studies of multiple shift types in the same participants. In general, the results of the meta-analysis suggest several new approaches for future studies of executive functions and attention shifting. One is to test multiple tasks in the same participants, and to focus on finding brain activity that discriminates among the tasks. Using the same approach, researchers can also try to find the psychological conditions necessary and sufficient to activate a particular brain region, which will strengthen inferences about psychological activity based on brain activation. Finally, studies of executive function and shifting attention would benefit from task designs that isolate particular components of switching based on theoretical and behavioral work (Allport et al., 1994; Mayr, 2003; Monsell et al., 2000).

Overlap between switching and WM

We observed a striking degree of overlap between attention shifting-related regions and regions shown to be selectively responsive to executive processes in WM. The high degree of overlap is broadly consistent with the idea that switching is one basic control process required in several more complex executive tasks. Thus, maintaining information in WM while processing other information, manipulating information in WM, and selecting which information among several sources should be stored in WM are all relatively complex processes that require shifting among both perceptual items and those stored in WM.

In support of this view, four out of seven regions commonly activated in switching tasks were common to executive processes in WM. Even those that were unique to switching-right parietal, left inferior temporal, and (at a lower threshold) bilateral anterior insula near the border with IFG—have all been observed in basic WM tasks as well, but were simply not significant in the [executive + storage] — [storage only] comparison. Thus, the difference between these areas and those that were significant for executive processes in WM is that these regions are commonly activated in basic working memory storage as well as when

executive processing is required (Berman and Colby, 2002; Wager and Smith, 2003). The existence of switching effects in these regions in the absence of executive demand suggests that switching is a component of WM rehearsal. This interpretation is plausible: for example, rehearsing a sequence of words stored in WM requires one to focus on each in turn, reinforce its representation, and then switch attention to the next item. As noted by Garavan (1998), the original studies of Sternberg (1966) on item recognition in WM revealed evidence for serial search through each item maintained, necessitating switching among items in response to WM probes.

Bilateral anterior prefrontal cortices were the only executive WM regions that were not also activated in switching at the lower switching threshold of P < 0.13. Activations in the anterior PFC have been reported in several studies of long-term memory encoding and retrieval (for a review, see Buckner and Petersen, 1996). While no areas in anterior PFC were significant in the switching meta-analysis, individual studies of switching have reported activations there (Dreher et al., 2002; Pollmann, 2001; Pollmann et al., 2000b). More research is required to test whether switching produces reliable activations in anterior prefrontal cortex, and if so, under what specific conditions? One possibility is that the long-term memory retrieval component of task switching activates anterior PFC (Dreher et al., 2002; Mayr and Kliegl, 2000).

Our results, taken as a whole, suggest that shifting attention may be a component of many executive processes involved in control of WM. Indeed, shifting attention has intuitive appeal as a basic control process that underlies many other types of executive processing. In a natural environment, a behaving animal shifts attention continuously, monitoring internal and external events in rapid succession. However, whether shifting activations reflect the operation of executive control mechanisms (Rubinstein et al., 2001), basic task processes that work harder when shifting (Dreher et al., 2002; Gilbert and Shallice, 2002), or interference among task-sets (Allport et al., 1994) remains to be discovered.

A major challenge is to understand how the decision to attend to one stimulus or task is made. In several current computational models of attention deployment, the decision process is applied to the model by the experimenter, who hard-codes which task is currently relevant (Cohen et al., 1990; Gilbert and Shallice, 2002; Yeung and Monsell, 2003). Presumably, the decision to selectively attend is the result of some congress of information processing mechanisms interacting. One line of current thinking is that the decision process is likely to involve integration of affective and cognitive information, and specifically dopamine systems related to reward (Cohen et al., 2002; O'Reilly et al., 2002; Rougier and O'Reilly, 2002).

Whatever the process is, the decision to attend is the beginning of the task-switching process, and it seems that it must ultimately involve consideration of the internal homeostatic milieu of the organism, and calculation of whether a particular task will confer benefits on the organism that outweigh any perceived costs. Thus, the process may have a great deal to do with reward mechanisms—an idea that has been investigated in animal models (Baxter et al., 2000; Roberts and Wallis, 2000) and modeled elegantly using neural networks (O'Reilly et al., 2002; Rougier and O'Reilly, 2002). Ultimately, the decision to deploy attention in a particular manner must be one that is made by a whole organism, integrating perceptual information with motivational drives, so it may operate

outside the framework of rules established in traditional laboratory tasks of shifting attention.

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