Don't Think of a White Bear: An fMRI Investigation of the Effects of Sequential Instructional Sets on Cortical Activity in a Task-Switching Paradigm

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Abstract: Using functional magnetic resonance imaging (fMRI), we investigated processes involved in switching between two ongoing tasks, thought to be paradigmatic of executive control processes. Subjects were considerably slower and less accurate when switching between two tasks than when repeatedly carrying out one task, so-called "switch costs." Switch costs, however, generally occur only when more than one task is associated with each stimulus type. This has led to the surmise that switch costs may be due largely to ongoing interference from previously learned stimulus-response (S-R) associations, which are no longer relevant for the task at hand. We used a paradigm that specifically assessed this hypothesis and investigated three stages. In Stage 1, a single task was carried out with each stimulus type; in Stage 2, a second novel task was introduced for each stimulus type; and in Stage 3, subjects reverted to carrying out solely the original tasks (as in Stage 1). In Stage 1, only one task was associated with each stimulus type, whereas two tasks were associated with each stimulus type in Stages 2 and 3. We compared images obtained during Stage 3 to those obtained during Stage 1 and show that during Stage 3, there was robust activation in the network of areas associated with the Stage 2 tasks, even though these tasks were no longer relevant. Our data strongly suggest that switch costs may derive largely from continued activation of areas associated with carrying out the now-irrelevant task(s). We posit that a large component of executive control processes involves resolution of competition between potentially relevant tasks. Our data also revealed widespread activation of a frontoparietal network of areas, and we discuss how this network might be involved in mediating this competition. *Hum. Brain Mapp.* 21:279–297, 2004.

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Key words: task switching; fMRI; switch costs; competition hypothesis; task sets; reconfiguration

Contract grant sponsor: National Institutes of Mental Health; Contract grant number: MH-63434, MH-49334, MH-63915; Contract grant sponsor: Burroughs Wellcome Fund.

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Received for publication 24 March 2003; Accepted 19 November 2003

DOI 10.1002/hbm.20003

INTRODUCTION

Switching from one task to another is an ability sufficiently common in our daily lives that its importance is overlooked easily. Editing a document on a computer, a task that is comprised of numerous smaller tasks, affords a good example. One frequently switches from writing text to reading text one has written previously. The stimuli and context afford both the reading and the writing tasks, yet we are able to switch freely and fluidly from one task to the other. Despite the importance of such switching, the mechanisms that underlie this ability remain very poorly understood. We used functional brain imaging (fMRI) to investigate this issue more fully, employing a paradigm that has been used to good effect in the behavioral literature on task switching [Allport et al., 1994].

Paradigms involving task switching can be used to study so-called executive control processes such as those that allow us to carry out an action that is consistent with our current goals rather than any one of several other potential actions. In a typical experiment of this type, subjects are given two tasks (Task A and B). On some trials, they are asked to repeatedly carry out each task (AA or BB); on other trials they are asked to switch from one task to the other (AB or BA). Trials that involve task switching are associated with slower response times (RT) and fewer correct responses than trials in which the same task is repeated. This performance cost in switch relative to repeat trials (the switch cost) has been interpreted by some as a reflection of the time it takes control processes to reconfigure the system from a readiness to carry out the task subjects are switching *from* to a readiness to carry out the task subjects are switching *to* [Meiran, 1996, 2001; Rogers and Monsell, 1995; Rubinstein et al., 2001]. This pattern reported initially by Jersild [1927], however, is found only when the stimuli do not uniquely cue the task to be carried out. As Jersild found, and Spector and Biederman [1976] later replicated, there is no cost associated with switching when the stimuli uniquely cue the task to be carried out, such that it is not possible to carry out Task A with stimuli associated with Task B (and vice versa). Switch costs are found only when the stimuli used for one task have been used previously for the other task.

The importance of having associated the stimuli with both tasks, within the experimental context, was demonstrated by Allport et al. [1994]. In their Experiment 4, they compared performance between two conditions. The first condition was comprised of two “pure” blocks. In one block, subjects were presented with color-word Stroop stimuli [Stroop, 1935] and asked to name the color of the word. In the other block, subjects were presented with number-numerosity Stroop stimuli (i.e., an array of between one to nine identical digits that could range in value from 1–9), and were asked to report the size (i.e., the number of digits present) of the array. In the second condition, subjects were asked to switch regularly between these two tasks. In this case, the stimuli uniquely cued the task to be carried out, and no switch costs were found.

Subjects were next asked to carry out the other task typically associated with these stimuli, i.e., they read the word of the color-word Stroop stimuli and reported the digit value of the number-numerosity Stroop stimuli. As in the first stage of the experiment, subjects worked through three blocks: one with the word-reading task alone, one with the digit-naming task alone, and one in which they regularly switched between the two tasks. Importantly, although the stimuli uniquely cued the task to be carried out within this stage, each stimulus type now had two stimulus-response (S-R) associations: one from Stage 1 and one from the current stage. When performance in the switching block was compared to the mean performance in the two pure blocks, there was now a reliable switch cost.

Finally, in the third stage of the experiment, subjects returned to the tasks that had been used in Stage 1. Unlike Stage 1, where no switch costs had been found, in Stage 3 subjects exhibited reliable switch costs. A different group of subjects worked through the experiment in a similar fashion but using the complimentary tasks in each stage, and the same pattern of results emerged: no switch costs in Stage 1 but robust switch costs in Stage 2 and Stage 3.

This result, in combination with others [Allport and Wylie, 1999, 2001; Mayr and Keele, 2000; Mayr and Kliegl, 2000; Waszak et al., 2003; Wylie and Allport, 2000; Wylie et al., 2003] has led some to conclude that switch costs are better thought of as reflecting interference between previously learned S-R associations rather than as reflecting a simple metric of control processes. One attempt to account for such results is embodied in the “competition hypothesis” [Wylie et al., 2003; see also Allport and Wylie, 2001; Wylie and Allport, 2000]. According to this hypothesis, which has some important similarities to other competition-based models [Duncan et al., 1997; Miller and Cohen, 2001], all S-R associations (tasks) that are potentially relevant (i.e., that have been associated with a given stimulus or stimulus type in a given context) compete on all trials. When only one response has been associated with a stimulus, this competition is won quickly by that single S-R association. When more than one response has been associated with a given stimulus, however, it takes the currently relevant S-R association longer to win the competition. This is true on all trials, but is particularly pronounced on switch trials because the competing task (the task relevant to the trial subjects are switching from) has just been carried out and is therefore a stronger competitor (because the processing pathway associated with that task remains somewhat active or because the S-R association is primed).

This is substantially different from that proposed by other researchers [DeJong, 2001; Meiran, 1996, 2001; Nieuwenhuis and Monsell, 2002; Rogers and Monsell, 1995; Rubinstein et al., 2001]. Although there are many differences between the models proposed by other researchers, most share the feature that the processes needed to reconfigure the system for a new task (i.e., switch tasks) are active only on switch trials. Such theories have trouble accounting for the growing body of functional imaging literature investigating task switching.

In many of these experiments, no statistically significant differences have been found in frontal regions between conditions in which subjects switched and conditions in which they did not [Dreher et al., 2002; Gurd et al., 2002; Kimberg et al., 2000]. Although other studies have reported reliable differences in frontal regions between switch and repeat conditions [DiGirolamo et al., 2001; Dove et al., 2000; Dreher and Berman, 2002; Sohn et al., 2000], it is not yet clear what the critical differences have been between paradigms that result in frontal activation and those that do not. The fact that all of these studies have specifically included switching as a factor and manipulations of this variable have not consistently activated frontal cortex raises the possibility that coupling between frontal cortex and task switching is not as tight as might be assumed. Manipulations of proactive interference, however, have been found to be associated more reliably with activation of lateral, prefrontal cortex (PFC) [D'Esposito et al., 1999; Dreher and Berman, 2002; Petrides et al., 1998]. It was observed that when an item presented had been paired recently with a response that is not currently relevant, activity was found in lateral PFC [D'Esposito et al., 1999; Petrides et al., 1998]. This effect has been generalized recently to include proactive interference from recent tasks [Dreher and Berman, 2002]. Although the frontal cortices do not seem consistently active in task switching paradigms, such paradigms seem to load on the parietal cortex somewhat more reliably [DiGirolamo et al., 2001; Dove et al., 2000; Gurd et al., 2002; Kimberg et al., 2000; Sohn et al., 2000]. Although the parietal cortex has been found to be critically involved in switching attention between spatial locations [Corbetta et al., 1993], its role in switching non-spatial attention is not yet clear.

Although some fMRI studies have found frontal regions to be involved on switch trials, the same regions seem involved on repeat trials, though typically to a lesser extent [DiGirolamo et al., 2001; Dove et al., 2000; Dreher et al., 2002; Gurd et al., 2002; Kimberg et al., 2000]. As yet, there is no evidence in the fMRI literature for any area that is associated specifically with switching processes. This pattern of results is consistent with the competition hypothesis because this hypothesis proposes that processes involved on repeat trials are largely the same as those involved on switch trials, although to a different extent (i.e., the competition is greater on switch trials).¹ This pattern, however, is troublesome for theories that propose there to be reconfiguration processes involved uniquely on switch trials. Such models should predict the presence of regions that are active on switch trials but not on repeat trials.

¹There is a growing body of functional imaging literature showing that irrelevant features of objects seem to be processed by the brain, despite having no current task relevance [e.g., O'Craven et al., 1999; Schoenfeld et al., 2003], thus extending what is known about venerable behavioral effects [e.g., Stroop, 1935]. Such findings suggest that some level of competition is the rule rather than the exception in the brain.

Although the fMRI literature is consistent with the competition hypothesis, this is only the case because of a consistent null effect (a lack of any frontal activation unique to switch trials). The present experiment was therefore devised to test directly the competition hypothesis. Specifically, we used an experimental paradigm that was logically identical to the one used by Allport et al. [1994] in their Experiment 4. We reasoned that if the competition hypothesis were correct, then the pattern of activated areas would differ across the three stages of the experiment, i.e., because in the first stage only one task was associated with each stimulus type, the areas associated with that task should be the ones that are most active. In Stage 2, when a new task is associated with each stimulus type, there should be competition from the task associated with each stimulus type in Stage 1 (if the competition hypothesis is correct). It was reasoned that this competition would result from the brain processing stimuli according to the task that was relevant in Stage 2 and the task that was relevant in Stage 1. The areas that had been active in Stage 1 therefore should also be active in Stage 2. This should also be the case in Stage 3, for similar reasons. Comparing activations in Stage 3 to those in Stage 1 thus should show activity in areas associated with the tasks subjects had carried out in Stage 2 (recall that subjects carry out the identical tasks during Stages 1 and 3).

Models that propose some sort of reconfiguration on switch trials that is completed on the switch trial (and absent on repeat trials) would not predict this pattern of results. Such models might predict some "leftover" activation from tasks carried out in Stage 2 to be found in Stage 3, but this would be confined to the very first trial of the very first block. In a block design like that employed in the present study, this transient activity should be imperceptible. Because these models do not include any mechanism whereby previous learning can persist for more than a single trial (the switch trial), they seem to predict that the pattern of brain activation in a block-design experiment should be indistinguishable in Stage 3 and Stage 1.

We did not use the same tasks as those used by Allport et al. [1994] for two reasons. First, one main innovation of the present design was the use of tasks that would "load" or target specific and dissociable regions of cortex that were readily distinguishable from one another. For example, the cortical regions associated with selective processing of color stimuli [area V4; see Bartels and Zeki, 2000] and with processing motion stimuli [regions of middle temporal cortex (MT/V5); see Sunaert et al., 2000] have been well characterized previously. By focusing on these established cortical networks, we were able to limit our survey of the brain to specific subregions and to take a region-of-interest (ROI) approach, thereby increasing the power of our statistical analyses. Second, we wished to use tasks that were not as "asymmetrical" in difficulty as those used by Allport et al. [1994], because some have suggested recently that effects observed by Allport et al. were due at least in part to this asymmetry in task difficulty [Monsell et al., 2000]. We therefore used: (1) a color discrimination task (color); (2) a face

discrimination task (face); (3) a spatial frequency discrimination task (thickness); and (4) a motion discrimination task (motion). These four tasks were mapped onto two stimulus types. For face and color tasks, faces that were converted to black and white images and then flooded with a homogeneous background color were used. For motion and thickness tasks, drifting square-wave gratings were used. In Stage 1, subjects were asked to carry out one task with each stimulus type (e.g., the color task with the colored face stimuli and the motion task with the drifting gratings). In Stage 2, they were asked to carry out the other task (the face task and the thickness task). In Stage 3, they were asked to carry out the same tasks they had carried out in Stage 1 (the color and motion tasks). In all cases, functional images and performance recorded in Stage 3 were compared to those in Stage 1.

To anticipate our results, when we compared brain activity in Stage 3 to that in Stage 1, we found activity in areas associated with the tasks carried out in Stage 2, which is precisely what the competition hypothesis predicts. This comparison (e.g., color in Stage 3 [Color 3] minus color in Stage 1 [Color 1]) is a conservative one, because the effect of practice would make subjects faster and more accurate in Stage 3 than in Stage 1, the opposite of what the competition model predicts and the opposite of what we found. Furthermore, the effect of practice is known to diminish the extent and intensity of cortical areas involved in carrying out a task [Jenkins et al., 1994], which is the opposite of what the competition model predicts, and the opposite of what we found. The same is true of priming effects: it has been found consistently that priming decreases the extent and intensity of brain areas involved [Buckner et al., 2000; Henson et al., 2000; Vuilleumier et al., 2002].

SUBJECTS AND METHODS

Subjects

Twenty-four young (mean age $\pm$ SD, 25 ± 4 years) neurologically normal, right-handed subjects participated (14 women, 10 men). All had normal color vision and sufficiently good acuity to discriminate the stimuli without their glasses at the distance used. All provided written, informed consent. These subjects were divided into two groups: Group 1 comprised 12 subjects (6 men, 6 women; mean age $\pm$ SD, 28 ± 3.7 years); Group 2 comprised the remaining 12 subjects (8 women, 4 men; mean age $\pm$ SD, 23 ± 3 years). The behavioral data from 3 subjects (2 from Group 1, and 1 from Group 2) were lost due to equipment failure. All subjects had been educated to a high school level or above.

Apparatus

A Siemens 1.5T VISION magnet was used for both the functional and anatomical data collection. Stimuli were delivered using an IFIS-SA stimulus delivery system (MRI Devices Corp., Waukesha, Wisconsin), which is equipped with a head-coil-mounted 640×480 LCD panel. This shielded LCD screen is mounted on the head-coil, directly in

the subjects' line of vision. Head motion was minimized using the standard Siemens head-holder.

The generation and sequencing of stimuli and the collection of subject responses were accomplished using the *ERTS* software package [Beringer, 1995] run on a Dell Latitude laptop that was interfaced with the IFIS system. Responses were collected using an MR-compatible, four-button response pad. Only the rightmost two buttons were used and all subjects responded with the index and middle fingers of their right hand.

Stimuli

Examples of the stimuli can be seen in Figure 1. There were two types of stimuli: faces with colored backgrounds and drifting square-wave gratings. The faces (subtending 5.5 degrees of visual angle in height $\times$ 5.15 degrees in width) were black and white bitmaps (Fig. 1). Two faces were of famous people and two were of nonfamous people. Faces were presented on a background tinted either red or blue. Two shades of each color were used: red, green, blue (RGB) values (range, 0–254) for red were (203, 118, 147) or (198, 124, 154); RGB values for blue were (124, 154, 198) or (109, 189, 206). On each trial involving one of these stimuli, both the face and color were chosen at random.

The spatial frequency of the drifting square-wave gratings (5.15 degrees $\times$ 5.15 degrees of visual angle) was either high or low (Fig. 1). Two values of each were used (the cycles per degree [CPD] for high spatial frequency were 3.3 or 2.18; CPD for low spatial frequency were 0.77 or 0.68). These gratings drifted to the right or left with equal probability at either a fast or a slow rate. Two rates were used for both the fast and slow rates: the fast-moving stimuli moved at either 20 or 40 msec per frame; the slow-moving stimuli moved at either 80 or 100 msec per frame. On each trial involving one of these stimuli, spatial frequency and speed were both chosen at random.

In all cases, the stimuli were presented at fixation and for 500 msec. There was always a 750-msec interval between successive stimuli, and each trial was 1.25 sec long.

Design

The experiment can be conceived of as consisting of three stages (Fig. 1).² The subjects were divided into two groups. The sequence for the first group was as follows.

²The design of this experiment includes, by necessity, a time effect. Although we interpret the differences between Stage 3 and Stage 1 as resulting from a change in competition or context, it is possible that, contrary to the practice/priming literature [Petersen et al., 1998; Raichle et al., 1994; Toni et al., 1998, 2001], these particular tasks result in greater BOLD signal across time. This seems a highly implausible hypothesis but is nevertheless possible, and it was for this reason that we balanced the experiment by running the two groups. One purpose of this design aspect was to replicate our findings with different tasks. Because our findings do replicate very well, the hypothesis that they are due to spurious (and highly unusual) time effects seems most unlikely.

Figure 1.

Experimental design. The design for the first two stages and examples of stimuli used are shown (Stage 3 design was exactly the same as that of Stage 1). Each block of trials (color, motion, switch color-motion, face, thickness, switch face-thickness) comprised 16 trials and lasted for 20 sec. Each block was preceded by a screen showing instructions, which was presented for 10 sec. Like experimental blocks, the blocks of rest were 20 sec long.

Stage 1

In the first stage, subjects worked through a block of 16 trials in which they categorized the face stimuli according to whether the faces were famous or not (i.e., only a single task is associated with this stimulus type, referred to as PURE blocks). Because each trial lasted for 1.25 sec, the block lasted for 20 sec (this was true for all blocks in the experiment). Subjects then worked through 16 trials in which they categorized the gratings according to whether they were high or low spatial frequency (a PURE block). They next worked though 16 trials in which they switched from the face task to the spatial frequency task on each successive trial (referred to as a SWITCH block), i.e., they regularly switched between the two tasks, and the stimuli cued the relevant task on every trial. Finally, they rested for a 20-sec block in which the word *rest* was presented in the center of the screen. This sequence of four blocks was repeated (i.e., Stage 1 was comprised of two sets of four blocks).

Stage 2

In Stage 2, subjects again worked through two sets of four blocks. In this stage, however, they carried out the other task with each stimulus type. Subjects first worked through a PURE block of 16 trials in which they categorized the colored (face) stimuli according to whether the background was red or blue, and then they categorized the moving (grating) stimuli according to whether they were moving quickly or slowly (16 trials; a PURE block). Subjects then switched between these two tasks on every successive trial (a SWITCH block), i.e., they regularly switched between the two tasks, and the stimuli cued the relevant task on every

trial (16 trials). Finally, they rested for 20 sec and then the sequence of four blocks was repeated.

Stage 3

The tasks used in Stage 3 were exactly the same as those used in Stage 1, except that the order in which the stimuli were presented was re-sorted randomly.

The second group of subjects worked through three stages in an analogous way. The only difference between the groups was that the tasks used in each stage were reversed. In Stage 1, the second group was asked to categorize the color of the colored (face) stimuli and to categorize the speed of the moving (grating) stimuli. In Stage 2, they were asked to categorize the face of the (colored) face stimuli and to categorize the spatial frequency of the (moving) grating stimuli. In Stage 3, they carried out the same tasks as in Stage 1 (categorizing the color of the colored [face] stimuli and the speed of the moving [grating] stimuli).

Procedure

All subjects were initially practiced on the tasks used in Stage 1. They worked through one complete set of four blocks of Stage 1 (both PURE, single-task blocks and a SWITCH block, as well as the rest break) before entering the magnet. Subjects were told that they would work through two sets of four blocks (like the blocks they had just completed) and that the instructions would change, so it was necessary to attend carefully to the instructions on every block. Furthermore, subjects were told that after they worked through two sets of four blocks with the new instructions, the instructions would change again and that this

would be the last time the instructions changed. Participants were never told what the instructions in the second and third stages would be.

Before each stage, two instruction screens were presented. Each screen showed examples of the stimuli (Fig. 1), told the subject which task to carry out with those stimuli, and depicted the appropriate response buttons to use. Each screen was presented for 10 sec.

Before each block, an instruction screen was presented that reminded subjects of the relevant task(s) for that block. This screen also indicated the appropriate response buttons to use for each judgment. Each of these screens was presented for 6 sec.

Collection of fMRI data

Information about the hemodynamic response evoked by the tasks was obtained using single-shot, T2*-weighted, echo planar imaging (EPI) sequences on the Siemens 1.5T. Images were acquired with a TR of 2 sec, a TE of 50 msec, and a flip-angle of 90 degrees. Each of the volumes consisted of 22 slices (voxel size = $3.91 \times 3.91 \times 5$ mm; matrix size = 64×64 voxels), which allowed for whole-brain coverage. One experimental block was run in which 335 volumes were acquired. Before data analysis, the first five volumes of each block were discarded to account for the time needed for the field to achieve a steady state. Onset of the volume acquisitions was triggered by a transistor-transistor logic (TTL) pulse generated by the ERTS stimulus delivery software (Beringer Inc.). Time ($T = 0$) was thus defined precisely for both the Siemens volume acquisitions and the beginning of stimulus delivery.

Anatomy

High-resolution whole brain images were acquired using the Siemens 1.5T magnet with a three-dimensional (3D) T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) sequence. Anatomical images (202 slices) were acquired (voxel size = 1 mm^3 , matrix size = 256×256 , TR = 11.6 msec, TE = 4.9 msec, flip angle = 8 degrees) for coregistration with the fMRI data.

Analyses of fMRI data

All images were realigned using Analysis of Functional NeuroImages (AFNI) [Cox, 1996]. Any blocks in which the subject moved more than one voxel in any dimension or more than a degree in pitch, roll, or yaw was discarded. Each raw time-series of signal strength for each subject was first time-shifted so that the slices were aligned temporally (i.e., shifted so that the slices had the same temporal origin), and any linear trends in the data were removed. All volumes in the time-series were then spatially registered, using an image midway through the time-series as the canonical image. All voxels outside the brain were eliminated from further analysis. The hemodynamic response was modeled by a delayed γ function, and this function was coded into the design matrix as a regressor. This has been shown to be a

robust method of estimating hemodynamic response when the precise timing of the onset of the rise of the hemodynamic response is not known [Ollinger et al., 2001]. Contrasts were specified using the General Linear Model.

A priori ROI analysis

ROIs were defined for each group based on the tasks they carried out in Stage 2. Group 1 carried out color and motion tasks in Stage 2. Previous studies have shown color processing to be associated with Brodmann area (BA) 18 and BA 19 [Barrett et al., 2001; Brefczynski and DeYoe, 1999], and motion processing to be associated with the human homologue of MT [as defined by Tootell et al., 1995]. ROIs were therefore established in these areas. The activation pattern associated with Stage 3 was then compared to that associated with Stage 1 for each of the tasks. In the following, we refer to the tasks performed in Stages 1 and 3 by the name of the task (e.g., "face") followed by the number of the stage: "face 3," thus, refers to the face task, performed in Stage 3. Face 3 was compared to Face 1, and because our hypothesis was that the areas associated with the tasks carried out in Stage 2 would continue in a heightened state of activation during Stage 3 (compared to Stage 1), we looked for activity in the ROI associated with color processing. Thickness 3 was compared to Thickness 1, and activity was assessed in the ROI associated with motion processing. Finally, switching in Stage 3 was compared to switching in Stage 1, and activity was assessed in the ROIs associated with both color and motion.

For Group 2, the tasks carried out in Stage 2 were Face and Thickness. Previous studies have shown face processing to be associated with the fusiform face area (FFA), or BA 19 [Kanwisher et al., 1997]. The processing of spatial frequency has been associated with a network of areas including extrastriate regions (BA 17/18), the cuneus (BA 19), occipitotemporal regions (BA 37), parietal areas (BA 7/40), frontal eye fields (BA 6), and prefrontal regions (BA 9/47) [Greenlee et al., 2000]. ROIs were therefore established in these areas, and the same analysis strategy used for Group 1 was followed. Color 3 was compared to Color 1, and activity was assessed in the ROI associated with face processing. Motion 3 was compared to Motion 1, and activity was assessed in the ROI associated with spatial frequency processing. Finally, switching in Stage 3 was compared to switching in Stage 1, and activity was assessed in the ROIs associated with both face processing and spatial frequency processing.

Data-led ROI analyses

In addition to the ROI analysis, which was driven by strong a priori hypotheses, we also wished to assess effects in other brain regions believed to be involved in cognitive control processes, such as regions of the frontal cortex and parietal attentional control areas. For this second level of analysis, we investigated the pattern of activation across the entire brain using the following ROI strategy to protect against Type 2 errors. A "mask" was created by comparing each task carried out in Stage 2 (color and motion for Group

TABLE I. Average response time and standard deviation for each task in each stage for Group 1 and Group 2

		Stage 1			Stage 2			Stage 3		
Group 1	Color	Motion	Switch	Face	Thickness	Switch	Color	Motion	Switch	
RT	452.8	607.5	604.8	510.0	492.6	571.5	492.8	625.6	647.0	
SD	73.1	135.8	125.8	76.2	99.1	90.0	139.6	141.9	105.9	
Group 2	Face	Thickness	Switch	Color	Motion	Switch	Face	Thickness	Switch	
RT	509.3	469.4	545.2	456.0	593.5	630.6	502.6	476.2	537.5	
SD	78.7	66.7	94.3	68.3	128.1	127.0	49.4	45.2	83.5	

Average response time (RT) and standard deviation (SD) for each task, in each stage of the experiment. For Group 1, there were reliable switch costs in Stage 3, but not in Stage 1. For Group 2, there were reliable switch costs in both Stage 3 and Stage 1. Values are expressed in milliseconds.

1, and face and thickness for Group 2) to the rest condition. As in the initial ROI analyses, our primary interest was in the pattern of results when the tasks carried out in Stage 3 were compared to the same tasks from Stage 1. Because we were primarily interested in areas that had been active in Stage 2, we used the mask to constrain our analyses. For instance, Group 1 carried out the face task in Stage 1 and 3 (and the color task in Stage 2). For these subjects, we compared face in Stage 3 to face in Stage 1 (Face 3–Face 1), masked by the areas associated with color processing in Stage 2 (Color–Rest). This strategy was used for PURE and SWITCH blocks, for both groups of subjects.

For both phases of our analyses, the effects were assessed with *t*-tests that compared the activation pattern resulting from the relevant linear contrast to the null hypothesis across subjects (i.e., a random effects model). In the first phase of our analyses, where strong a priori hypotheses were used to define the ROIs, an α criterion of $P < 0.05$ was applied to identify regions showing significant differences in blood oxygenation level-dependent (BOLD) signal between conditions. Because in the second phase of our analyses, our hypotheses were not as strong regarding the network of areas that might be involved (excepting regions of the frontoparietal attention network), the results of this analysis were corrected for multiple comparisons using a very strict corrected α level of $P < 0.001$. To make this correction, we ran a Monte Carlo simulation using *AlphaSim*, one of the fMRI analysis tools in the AFNI suite, which determined that for these data a threshold of $P < 0.01$ and a cluster size of at least six contiguous voxels resulted in a corrected α level of $P < 0.001$.

RESULTS

Behavioral Results

For each group of 12 subjects, we analyzed the RT and error rate (ER) data using a 2×2 repeated measures analysis of variance (ANOVA). For each subject, the median RT and the mean ER were computed for each of the three conditions within the three stages (two conditions in which subjects carried out only one task, and one in which they switched between the two tasks). Only data from Stages 3 and 1 were

analyzed further. For all analyses, the factors were Stage (Stage 3 vs. Stage 1) and Block (PURE task block vs. SWITCH block). The PURE task block comprised the mean of both single-task blocks within a stage.

Group 1: color and motion in Stage 1 and 3

In the RT data, the only effect to reach significance was that of Block ($F_{1,9} = 8.37$, $P = 0.018$). This was because subjects responded with longer latencies in the SWITCH blocks than in the single-task blocks (see Table I). Because we had prior hypotheses regarding the differential effect of Block in the different Stages, we also carried out paired *t*-tests on the data, comparing the single-task blocks and the SWITCH blocks in Stage 1 and Stage 3. Only in Stage 3 was the difference between single-task and SWITCH block reliable ($P < 0.001$).

The error data showed a similar pattern. The only effect to approach significance was that of Block ($F_{1,9} = 4.73$, $P = 0.058$). When the same *t*-tests that had been used on the RT data were applied, however, the difference in neither Block was reliable.

Group 2: face and thickness first in Stage 1 and 3

The results from the analysis of these data were similar to those from Group 1; the only effect to reach significance was that of Block ($F_{1,10} = 15.72$, $P = 0.003$). This was because subjects responded with longer latencies in the SWITCH blocks than in the single-task blocks (see Table I). Unlike Group 1, however, planned comparisons showed a reliable effect of Block in both Stage 3 ($P < 0.01$) and Stage 1 ($P < 0.01$).

When the same analysis was applied to the error data, only the interaction was reliable ($F_{1,10} = 6.47$, $P < 0.03$). This resulted from subjects reliably making more errors in the SWITCH block of Stage 3 ($P < 0.05$) than in any of the other conditions.

fMRI Results

In the sections that follow, we will focus primarily on the brain activations that we hypothesized would be

TABLE II. Talairach coordinates for the most highly reliable voxel of activated regions in each of three contrasts from Group I

Area/structure	Hemisphere	BA	Switch 3-Switch 1					Color 3-Color 1					Motion 3-Motion 1				
			<i>x</i>	<i>y</i>	<i>z</i>	Vox	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>	Vox	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>	Vox	<i>t</i>
Frontal																	
Superior frontal gyrus	Left	6	—	—	—	—	—	−2	23	56	52	3.54	−6	3	64	20	3.23
		6	—	—	—	—	—	−26	−5	68	11	3.95	—	—	—	—	—
Middle frontal gyrus	Left	6	−34	−5	60	78	2.76	−46	3	40	83	3.34	−50	3	40	49	4.23
	Right	9	46	19	32	11	4.06	—	—	—	—	—	—	—	—	—	—
Inferior frontal gyrus	Right	10	—	—	—	—	—	30	51	20	6	3.12	—	—	—	—	—
		45	—	—	—	—	—	46	31	4	19	3.92	—	—	—	—	—
		Left	47	−46	15	−4	23	2.32	−42	19	−4	19	3.52	−22	35	−8	45
Precentral gyrus	Right	47	—	—	—	—	—	—	—	—	—	—	42	35	−4	402	2.51
	Right	9	50	3	24	85	2.24	46	19	36	217	3.38	46	19	36	76	4.27
Parietal																	
Superior parietal lobule	Left	7	−42	−61	48	26	3.12	−34	−65	44	21	4.43	—	—	—	—	—
	Right	7	30	−69	48	16	3.32	30	−61	44	16	3.60	30	−61	44	12	3.99
Inferior parietal lobule	Left	40	−54	−37	24	11	2.48	−42	−53	44	26	4.93	−42	−37	44	7	3.45
	Right	40	—	—	—	—	—	46	−53	48	60	3.71	—	—	—	—	—
Precuneus	Left	19	−30	−65	40	8	3.72	—	—	—	—	—	−30	−65	44	6	3.29
Temporal																	
Superior temporal gyrus	Right	39	—	—	—	—	—	46	−53	8	9	4.65	—	—	—	—	—
Middle temporal gyrus	Right	37	46	−65	4	7	3.28	46	−65	0	6	3.88	46	−65	−4	20	3.16
Occipital																	
Fusiform gyrus	Left	19	—	—	—	—	—	−30	−61	−16	72	3.13	—	—	—	—	—
	Right	19	22	−57	−16	9	3.55	38	−69	−12	102	3.89	26	−61	−12	28	4.03
Middle occipital gyrus	Left	19	−54	−73	8	8	2.32	—	—	—	—	—	−34	−93	4	8	2.38
	Right	19	—	—	—	—	—	42	−73	8	13	3.20	—	—	—	—	—
Lingual gyrus	Left	18	−6	−81	−16	28	2.51	—	—	—	—	—	−10	−97	−8	5	2.28
	Right	18	—	—	—	—	—	22	−97	0	16	3.20	—	—	—	—	—
Cuneus	Left	19	−22	−85	32	8	2.44	—	—	—	—	—	−26	−89	24	2	2.65
	Right	19	—	—	—	—	—	—	—	—	—	—	22	−89	24	8	3.39

The *x*, *y*, and *z* coordinates (in Talairach space) of the most highly reliable voxel (see *t*-value associated with each region) of the activated regions in each of the three contrasts from Group 1. Only those areas are shown that were reliable with an α level of $P < 0.001$, corrected for multiple comparisons (in cases where we had no prior hypotheses), or with an α level of $P < 0.05$ (in cases where we did have prior hypotheses). Volume is reported as the number of voxels (Vox) in the activate region. Areas for which we had prior hypotheses are shown in bold.

BA, Brodmann's area.

active, i.e., on the results of the initial ROI analyses. A full list, however, of all areas activated above threshold including those uncovered during the second phase of our analyses, are shown in Table II and III (Group 1 in Table II, Group 2 in Table III).

Color 3–Color 1

In this comparison, we hypothesized that areas associated with face processing would be substantially more active during Stage 3 than during Stage 1. Subjects carried out exactly the same tasks in Stage 3 and Stage 1, with the exact same stimuli. Nevertheless, as Figure 2 shows, when images acquired during Stage 3 were compared to those acquired during Stage 1, the fusiform face area [BA 19; Kanwisher et al., 1997] was reliably active across the 12

subjects, despite the fact that subjects were not carrying out a face-recognition task at any point during Stage 3 ($t_{1,11} = 3.89$, $P = 0.003$).

Motion 3–Motion 1

In this comparison, we hypothesized that areas associated with processing spatial frequency would be more active in Stage 3 than they had been during Stage 1 (for the same reasons as obtained in the comparison of Color 3 to Color 1). As Figure 3 shows, this was confirmed. Areas of significantly higher activation included extrastriate regions (BA 18; $t_{1,11} = 2.38$, $P = 0.036$), the cuneus (BA 19; $t_{1,11} = 3.39$, $P = 0.006$), occipitotemporal regions (BA 37; $t_{1,11} = 3.15$, $P = 0.01$), parietal areas (BA 7/40; $t_{1,11} = 3.99$, $P = 0.002$), frontal eye fields (BA 6; $t_{1,11} = 4.23$, $P = 0.006$), and prefrontal regions (BA 9/47; $t_{1,11} = 4.27$, $P = 0.01$). These cortical

TABLE III. Talairach coordinates of the most highly reliable voxel of the activated regions in each of the three contrasts from Group 2

Area/structure	Hemisphere	BA	Switch 3-Switch 1					Face 3-Face 1					Thickness 3-Thickness 1				
			<i>x</i>	<i>y</i>	<i>z</i>	Vox	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>	Vox	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>	Vox	<i>t</i>
Frontal																	
Superior frontal gyrus	Left	6	—	—	—	—	—	-2	11	52	7	4.04	—	—	—	—	—
	Right	6	—	—	—	—	—	—	—	—	—	—	2	7	56	21	3.97
	Left	8	-2	15	52	8	3.50	—	—	—	—	—	—	—	—	—	—
Middle frontal gyrus	Right	6	—	—	—	—	—	30	-5	60	11	3.26	38	-1	56	18	3.72
	Left	8	—	—	—	—	—	-50	15	40	30	3.32	—	—	—	—	—
	Right	8	—	—	—	—	—	—	—	—	—	—	50	15	40	102	3.4
	Left	9	-54	11	36	46	4.76	—	—	—	—	—	-50	11	36	40	4.18
	Right	10	—	—	—	—	—	—	—	—	—	—	34	55	8	9	3.46
Precentral gyrus	Left	6	-34	-13	60	8	4.10	-46	-1	56	32	3.21	-42	-5	60	13	3.18
	Right	9	42	7	36	28	4.22	42	7	36	20	4.72	—	—	—	—	—
Parietal																	
Superior parietal lobule	Left	7	-34	-53	48	71	3.82	—	—	—	—	—	-30	-61	56	15	2.83
	Right	7	30	-65	52	69	3.60	26	-61	52	114	3.43	26	-61	52	91	3.77
Inferior parietal lobule	Left	40	-46	-37	44	27	4.12	—	—	—	—	—	—	—	—	—	—
	Right	40	—	—	—	—	—	—	—	—	—	—	50	-45	48	9	3.17
Precuneus	Left	19	—	—	—	—	—	-30	-69	44	145	3.34	-30	-49	48	10	3.41
	Left	7	—	—	—	—	—	-6	-61	60	6	3.17	—	—	—	—	—
Postcentral gyrus	Left	1	-50	-25	52	9	3.50	—	—	—	—	—	—	—	—	—	—
Sub-lobar																	
Insula	Left	13	-34	15	12	6	3.32	—	—	—	—	—	—	—	—	—	—
	Right	13	30	19	16	13	4.00	—	—	—	—	—	30	23	4	13	3.35
Temporal																	
Fusiform gyrus	Right	37	38	-53	-16	2,053	3.78	38	-53	-16	380	3.98	—	—	—	—	—
Middle temporal gyrus	Right	37	—	—	—	—	—	—	—	—	—	—	42	-57	0	6	4.29
Occipital																	
Fusiform gyrus	Left	19	-34	-69	-12	52	3.70	—	—	—	—	—	—	—	—	—	—
	Right	19	34	-53	-16	68	3.80	—	—	—	—	—	18	-65	-12	275	3.16
Lingual gyrus	Right	19	—	—	—	—	—	26	-73	0	6	3.61	—	—	—	—	—
Middle occipital gyrus	Right	18	—	—	—	—	—	26	-93	8	22	3.72	—	—	—	—	—
Inferior occipital gyrus	Left	18	—	—	—	—	—	-34	-85	-4	9	3.75	—	—	—	—	—
Cuneus	Left	17	—	—	—	—	—	-14	-97	0	9	3.71	—	—	—	—	—
Limbic																	
Parahippocampal gyrus	Left	35	-14	-13	-28	6	4.10	—	—	—	—	—	—	—	—	—	—
Sub-lobar																	
Thalamus	Left		-10	-17	16	9	4.23	—	—	—	—	—	—	—	—	—	—
Thalamus	Right		2	-21	16	29	3.50	—	—	—	—	—	—	—	—	—	—
Lentiform nucleus	Left		—	—	—	—	—	-18	7	8	13	3.45	—	—	—	—	—
Caudate	Left		-22	7	20	6	3.42	-18	7	20	11	3.61	—	—	—	—	—
	Right		—	—	—	—	—	14	11	4	12	3.81	—	—	—	—	—

The *x*, *y*, and *z* coordinates (in Talairach space) of the most highly reliable voxel (see *t*-value associated with each region) of the activated regions in each of the three contrasts from Group 2. Only those areas were shown that were reliable with an α level of $P < 0.001$, corrected for multiple comparisons (in cases where we had no prior hypotheses), or with an α level of $P \leq 0.05$ (in cases where we did have prior hypotheses). The volume is reported as the number of voxels (Vox) in the activated region. Areas for which we had prior hypotheses are shown in bold.

BA, Brodmann's area.

areas have all been shown to be involved when subjects were engaged in a spatial frequency discrimination task [Greenlee et al., 2000]. This pattern was found despite the fact that subjects were not carrying out a spatial frequency discrimination task at any point during Stage 3 nor expecting to perform such a task again later.

Switch Color-Motion 3-Switch Color-Motion 1

In this comparison, we hypothesized that we would find activity in areas associated with both face processing and spatial frequency processing. Because subjects carried out both color and motion tasks during the SWITCH blocks, we

Figure 2.

Color task blocks in Stage 3 vs. Stage 1 from Group 1. Color 3–Color 1 rendered in 3-D space (i). Rendering for all figures done using the structural image of a single subject, from a vantagepoint behind, to the right, and above the head. Axial (ii), coronal (iii), and sagittal (iv) views are shown for an area known to be involved in face processing, the fusiform face area on the right ($x, y, z = 38, -69, -12$), and also on the left ($x, y, z = -30, -61, -16$). Activations shown on a structural image that is the average of all subjects in the group.

hypothesized that there would be activation in the areas associated with both of the competing tasks (i.e., face and thickness) when Stage 3 was compared to Stage 1. This hypothesis was confirmed (Table II). Furthermore, the second phase of analysis revealed additional activations in a network of areas thought to play an important role in the control of behavior (see Fig. 4, Table II), including the dorsolateral prefrontal cortex (DLPFC) (BA 9: $t_{1,11} = 2.24$, $P = 0.04$) as well as in other frontal regions (BA 6: $t_{1,11} = 2.76$, $P = 0.02$ and BA 47: $t_{1,11} = 2.32$, $P = 0.04$) and in parietal cortex (BA 40: $t_{1,11} = 2.48$, $P = 0.03$).

Face 3–Face 1

In this comparison, face processing in Stage 3 was compared to face processing in Stage 1. Subjects did not carry out a task related to color processing at any point in either of these stages. Nevertheless, the competition hypothesis predicts that because subjects carried out a color discrimination task in Stage 2 with the same stimuli, we should find activity in areas that have been found to be activated in studies involving color processing, including BA 18 and 19 [Barrett et al., 2001; Brefczynski and DeYoe, 1999]. As Figure 5

Figure 3.

Motion task blocks in Stage 3 vs. Stage 1 from Group 1. The comparison of Motion 3–Motion 1 rendered onto a single subject's structural image (i). Axial (ii), coronal (iii), and sagittal (iv) views are shown for an area known to be involved in processing spatial frequency, the middle temporal gyrus (BA 37; $x, y, z = 46, -65, -4$). Activations are shown on a structural image that is the average of all subjects in the group. Several other areas also implicated in spatial frequency processing, including visual areas and parietal areas, are evident (i).

Figure 4.

Switching between color and motion tasks in Stage 3 vs. Stage 1. Switch Color-Motion 3–Switch Color-Motion 1 rendered onto a single subject's structural image (**A**). **B**: Axial (**i**) and sagittal (**ii**) views of frontal activation as well as axial (**iii**) and sagittal (**iv**) views of parietal activation. Activations are shown on a structural image that is the average of all subjects in the group. These areas (and

others, see Table II) comprise a network of areas thought to be involved in control processes. Talairach coordinates of frontal region: $x, y, z = 46, 19, 32$; parietal region: $x, y, z = 30, -69, 48$. **C**: The same slice when subjects were not switching: comparison of Color 3–Color 1 (**i**) and Motion 3–Motion 1 (**ii**) show robust activity in the same network.

shows, this was confirmed ($t_{1,11} = 3.98, P = 0.002$; see also Table III).³

³This area is just superior and posterior to the fusiform face area (FFA), which was found to be active when the analogous contrast was computed for Group 1. To be certain that this area was not coextensive with

the FFA, we compared Face 1 to Rest (for Group 2). This comparison should reveal the entire network of areas that Group 2 used for the face judgment task, particularly the FFA. Although the comparison of Face 1 to Rest revealed activity in an area more inferior and anterior to that shown when Face 3 was compared to Face 1 (presumably this was the FFA for Group 2), there was no reliable activity in the voxels found to be most active in the Face 3–Face 1 comparison.

Figure 5.

Face task blocks in Stage 3 vs. Stage 1 from Group 2. Face 3–Face 1 rendered onto a single subject's structural image (i). Axial (ii), coronal (iii), and sagittal (iv) views shown for an area known to be involved in color processing, the fusiform gyrus ($x, y, z = -38, -53, -16$). Activations are shown on a structural image that is the average of all subjects in the group.

Thickness 3–Thickness 1

In this comparison, spatial frequency judgments in Stage 3 were compared to the same judgments in Stage 1. The competition hypothesis predicts that areas associated with the processing of motion would be more active in Stage 3 than in Stage 1 because a motion discrimination task was carried out in Stage 2 (with the same stimuli). As Figure 6 shows, this prediction was confirmed: the human homologue of MT [as defined by Tootell et al., 1995] is part of a large region of activity that extends down through ventral regions and into the cerebellum ($t_{1,11} = 4.29, P = 0.001$; see also Table III).

Switch Face-Thickness 3–Switch Face-Thickness 1

In the comparison of SWITCH blocks, the competition hypothesis predicts that areas associated with both tasks carried out in Stage 2 should continue to be active in Stage 3; therefore, if switching in Stage 3 is compared to that in Stage 1, we should find activity in color and motion processing areas. As Table III shows, this prediction was confirmed. In addition, our secondary analysis phase revealed that Group 2, like Group 1, displayed significantly increased activity in a frontoparietal network that included DLPFC (left, BA 8/9; $t_{1,11} = 4.75, P < 0.0001$) and parietal cortex

Figure 6.

Thickness task blocks in Stage 3 vs. Stage 1 from Group 2. Thickness 3–Thickness 1 rendered onto a single subject's structural image (i). Axial (ii), coronal (iii), and sagittal (iv) views are shown for an area known to be involved in motion processing, the human homologue of MT (BA 37; $x, y, z = -42, -57, 0$). Activations are shown on a structural image that is the average of all subjects in the group.

Figure 7.

Switching between face and thickness tasks in Stage 3 vs. Stage 1. Switch Face-Thickness 3-Switch Face-Thickness 1 rendered onto single subject's structural image (**A**). **B**: Axial (**i**) and sagittal (**ii**) views of frontal activation as well as the axial (**iii**) and sagittal (**iv**) views of the parietal activation. Activations are shown on a structural image that is the average of all subjects in the group. These areas (and others, see Table II) comprise a network of areas thought to be involved in control processes. Talairach coordinates of frontal region: $x, y, z = 42, 7, 36$; parietal region: $x, y, z = 30, -65, 52$. **C**: Same slice when subjects were not switching: the comparison of Face 3-Face 1 (**i**) and the comparison of Thickness 3-Thickness 1 (**ii**) show robust activity in the same network.

(left, BA 40; $t_{1,11} = 4.12, P = 0.002$). This is shown in Figure 7 and Table III. Group 2 also showed reliable activity in the insula (BA 13; $t_{1,11} = 3.95, P = 0.002$), and on the medial surface of the superior frontal gyrus (BA 8; $t_{1,11} = 3.49, P = 0.005$). Although this region of activation directly neighbors anterior cingulate cortex (ACC), it did not extend ventrally into ACC. Despite expectations, we did not find any activation in the ACC proper. This was even the case when the threshold was lowered to $P < 0.05$.

DISCUSSION

This study investigated whether stimuli that had been associated with two tasks, one of which was no longer relevant, would continue to invoke processing in brain areas associated with the now-irrelevant task. Our central hypothesis was that switch costs typically found during task-switching paradigms might be due largely to ongoing interference from previously learned S-R associations. To address this hypothesis, we compared images obtained during Stage 3 to those obtained during Stage 1, and showed that during Stage 3, there was robust activation in the network of areas associated with the tasks carried out during the intervening

Stage 2, even though these tasks were no longer relevant (nor would they be relevant again). This observation suggests that either subjects were not using control processes or control processes *do not* affect control by simply "turning on" areas involved in carrying out the currently relevant task and "turning off" areas associated with all other, potentially relevant tasks. The first alternative is clearly untenable, because subjects were able to carry out the appropriate tasks. The second alternative, however, that control is not effected through a simple gating mechanism, is consistent with a growing body of literature on control processes [Allport et al., 1994; Allport and Wylie, 2001; Wylie and Allport, 2000; Wylie et al., 2003].

Although our results are consistent with the findings of Allport et al. [1994], they initially seem to present something of a puzzle. Control was exerted manifestly by subjects (because they correctly carried out the relevant task in each stage), yet the brain areas associated with the irrelevant task were clearly more active in Stage 3 than in Stage 1. One interpretation of this is that the control that was exerted was not directed "down" toward areas involved in the lower level processing of a given task. Had this been the case,

activation of lower level processing areas would be expected to be very similar during Stage 3 and Stage 1, which is clearly not the case. Rather, the control that was exerted seems to have affected processing in a fundamentally different way (discussed below).

The results from the PURE blocks of Stage 3 show that subjects continued to process the stimuli according to both tasks that had been relevant in the experimental context. The results from the SWITCH blocks serve to clarify our understanding of how control is implemented in the brain. In both Stage 3 and Stage 1, subjects were switching between two tasks and in both cases, the stimuli could be used as a cue for the task to carry out. In Stage 3, however, subjects showed larger switch costs than in Stage 1 (in RTs and error rates; this was true for Group 1 but not Group 2, discussed below), suggesting that tasks learned in Stage 2 were interfering with processing, despite the fact that they were irrelevant. Indeed, subjects were told explicitly that the third stage was the last, and therefore knew that the tasks learned in Stage 2 would never be used again. In addition, the pattern of brain activity in Stage 3 was very different from that in Stage 1. In Stage 3, the areas believed to be involved in exerting control were significantly more active than they had been in Stage 1. These included the DLPFC and parietal cortices, and the medial superior frontal gyrus (only Group 2). Although these areas have often been found to be active when subjects are required to switch between tasks, using bivalent stimuli, they are typically also active when subjects are required to repeat tasks. The current finding that these areas were considerably more active in Stage 3 (when subjects had to switch between two tasks using stimuli that have been associated with two tasks) than in Stage 1 (when subjects had to switch between the same tasks, but the stimuli had been associated only with one task) allows us to begin to make sense of previous research.⁴

Implications for Functional Models of Control

Our data do not seem to accord well with one of the most prominent models of cognitive control processes in the literature [Carter et al., 1998, 2000; Cohen et al., 2000; Miller and Cohen, 2001; van Veen et al., 2001; van Veen and Carter, 2002]. Cohen, Carter and colleagues have proffered the hypothesis that the ACC is responsible for detecting conflict or interference and the DLPFC is responsible for exerting top-down control, which serves to ameliorate this conflict. Under the model, these two mechanisms are linked closely such that when the DLPFC is not exerting sufficient top-down control, interference in the system can increase. Any such increase is detected by the ACC and relayed to the DLPFC. The DLPFC, alerted to the conflict, is able to exert top-down

control and thereby reduce the conflict in the system. In a study reported by MacDonald et al. [2000], subjects who exhibited small interference effects had greater activation in DLPFC whereas subjects who showed larger interference effects had greater activation in ACC. In the current study, we found robust activation of the DLPFC but did not find activity in the ACC, despite the fact that our design specifically manipulated the amount of conflict present in the system. Rather, the only frontal midline activity that we found was in the neighboring midline region of the superior frontal gyrus, and this was found for only one of our experimental groups. Our data, however, do provide strong evidence for conflict in the system; subjects continued to process the stimuli according to task rules relevant in Stage 2 and those relevant in Stage 3. The lack of ACC activation during Stage 3 when conflict was patently high is difficult to account for by this model. In addition, the absence of ACC activity in our task is certainly not unique in the task-switching literature. A survey of nine recent functional imaging studies of switching reveals that only four found ACC activity during putative conflict conditions (i.e., switching tasks) [DiGirolamo et al., 2001; Dreher and Berman, 2002; Rushworth et al., 2002; Sylvester et al., 2003], and five did not [Dreher et al., 2002; Dove et al., 2000; Gurd et al., 2002; Kimberg et al., 2000; Sohn et al., 2000].

At least for the present tasks and design, the control exerted does not involve a simple top-down gating of relatively low level processing in the visual system. On the contrary, the areas associated with carrying out the constituent tasks are robustly active. This too represents a potential problem for models like that proposed by Cohen, Carter and colleagues. Surely the simplest way to decrease interference in this experiment would be to turn off or strongly suppress the areas that carry out the irrelevant tasks; however, this does not seem to be the way that the brain has instantiated control in this case.⁵

What then is the role of the DLPFC? We favor an interpretation in which the DLPFC maintains a representation of the currently relevant goal. This is consistent with the working memory literature [Courtney et al., 1997; Fuster, 1985; Goldman-Rakic, 1987; Petrides, 2001; Rushworth and Owen, 1998] and has certain similarities to the models proposed by Miller and Cohen [Miller and Cohen, 2001]. Under this view, the DLPFC is more active in Stage 3 than in Stage 1 because subjects have acquired a second S-R association (and therefore goal) in Stage 2 for each stimulus type. To carry out the correct tasks in Stage 3, the currently relevant goal must be more highly activated than it was in Stage 1, when subjects had learned only one S-R association per stimulus type. A second and potentially complementary possibility is that

⁴When switching in Stage 3 was compared to switching in Stage 1, activity was also found in the parahippocampal gyrus for one of the groups (see Table III). Because this activity could be related to the retrieval of S-R associations, we interrogated the same region in the first group, at a relaxed threshold of $P < 0.05$, uncorrected. At this α level, activity was evident in Group 1 as well ($x-y-z = 14 - 13 - 16$).

⁵Although our data show that there is not a strong top-down suppression of activity in the early visual circuitry for the irrelevant task, they do not rule out a top-down modulatory component. Indeed, we believe that such modulation does occur under certain circumstances [Foxy et al., 1998; Fu et al., 2001; Worden et al., 2000; Wylie et al., 2003].

DLPFC serves an inhibitory function, filtering out distracting information, proceeding in this case from the ongoing processing of the irrelevant stimulus dimension. This notion is consistent with the finding that patients with prefrontal lesions have severe difficulties with tasks that require inhibition or filtering of distracting stimuli [Chao and Knight, 1995, 1998; Richer et al., 1993; Shimamura, 1995].

Implications for Behavioral Models of Control

The present data are also difficult to reconcile with several behavioral models of task switching that imply that switching (i.e., reconfiguration of the system) is carried out only on the switch trial [Meiran, 1996; Rogers and Monsell, 1995; Rubinstein et al., 2001]. This is perhaps demonstrated most easily by considering the PURE blocks. If the system was able to reconfigure itself during the course of the switch trial such that after the switch trial, the system was fully prepared for the new task, the comparison of Stage 3 to Stage 1 would have yielded no effects. This is simply because we used a blocked experimental design, and therefore only one of forty trials (in the PURE blocks) was a switch trial, i.e., the very first trial in the very first block. Even if the areas associated with the tasks carried out in Stage 2 were active on this switch trial, this activity would have been absent on the remaining 39 trials, and would therefore have been almost certainly undetectable. To address this directly, we reanalyzed the data excluding the first block of each condition in each stage, which excluded all switch trials from the PURE blocks. The same pattern of results was found. The activity in areas associated with the tasks carried out in Stage 2 thus persists well beyond the initial switch back to the tasks carried out in Stage 3. This result constrains what reconfiguration can mean.

One interpretation of models that propose reconfiguration on switch trials to consist of “enabling and disabling connections between processing modules” [Monsell, 1996], or the “chain[ing] together and configur[ation of] an appropriate set of processes” [Rogers and Monsell, 1995] is that reconfiguration consists of enabling the relevant processing pathway and disabling the irrelevant one. As discussed above, the fact that processing for the irrelevant task clearly continues to be active in Stage 3 calls this interpretation into considerable doubt. Although the irrelevant processing pathway is not driving behavior, it is certainly active (it is not disabled). We therefore favor a biasing account in which both processing pathways continue to be active and compete for dominance but in which the currently relevant processing pathway is biased to win the competition.

The Competition Model

A different class of model is embodied in the competition hypothesis [Wylie et al., 2003; see also Allport and Wylie, 2001; Wylie and Allport, 2000]. This hypothesis represents an attempt to marry what is known about learning and memory to the literature of control processes, and it is perhaps explained most easily by first considering the brain’s response when confronted with a new task. In a typical

psychological experiment, subjects are given relatively simple, novel tasks. They are told the task rules (i.e., how to respond to the stimuli) and are then allowed some few trials of practice. One of the most highly replicated findings in the psychological literature is that subjects are able to transform the highly abstract representation of the task rules, as explained by the experimenter, into (S-R) mappings that traverse many brain structures.

Although little is known about how this transformation is achieved by the brain, it is known that large areas of cortex are active early in practice, whereas later in practice activated areas become much more circumscribed [Garavan et al., 2000; Jansma et al., 2001; Petersen et al., 1998; Raichle et al., 1994; Toni et al., 1998, 2001]. One interpretation of this finding has been that when the brain is first confronted with a novel task, it brings to bear as many resources and processes as possible in an attempt to convert the representation of the stimulus into a representation of a response. This approach may not be elegant, or even efficient, but it does result in a stimulus-to-response transformation (although sometimes not the correct one). As practice progresses, the irrelevant processes are discarded through Hebbian learning (or some equivalent process) such that after sufficient practice, only those areas necessary to carry out the task are activated, i.e., over successive trials, the processes that were initially active compete with one another. The processes necessary for the task (those that consistently lead to correct responses) compete more effectively because they receive support from reward-related processes when the task is completed correctly [O’Doherty et al., 2001]. The processes that compete more effectively become associated with the stimuli (in the current context), whereas those that compete ineffectively do not. Competition thus leads to the observed reduction in the areas activated by the task across practice.⁶

In task-switching experiments, switch costs are found only when two (or more) tasks are associated with each stimulus type [Jersild, 1927; Spector and Biederman, 1976]. The results reported here show that when two tasks have been associated with each stimulus type, the stimuli are processed by brain areas associated with both tasks. The competition hypothesis proposes that this is due to a mechanism similar to that used in learning.

When two tasks have been associated with a given stimulus type in a particular context, it is usually the case in the real world that both tasks are potentially relevant in that context. It would be sensible, therefore, to process the stimuli according to the rules of both tasks, to the extent that this is possible. Furthermore, some stimulus processing must occur before the brain “knows” what the stimulus is. Although there might be some predisposition to carry out one

⁶It is probable that some areas seen to attenuate with repetition/practice of a novel task are not involved directly in the competition process but serve as modulators of the competition process. An example would be regions of the sustained attention network (e.g., posterior parietal cortices), because during the difficult learning period there is often a need for sustained attentional processes.

task rather than another (based on prior instructions), the stimulus that is actually presented determines whether a given task can be carried out. The stimulus must be processed to some level before it can be determined whether the currently relevant task can be carried out at all. This processing might well cascade through the system to any and all processing systems that have been associated previously with that stimulus type. Given these reasons and the results from the current experiment, it seems likely that stimuli are processed (to some extent) according to all of the potentially relevant task-rules that have been learned previously in a given context.

If this is the case, the question that needs to be addressed in task-switching experiments is not how the brain is able to carry out the currently relevant task on switch trials relative to repeat trials. Instead, the question that should be addressed is how the brain settles on a response consistent with the currently relevant task (on switch trials and on repeat trials). We suggest that this is accomplished through competition. The currently relevant task is specified by the instructions provided by the experimenter and a representation of the currently relevant task is certainly maintained somewhere in the brain (e.g., DLPFC). On any given trial, the stimulus is processed (to some extent) according to all task rules that have been associated with that stimulus type in that context, but only one is consistent with the currently dominant task representation. Although several outputs might be generated by the processing pathways associated with each task, and these will all compete with one another, only the one that is consistent with the currently relevant task-representation will receive support from the task-representation; therefore, only one will win the competition.⁷

In summary, we feel the competition hypothesis provides a physiologically plausible account of some of the mechanisms underlying control of action, an account consistent with results of behavioral, electrophysiologic, and neuroimaging studies.

Additional Considerations

As was noted previously, the design of this experiment mandated the inclusion of a time-effect: Stage 3 always followed Stage 1 in time. In the fMRI literature, it has been shown repeatedly that practice and priming result in decreases rather than increases in BOLD signal across time

[Petersen et al., 1998; Raichle et al., 1994; Toni et al., 1998, 2001]. Nevertheless, it could be suggested that the observed effects in our study were due to the operation of some mechanism that produced increases rather than decreases in BOLD signal over time and practice. Given the pattern of results in these data, this hypothesis would posit that contrary to what has been shown previously in the literature on practice effects, something peculiar to the paradigm employed here resulted in an increase in activity in certain brain areas in Stage 3 relative to Stage 1, an increase specific to areas associated with tasks carried out in Stage 2. Based on prior research, we feel that a simple practice account for our findings is highly unlikely. Furthermore, we know of no model (other than the competition model itself) that would predict increases in activity in areas specifically associated with the now-irrelevant tasks across time and practice.

Another issue that deserves comment involves the comparison of the RTs from the PURE blocks of Stage 3 relative to Stage 1. The competition hypothesis predicts that RTs should be longer in Stage 3 than in Stage 1, a prediction consistent with findings of Allport et al. [1994] in their Experiment 4 and with previous research [Allport and Wylie, 1999; Wylie and Allport, 2000]. Although three of four tasks showed numerically longer RTs in Stage 3 relative to Stage 1 (Table I), these differences were not reliable. Nevertheless, reliable switch costs were found in Stage 3 for both groups. Because the competition hypothesis proposes that switch costs derive largely from competition and because competition from previously learned S-R associations should have been nearly the same in PURE and SWITCH blocks in Stage 3, a question arises regarding the source of the extra RT cost in the switching blocks. There are several possibilities; however, these data are not able to distinguish between them. It could be that the processing pathway associated with each task remained somewhat active after the execution of that task. During PURE blocks, each trial thus benefited from the fact that the same task was carried out on the previous trial. During SWITCH blocks, this putative persisting activation would have been less for each task because of the regular alternation of (unrelated) tasks in these blocks. The SWITCH blocks in Stage 3 might have shown larger RT costs because each task benefited less from persisting activation and was therefore more prone to interference from the competing task learned in Stage 2. An alternative hypothesis is that SWITCH trials involve some extra processing that is not needed on repeat trials, and that this additional processing results in the additional cost found during SWITCH blocks. Further work will be required to decide between these hypotheses.

One further issue that needs to be addressed is that Group 2 showed a behavioral switch cost in RT both in Stage 3 as we had predicted, but also in Stage 1, which was not our prediction. This does not weaken the fMRI findings. On the contrary, because there was no great performance difference between Stages 1 and 3, it is all the more striking that we found strong differences in the BOLD signal. The switch costs found in Stage 1, however, were somewhat puzzling.

⁷In this model, the representation of the currently relevant task holds no privileged place in the system. It biases the settling of the system, but the information in the rest of the system affects it as well. The information in the rest of the system can thus in certain cases override the representation of the currently relevant task. Indeed, it has been shown that when a stimulus has been paired consistently with a given task, subjects will frequently find themselves compelled to perform that task, even when it is not currently relevant [Stroop, 1935; for review see MacLeod, 1991]. This presumably occurs because when a given task has been associated consistently with a given stimulus set, those stimuli strongly cue or potentiate that task [MacLeod and Dunbar, 1988].

We suspected that they might have occurred because subjects had not been given very much practice at the tasks (despite the fact that subjects in Group 1 were given precisely the same amount of practice). We therefore ran four additional subjects on a behavioral variant of the paradigm used here. The only difference was that there were six replications of each condition in each stage, rather than only two. This allowed us to assess whether the switch cost would be reduced by sufficient practice. When the average RT from the PURE blocks in Stage 1 was compared to the average RT from the SWITCH block in Stage 1 (using a *t*-test), the difference was not reliable. When the same comparison was conducted using RTs in Stage 3, however, the difference was highly reliable ($P = 0.001$). The reliable switch cost shown by subjects in Stage 1 of the main experiment was therefore likely the result of the small amount of practice they were afforded. Given that face processing is known to rely to some extent on spatial frequency information, this finding is perhaps not surprising. It is possible that early in practice, each task produced a form of proactive interference in the areas associated with processing spatial frequency information. This sort of interference, however, would be expected to minimize any differences between Stages 1 and 3, rather than amplify them. Because this choice of tasks might have been suboptimal in this respect, the robustness of our findings are all the more striking.

The finding that switch costs disappear across the course of Stage 1 (provided sufficient practice) but are highly robust across Stage 3 shows an important point: the interpretation of behavioral switch costs is not always straightforward [Allport and Wylie, 1999]. For instance, it could well be that switch costs evident in Stage 1 are due to a different mechanism (or set of mechanisms) than the switch costs seen in Stage 3. The difficulty in ascertaining the mechanism(s) underlying switch costs from behavior alone underscores the importance of complementing behavioral experiments with experiments that investigate physiologic changes, like those reported here. In addition, it is perhaps important to point out that the competition hypothesis predicts that competition between tasks (S-R associations) in a paradigm like the one used here will result in switch costs; however, this does not mean that switch costs can always be attributed to competition. For instance, it was our prediction that there would be competition between tasks in Stage 3 and we would therefore find switch costs in Stage 3. This prediction was clearly supported. We also predicted that there would be far less competition in Stage 1 than in Stage 3, but this does not necessarily mean that there should be no switch costs in Stage 1 because switch costs can potentially result from several mechanisms. It is clearly unsatisfactory to have such ambiguity in a dependent measure [see Allport and Wylie, 1999, 2001; Wylie and Allport, 2000].

CONCLUSIONS

This experiment shows that under the conditions employed here, once stimuli have become associated with processing in a given processing pathway, those stimuli con-

tinue to be processed in that processing pathway (to some extent) even when such processing is inappropriate. This finding has important implications for our understanding of control processes, because it suggests strongly that control is not achieved in the brain by simply activating the relevant processing pathway and deactivating the irrelevant processing pathway(s). Rather, control seems to be achieved by biasing the competition between the outputs of these processing pathways. This finding, however, has much larger scope. It points to the importance of a subject's history in the experimental context. If one is interested in establishing a pure measure of performance, or of neural activity, on a given task, it is imperative that the stimuli used for that task have not been associated previously with a different task within the experimental context.

ACKNOWLEDGMENTS

This work was supported by the National Institutes of Mental Health (MH-63434 to J.J.F., MH-49334 to D.C.J., and MH-63915 to G.R.W.) and the Burroughs Wellcome Fund. We thank Ms. D. Foxe and Mr. P. O'Donnell for their unflagging technical support and thank Dr. A. Martinez for her helpful suggestions. We also thank two anonymous reviewers for their helpful comments and suggestions on an earlier version of this article.

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