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Dissociable Contributions of Prefrontal and Parietal Cortices to Response Selection

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The ability to select between possible responses to a given situation is central to human cognition. The goal of this study was to distinguish between brain areas representing candidate responses and areas selecting between competing response alternatives. Event-related fMRI data were acquired while 10 healthy adults performed a task used to examine response competition: the Eriksen flanker task. Left parietal cortex was activated by either of two manipulations that increased the need to maintain a representation of possible responses. In contrast, lateral prefrontal and rostral anterior cingulate cortices were specifically engaged by the need to select among competing response alternatives. These findings support the idea that parietal cortex is involved in activating possible responses on the basis of learned stimulus-response associations, and that prefrontal cortex is recruited when there is a need to select between competing responses. © 2002 Elsevier Science (USA)

INTRODUCTION

For any given situation in which we find ourselves, several possible responses may come to mind before we select one and carry it out. In the present study, we examined the neural substrates underlying the representation of responses and the selection of an appropriate response from among competing response alternatives. The goal of this study was to examine the differential contributions to these processes of lateral prefrontal and parietal cortices, two brain regions implicated in the planning and execution of movements.

Studies of brain-damaged patients and nonhuman primates have emphasized the importance of prefrontal cortex (PFC) in goal-directed behavior (Milner, 1963; Fuster, 1980; Goldman-Rakic, 1987; Stuss and Benson, 1986; Owen *et al.*, 1990). Carrying out a goal requires the ability to maintain goal-relevant information in mind—a function referred to as working memory—while ignoring distractions and inhibiting inappropriate responses, functions referred to as behavioral inhibition (Luria, 1966). PFC, however, is strongly interconnected with parietal cortex (Petrides and Pandya, 1984; Schwartz and Goldman-Rakic, 1984). Temporary inactivation of one region, via cooling, changes the response properties of neurons in the other (Quintana *et al.*, 1989; Chafee and Goldman-Rakic, 2000), suggesting close functional connectivity between the two regions. Brain imaging studies have demonstrated coactivation of PFC and parietal cortex across a wide variety of cognitive tasks, including those invoking working memory (e.g., Friedman and Goldman Rakic, 1994; Jonides *et al.*, 1998a; for review see Cabeza and Nyberg, 2000) and behavioral inhibition (Pardo *et al.*, 1990; Sweeney *et al.*, 1996; Garavan *et al.*, 1999; Hazeltine *et al.*, 2000).

The close functional relationship between prefrontal and parietal cortices has hindered efforts to differentiate their functions in the intact brain. Imaging studies of verbal working memory have provided some evidence of functional dissociations between the two regions, such that PFC is thought to be involved in actively rehearsing phonological information stored in parietal cortex (Paulesu *et al.*, 1993; Awh *et al.*, 1996; Jonides *et al.*, 1998a; Bunge *et al.*, 2000). A clear functional dissociation between these regions, however, has not been apparent among imaging studies of behavioral inhibition. The aim of the present study was to dissociate prefrontal and parietal contributions to the control of action by examining brain activation related to the planning of motor responses in the face of distracting information.

We examined brain activation associated with a task in which we could separately manipulate, first, the number of responses which are brought to mind and, second, the need to select among competing responses. Subjects performed a variant of the Eriksen flanker task (Eriksen and Eriksen, 1974) during functional magnetic resonance imaging. Prior to scanning, sub-

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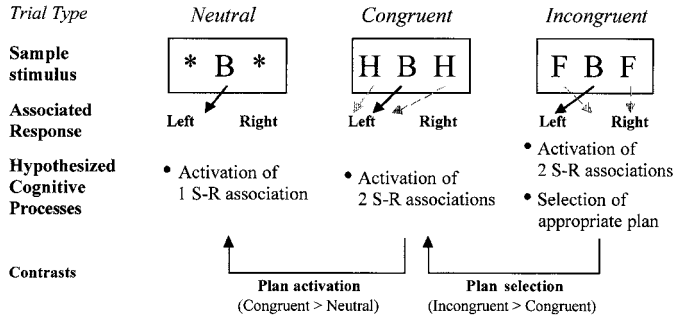

FIG. 1. Trial types performed in the scanner. From top to bottom: sample stimuli presented on the screen; S-R associations learned prior to test; hypothesized cognitive processes invoked by tasks; hypothesized processes isolated by contrasts between conditions.

jects learned to associate four visually presented letters with one of two button press responses to be made with one of two fingers (two letters per button). During the scans, subjects responded on the basis of a central target letter while ignoring two flanking stimuli presented to the left and right of the central letter. The flankers differed from the target stimulus on every trial, so it was necessary on any given trial to focus on the target stimulus in order to respond quickly and accurately. The identity of the flanker stimuli was manipulated across trial types. Flankers were either associated with no response (Neutral trials), the same response as the target (Congruent trials), or a different response from the target (Incongruent trials; Fig. 1). Many studies have shown that subjects involuntarily process the surrounding flankers despite their irrelevance for the task requirement of responding to the central target. This processing is evidenced by a slowing of response times when the flankers signify a response incongruent with the central target (Eriksen and Eriksen, 1974), as well as by event-related potentials recorded in response to the flankers (Gratton *et al.*, 1988).

Brain regions involved in the activation of possible responses on the basis of previously learned stimulus-response (S-R) associations should be more active during the performance of Congruent than Neutral trials. Congruent trials are hypothesized to activate two S-R associations—one for the target and another for the flankers—whereas Neutral trials are hypothesized to activate only the one S-R association for the target. In contrast, brain regions involved in selecting between competing responses should be more active during performance of Incongruent than Congruent trials. Both Incongruent and Congruent trials ought to activate two S-R associations, but only the Incongruent trials should lead to the activation of two different, competing responses (a left and right button press). We examined the dissociability of processes involved in response activation and response selection by determining whether there were regions which were exclusively activated by one of these two contrasts of interest (Incongruent vs Congruent or Congruent vs Neutral).

Lesion studies in animals have identified several brain regions that are important for learning S-R associations, including PFC (Petrides, 1985; Rushworth *et al.*, 1997), premotor cortex, the basal ganglia, and medial temporal lobes (Murray *et al.*, 2000). Learning-related changes in activation during performance of a conditional association task have been observed in a number of these areas (Deiber *et al.*, 1997; Toni *et al.*, 2001; Passingham *et al.*, 2000a). In the current study, subjects were scanned after having learned the S-R associations, and comparisons were made between conditions involving the same set of four stimuli. Therefore, the activations observed in the present study were associated with the performance of well-learned S-R associations, rather than the initial learning of those associations.

MATERIALS AND METHODS

Subjects

Paid volunteers were recruited from Stanford University and around the Bay Area. Ten healthy right-handed volunteers (5 males, 5 females; ages 18–44, $M = 27$) were included in the study. Three additional subjects were excluded; one on the basis of poor behavioral performance (average accuracy of 53%) and two on the basis of poor normalization of their anatomical volumes to the standard template brain.

Experimental Procedure

Prior to being scanned, subjects learned arbitrary S-R associations for each task. Subjects were told to press the left button for the letter "B" or "H" and the right button for the letter "F" or "T". Subjects first practiced responding to single letters presented centrally on the basis of the learned S-R associations. They then performed 10–20 trials of the flanker task prior to the start of the scan session. Psyscope (Cohen *et al.*, 1993) was used to generate stimuli and collect responses.

Subjects performed 250, 3-s trials of the flanker task over the course of two scans while whole-brain functional MRI data were acquired. On a given trial, a horizontal array of three visually presented stimuli, including a central letter and two flanking stimuli (identical stimuli which differed from the central letter), was presented for 1500 ms (Fig. 1). Each stimulus subtended approximately 1.0° of visual angle and was separated from its nearest neighbors by approximately 0.4°. Subjects used the index and middle fingers of their right hand to press one of two buttons in response to the central stimulus on the basis of the learned S-R

associations. Presentation of the stimulus array was followed by a fixation period, in which a crosshair was presented on the screen for 1300 ms, and a 200 ms blank screen prior to the start of the next trial. On fixation trials, subjects viewed a crosshair for 2800 ms and a blank screen for 200 ms.

Each scan included 3 experimental conditions: Congruent, Incongruent, and Neutral trials, as well as additional fixation trials. On Congruent trials, the flanking letters were associated with the same response as the central letter. On Incongruent trials, the flanking letters were associated with the opposite response from the central letter. On Neutral trials, the flankers were symbols (asterisks) which were not associated with any response. The order of the trials was constrained so that the identity of the target was not repeated on successive trials.

The tasks followed a rapid event-related design with a 3-s intertrial interval. The order of presentation of trials was specified according to a stochastic design in SPM99, in which the probability of each trial type varied sinusoidally over a 30-s period. There were 68 Incongruent, 68 Congruent, 71 Neutral, and 33 fixation trials over the course of the two scans.

Data Acquisition

Whole-brain imaging data were acquired on a 3 T MRI Signa LX Horizon Echospeed scanner (G.E. Medical Systems, 8.2.5 systems revision). T2-weighted flow-compensated spin-echo anatomical images (2000 ms TR; 85 ms TE) were acquired in 16 contiguous 7-mm axial slices. Functional images were acquired in the same set of slices using a T2*-sensitive gradient-echo spiral-pulse sequence 48 (1500 ms TR, 30 ms TE, 1 interleave, 60° flip angle, 24 cm field of view, 64 × 64 data acquisition matrix; Glover and Lai, 1998).

Data Analysis

Functional images were motion-corrected and normalized with SPM99 (Wellcome Department of Cognitive Neurology), interpolated to 2×2×2 mm voxels, spatially smoothed with a Gaussian filter (6 mm full width-half-maximum) and temporally filtered (low pass filter: 4 ms Gaussian; high-pass filter: SPM default calculated on the basis of trial frequency). Single subjects' data were analyzed with a fixed effects model, and group data were analyzed using a random effects model (Holmes, 1998). For the group analysis, images were averaged to create one image of mean activity per trial type and subject. These images were globally scaled to a mean signal intensity of 100 at the group level. *T* tests were performed on these average images to create a series of SPM maps depicting differences in brain activity between trial types. Maxima were reported in MNI stereotaxic coordinates for foci exceeding a height threshold of $P < 0.001$ uncorrected for multiple comparisons and an extent threshold of 5 voxels (see Table 1).

Regions of interest (ROIs) were identified functionally from a comprehensive contrast—Incongruent vs Neutral—for which activation encompassed all the activations associated with the two contrasts of greatest interest: Incongruent vs Congruent and Congruent vs Neutral. The group-averaged parameter estimates were calculated for these two contrasts within each of the regions of interest. ROIs were generated from a statistical map thresholded at the standard threshold of $P < 0.001$ (see Table 1). ROI analyses were also performed at a more conservative threshold ($P < 0.0005$ uncorrected for multiple comparisons) to allow for the separation of peaks of activation in parietal cortex (see Fig. 2).

RESULTS

Behavioral Results

Performance in the scanner was highly accurate (Neutral, 98 ± 0.8%; Congruent, 99 ± 0.5%; Incongruent, 99 ± 0.7%; mean ± SEM), and there were no differences in accuracy across conditions ($F(2,9) = 0.92$; $P = 0.42$). Response latencies differed across conditions (Neutral, 693 ± 39 ms; Congruent, 696 ± 40 ms; Incongruent, 718 ± 40 ms; ($F(2,9) = 3.87$; $P = 0.04$; mean response times excluding responses more than 2 SD away from the mean). Planned contrasts revealed that subjects responded more slowly on Incongruent than Congruent trials ($F(1,9) = 4.89$; $P = 0.04$, two-tailed) but that response times for Congruent and Neutral trials did not differ from one another ($F(1,9) = 0.12$; $P = 0.73$, two-tailed).

Brain Imaging Results

Regions that were more activated by Incongruent than Neutral trials included all the regions identified by either of the two contrasts of interest, namely Incongruent vs Congruent and/or Congruent vs Neutral. Prefrontal regions activated by Incongruent vs Neutral included right middle frontal gyrus (B.A. 8, 46), left inferior frontal sulcus and middle frontal gyrus (B.A. 9), bilateral superior frontal gyri (B.A. 8), and right inferior frontal gyrus (B.A. 45; see Table 1). Parietal regions activated by this contrast included left-lateralized intraparietal sulcus, superior and inferior parietal lobules, right-lateralized inferior parietal lobule (B. A. 40), and bilateral postcentral sulcus. Additional activations were observed in the anterior and posterior cingulate cortices (B.A. 32, 31) and the thalamus.

Prefrontal and parietal activations identified by the Incongruent vs Neutral contrast were further characterized via ROI analyses to determine which of these areas might be involved in the activation of responses

TABLE 1

Regions Activated by Incongruent vs Neutral

Brain region	B.A.	Talairach *x*	Talairach *y*	Talairach *z*	Volume	*Z* score	*P* values CvsN	*P* values IvsC
Prefrontal								
L IF sulc., MFG	9	−34	8	38	1312	3.83	0.92	0.03
R MFG	46	42	32	26	192	3.81	0.44	0.04
R IFG	45	52	20	22	80	3.39	0.26	0.08
R MFG	8	34	24	38	1032	5.00	0.78	0.01
	8	34	44	40	48	3.42	0.11	0.10
L SFG	8	−14	18	52	144	4.03	0.25	0.13
R SFG	8	14	22	48	176	3.95	0.11	0.04
Parietal								
L IP sulcus		−34	−60	34	224	3.69	0.03	0.03
L IP sulcus*		−34	−40	54	local	4.32	0.02	0.001
R inf. parietal	40	40	−44	56	184	3.42	0.89	0.14
L postC sulcus		−52	−18	46	1000	4.19	0.003	0.64
R postC sulcus		56	−22	44	96	3.74	0.01	0.35
R postC	3/1/2	50	−26	54	264	4.09	0.32	0.56
Motor, premotor, and supplementary motor cortices								
L central sulc.		−16	−36	70	104	3.25	0.24	0.54
		−22	−28	66	256	3.94	0.004	0.70
L premotor	6	−18	−4	64	5528	4.47	0.0006	0.03
	6	−12	−18	58	456	3.86	0.07	0.09
R premotor	6	26	8	66	1248	4.67	0.24	0.02
L SMA	6	−4	−22	58	160	3.43	0.17	0.17
Cingulate cortex								
R anterior	32	10	32	22	96	3.48	0.68	0.004
	32	10	18	38	72	3.34	0.07	0.06
L anterior	32	−8	12	38	64	3.59	0.06	0.13
L posterior	31	−10	−34	36	64	3.32	0.88	0.06
R posterior	31	16	−34	34	56	3.71	0.93	0.07
L thalamus		−16	−24	12	216	3.96	0.06	0.04
R thalamus		20	−18	10	272	4.08	0.02	0.26
R post. insula	13	46	−40	18	72	3.36	0.16	0.63

Note. $P < 0.001$ uncorrected for multiple comparisons. B.A. = Brodmann's areas. *x*, *y*, and *z* are MNI stereotaxic coordinates. IvsC and CvsN show *P* values for two-tailed *t* tests comparing parameter estimates of activation for Incongruent vs Congruent and Congruent vs Neutral conditions, respectively (shaded values: $P < 0.05$). Volume is measured in mm^3. PreC, precentral gyrus; postC, postcentral gyrus; SMA, supplementary motor cortex; IP, intraparietal.

* Local maximum of activation centered in L premotor cortex; includes superior and inferior parietal lobules. ROI analysis for this region based on activation thresholded at $P < 0.0005$.

(Congruent vs Neutral contrast) and/or the need to select among competing responses (Incongruent vs Congruent contrast). This analysis demonstrated a clear dissociation between dorsolateral prefrontal and parietal regions exhibiting significant activation for at least one of the two contrasts of interest (Table 1). Inferior and superior portions of left parietal cortex were activated by both Congruent vs Neutral and Incongruent vs Congruent trials. In contrast, lateral prefrontal regions were exclusively activated by Incongruent vs Congruent trials. An examination of the largest activations revealed a rostral-caudal progression whereby more anterior regions of the brain showed greater selectivity for activation by Incongruent vs Congruent (Fig. 2).

Within the anterior cingulate cortex, two patterns of results were observed. A rostral portion ($y = 32$), located in RCZa (Picard and Strick, 2001), was activated by Incongruent vs Congruent but not by Congruent vs Neutral trials. In contrast, more caudal foci ($y = 18$, $y = 12$) were not significantly activated by either manipulation, but exhibited a marginal tendency toward activation by Congruent vs Neutral as well as Incongruent vs Congruent trials.

DISCUSSION

As expected from previous studies involving flanker tasks (Eriksen and Eriksen, 1974; Cohen and Shoup, 1997), subjects were slower to respond on Incongruent than Congruent trials. Because the only difference between these two trial types was that the flankers and target were associated with the same response on Congruent trials and with different responses on Incongru-

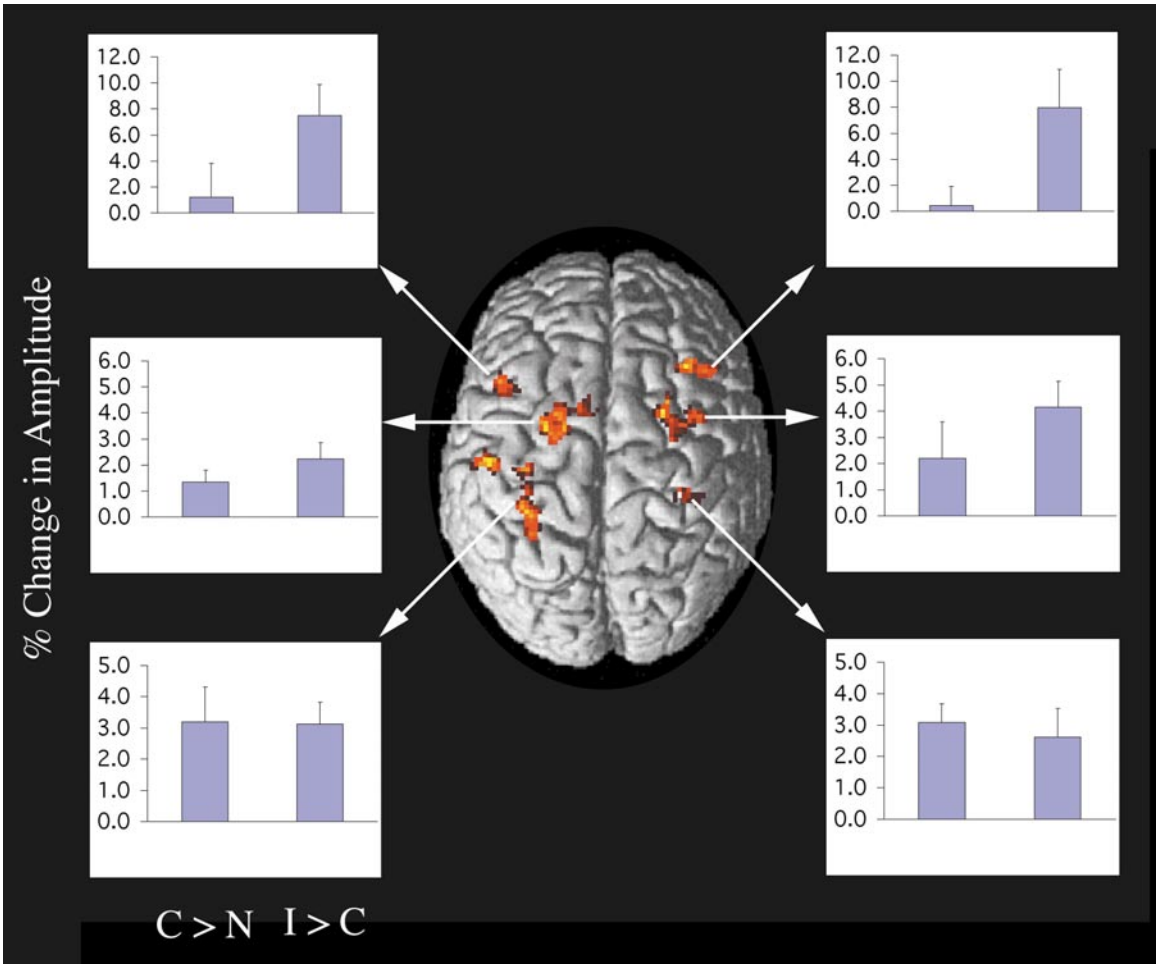

FIG. 2. Rendering of group-averaged activations for Incongruent vs Neutral trials (view from top of brain; front of brain toward the top of the image); $P < 0.0005$ uncorrected for multiple comparisons. Region-of-interest analyses displaying % change in activation (parameter estimate increases) for Congruent vs Neutral trials and Incongruent vs Congruent trials. The regions of interest, from top to bottom, were as follows. *Left hemisphere*: inferior frontal sulcus/middle frontal gyrus, premotor cortex, parietal cortex (lateral and medial portions of the intraparietal sulcus; inferior and superior parietal lobules). *Right hemisphere*: middle frontal gyrus, premotor cortex, postcentral gyrus. Additionally displayed on the rendered brain is an activation in left postcentral gyrus.

ent trials, this increased latency is thought to be related to the need to select between competing responses. In contrast, there were no significant differences in accuracy or performance between Congruent and Neutral trials. Although some studies have observed a speeding of responses for Congruent relative to Neutral trials (e.g., Cohen and Shoup, 1997), the presence of this facilitation depends on stimulus properties and task demands (Grice *et al.*, 1984).

The present study provides evidence for a dissociation between lateral prefrontal and parietal contributions to planning a response in the face of distracting information. Left parietal cortex was activated by either of two manipulations—Incongruent vs Congruent and Congruent vs Neutral trials—that increased the need to maintain a representation of possible responses. In contrast, bilateral prefrontal regions were exclusively activated by the manipulation that required selection among competing responses—Incongruent vs Congruent trials. These data support two hypotheses: first, that parietal cortex serves to represent candidate responses and, second, that prefrontal cortex plays a role in selecting an appropriate response from among competing responses.

Parietal Cortex

The present results, in the context of convergent evidence, favor the view that parietal cortex mediates the representation of possible responses invoked by the environment (i.e., the visual display). As predicted, activation in parietal cortex was greater for Congruent than Neutral trials, despite the lack of a difference in performance between these two trial types. Because Congruent trials were assumed to be associated with activation of more S-R associations than Neutral trials,

this finding supports the idea that parietal cortex is involved in activating motor responses on the basis of S-R associations (Andersen, 1987; Snyder *et al.*, 2000). Similar regions in parietal cortex have been activated across a wide variety of neuroimaging studies involving the planning, imagining, or perception of actions (Deiber *et al.*, 1996; Hazeltine *et al.*, 1997; Jenkins *et al.*, 1994; Decety *et al.*, 1994; Grafton *et al.*, 1996). A region in left inferior parietal cortex (supramarginal gyrus) near the region activated in the present study is activated when subjects covertly attend to either right-handed or left-handed hand movements (Rushworth *et al.*, 2001b), and repetitive transcranial magnetic stimulation of this region disrupts this motor attention (Rushworth *et al.*, 2001a). The medial bank of the intraparietal sulcus and adjacent superior parietal lobule—regions activated in the present study—have been shown to be engaged when subjects are visually cued to switch between selecting responses according to either of two rules (Rushworth *et al.*, 2001c). Thus, the left parietal activation observed in the present study is likely to be related at least in part to the cue-driven activation of, and attention to, responses associated with the hand.

Convergent evidence for the idea that parietal cortex houses response representations comes from neuropsychological experiments (Goodale and Milner, 1992). Damage to parietal or prefrontal cortices or to the connections between these two regions (particularly left-lateralized) can result in ideomotor apraxia, a syndrome characterized by the inability to translate goals into movements (Geschwind, 1975; Heilman *et al.*, 1982). Apraxic patients with frontal and parietal damage both have difficulty executing appropriate movements. However, parietal patients are additionally impaired at simulating movements mentally (Sirigu *et al.*, 1996) and judging the movements of others (Kolb and Milner, 1981) and their own movements (Sirigu *et al.*, 1999), suggesting that parietal cortex is particularly important for representing knowledge about actions.

There are several additional (and not mutually exclusive) explanations for the left parietal activations observed for Congruent relative to Neutral trials, in addition to response code activation. Congruent stimuli may require greater visuospatial attention than Neutral stimuli because they involve a greater number of potentially relevant visual stimuli. A large body of evidence suggests, however, that right—and not left—parietal cortex (around the angular gyrus) is particularly important for visuospatial attention (see Rushworth *et al.*, 2001a,b). In contrast, a more anterior region in left parietal cortex, near a region activated in the present study, has been implicated in attention to hand movements (see Rushworth *et al.*, 2001a,b). A second possible explanation for the parietal activation for Congruent relative to Neutral trials is that parietal cortex is sensitive to the number of letter stimuli presented. This account is plausible, given data from the working memory literature suggesting that parietal cortex stores phonological information (Awh *et al.*, 1996; Jonides *et al.*, 1998a; Bunge *et al.*, 2001). Only further experiments can determine with certainty whether the parietal activation in the current study at least in part reflects the activation of S-R associations, as we propose.

In addition to being activated by Congruent relative to Neutral trials, left parietal cortex was also activated by Incongruent vs Congruent trials in the present experiment. On the basis of evidence that parietal cortex is involved in representing possible responses, we propose that greater parietal activation for Incongruent than Congruent trials is not specifically related to selection between competing responses. Rather, this activation may reflect sustained activation of competing responses during the period in which the prefrontal regions guide selection of the appropriate response. This period is longer for Incongruent than Congruent trials because of the additional demands on response selection. Parietal activation has been observed previously for incongruent relative to congruent or neutral flanker trials (e.g., Carter *et al.*, 2000; Casey *et al.*, 2000; Bunge *et al.*, 2002). However, this activation depends on the proportion of incongruent to congruent trials (Casey *et al.*, 2000), suggesting that it is not important for resolving response competition on a trial-by-trial basis. A second piece of evidence suggesting that parietal cortex represents possible responses rather than being specifically involved in response selection comes from studies employing the go/no-go paradigm. Cells in the parietal cortex of nonhuman primates are active in response to cues instructing them to withhold a response as well as by cues instructing them to make a response (Kalaska and Crammond, 1995); this finding has been replicated with neuroimaging in humans (Toni *et al.*, 2001).

Like left parietal cortex, a region in left dorsal premotor cortex was engaged by both Congruent vs Neutral and Incongruent vs Congruent trials. This region is strongly associated with movement preparation and generation (see Picard and Strick, 2001), and the present findings are consistent with the involvement of this region in activating plans for movement.

Postcentral Sulcus

Unlike the more posterior parietal foci discussed above, bilateral foci in the postcentral sulcus were engaged by Congruent vs Neutral trials but not by Incongruent vs Congruent trials (Table 2). It is likely that these activations reflect neural activity in the adjacent anterior superior parietal lobule rather than somatosensory cortex, because the tactile demands were matched across conditions. We speculate that these

regions may be transiently involved in activating S-R associations, but may not maintain these associations or interact with prefrontal cortex throughout the period of response selection.

Prefrontal Cortex

Bilateral regions in PFC were activated by Incongruent vs Congruent trials, presumably reflecting the need to select between competing responses on Incongruent trials. Unlike parietal cortex, these regions were not activated by Congruent relative to Neutral trials. The absence of prefrontal activation for Congruent vs Neutral trials cannot be explained by a lack of power to detect it, because this contrast elicited activations in other regions, including parietal and premotor cortices, which were equal or greater in magnitude than that for Incongruent vs Congruent trials.

The finding that PFC was activated on Incongruent but not Congruent trials enables us to disambiguate between alternative interpretations of the role of PFC in the flanker task. It has previously been suggested that PFC is required for maintaining the representation of S-R associations in working memory (Rafal *et al.*, 1996). If this were the case, one might expect to observe greater PFC activation on Congruent than Neutral trials, because of the need to maintain two S-R associations in working memory rather than just one. In effect, this pattern of results was observed in parietal and premotor—but not prefrontal—cortices. Additional evidence against the idea that PFC is necessary for maintaining S-R associations in working memory is provided by lesion data from nonhuman primates demonstrating that PFC is important for acquiring S-R associations, but not for retaining them once they have been learned (Petrides, 1985; Rushworth *et al.*, 1997; see also Passingham *et al.*, 2000). In the present study, the S-R associations had been learned prior to scanning, and PFC was selectively activated by a condition in which multiple, conflicting response alternatives were activated by the environment and there was a need to select a contextually appropriate response. The right dorsolateral PFC focus in the present study is very similar to a region that has been associated previously with response selection, in the context of a spatial working memory task (Rowe *et al.*, 2000).

Prefrontal activation in the present study was bilateral and primarily dorsolateral, as has been observed previously with a letter flanker task (Van Veen *et al.*, 2001). Other flanker studies have found right-lateralized activation in dorsolateral and/or ventrolateral PFC (Hazeltine *et al.*, 1997; Bunge *et al.*, 2002; Casey *et al.*, 2000). In a companion study, we have shown that the location of PFC activations in a flanker task depends in part on the type of stimulus materials used (verbal vs non-verbal; Hazeltine *et al.*, under review). Differences in prefrontal regions implicated across flanker studies may also depend on such factors as whether the S-R associations are arbitrary or not (e.g., letters vs arrows indicating whether a left or right button should be pressed) and whether these S-R associations have been well-learned prior to scanning. Mid-dorsolateral and/or mid-ventrolateral PFC regions are recruited by tasks involving response competition (see Duncan and Owen, 2000), but the nature of their relative contributions to response selection is not yet clear.

Anterior Cingulate Cortex

A number of studies have provided evidence suggesting that a rostral portion of the anterior cingulate cortex, corresponding to RCZa (Picard and Strick, 2001), detects conditions of conflict (Botvinick *et al.*, 1999; Casey *et al.*, 2000; Van Veen *et al.*, 2001). In the present study, a region in right RCZa ($y = 32$) was selectively recruited when conflicting response alternatives were activated (i.e., for Incongruent relative to Congruent trials, but not for Congruent relative to Neutral trials; see Table 1). This pattern of results is broadly consistent with that observed using a similar letter flanker paradigm (Van Veen *et al.*, 2001). Van Veen and colleagues reported that a region in rostral ACC ($y = 32$) was engaged by response conflict (i.e., for incongruent relative to congruent trials) but not by stimulus conflict (i.e., for congruent trials relative to trials in which the flankers were visually identical to the target). In the present study, as in others (see Picard and Strick, 2001, for review), more caudal activations in the anterior cingulate cortex ($y = 18$, $y = 12$) did not exhibit a pattern consistent with conflict detection. The present study was not designed to dissociate prefrontal and anterior cingulate function. However, the finding that both DLPFC and rostral anterior cingulate were specifically recruited under conditions of response competition is consistent with the hypothesis that rostral anterior cingulate detects conflict and engages lateral PFC to allocate control (Botvinick *et al.*, 1999, 2001; Casey *et al.*, 1997, 1999; Carter *et al.*, 2000; MacDonald *et al.*, 2000).

Prefrontal and Parietal Contributions to Response Selection

The present study identified a functional dissociation between prefrontal and parietal contributions to the planning of a motor response in the face of distraction. Unlike studies of behavioral inhibition which have compared a high-conflict condition with a low-conflict condition and which have generally observed coactivation of prefrontal and parietal cortices, the present study made use of three different conditions associated with a graded increase in the number of postulated processes. Based on the present findings, it

is suggested that S-R associations are stored in parietal cortex, and that these associations are activated in a bottom-up fashion that is driven by perception of salient environmental cues. Parietal activation occurred despite the task irrelevance of the flankers, and even when those cues did not influence behavior in the Congruent relative to Neutral trials.

By contrast, this and other brain imaging studies suggest that PFC is important for selecting among competing stimuli, responses, or memoranda (Taylor *et al.*, 1997; Thompson-Schill *et al.*, 1997; Desmond *et al.*, 1998; Jonides *et al.*, 1998b; Konishi *et al.*, 1998, 1999; Casey *et al.*, 2000; Leung *et al.*, 2000; Hazeltine *et al.*, 2000). PFC, which is thought to maintain representations of context, goals, and rules during performance of a cognitive task (Braver *et al.*, 1999), may effect control over voluntary behavior via top-down inputs to association and motor cortices (Cohen *et al.*, 1996; Miller and Cohen, 2001; Tomita *et al.*, 1999). In the context of the task demands of the present study, PFC may enhance the representation of the task-appropriate motor response relative to task-inappropriate responses in parietal cortex.

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