

# Two Attentional Processes in the Parietal Lobe

Gordon L. Shulman<sup>1</sup>, Giovanni d'Avossa<sup>1,3</sup>, Aaron P. Tansy<sup>2</sup> and Maurizio Corbetta<sup>1,2,4</sup>

<sup>1</sup>Department of Neurology and Neurological Surgery, Washington University, <sup>2</sup>Department of Radiology, Washington University, <sup>3</sup>Alzheimer's Disease Research Center, Washington University and <sup>4</sup>Department of Anatomy and Neurobiology, Washington University, St Louis, MO 63110, USA

**We report fMRI evidence for two attentional processes in parietal cortex. Subjects matched a feature, cued by a word, to a test display of moving colored dots. Either color (red, green) or motion direction (left, right) was cued on mixed scans while only one dimension was cued on blocked scans. An event-related paradigm separated the preparatory activity generated by the cue from the subsequent activity related to the test display. One attentional process specified task information while a second process was motion selective. During the cue period, a pure effect of task specification was observed in left frontal cortex while combined effects of task specification and motion selectivity were observed in left posterior parietal cortex. The frontal task-specification signal may have been the source of the corresponding signal in parietal cortex. Effects of task specification generalized over cue dimension, indicating that the information was coded in a sufficiently abstract form to affect color and motion processing. During the subsequent test period, task-specification and motion-selective signals were again observed in left parietal cortex. Task specification did not significantly affect occipital motion-selective regions, such as MT+, however, indicating that this process did not influence the lower cortical tier of the motion processing stream. These results provide evidence for general and specialized task representations within left parietal cortex during task preparation and execution.**

## Introduction

Selection of task-relevant information is a fundamental aspect of attention. Psychological studies have investigated two related aspects of selective visual processing. One reflects the specification of task-relevant information. Depending on a person's current goals or expectations, different visual dimensions (e.g. color or motion) of objects within a scene may be of particular importance and require specific responses. Studies have examined how people specify task-relevant information (Allport *et al.*, 1994; Rogers and Monsell, 1995) by looking at their ability to switch between task-sets involving different visual dimensions and responses. Second, selection of visual information involves the modulation of pathways corresponding to the specified dimension. An extensive behavioral literature has concerned the selective processing of visual attributes such as location (Eriksen and Hoffman, 1972; Posner *et al.*, 1980) and direction of motion (Ball and Sekuler, 1980, 1981).

Selective processing of motion may involve modulations of parietal cortex. The parietal lobe receives extensive projections from motion-selective regions such as MT and MST, and contains cells that are directionally tuned and sensitive to moving patterns such as optic flow (Maunsell and Van Essen, 1983; Ungerleider and Desimone, 1986; Colby *et al.*, 1993; Siegel and Read, 1997). Neuroimaging studies have reported modulations in parietal cortex during speed judgments but not judgments of shape or hue (Corbetta *et al.*, 1991; Beauchamp *et al.*, 1997).

While selective processing of particular dimensions involves modulations of specialized pathways (e.g. the motion pathway),

task specification involves the specification of inputs (e.g. color or motion), outputs (e.g. left and right hand, or hand and eye movements), and the mapping between them. There is some evidence for this process within the parietal lobe (Le *et al.*, 1998; Kimberg *et al.*, 2000; Sohn *et al.*, 2000; Rushworth *et al.*, 2001). However, it is unknown if regions coding this information generalize over the type of input and output rather than being specialized for particular types. Generalization would suggest that these regions involve relatively abstract representations that can code a wide range of tasks.

Finally, it is important to distinguish preparatory signals for selective processing and task specification from the signals these processes produce during stimulus presentation. One way to accomplish this is to provide advance information that indicates the appropriate set prior to stimulus onset. Recent event-related fMRI studies have successfully used this technique to separate signals involved in task preparation and execution [for a review, see Corbetta and Shulman (Corbetta and Shulman, 2002)].

In the present study, we test the hypothesis that parietal cortex carries signals involved in task specification and selective processing of motion. Signals related to task specification were isolated by comparing scans in which the task-relevant dimension changed over trials or was constant. Signals related to motion selectivity were isolated by comparing trials in which motion or color was cued. The isolation of both task-specification and motion-selective signals within the same study allowed us to characterize their functional and anatomical relationship. Finally, event-related techniques were used to separate preparatory signals for these processes from the signals these processes produce during stimulus presentation.

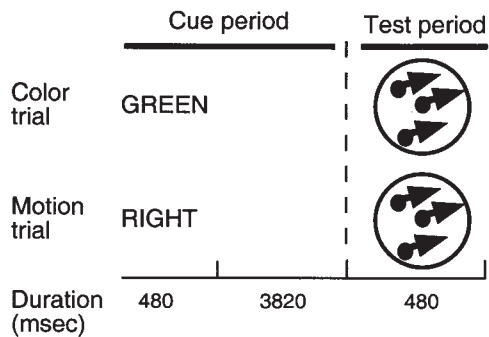
## Materials and Methods

### Subject and Stimuli

Nineteen right-handed subjects gave informed consent in accordance with guidelines set by the Human Studies Committee of Washington University. Fifty colored moving dots were randomly positioned on a black background within a 3.25° circular aperture. Speed of motion was 4.2°/s. A central fixation cross was present throughout the trial and subjects were instructed to maintain fixation.

### Procedure

A visual word cue indicated the feature that subjects were required to process during the subsequent test period (Fig. 1). One of four words ('red', 'green', 'left' or 'right') was presented for 480 ms at the onset of the cue period, which lasted for 4.32 s. On 25% of the trials (cue trials), the trial ended with the completion of the cue period. The end of a trial was signaled by a brief dimming of the fixation point. For the other 75% of the trials (cue + test trials), following the cue period, a moving colored random dot pattern was presented for 480 ms. Subjects pressed a key with their right hand as quickly as possible if the cued feature in the test pattern matched a standard feature that subjects had previously been taught (see below). For example, if the cue word was 'red', subjects pressed the right key if the red hue of the moving dots matched a



**Figure 1.** Examples of trials involving color and motion cues.

'standard' red hue and pressed the left key if the red hue was 'non-standard' (i.e. following a red cue, red dots were always presented but they could be of variable red hue). For a particular hue (e.g. red), only one non-standard hue was presented, and this hue was determined for each subject in a pre-session (see below) to yield ~80% correct responses. The four cue types (red, green, left, right) occurred with equal frequency. On half the trials, the task-relevant dimension of the test stimulus involved a standard feature while on the other half the task-relevant dimension involved a non-standard feature. A similar constraint held for the feature of the irrelevant-task dimension. The interval between each trial was randomly varied from 3.82 to 8.14 s.

Subjects received eight scanning runs in which all four cue words might be presented on any trial (mixed scans), four scanning runs in which only color cues were presented (blocked color scans), and four scanning runs in which only motion cues were presented (blocked motion scans). Because of the variable inter-trial interval, the number of trials varied slightly between scanning runs but the average was 25. Subjects were trained in a behavioral pre-session so that the standard/non-standard discrimination on both the color and motion dimensions was made with ~80% accuracy. The standard leftward and rightward directions was 20° upward from horizontal. Non-standard motions involved directions slightly greater than 20°, the exact direction determined separately for each subject. To avoid non-uniform displacements along oblique directions caused by screen pixellation, the virtual position of the dots was dithered by independent Gaussian noise with a standard deviation of 0.1 pixels. This procedure yielded displays with smooth appearing oblique motions. The standard red and green hues were obtained by activating only the red and green channels of the LCD projector, respectively. Non-standard reds and greens were obtained by activating the blue channel while decreasing the activation of the red and green channel to maintain equivalent CIE luminance. In order to prevent subjects from using residual luminance differences between standard and non-standard stimuli as a cue, the overall luminances of standard and non-standard stimuli were varied randomly on each trial by up to ±10%.

### Imaging Methods

MRI scans were collected on a Siemens 1.5 T Vision system, using an asymmetric spin-echo EPI sequence sensitive to BOLD contrast ( $T_2^*$ ) ( $T_R = 2360$  ms,  $T_2^*$  evolution time = 50 ms, flip angle = 90°). During each scanning run, 128 2.36 s MR frames were acquired, where each frame contains an image of the brain consisting of 16 contiguous 8 mm axial slices (3.75 × 3.75 mm in-plane). Structural images were collected with a sagittal MP-RAGE  $T_1$ -weighted sequence ( $T_R = 9.7$  ms, echo time  $T_E = 4$  ms, flip angle = 12°, inversion 300 ms) and a  $T_2$ -weighted spin-echo sequence ( $T_R = 3800$  ms,  $T_E = 90$  ms, flip angle = 90°).

### Data Analysis

Functional data were realigned within and across scanning runs to correct for head movement, using six-parameter rigid-body realignment. A whole-brain normalization was applied to each scanning run to correct for changes in signal intensity between runs. Differences in the time of acquisition of each slice within a frame were compensated by sinc interpolation. For each subject, an atlas transformation (Talairach and Tournoux, 1988) was computed based on an average of the first frame of

each functional run and the  $T_2$  and MP-RAGE structural images. The BOLD signal in each subject was analyzed with a 'within-trial' linear regression model that estimated separate time-courses during the cue and test periods for each trial type (e.g. 'red' cue, 'standard' test stimulus), without assuming a shape for the hemodynamic response (Shulman *et al.*, 1999; Ollinger *et al.*, 2001a,b). A second 'between-trial' model was also generated that estimated separate time-courses for each trial, rather than for periods within a trial. Both models included terms on each scanning run for an intercept, linear trend, and temporal high-pass filter with a cut-off frequency of 0.009 Hz. For all differences between conditions (e.g. color task versus motion task) that are reported for the cue or test periods from the within-trial model, we verified that a similar difference was observed in the corresponding time-courses generated from the between-trial model. For example, if a difference between the color and motion conditions was reported during the test period (within trial model), then a similar difference was observed during later frames of cue + test trials (between trial model). The analysis of the test period included both correct and incorrect trials.

Time-courses from the within-trial linear model were put into atlas space and smoothed by a filter with a full-width-at-half-maximum of 4 mm. Group analyses were conducted using voxel-level ANOVAs. Subjects were treated as a random effect so that all results generalized across the population. Correlations across time-points were corrected by adjusting the degrees of freedom (Ollinger and McAvoy, 2000). Statistical images were corrected for multiple comparisons over the whole brain ( $P < 0.05$ ), using a magnitude threshold derived from Monte-Carlo simulations that takes into account the number of contiguous activated voxels (Forman *et al.*, 1995). The coordinates of responses in multiple-comparison corrected maps were identified by an automated algorithm that searched for local maxima and minima (Mintun *et al.*, 1989).

Voxels that were activated by the motion and color tasks during the cue or test periods were determined by the Main effect of MR frame (for frames 1–8) in a voxel-level ANOVA. The resulting  $F$ -statistic isolated regions that showed a time-course that significantly differed from a flat line. Voxels differentially activated by the motion and color tasks were determined by the interaction of Cue Dimension (motion, color) and MR frame (1–8). The resulting  $F$ -statistic isolated regions that showed a different time-course following color and motion cues. Similarly, voxels differentially activated during blocked and mixed scans were determined by the interaction of Cue Mode (blocked, mixed) and MR frame (1–8). Results are only presented for positive activations. Deactivations are not considered in this report.

## Results

### Behavior

Subjects saw a cue word specifying either a hue (red, green) or motion direction (left, right) and then saw a test display of moving colored dots. Their task was to indicate whether the cued feature in the test display matched a 'standard' feature that had previously been taught. For example, if the cue word was 'red', subjects pressed one key if the red hue of the moving dots matched the 'standard' red hue, and pressed another key if the red hue was 'non-standard'.

Subjects correctly made the standard/non-standard discrimination during the color and motion tasks on 77.2 and 78.2% of trials, respectively. These percentages were not significantly different and indicate that both discrimination tasks were very difficult, with performance at or near threshold. Under conditions with high error rates, reaction times are difficult to interpret. Both tasks involved reaction times that were quite long relative to most simple two-choice discrimination, emphasizing the difficult nature of the discriminations. Correct reaction time in the motion task (1192 ms) was 79 ms slower than in the color task (1113 ms) [ $F(1,18) = 6.7$ ,  $P < 0.05$ ].

Error rates and reaction times for each task were not significantly different on mixed and blocked scans. The absence of a task-switching cost on mixed scans (Allport *et al.*, 1994)

probably reflected several factors. The preparation interval was over 4 s, which would reduce switch costs by allowing subjects to prepare for the upcoming stimulus (Meiran, 1996). The inter-trial interval was relatively long (~4–8 s), which would dissipate effects from the previous trial (Meiran *et al.*, 2000). Finally, the limiting factor on performance was discriminability rather than the speed of stimulus–response translation.

The data from mixed scans were examined to determine if performance depended on whether the cued dimension and feature on a given trial matched those on the previous trial. There was no reliable effect of this variable on accuracy. However, reaction time was faster when both the relevant dimension and feature was repeated (i.e. red was cued on both trial  $n - 1$  and trial  $n$ ) [ $F(2,24) = 8.55, P < 0.002$ ]. *Post hoc* analyses indicated that repeating the relevant dimension and feature produced faster reaction times (1100 ms) than repeating only the relevant dimension (i.e. green on trial  $n - 1$  and red on trial  $n$ ; 1160 ms) [ $F(1,13) = 19.8, P < 0.001$ ], or changing both the relevant feature and dimension (i.e. green on trial  $n - 1$ , left on trial  $n$ ; 1172 ms) [ $F(1,13) = 9.4, P < 0.01$ ]. The latter two conditions did not differ. However, on blocked scans, trials in which the relevant dimension and feature were repeated (1149 ms) were actually slightly slower (although non-significantly) than trials in which the feature was changed (1136 ms). Therefore, the interpretation and reliability of the reaction time effect on mixed scans is open to question. As noted, reaction time data should be treated cautiously when error rates are high.

Further analyses examined whether the irrelevant stimulus dimension (i.e. if a trial involved a motion cue, then color was irrelevant) affected the subject's judgment of the relevant dimension. On incongruent trials, the feature of the task-relevant dimension called for a different response than the feature of the task-irrelevant dimension. For example, the relevant dimension might involve a standard feature, calling for a right hand response, while the irrelevant dimension might involve a non-standard feature, which would call for a left hand response if it were relevant. On congruent trials, both the relevant and irrelevant dimensions called for the same response. Subjects were more accurate on congruent than incongruent trials [79.4% versus 76.1%;  $F(1,18) = 16.2, P < 0.001$ ], reflecting an effect of the task-irrelevant dimension, but there were no reliable differences in reaction time. Although the congruency effect was slightly larger on mixed scans than blocked scans (4.5% versus 2.1%), this difference was not significant [ $F(1,18) = 1.02$ ].

### Imaging

Changes in the BOLD signal are first discussed for the cue period, in which verbal motion or color cues were presented, and then for the test period, in which color or motion judgments were made on the same visual stimulus. The terms 'task preparation' and 'task execution', respectively, are used in the text to describe processes engaged during the cue and test periods. Each section considers three main questions. First, were any voxels differentially activated in the motion and color conditions (e.g. effects of Cue Dimension)? These analyses isolated voxels that were involved in a dimension-specific attentional process. Second, were any voxels differentially activated during mixed scans, in which the task-relevant dimension changed over trials, compared to blocked scans, in which the task-relevant dimension was constant (e.g. effects of Cue Mode)? These analyses isolated voxels that were involved in specifying task information. Finally, what was the relationship between the two variables, as indicated by joint effects of Cue Mode and Cue Dimension?

### Cue Period: Effects of Cue Dimension

Figure 2 (top left panel) shows that motion cues yielded greater activity than color cues near the cortical surface of left IPs (intraparietal sulcus), extending medially into SPL (superior parietal lobule) (see Table 1 for coordinates).

### Cue Period: Effects of Cue Mode

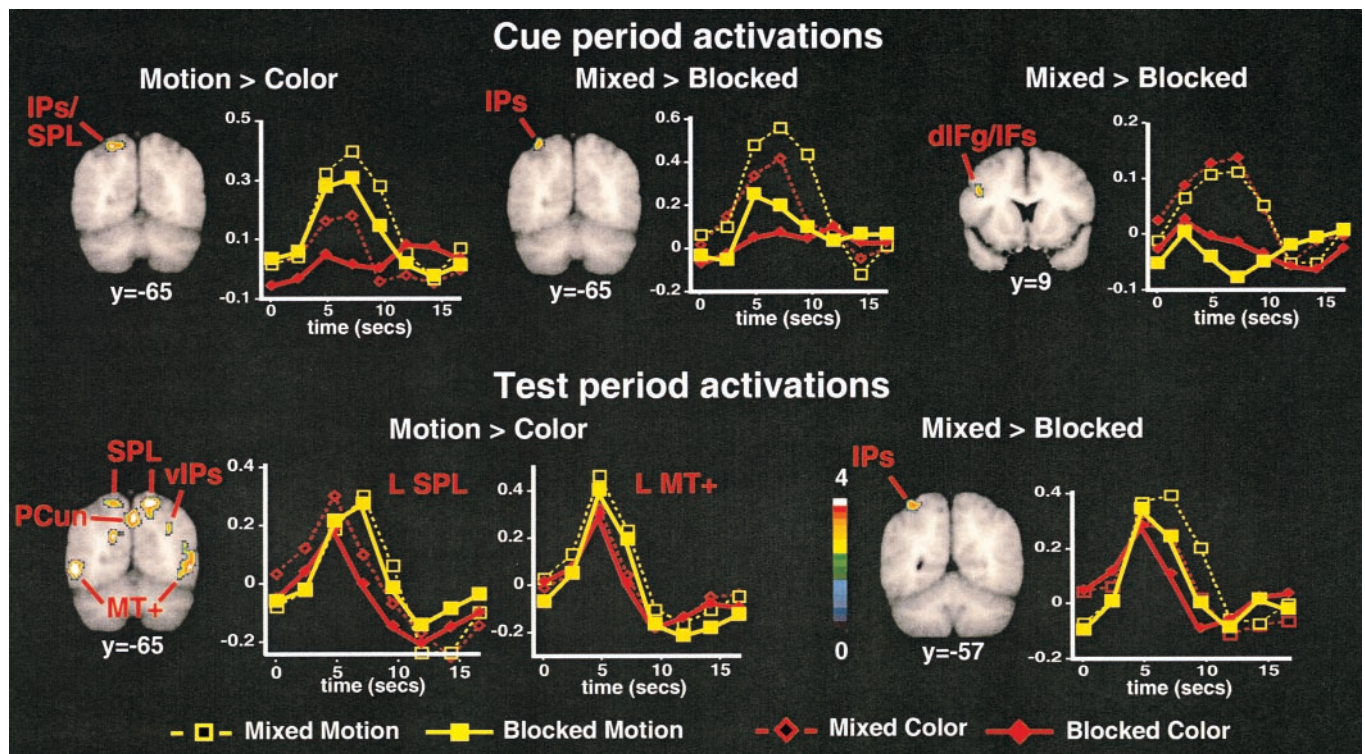
Greater activation on mixed scans than blocked scans was observed near the cortical surface of left IPs (Fig. 2, top middle panel; see Table 2 for coordinates), very similar to the region showing an effect of Cue Dimension. A significantly larger signal on mixed than blocked scans was also observed in the left dorsal inferior frontal gyrus/sulcus (dlFG/IFs) (Fig. 2, top right panel). As indicated by the time-course, this frontal region was only affected by task specification, with no evidence of motion selectivity.

Increased activity on mixed scans might reflect more processing when the cued dimension/feature on the current trial was changed from the previous trial. Therefore, each trial on mixed scans was categorized by whether it involved the same dimension and feature, same dimension but different feature, or different dimension and feature as the preceding trial. A voxel-based ANOVA yielded no significant effects of the preceding trial. This result suggests that during mixed scans, subjects encoded the cue on each trial, independently of the information cued on the previous trial.

### Cue Period: Relationship Between Effects of Cue Mode and Cue Dimension

The left parietal regions sensitive to Cue Mode and Cue Dimension were spatially overlapping. One hundred and thirty voxels ( $1040 \text{ mm}^3$ ) were sensitive to Cue Dimension, 45 voxels ( $360 \text{ mm}^3$ ) were sensitive to Cue Mode, and 7 voxels ( $56 \text{ mm}^3$ ) were sensitive to both variables. Because of the conservative nature of whole-brain corrected, voxel-level statistics, the actual number of voxels sensitive to both task specification and motion selection was probably greater than indicated by these quantities. While individual voxels in the group statistical map were more sensitive to one or the other variable, these voxels did not show a consistent anatomical segregation (i.e. medial–lateral or anterior–posterior) and this was reflected in the similar coordinates for the group foci shown in Tables 1 and 2. Overlap in the spatial distribution of the two variables was also supported by an examination of individual data. Figure 3 shows spatial  $z$ -maps in individual subjects for the different cueing conditions: motion versus color cues (collapsed over the mixed-blocked variable), and mixed versus blocked scans (collapsed over the Cue Dimension variable). Subjects showed more activation in the motion and mixed conditions and these activations occurred in very similar spatial locations. Therefore, while it is possible that the two processes were segregated in a 'mosaic' or that the spatial extent of the motion-selective process was broader than that for task specification, the main conclusion is that the two processes occurred within similar regions of left posterior parietal cortex. In contrast, the two processes were clearly segregated outside of parietal cortex. The left frontal focus (Fig. 2, upper right panel) only showed effects of task specification, with no evidence of motion selectivity. Finally, the higher-order interaction of Cue Dimension by Cue Mode by MR Frame was not significant for any voxel, indicating that the null hypothesis of additivity between the two variables could not be rejected.

In summary, during the cue period, overlapping regions in left posterior parietal cortex were affected by task specification



**Figure 2.** Statistical maps of significant voxels from voxel-wise, random-effects, multiple-comparison corrected ANOVAs and the associated group mean time-course of the BOLD signal. Statistical maps are superimposed on group-averaged anatomy images. Images are displayed such that the left and right hemispheres are on the left and right side, respectively. The color scale refers to the equivalent z-score for the ANOVA, ranging from 0 (blue) to 4 or higher (white). Time-courses were determined within the ROI defined by the intersection of the voxels in the statistical map and a sphere of diameter 10mm, centered on the peak voxel for the displayed focus (see Tables 1 and 2 for coordinates). The y-axis on the graphs refers to percent signal change. *Top row:* Significant activations during the cue period. The left panel shows greater activity in left posterior parietal cortex following motion cues than color cues, while the middle panel shows that a similar parietal region was more activated on mixed than blocked scans. *Bottom row:* Significant activations during the test period. The left panel shows voxels with significantly greater activity for motion trials than color trials at the same coronal slice shown for the cue period. The right panel shows a region in left parietal cortex with greater activity on mixed than blocked scans. IPs = intraparietal sulcus, SPL = superior parietal lobule, IFg/IFs = inferior frontal gyrus/sulcus, PCun = precuneus. v = ventral.

**Table 1**  
Talairach coordinates and z-scores of voxels showing effects of motion selectivity

		Motion > color								
		x	y	z	z-score	x	y	z	z-score	
<b>Cue period</b>										
L IPs/SPL		-23	-67	50	4.3					
L IPs		-31	-57	56	3.7					
<b>Test period</b>					<b>Test period</b>					
L SPL		-15	-67	52	3.5	L MT+	-49	-67	-6	5.1
R SPL		13	-65	52	5.0	R MT+	47	-59	-2	6.5
L Precuneus		-9	-69	26	3.7	R Precentral/SFs	31	-5	44	4.8
R Precuneus		1	-69	42	4.6	R vPrecentral	23	1	48	3.9
R Postcentral/IPs		51	-31	42	3.8					4.2
		37	-41	42	3.8					
		29	-45	42	3.6					
		41	-45	52	3.7					
R vIPs		31	-77	34	4.4					
		31	-67	32	3.6					
R TOs		35	-77	22	4.5					

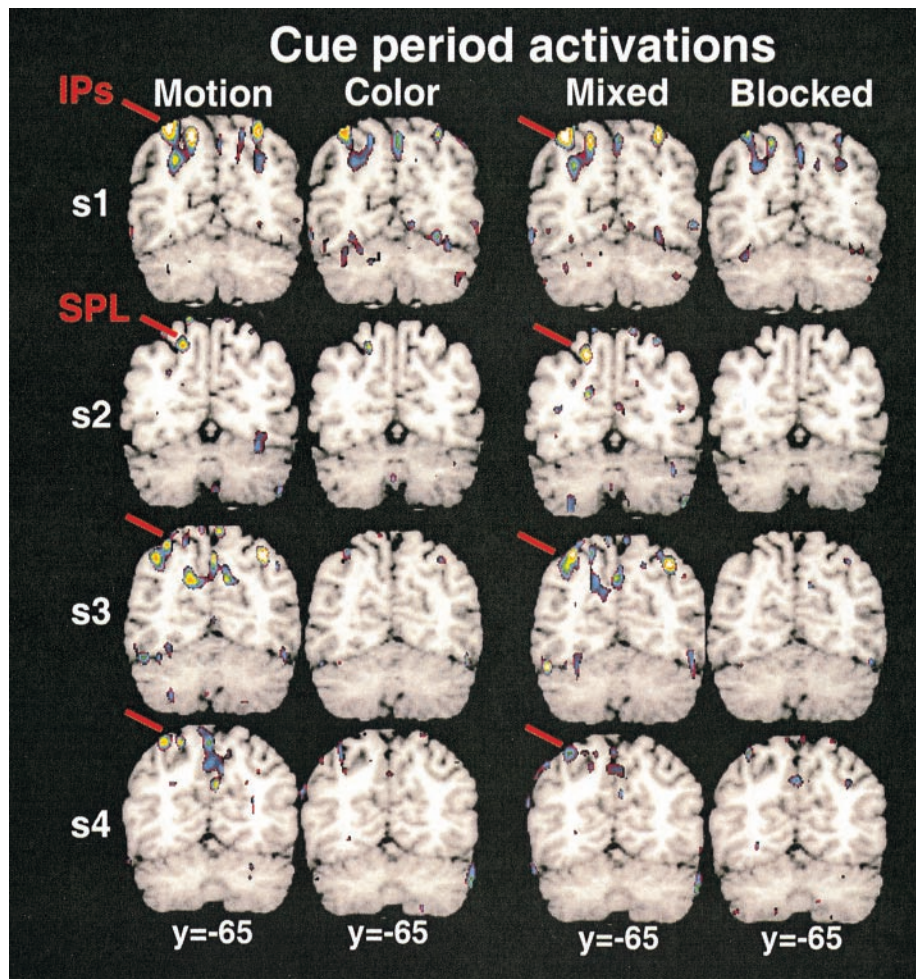
SPL, superior parietal lobule; s, sulcus; IP, intraparietal; v, ventral; TO, transverse occipital; SF, superior frontal.

and motion selection. In addition, a left frontal region showed only an effect of task specification.

**Test Period: Effects of Cue Dimension**

A larger signal on motion trials than color trials was observed in

precentral regions, parietal regions, including bilateral SPL, bilateral precuneus, right vIPs, right IPs and postcentral sulcus, and occipital regions, including bilateral MT+ and the right transverse occipital sulcus. Activations in SPL, precuneus, vIPs and MT+ are shown in Figure 2 (bottom left panel) at the same



**Figure 3.** Individual z-maps for four subjects. Motion and color conditions were collapsed over the mixed and blocked conditions, while mixed and blocked conditions were collapsed over the motion and color conditions.

**Table 2**  
Talairach coordinates and z-scores of voxels showing effects of task specification

Mixed > blocked									
	x	y	z	z-score		x	y	z	z-score
Cue period					Test period				
L IPrs	-31	-65	52	3.5	L IPrs	-35	-57	56	4.1
L dlFg/IFs	-41	9	26	3.6	L Precentral	-43	-7	36	4.0
L MFg	-47	11	38	3.9		-43	-7	46	3.9
R Central s	45	-17	54	4.0	L Cblm	-17	-69	-40	3.9

IP, intraparietal; s, sulcus; IF, inferior frontal; g, gyrus; Cblm, cerebellum.

slice shown for the cue period, while time-courses are shown for the activations in SPL and MT+.

The motion-selective activation in left SPL was less robust than the activation in right SPL, but overlapped the left parietal motion-selective activation from the cue period (Fig. 2, top left panel). Motion selectivity was observed in 130 left parietal voxels (1040 mm<sup>3</sup>) during the cue period, 54 voxels (432 mm<sup>3</sup>) during the test period, and 34 voxels (272 mm<sup>3</sup>) during both periods. Therefore, some left parietal voxels showed motion-selective signals during both task preparation and execution.

#### Test Period: Effects of Cue Mode

A significantly larger signal was observed on mixed scans than blocked scans in left IPrs (Fig. 2, bottom right panel) and left precentral regions (see Table 2 for coordinates). The IPrs region overlapped the IPrs region affected by Cue Mode during the preceding cue period. Task specification affected 45 left parietal voxels (360 mm<sup>3</sup>) during the cue period, 56 voxels (448 mm<sup>3</sup>) during the test period, and eight voxels (64 mm<sup>3</sup>) during both periods. Therefore, some left parietal voxels showed task-specification signals during both preparation and execution.

A voxel-based ANOVA was conducted to determine if the BOLD signal in any voxel depended on whether the information cued on the current trial differed from the information cued on the preceding trial. A significant effect was found in the left central sulcus (-47, -29, 46). Examination of the time-courses in this region indicated that on trials in which the task-relevant feature/dimension was the same as the previous trial (e.g. red was cued on both trials), the BOLD signal rose slightly faster and decayed slightly more quickly than on trials in which either the task-relevant feature or dimension was different.

#### *Test Period: Relationship Between Effects of Cue Mode and Cue Dimension*

There was no spatial overlap during the test period between the left parietal voxels significantly sensitive to Cue Dimension and Cue Mode. However, the time-course shown in Figure 2 (bottom right panel) for the left IPs region sensitive to Cue Mode indicates that some sensitivity to motion selection may have been present in this region, suggesting caution in drawing strong inferences concerning segregation. Moreover, an examination of individual *z*-maps did not show clear evidence for segregation of the two variables, again suggesting caution. Therefore, the data do not allow strong claims that the spatial distributions of the two variables in left parietal cortex during the test period were different. Rather, a reasonable conclusion is that both processes occurred within similar, but perhaps not identical, regions of left posterior parietal cortex. In contrast, significant effects of motion selectivity were observed in many occipital regions that did not show significant effects of task specification (compare Tables 1 and 2), indicating greater segregation of the two variables outside of left parietal cortex. Finally, the higher-order interaction of Cue Dimension by Cue Mode by MR Frame was not significant for any region or voxel, indicating that the null hypothesis of additivity between the two variables could not be rejected.

In summary, during the test period, left posterior parietal cortex was significantly affected by task specification and motion selection. However, the two processes were more segregated in other cortical regions. Left posterior parietal voxels were sensitive to task specification or motion selection during both cue and test periods, indicating that overlapping regions were involved in task preparation and execution.

#### *Hemispheric Asymmetries*

Effects of motion selectivity and task specification were primarily observed in the left hemisphere during the cue period, in which task-relevant information was verbally cued. In contrast, during the test period, many regions only showed motion selectivity in the right hemisphere and those regions that were bilaterally activated showed larger *z*-scores in the right hemisphere (see Table 1; although left MT+ appears more activated than right MT+ in Fig. 2, this simply reflects the fact that the slice shown was closer to the left MT+ focus. The peak *z*-score was greater for right than left MT+).

A quantitative analysis of the asymmetry of motion-selectivity during the cue period in left parietal cortex was conducted. Since right hemisphere regions were poorly activated during the cue period (even in images simply reflecting the main effect of MR frame), right hemisphere ROIs could not be defined from the cue period images. Moreover, using the homologous coordinate from the activated left hemisphere to define the right hemisphere focus would bias the results. Therefore, left and right hemisphere regions were defined from the functional data from the test period. Specifically, ROIs for left and right parietal

cortex were defined by centering a 10 mm diameter sphere on the parietal voxel in the left (coordinate = -15, -67, 52) and right (coordinate = 13, -65, 52) hemisphere that showed the peak *z*-score for the interaction of Cue Dimension and MR Frame. A significant interaction of Hemisphere by Cue Dimension by MR Frame was observed [ $F(7,126) = 2.31, P < 0.05$ ], confirming the presence of significant hemispheric asymmetries in motion selectivity during the cue period.

#### **Discussion**

Two types of attentional modulations were observed in human posterior parietal cortex. One type reflected selective processing of motion information, as indicated by more activity during the motion than color tasks. The other type reflected the specification of the task-relevant dimension on both color and motion trials, as indicated by greater activity when the task-relevant dimension changed over trials than when it remained fixed. Both types of modulations were involved in activating the appropriate neural pathways during mixed scans involving the motion task.

#### *Selective Processing of Motion*

One type of preparatory modulation involved selective processing of motion. Strong motion selectivity during the cue period was observed in a left posterior parietal region very similar to that activated in our previous study of preparatory processes related to motion detection (Shulman *et al.*, 1999). Since the control task in the current study involved an active discrimination (color matching) rather than passive viewing (the control in the prior study), the present results show that these activated regions were motion selective. Interestingly, motion-selective activations were observed on blocked scans as well as on mixed scans, indicating that the motion-selective process was engaged when the task-relevant dimension was fixed and the cue only provided direction information. This result is consistent with prior evidence that the motion-selective process is directionally specific (Shulman *et al.*, 1999).

Preparatory activity for the selective processing of motion was not observed in occipital regions. In our previous study, cue direction was specified by an arrow rather than by a word. Although MT+ activation was significantly greater following an arrow cue than a passive viewing cue, this activation was transient (Shulman *et al.*, 1999), indicating that MT+ was not involved in maintaining the cue information. Similar transient MT+ responses were produced by an arrow cue specifying the location of a target (Corbetta *et al.*, 2000). These results indicate that top-down control signals do not invariably produce sustained pre-activations of early visual areas in anticipation of a target (Chawla *et al.*, 1999; Kastner *et al.*, 1999).

Motion-selective modulations of stimulus-evoked BOLD signals were also observed during the test period (Culham *et al.*, 1998). The magnitude of the BOLD signal in a variety of dorsal areas was larger for motion than color judgments involving the identical stimulus. Some modulations occurred in a left posterior parietal region that was also modulated during the cue period, indicating that it engaged both preparatory and stimulus-evoked attentional processes. However, stimulus-evoked modulations were also observed uniquely in a larger set of regions in frontal (R precentral/SFs), parietal (R SPL and IPs, R bilateral precuneus), and occipital cortex (bilateral MT+, right TOs). The motion-selective preparatory signal in left posterior parietal cortex may have been the instruction signal for these additional modulations during the test period.

### **Specification of Task-relevant Information**

Since the test stimulus was the same during the motion and color tasks, it was necessary to specify which dimension should be selectively processed. On blocked scans, this information could be tonically maintained. On mixed scans, however, the appropriate modulation had to be generated each trial, accounting for the observed difference in the BOLD signal on mixed and blocked scans. The BOLD signal in regions affected by Cue Mode, as well as behavioral accuracy, was not affected by whether the task-relevant dimension on the previous trial was the same or different. This result indicates that a task set and corresponding modulation was generated each trial, regardless of the task set on the previous trial.

The present study manipulated the task-relevant stimulus dimension (e.g. color and motion), thereby changing how the test stimuli were mapped onto responses. We suggest that the process indexed by Cue Mode was involved in specifying which input should control the response. This hypothesis explains why it was not engaged on blocked scans, even though the cued feature changed over trials (e.g. leftward and rightward motion were cued on different trials). Since only one motion direction and one hue appeared in the test stimulus (e.g. red dots moving left), knowledge of the task-relevant dimension was sufficient to specify which input should be linked to a response. If two superimposed dot patterns had been presented (e.g. red dots moving left, green dots moving right), then knowledge of the task-relevant feature (e.g. left), not just the dimension, would have been necessary to link an input to a response. The current hypothesis predicts that under these conditions, task-specification signals would have been generated in scans in which the cue dimension was blocked.

Preparatory neural correlates of task specification were observed in left frontal cortex and left IPs. During the cue period, a region in left dlFg/IFs showed only an effect of task specification, with no modulation related to the task-relevant dimension, indicating that the task-specification signals generalized over dimensions. A very similar region has been activated in encoding tasks involving materials that can be verbally coded (e.g. words, namable objects) (Kelley *et al.*, 1998). We suggest that this left frontal region was engaged in the current study by verbal coding processes related to the specification of task information and sent this information to left posterior parietal cortex. The left frontal region did not show significant task-specification effects during the subsequent test period. Although this is a null result, it is consistent with the hypothesis that it was primarily involved in the initial coding of task specification. In contrast, left parietal cortex did show significant task-specification effects during the test period, possibly reflecting on-line maintenance of task information as the trial proceeded.

Task-specification signals in left posterior parietal cortex were observed for both color and motion cues, indicating that they generalized over dimensions. Other studies (Kimberg *et al.*, 2000; Sohn *et al.*, 2000) have reported that when subjects switched between task sets involving letters and digits, activation related to the switch was confined to a similar left parietal region, indicating that this region was activated by task-specification processes related to shape/identity. Therefore, the current results show that this region codes information in a sufficiently abstract form that many different types of inputs can be represented.

### **Relationship Between Task Specification and Motion Selectivity**

Unlike left frontal cortex, left posterior parietal cortex showed

effects of both task specification and motion selectivity. The two variables were roughly additive in this region. Acceptance of additivity must be treated cautiously since it is based on the null hypothesis and subtle interactions may well have been present. The main point, however, is that roughly similar effects of task specification were observed on color and motion trials, and roughly similar effects of motion selectivity were observed on mixed and blocked scans (see time-courses in Fig. 2). A standard interpretation of additivity is independence; task-specification and motion-selective processes involved independent functions. In this view, the involvement of both processes within the same overall tissue remains unexplained. This interpretation of additivity also involves assumptions about the appropriate underlying scale of BOLD activity (e.g. linear, logarithmic).

An alternative hypothesis is that abstract task representations affected motion-selective pathways. Left frontal regions involved in task specification may have sent signals to left parietal motion-selective regions. On motion trials, these task-specification signals facilitated motion processing, while on color trials, these signals attenuated motion processing. Interestingly, significant task-specification signals were not observed in occipital motion-selective regions, such as MT+, indicating that task specification did not influence the lower cortical tier of the motion processing stream. This result suggests that these signals may have affected higher-order representations involved in categorizing the stimulus motion with respect to the cue. In summary, the combined effects of task specification and motion selectivity within left parietal cortex may reflect influences of abstract task representations on more specialized motion pathways.

### **Left Hemisphere Dominance and Verbal/Symbolic Coding during the Cue Period**

During the cue period, significant effects of motion selectivity and task specification in parietal cortex were confined to the left hemisphere. This left hemisphere bias likely reflected the use of verbal cues, although it may be observed with other symbolic formats. A left hemisphere bias during the cue period was much less marked in a previous study using arrow cues (Shulman *et al.*, 1999), which specified direction in an analog format. It is interesting that the format specifying the appropriate task set had such a strong impact on the parietal system preparing that set.

### **Eye Movements and Task Difficulty Do Not Explain the Results**

During the cue period, it is very unlikely that subjects differentially moved their eyes following the foveal color and motion word cues and this supposition is strongly supported by the results. Differential activations did not occur in routinely observed eye movement regions such as the supplementary eye fields (Petit *et al.*, 1997; Corbetta *et al.*, 1998; Luna *et al.*, 1998). Second, the cue period activations showed a left hemisphere dominance, consistent with encoding of the verbal cue, but inconsistent with eye movements, which produce bilateral activations (Petit *et al.*, 1997; Corbetta *et al.*, 1998; Luna *et al.*, 1998). Finally, there is no plausible eye movement account for the effects of Cue Mode, particularly since these effects were observed on both color and motion trials. Effects of Cue Mode overlapped the parietal regions that showed effects of motion selectivity. With respect to issues of task difficulty, both the motion and color tasks were quite difficult, with performance at or near threshold and reaction times of over a second. Moreover, no significant performance differences were observed between the mixed and blocked scans.

## Conclusion

Left posterior parietal cortex combines preparatory signals involved in the specification of task-relevant information and motion-selective processing. Preparatory signals restricted to task specification were observed in left frontal cortex, which may have been the source of the corresponding preparatory signals observed in parietal cortex. Preparatory task-specification signals in both frontal and parietal cortex generalized over cue dimension, indicating that this information was coded in a sufficiently abstract form to affect both color and motion tasks. During task execution, task-specification and motion-selective signals were also observed in left parietal cortex. However, motion-selective regions in bilateral occipital cortex, such as MT+, did not show significant effects of task specification, indicating that this process did not influence the lower cortical tier of the motion processing stream. These results provide evidence for general and specialized task representations within left parietal cortex during task preparation and execution.

## Notes

This work was supported by NIH grants EY12148 and EY00379. We thank John Ollinger, Mark McAvoy, Tom Conturo, Erbil Akbudak, Abraham Snyder and Fran Miezin for software and hardware development.

Address correspondence to Gordon Shulman, Department of Neurology, Box 8111, 660 S. Euclid, St Louis, MO 63110, USA. Email: gordon@npg.wustl.edu.

## References

- Allport A, Styles EA, Hsieh S (1994) Shifting intentional set: exploring the dynamic control of tasks. In: Attention and performance XV (C Umiltà, M Moscovitch, eds), pp. 421–452. Cambridge, MA: MIT Press.
- Ball K, Sekuler R (1980) Models of stimulus uncertainty in motion perception. *Psychol Rev* 87:435–469.
- Ball K, Sekuler R (1981) Cues reduce direction uncertainty and enhance motion detection. *Percept Psychophys* 30:119–128.
- Beauchamp MS, Cox R, DeYoe EA (1997) Graded effects of spatial and featural attention on human area MT and associated motion processing regions. *J Neurophysiol* 78:516–520.
- Chawla D, Rees G, Friston KJ (1999) The physiological basis of attentional modulations in extrastriate visual areas. *Nat Neurosci* 2:671–676.
- Colby CL, Duhamel J-R, Goldberg ME (1993) Ventral intraparietal area of the macaque: anatomic location and visual response properties. *J Neurophysiol* 69:902–914.
- Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3:201–215.
- Corbetta M, Miezin FM, Dobmeyer S, Shulman GL, Petersen SE (1991) Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *J Neurosci* 11:2383–2402.
- Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman GL (1998) A common network of functional areas for attention and eye movements. *Neuron* 21:761–773.
- Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL (2000) Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci* 3:292–297.
- Culham JC, Brandt SA, Cavanagh P, Kanwisher NG, Dale AM, Tootell RBH (1998) Cortical fMRI activation produced by attentive tracking of moving targets. *J Neurophysiol* 80:2657–2670.
- Eriksen CW, Hoffman JE (1972) Temporal and spatial characteristics of selective encoding from visual displays. *Percept Psychophys* 12:201–204.
- Forman SD, Cohen JD, Fitzgerald M, Eddy WF, Mintun MA, Noll DC (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magn Reson Med* 33:636–647.
- Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG (1999) Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* 22:751–761.
- Kelley WM, Miezin FM, McDermott KB, Buckner RL, Raichle ME, Cohen NJ, Ollinger JM, Akbudak E, Conturo TE, Snyder AZ, Petersen PE (1998) Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron* 20:927–936.
- Kimberg DY, Aguirre GK, D'Esposito M (2000) Modulation of task-related neural activity in task-switching: an fMRI study. *Cognit Brain Res* 10:189–196.
- Le TH, Pardo JV, Hux (1998) 4T-fMRI study of nonspatial shifting of selective attention: cerebellar and parietal contributions. *J Neurophysiol* 79:1535–1548.
- Luna B, Thulborn KR, Strojwas MH, McCurtain BJ, Berman RA, Genovese CR, Sweeney JA (1998) Dorsal cortical regions subserving visually-guided saccades in humans: an fMRI study. *Cereb Cortex* 8:40–47.
- Maunsell JHR, Van Essen DC (1983) The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *J Neurosci* 3:2563–2586.
- Meiran N (1996) Reconfiguration of processing mode prior to task performance. *J Exp Psychol Hum Learn Mem* 22:1423–1442.
- Meiran N, Chorev Z, Sapir A (2000) Component processes in task switching. *Cognit Psychol* 41:211–253.
- Mintun MA, Fox PT, Raichle ME (1989) A highly accurate method of localizing regions of neuronal activation in the human brain with positron emission tomography. *J Cereb Blood Flow Metab* 9:96–103.
- Ollinger J, McAvoy M (2000) A homogeneity correction for *post-hoc* ANOVAs in fMRI. Proceedings of the Sixth Annual Meeting of the Organization for Human Brain Mapping.
- Ollinger JM, Corbetta M, Shulman GL (2001a) Separating processes within a trial in event-related functional MRI II. Analysis. *Neuroimage* 13:218–229.
- Ollinger JM, Shulman GL, Corbetta M (2001b) Separating processes within a trial in event-related functional MRI I. The method. *Neuroimage* 13:210–217.
- Petit L, Clark VP, Ingelholm J, Haxby JV (1997) Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. *J Neurophysiol* 77:3386–3390.
- Posner MI, Snyder CRR, Davidson BJ (1980) Attention and the detection of signals. *J Exp Psychol Gen* 109:160–174.
- Rogers RD, Monsell S (1995) The cost of a predictable switch between simple cognitive tasks. *J Exp Psychol Gen* 124:207–231.
- Rushworth MFS, Paus T, Sipila PK (2001) Attention systems and the organization of the human parietal cortex. *J Neurosci* 21:5262–5271.
- Shulman GL, Ollinger JM, Akbudak E, Conturo TE, Snyder AZ, Petersen SE, Corbetta M (1999) Areas involved in encoding and applying directional expectations to moving objects. *J Neurosci* 19:9480–9496.
- Siegel RM, Read HL (1997) Analysis of optic flow in the monkey parietal area 7a. *Cereb Cortex* 7:327–346.
- Sohn MH, Ursu S, Anderson JR, Stenger VA, Carter CS (2000) Inaugural article: the role of prefrontal cortex and posterior parietal cortex in task switching. *Proc Natl Acad Sci USA* 97:13448–13453.
- Talairach J, Tournoux P (1988) Co-planar stereotaxic atlas of the human brain. New York: Thieme.
- Ungerleider LG, Desimone R (1986) Cortical connections of visual area MT in the macaque. *J Comp Neurol* 248:190–222.