



ACADEMIC  
PRESS

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

NeuroImage

NeuroImage 20 (2003) 2135–2141

[www.elsevier.com/locate/ynimg](http://www.elsevier.com/locate/ynimg)

## Parametric manipulation of conflict and response competition using rapid mixed-trial event-related fMRI

S. Durston,<sup>a,b,\*</sup> M.C. Davidson,<sup>a</sup> K.M. Thomas,<sup>c</sup> M.S. Worden,<sup>a</sup> N. Tottenham,<sup>a,c</sup>  
A. Martinez,<sup>a</sup> R. Watts,<sup>a</sup> A.M. Ulug,<sup>a</sup> and B.J. Casey<sup>a</sup>

<sup>a</sup> *Sackler Institute for Developmental Psychobiology, Weill Medical College of Cornell University, New York, NY 10021, USA*

<sup>b</sup> *Dept. of Child and Adolescent Psychiatry, University Medical Center, Utrecht, The Netherlands*

<sup>c</sup> *Institute of Child Development, University of Minnesota, Minneapolis, MN*

Received 20 May 2003; revised 28 July 2003; accepted 4 August 2003

### Abstract

In the current study we examined the influence of preceding context on attentional conflict and response competition using a flanker paradigm. Nine healthy right-handed adults participated in a rapid mixed trial event-related functional magnetic resonance imaging (fMRI) study, in which increasing numbers of either compatible or incompatible trials preceded an incompatible trial. Behaviorally, reaction times on incompatible trials increased as a function of the number of preceding compatible trials. Several brain regions showed monotonic changes to the preceding context manipulation. The most common pattern was observed in anterior cingulate, dorsolateral prefrontal, and superior parietal regions. These areas showed an increase in activity for incompatible trials as the number of preceding *compatible* trials increased and a decrease in activity for incompatible trials as the number of preceding *incompatible* trials increased. Post hoc analysis showed that while the MR signal in the anterior cingulate and dorsolateral prefrontal regions peaked before the superior parietal region, the dorsolateral prefrontal MR signal peaked early and remained at this level. These findings are consistent with the conflict monitoring theory that postulates that the anterior cingulate cortex detects or monitors conflict, while PFC is involved in control adjustments that may then lead to modulation of superior parietal cortex in top-down biasing of attention.

© 2003 Elsevier Inc. All rights reserved.

A primary component of cognitive control is resolving conflict when competing responses or information are present (e.g., Allport, 1987; Cohen and Servan-Schreiber, 1992; Ninio and Kahneman, 1974). Several imaging studies have implicated a network of brain regions including the anterior cingulate, and prefrontal and superior parietal cortices in this process (e.g., Bench et al., 1993; Bunge et al., 2002; Carter et al., 1995, 1998; Duncan, 2001; Pardo et al., 1990; Van Veen et al., 2001). Dissociations among and within these regions have been shown in a number of studies using a variety of tasks (e.g., MacDonald et al., 2000; Bunge et al., 2002; Casey et al., 2000; Corbetta et al., 2000; Hopfinger et al., 2000; Pessoa et al., 2002; Shulman

et al., 2002). Accordingly, the anterior cingulate cortex has been shown to play a role in conflict detection and error monitoring (e.g., Gerhing et al., 1993; MacDonald et al., 2000; Botvinick et al., 2001; Nieuwenhuis et al., 2003; Ridderinkhof et al., 2003; Van Veen et al., 2001; Jones et al., 2002), while the dorsolateral prefrontal cortex has been implicated in the resolution of conflict, presumably through top-down biasing of posterior systems (e.g., parietal cortex) (e.g., Desimone and Duncan, 1995; Corbetta and Shulman, 2002) that in turn reduce conflict (Cohen and Servan-Schreiber, 1992; Awh and Jonides, 1998; Rainer et al., 1998). Further, dissociations within posterior systems (e.g., Corbetta et al., 2000; Hopfinger et al., 2000) suggest that regions in orienting and top-down modulation of attention (e.g., intraparietal sulcus) are anatomically distinct from those involved in detecting unattended, but behaviorally relevant stimuli (e.g., temporoparietal junction).

The current study methodically builds on our previous

\* Corresponding author. Sackler Institute for Developmental Psychobiology, Weill Medical College of Cornell University, 1300 York Avenue, Box 140, New York, NY 10021. Fax: +1-212-746-5755.

E-mail address: [S.Durston@azu.nl](mailto:S.Durston@azu.nl) (S. Durston).

work (Casey et al., 2000) showing dissociations *between* prefrontal and posterior systems and *within* posterior regions using a version of a flanker task (Eriksen and Eriksen, 1974). The number of preceding compatible (> > > > >) and incompatible (> > < > >) flanker trials were parametrically manipulated to examine the effect of subtle changes in context on cognitive and neural processes of conflict and cognitive control. Gratton et al. (1992) have shown that the balance between conflict from, and suppression of, flankers is determined by the compatibility between the flankers and the target on preceding trials. With consecutive incompatible trials, attention becomes increasingly directed to the target rather than to the flanking stimuli, resulting in increased selective attention (Allport, 1987) typically evidenced by fewer errors and decreased response latency. With consecutive compatible trials, attention becomes less focused on the target, resulting in increased conflict from the flankers in the form of response competition evidenced behaviorally by longer reaction times (Cohen and Servan-Schreiber, 1992; Coles et al., 1985; Eriksen and Eriksen, 1974; Jones et al., 2002; Mayr et al., 2003). In our previous study, we used a post hoc procedure within a block design to examine MR signal change during blocks of compatible and incompatible trials (Casey et al., 2000). In that study, we showed dissociations *between* prefrontal (anterior cingulate and dorsolateral prefrontal cortex) and posterior systems (superior parietal cortex) and *within* posterior regions (superior and inferior parietal regions), but no dissociations between anterior cingulate and dorsolateral prefrontal regions.

In the current study, we examined the effects of parametrically manipulating the number of incompatible or compatible trials preceding an incompatible flanker trial in a rapid mixed trial design. The goal was to further dissociate brain regions involved in selective attention and response competition. We predicted that regions sensitive to the preceding trial type in our previous study (Casey et al., 2000) would display monotonic changes in MR signal as a function of preceding number of compatible or incompatible trials, in a manner similar to the changes shown in our previous work using a parametric manipulation of a go nogo task (Durston et al., 2002a). This type of manipulation is key in developmental and clinical studies when trying to equate level of performance (task difficulty) between groups within the same task (Durston et al., 2002b). As such, we predicted poorer performance and greater recruitment of prefrontal regions for incompatible trials preceded by several compatible trials and better performance and greater recruitment of parietal regions for incompatible trials preceded by several other incompatible trials. Further, we predicted the onset and duration of MR signal change in these regions would significantly differ with the hemodynamic response in the anterior cingulate cortex, peaking earlier in detection of conflict and the MR signal in dorsolateral prefrontal peaking early but remaining high relative to anterior cingulate activity. In contrast, we predicted that pari-

etal regions would peak later, presumably from top-down biasing of attention from dorsolateral prefrontal regions.

## Methods

### Paradigm

Subjects were asked to perform a variant of the flanker task in the MR scanner. An equal number of compatible (e.g., > > > > >) and incompatible trials (e.g., < < > < <) were presented. Subjects were instructed to press a left or right response button based on the directionality of the center arrow in the display, with the highest possible speed and accuracy. We manipulated preceding context for incompatible trials by varying the number of trials (compatible or incompatible) preceding a given trial in order to manipulate the amount of response conflict on the trial of interest. Therefore any incompatible trial could be preceded by one to six compatible trials. Alternatively, to manipulate the degree of focus on the central arrow, incompatible trials could be preceded by one to five other incompatible trials. Stimuli were presented for 1000 ms with a 3.0 s interstimulus interval, resulting in a total trial length of 4.0 s. The total task consisted of four runs that lasted 4 min and 48 s each. There were 72 trials within each run, with equal numbers of compatible and incompatible trials intermixed pseudorandomly, while adhering to the context manipulations, resulting in a total of 144 incompatible trials. In order to include a reasonable number of incompatible trials in each cell of the design, incompatible trials were included in one of six cells based on their preceding context, with either low (1), medium (2–3), or high (>3) numbers of compatible or incompatible trials preceding the trial of interest. This resulted in approximately 30 correct trials in each of the cells. Reaction time and accuracy measures were collected throughout the four runs.

### Subjects

Nine healthy right-handed adults participated in this study (mean age = 25.7 years, four females). All subjects were screened for any contraindications for an MRI. We obtained written consent from all subjects prior to scanning.

### Scan acquisition

EPI BOLD images were acquired in 24 axial slices on a 1.5 T GE Signa scanner, covering all but the frontal and occipital poles (TR = 2000, TE = 40, 64 × 64, FOV = 20, 4 mm slice thickness, resulting in 3.125 × 3.125 mm in-plane resolution). Anatomical spin echo images were collected (TR = 500, TE = min, 256 × 256, FOV = 20, 4 mm slice thickness) in the same locations as the functional slices. Stimuli were presented using the integrated functional imaging system (IFIS) (PST, Pittsburgh, PA), which

uses a LCD video display in the bore of the MR scanner and a fiberoptic response collection device.

### Analysis

AIR (Automated Image Registration) version 3.08 (Woods et al., 1992) was used for motion correction, image smoothing (2 mm), and cross registration of data similar to previous published studies (Braver et al., 1997; Thomas et al., 1999; Casey et al., 2000, 2001). Three “whole-brain” voxelwise multifactorial analyses of variance (ANOVAs) were performed averaging across all nine subjects’ pooled data. The first voxelwise, 9 (subjects)  $\times$  2 (trial types) ANOVA examined MR signal intensity for incompatible trials vs compatible trials. The second multifactorial 9 (subjects)  $\times$  4 (condition) ANOVA examined changes in MR signal intensity for incompatible trials preceded by (1) one compatible trial; (2) two to three compatible trials; or (3) four to six compatible trials, relative to compatible trials preceded by on average three compatible trials. The third ANOVA examined the change in MR signal for incompatible trials preceded by (1) one incompatible trial; (2) two to three incompatible trials; or (3) four to six incompatible trials, relative to compatible trials preceded by on average three compatible trials. The ANOVAs consisted of two scan points for each behavioral trial, at 4 and 6 s after stimulus onset. Only correct trials were analyzed. Regions of four or more contiguous voxels ( $P < 0.025$ , estimated correction  $P < .00025$ ) were identified (Forman et al., 1995). Images were warped into stereotaxic space using AFNI (Cox, 1996) to localize regions of activity, based on the coordinate system of the Talairach atlas (Talairach and Tournoux, 1988).

A post hoc scan-by-scan analysis was performed similar to one we have used previously (Casey et al., 2000; Durston et al., 2002a,b, 2003) and was performed on brain regions identified as having significant MR signal change for the 9 (subjects)  $\times$  2 (trial types) ANOVA. MR signal was averaged per subject per trial type to test for a differential response on incompatible trials dependent on preceding context. Plots of percent signal were then created to determine whether signal changes showed a monotonic function. MR signal for those regions showing monotonic changes to the context manipulation were compared at 4 and 6 s after stimulus onset to test for differences in peak and duration of MR signal change.

## Results

### Behavioral results

None of the subjects became explicitly aware of the contextual manipulation, based on self-report at the end of the study. Overall reaction time was significantly faster on compatible than incompatible trials ( $RT = 534 \pm 76$  ms;

Table 1

Regions from 9 (subjects)  $\times$  2 (trial type) ANOVA that demonstrated monotonic signal change on post hoc analysis

| Area                 | Brodmann | Side | Talairach      | Max <i>F</i> | Context |
|----------------------|----------|------|----------------|--------------|---------|
| Med. frontal gyrus   | 8/9      | L    | (−38, 18, 37)  | 14.55        | ↑ C ↓ I |
| Sup. frontal gyrus   | 8        | R    | (19, 38, 37)   | 18.53        | ↑ C ↓ I |
| Ant. cingulate gyrus | 32       | R/L  | (3, 42, 17)    | 29.87        | ↑ C ↓ I |
| Sup. parietal lobe   | 7        | L    | (−32, −47, 53) | 67.47        | ↑ C ↓ I |
| Sup. parietal lobe   | 7        | R    | (29, −55, 49)  | 13.36        | ↑ C —   |
| Intraparietal sulcus | 40       | R    | (32, −43, 43)  | 11.65        | — ↑ I   |
| Fusiform gyrus       | 19/37    | L    | (−39, −57, 1)  | 10.21        | ↓ C —   |

*Note.* ↑, activation increases; ↓, activation decreases; C, as a function of the number of preceding compatible trials; I, as a function of the number of preceding incompatible trials; ant., anterior; inf., inferior; med., medial; sup, superior; L, left; R, right.

$598 \pm 78$  ms  $t = 2.48$ ;  $P = 0.048$ , respectively). Mean accuracy was high across both trial types (accuracy =  $1.0 \pm 0.0$  for compatible trials;  $0.98 \pm 0.04$  for incompatible trials;  $t = 1.23$ ;  $P = 0.26$ ). Reaction time increased for incompatible trials as a function of the number of preceding compatible trials (RT =  $583 \pm 71$  ms for incompatible trials preceded by one compatible trial;  $597 \pm 52$  ms for incompatible trials preceded by two to three compatible trials; and  $611 \pm 90$  ms for incompatible trials preceded by more than three compatible trials;  $P < 0.001$ ). Differences in reaction time on incompatible trials preceded by different numbers of incompatible trials decreased overall, but did not reach significance (RT =  $614 \pm 109$  ms for incompatible trials preceded by one incompatible trial;  $581 \pm 69$  ms for incompatible trials preceded by two to three incompatible trials;  $604 \pm 87$  ms for incompatible trials preceded by more than three incompatible trials;  $t = 0.46$ ;  $P = 0.66$ ).

### Imaging results

The 9 (subjects)  $\times$  2 (trial types) ANOVA revealed regions in the bilateral dorsolateral prefrontal cortex (BA 8/9), anterior cingulate gyrus (BA 32), bilateral superior parietal cortex (BA 7), inferior parietal cortex (BA 40), temporo-occipital cortex (BA 19/37), and temporal lobe (BA 19/39) and showed significant changes in MR signal intensity for incompatible relative to compatible trials. Post hoc comparison of the MR signal change in these regions showed three distinct patterns (see Table 1 and Fig. 1). The most common pattern was found in regions of anterior cingulate, dorsal prefrontal, and superior parietal cortex. MR signal increased for incompatible trials as a function of the number of compatible trials preceding them, but decreased to incompatible trials that were preceded by other incompatible trials as a function of their number. A region in the right inferior parietal lobe showed MR signal increases to incompatible trials as a function of the number of preceding incompatible trials, but no monotonic relationship for preceding compatible trials. In a region of fusiform

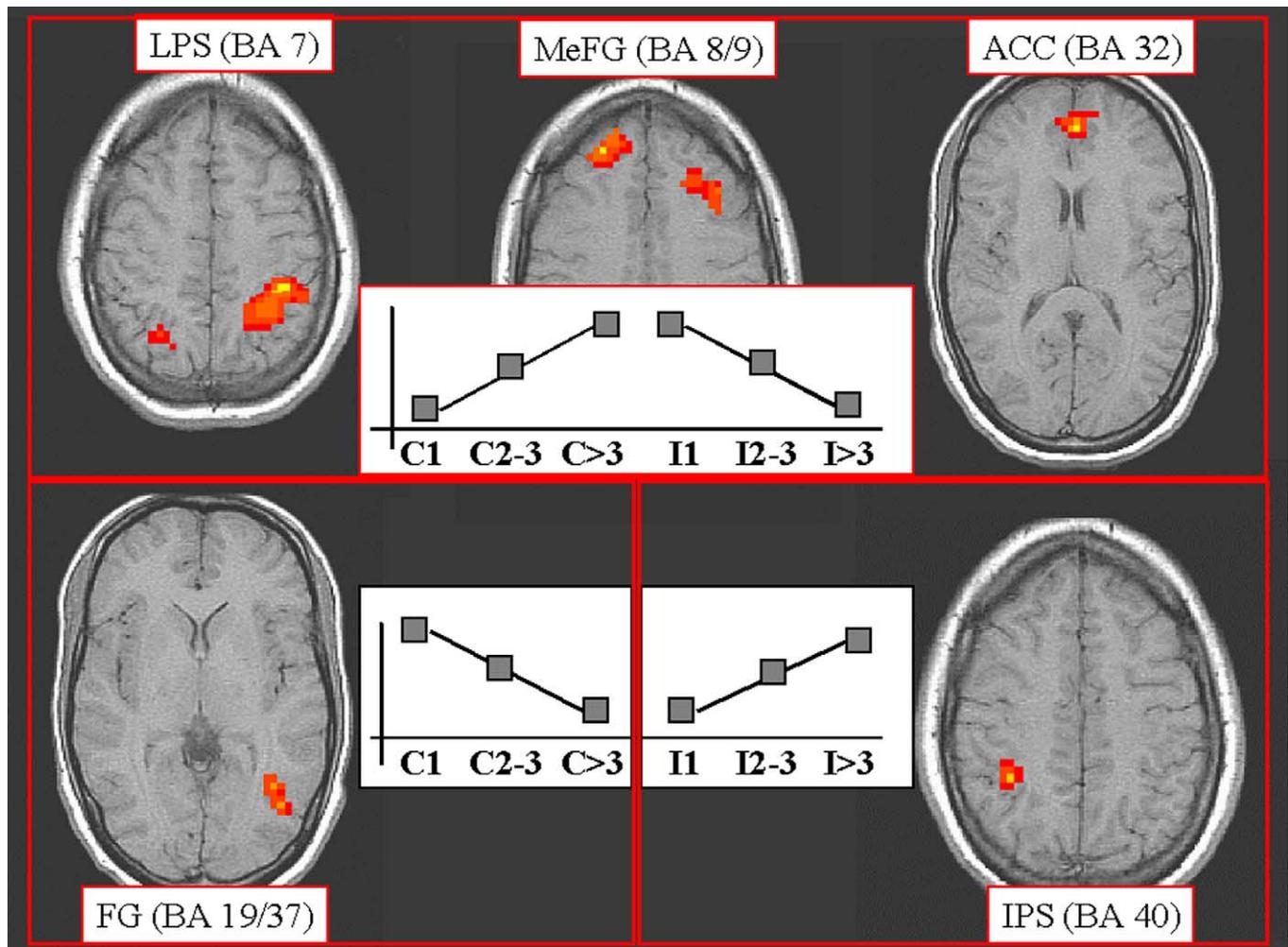


Fig. 1. Schematic rendering of percent change in MR signal on incompatible trials following (from left to right in graph) 1, 2–3, or >3 compatible trials and 1, 2–3, or >3 incompatible trials for ROIs in the superior parietal lobe (LPS), medial frontal gyrus (MeFG), anterior cingulate gyrus (ACC) (upper box), fusiform gyrus (FG) (left lower box), and intraparietal sulcus (IPS) (right lower box). Patterns correspond to signal changes observed in the brain areas shown within the same box.

gyrus, MR signal decreased for incompatible trials as the number of preceding compatible trials increased, but showed no monotonic change when the preceding trials were incompatible.

The comparison of MR signal intensity at 4 and 6 s scans (period of 4 to 8 s) following stimulus onset for the regions of the anterior cingulate, dorsal prefrontal, and superior parietal cortex showed dissociations among these three regions. The MR signal change was larger at 4 to 6 than at 6 to 8 s for the anterior cingulate cortex ( $P < .05$ ), not different for the dorsolateral prefrontal cortex across these time points, and larger at 6 to 8 than at 4 to 6 s for parietal areas ( $P < .05$ , see Fig. 2).

### Modeling

Increases in reaction time on incompatible trials as a function of the number of preceding compatible trials sup-

ports our prediction that interference from flanking arrows increases in this context. Several regions showed an increase in MR signal that mirrored this effect. These regions may be recruited more as task demands increase, as a result of increased interference (i.e., requiring the subject to ignore incompatible flanking arrows after multiple compatible trials, where the flanking arrows did not conflict with the relevant central arrow).

We wanted to exclude the possibility that the increase in MR signal might be based on an artifactual summation of blood oxygen level dependent (BOLD) responses due to the randomization scheme within our flanker paradigm. In order to test this possibility, we modeled our randomization scheme using a previously described method (Durston et al., 2002a). We combined a model of the hemodynamic response (Boynton et al., 1996) with the randomization scheme of this paradigm. This resulted in models for the average BOLD response for all types of incompatible trials.

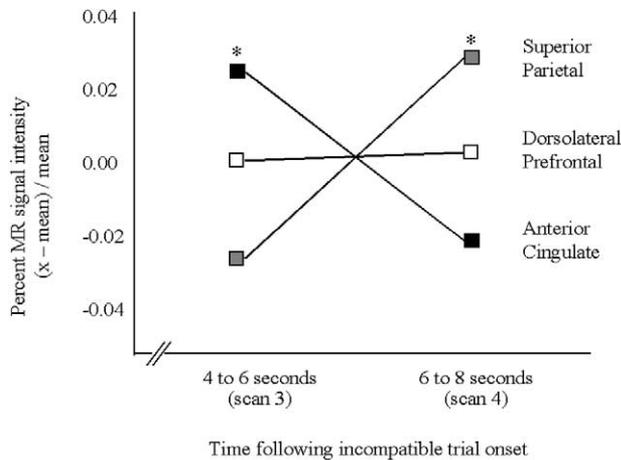


Fig. 2. Comparison of MR signal change from scan 3 to scan 4 (period of 4 to 8 s) following stimulus onset of incompatible trials for the regions of the anterior cingulate, dorsolateral prefrontal, and superior parietal cortex plotted as a percent change in MR signal intensity from scan 3 to scan 4. MR signal change decreased from scan 3 to scan 4 for the anterior cingulate cortex ( $*P < .05$ ) and increased from scan 3 to scan 4 for parietal cortex ( $*P < .05$ ).

Under the null hypothesis that there was no effect of preceding context (i.e., the amplitude of the BOLD curve following an incompatible trial was the same regardless of the trials preceding it), the model predicted no artifactual effect of context for either preceding compatible or incompatible trials.

## Discussion

Overall, our findings show that the anterior cingulate, dorsolateral prefrontal, and parietal cortex regions are sensitive to subtle changes in conflict, consistent with previous studies (e.g., Bench et al., 1993; Bunge et al., 2002; Carter et al., 1995, 1998; Nieuwenhuis et al., 2003; Pardo et al., 1990; Ridderinkhof et al., 2003; Van Veen et al., 2001). These areas showed an increase in activity on incompatible trials as a function of the number of preceding compatible trials and decreased as a function of the number of preceding incompatible trials. In general, this pattern parallels the behavioral results, in that mean reaction time increased for incompatible trials as the number of preceding compatible trials increased (see also Gratton et al., 1992) and overall reaction time decreased when there was more than one incompatible trial preceding another incompatible. These results are largely consistent with our previous study showing a positive correlation between activity in the anterior cingulate and prefrontal regions and reaction time on a similar task (Casey et al., 2000).

Our parametric manipulation successfully perturbed three brain regions previously implicated in conflict detection, resolution, and selective attention. However, this manipulation, at least on the surface, did not seem to dissociate

among these three regions. As such, we performed a post hoc analysis to examine differences in onset of peak and duration of the hemodynamic response in these three regions. We compared MR signal change during incompatible trials for the scans occurring at 4 and 6 s after stimulus onset. Based on this analysis, we saw a significant difference between the anterior cingulate and parietal regions. Accordingly, MR signal intensity in the anterior cingulate cortex was greater (peaked) between 4 and 6 s and then began to decrease between 6 and 8 s. In contrast, MR signal intensity in superior parietal cortex did not peak until 6 to 8 s, showing a gradual increase between 4 to 6 s and 6 to 8 s scans. The pattern observed in MR signal change for dorsolateral prefrontal cortex was constant (high) across both scans for the period of 4 to 8 s following stimulus onset. These data are consistent with the conflict monitoring theory that anterior cingulate cortex monitors or detects conflict, while the prefrontal cortex is involved in control adjustments that may then lead to modulation of superior parietal cortex by top-down biasing. (e.g., Botvinick et al., 2001; Jones et al., 2002).

Two other patterns of activity were shown with the parametric manipulation of preceding context. One of these was shown in right inferior parietal cortex and behaved similarly to parietal findings published previously by our group (Casey et al., 2000). This region increased when incompatible trials were preceded by other incompatible trials, but not when preceded by compatible trials. This pattern may reflect the top-down modulation of attention, with subjects increasingly focusing attention on the center arrow away from flanker stimuli in order to reduce conflict. Thus, increases in activity in this region as the number of preceding incompatible trials increased may be related to increased allocation of attentional resources.

A second distinct pattern of activity was shown in the left fusiform gyrus. Activity in this region decreased monotonically for incompatible trials preceded by an increasing number of compatible trials. We speculate that this activity is related to perceptual processing, as this region has been implicated in studies of configural and featural processing (Gauthier and Tarr, 2002). After multiple compatible trials with identical flankers and targets (all arrows pointing in the same direction), the subject may process the stimuli in a more configural manner (featural processing would not be necessary to perform these trials successfully). However, on the subsequent presentation of an incompatible trial, this system would then need to be suppressed to the extent that configural processing had been engaged. Suppression of activity in this region could also be associated with the increase in superior parietal activity during this manipulation. Indeed, previous studies have shown that fusiform gyrus activity may be modulated by attention (Haxby et al., 1994; Vuilleumier, et al., 2001; Wojciulik et al., 1998).

A recent paper challenging the conflict resolution theory argues that repetition priming may play a significant role (Mayr et al., 2003). The authors showed that there is a

reaction time advantage on trials that are preceded by an identical trial (Mayr et al., 2003). In the flanker paradigm, incompatible trials preceded by an incompatible trial are identical to the previous stimulus on 50% of trials, whereas they are never identical in the case of compatible trials preceding an incompatible trial. Studies using other paradigms that do not involve the repetition of the same stimuli over multiple consecutive trials have also demonstrated the influence of preceding context on response conflict (e.g., Botvinick et al., 2001; Durston et al., 2002a). Although repetition priming may affect reaction time within a flanker paradigm, this does not necessarily argue against an (opposite) effect for conflict on preceding trials.

An advantage of parametric manipulations such as the one incorporated in this paradigm is that they will allow the comparison of groups, across different levels of task difficulty. In a developmental study using a parametric go nogo task we were able to demonstrate that improvement in performance on this task with age was related to a more adultlike pattern of activation in related circuitry (Durston et al., 2002b). In a follow-up study we showed that differences in performance on this task between young children with and without ADHD did not account for differential patterns of activation associated with inhibiting a response (Durston et al., 2003). Typically, studies examining developmental or patient populations using these types of tasks have not been able to dissociate performance differences from other effects. The incorporation of parametric manipulations may allow for such dissociations.

In sum, we have shown both a behavioral and a biological effect of preceding context on response conflict using a flanker task. We have replicated previous work demonstrating the relevance of preceding context, and have shown differential activation of regions involved in conflict and response competition and those involved in the top-down modulation of attention. Finally, our behavioral task and experimental design manipulations have implications for future studies. Manipulating the number and type of preceding targets affected task difficulty as indicated by reaction time on incompatible trials. This finding suggests that parametric manipulations of preceding context may be useful for titrating task difficulty when studying subjects of different ages, or from different clinical populations.

## Acknowledgments

The authors thank two anonymous reviewers for their thoughtful and helpful suggestions. This work was supported in part by R21 DA15882, R01 MH63255, and P01 MH62196 to BJC.

## References

Allport, A., 1987. Selection for action: some behavioral and neurophysiological considerations of attention and action, in: Heuer, H., Sanders,

- A.F. (Eds.), *Perspectives on Perception and Action*, Erlbaum, Hillsdale, NJ, pp. 395–419.
- Awh, E., Jonides, J., 1998. Spatial selective attention and spatial working memory, in: Parasuraman, R. (Ed.), *The Attentive Brain*, MIT Press, Cambridge, MA, pp. 353–380.
- Bench, C.J., Frith, C.D., Grasby, P.M., Friston, K.J., Paulesu, E., Frackowiak, R.S., Dolan, R.J., 1993. Investigations of the functional anatomy of attention using the Stroop test. *Neuropsychologia* 31 (9), 907–922.
- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. *Psychol. Rev.* 108 (3), 624–652.
- Braver, T.S., Cohen, J.D., Nystrom, L.E., Jonides, J., Smith, E.E., Noll, D.C., 1997. A parametric study of prefrontal cortex involvement in human working memory. *NeuroImage* 5, 49–62.
- Bunge, S.A., Hazeltine, E., Scanlon, M.D., Rosen, A.C., Gabrieli, J.D., 2002. Dissociable contributions of prefrontal and parietal cortices to response selection. *NeuroImage* 17 (3), 1562–1571.
- Carter, C.S., Mintun, M., Cohen, J.D., 1995. Interference and facilitation effects during selective attention: an H2150 PET study of Stroop task performance. *NeuroImage* 2 (4), 264–272.
- Carter, C.S., Braver, T.S., Barch, D.M., Botvinick, M.M., Noll, D., Cohen, J.D., 1998. Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* 280 (5364), 747–749.
- Casey, B.J., Forman, S.D., Franzen, P., Berkowitz, A., Braver, T.S., Nystrom, L.E., Thomas, K.M., Noll, D.C., 2001. Sensitivity of prefrontal cortex to changes in target probability: a functional MRI study. *Hum. Brain Mapping* 13, 26–33.
- Casey, B.J., Thomas, K.M., Welsh, T.F., Badgaiyan, R.D., Eccard, C.H., Jennings, J.R., Crone, E.A., 2000. Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. *Proc. Natl. Acad. Sci. USA* 97, 8728–8733.
- Cohen, J.D., Servan-Schreiber, D., 1992. Context, cortex, and dopamine: a connectionist approach to behavior and biology in schizophrenia. *Psychol. Rev.* 99, 45–77.
- Coles, M.G.H., Gratton, G., Bashore, T.R., Eriksen, C.W., Donchin, E., 1985. A psychophysiological investigation of the continuous flow model of human information processing. *J. Exp. Psychol. Hum. Perception Performance* 11, 529–553.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3 (3), 201–215.
- Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., Shulman, G.L., 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* 3 (3), 292–297.
- Cox, R.W., 1996. AFNI: software for analysis and visualization of functional magnetic resonance images. *Comput. Biomed. Res.* 29, 162–173.
- Desimone, R., Duncan, J., 1995. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18, 193–222.
- Duncan, J., 2001. An adaptive coding model of neural function in prefrontal cortex. *Nat. Rev. Neurosci.* 2 (11), 820–829.
- Durston, S., Thomas, K.M., Worden, M.S., Yang, Y., Casey, B.J., 2002a. The effect of preceding context on inhibition: an event-related fMRI study. *NeuroImage* 16 (2), 449–453.
- Durston, S., Thomas, K.M., Yang, Y., Ulug, A.M., Zimmerman, R.D., Casey, B.J., 2002b. A neural basis for the development of inhibitory control. *Dev. Sci.* 5, F9–F16.
- Durston, S., Tottenham, N.T., Thomas, K.M., Davidson, M.C., Eigsti, I.M., Yang, Y., Ulug, A.M., Casey, B.J., 2003. Differential patterns of striatal activation young children with and without ADHD. *Biol. Psychiatry* 53, 871–878.
- Eriksen, B.A., Eriksen, C.W., 1974. Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept Psychophys.* 16, 143–149.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D.C., 1995. Improved assessment of significant activation in

- functional magnetic resonance imaging (fMRI). *Magn. Reson. Med.* 33, 636–647.
- Gauthier, I., Tarr, M.J., 2002. Unraveling mechanisms for expert object recognition: bridging brain activity and behavior. *J. Exp. Psychol.: Hum. Perception Performance* 28 (2), 431–446.
- Gehring, W.J., Goss, B., Coles, M.G.H., Meyer, D.E., Donchin, E., 1993. A neural system for error detection and compensation. *Psychol. Sci.* 4, 385–390.
- Gratton, G., Coles, M.G., Donchin, E., 1992. Optimizing the use of information: strategic control of activation of responses. *J. Exp. Psychol. Gen.* 121(4), 480–506.
- Haxby, J.V., Horowitz, B., Ungerleider, L.G., Maisog, J.M., Pietrini, P., Grady, C.L., 1994. The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *J. Neurosci.* 14, 6336–6353.
- Hopfinger, J.B., Buonocore, M.H., Mangun, G.R., 2000. The neural mechanisms of top-down attentional control. *Nat. Neurosci.* 3 (3), 284–291.
- Jones, A.D., Cho, R.Y., Nystrom, L.E., Cohen, J.D., Braver, T.S., 2002. A computational model of anterior cingulate function in speeded response tasks: effects of frequency, sequence, and conflict. *Cogn. Affect. Behav. Neurosci.* 2 (4), 300–317.
- MacDonald, A.W., Cohen, J.D., Stenger, V.A., Carter, C.S., 2000. Dissociating the role of the dorsolateral prefrontal cortex and anterior cingulate cortex in cognitive control. *Science* 288, 1835–1838.
- Mayr, U., Awh, E., Laurey, P., 2003. Conflict adaptation effects in the absence of executive control. *Nat. Neurosci.* 6 (5), 450–452.
- Nieuwenhuis, S., Yeung, N., Van den Wildenberg, W., Ridderinkhof, K.R., 2003. Electrophysiological correlates of anterior cingulate function in a Go/NoGo task: effects of response conflict and trial-type frequency. *Cogn. Aff. Behav. Neurosci.* 3, 17–26.
- Ninio, A., Kahneman, D., 1974. Reaction time in focused and in divided attention. *J. Exp. Psychol.* 103, 394–399.
- Pardo, J.V., Pardo, P.J., Janer, K.W., Raichle, M.E., 1990. The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proc. Natl. Acad. Sci. USA* 87, 256–259.
- Pessoa, L., Kastner, S., Ungerleider, L.G., 2002. Attentional control of the processing of neutral and emotional stimuli. *Brain Res. Cogn. Brain Res.* 15 (1), 31–45.
- Rainer, G., Asaad, W.F., Miller, E.K., 1998. Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature* 393, 577–579.
- Ridderinkhof, K.R., Nicuwcnhuis, S., Bashore, T.R., 2003. Errors are foreshadowed in brain potentials associated with action monitoring in cingulate cortex. *Neurosci. Lett.* 348(1), 1–4.
- Shulman, G.L., d'Avossa, G., Tansy, A.P., Corbetta, M., 2002. Two attentional processes in the parietal lobe. *Cereb. Cortex* 12 (11), 1124–1131.
- Talairach, J., Tournoux, P., 1988. *Co-planar Stereotaxic Atlas of the Human Brain*. Thieme, New York.
- Thomas, K.M., King, S.W., Franzen, P.L., Welsh, T.F., Berkowitz, A.L., Noll, D.C., Birmaher, V., Casey, B.J., 1999. A developmental functional MRI study of spatial working memory. *NeuroImage* 10(3), 327–338.
- Van Veen, V., Cohen, J.D., Botvinick, M.M., Stenger, V.A., Carter, C.S., 2001. Anterior cingulate cortex, conflict monitoring, and levels of processing. *NeuroImage* 14 (6), 1302–1308.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron* 30 (3), 829–841.
- Wojciulik, E., Kanwisher, N., Driver, J., 1998. Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *J. Neurophysiol.* 79, 1574–1578.
- Woods, R.P., Cherry, S.R., Mazziotta, J.C., 1992. Rapid automated algorithm for aligning and reslicing PET images. *J. Comput. Assist. Tomogr.* 16, 620–633.