

# Anterior Cingulate Cortex, Conflict Monitoring, and Levels of Processing

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**It has been hypothesized that the anterior cingulate cortex (ACC) contributes to cognition by detecting conflicts that might occur during information processing, to signal the need to engage top-down attentional processes. The present study was designed to investigate which levels of processing are being monitored by the ACC for the presence of conflict. Event-related fMRI was used to measure the response of the ACC during an interference task in which distracting information could be congruent, conflicting at the level of stimulus identification, or conflicting at the response level. Although both types of conflict caused reaction time interference, the fMRI data showed that the ACC is responsive only to response conflict, even when controlling for reaction times. These results suggest a highly specific contribution of the ACC to executive functions, through the detection of conflicts occurring at later or response-related levels of processing.** © 2001

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## INTRODUCTION

The anterior cingulate cortex (ACC) is often associated with the neural implementation of attentional control (Devinsky *et al.*, 1995; Posner and Petersen, 1990). This region has been shown to be activated during underdetermined response selection such as verb generation (Barch *et al.*, 2000; Crosson *et al.*, 1999; Petersen *et al.*, 1988), dual-task situations (D'Esposito *et al.*, 1995), interference tasks such as the Stroop task (Bench *et al.*, 1993; Carter *et al.*, 2000; George *et al.*, 1994; Pardo *et al.*, 1990; Taylor *et al.*, 1997), and errors (Carter *et al.*, 1998; Dehaene *et al.*, 1994; Gehring and Knight, 2000; Kiehl *et al.*, 2000), among others (Bush *et al.*, 2000). Both the ACC and the lateral parts of the prefrontal cortex are widely believed to play an important part in attentional control (Smith and Jonides, 1999). However, it is still controversial what role exactly is played by these two systems and how they interact with each other (Bush *et al.*, 2000; Gehring and Knight, 2000).

We have recently proposed that the function of the ACC is to detect the occurrence of processing conflicts (Barch *et al.*, 2000; Botvinick *et al.*, 1999, 2001; Carter *et al.*, 1998, 2000; Cohen *et al.*, 2000; MacDonald *et al.*, 2000). Specifically, according to this theory, the ACC does not implement a top-down attentional control mechanism, but rather detects competition between processes that conflict during task performance and signals the extent to which attentional control is required (Botvinick *et al.*, 2001). A series of experiments designed to test this hypothesis has shown that the ACC is indeed more active under conditions of high conflict and that its activity is dissociable from top-down control (Botvinick *et al.*, 1999; Carter *et al.*, 1998; MacDonald *et al.*, 2000). Furthermore, top-down attentional mechanisms implemented in the prefrontal cortex are thought to regulate information processing in posterior representational cortex (Cohen *et al.*, 1996; Desimone and Duncan, 1995; Miller, 2000; Smith and Jonides, 1999). We propose that the prefrontal cortex itself is regulated by an ACC-based monitoring system that is responsive to processing conflicts. Thus, these mechanisms form a “feedback loop” (Botvinick *et al.*, 2001).

One unresolved issue about this psychological theory is to what kinds of conflict the ACC responds. In cognitive psychology, information processing is often thought of as occurring at a number of different levels, which might correspond to the different phases of task processing, for example stimulus encoding, target detection, response selection, and response execution. Theoretically, conflicts might occur at any or all of these levels. In particular, Kornblum and colleagues (Kornblum, 1994; Kornblum *et al.*, 1990, 1999; Zhang *et al.*, 1999) have argued that interference tasks, such as the Stroop task or the Eriksen flanker task, involve conflict not only at the response level, but also at a stimulus-identification (or target-detection) level. So far, we have tested our theory using tasks that involve interference at both these earlier and later levels of processing. Computational modeling studies have

shown that response-level monitoring is sufficient to account for much of the existing data related to the online modulation of attentional control (Botvinick *et al.*, 2001; Cohen *et al.*, 2000). However, it remains an open question as to whether conflict occurring at other levels of processing also engages the ACC.

To start addressing this issue, we used the flanker task, originally designed by Eriksen and Eriksen (1974), to separate response conflict from conflict occurring at the level of stimulus processing (Zhang *et al.*, 1999). In this task, the subject has to respond to the identity of a centrally presented target letter and to ignore the flanker letters that are presented simultaneously on both sides of the target. When these flankers are identical to the target letter, reaction times (RTs) are fastest ("congruent" condition, CO); if the flankers are part of the response set that is mapped onto the opposite response, RTs are slowest (Eriksen and Eriksen, 1974). We will refer to this as the "response-incongruent" condition (RI). If the distracting stimuli are not identical to the target, but are mapped onto the same response, RTs are slower than to CO stimuli, but faster than to RI stimuli (Eriksen and Schultz, 1979). This effect is considered to reflect the occurrence of conflict at an earlier processing level, in absence of conflict at a response level (Zhang *et al.*, 1999). We will refer to this as the "stimulus-incongruent" condition (SI). We expect RTs to increase with increasing levels of conflict. The ACC could respond in various ways to these different kinds of conflict. If the ACC responds to general conflict, we would expect the ACC activation to increase with levels of conflict, mirroring reaction times. Second, if different ACC regions are responsive to conflict occurring at different levels of processing, we expect one region of the ACC to show increased activity to both SI and RI stimuli (reflecting detection of stimulus conflict) and a different region to show increased activity only to RI stimuli (reflecting detection of response conflict). Last, if the ACC were selectively responsive to response conflict, we would expect the largest activation to RI stimuli, with no difference between the activation patterns to CO and SI stimuli.

In the established literature, the effect of stimulus conflict on RT may be rather small (Eriksen and Eriksen, 1974; Eriksen and Schultz, 1979). For this reason we used a majority of CO trials and relatively smaller percentages of SI and RI trials, to increase the effects of both stimulus conflict and response conflict on RTs. It has been found that the amount of conflict in an interference task is modulated by the relative proportions of congruent and incongruent trials (Lindsay and Jacoby, 1994; Logan and Zbrodoff, 1979; Tzelgov *et al.*, 1992). Presumably, this is because the overall context of the block influences attentional engagement. During mostly congruent blocks, interference on the (infrequent) incongruent trials is greater, compared to

mostly incongruent blocks. During mostly congruent blocks, subjects are thought to assume a strategy in which they rely relatively more on the information in the irrelevant channel, which benefits performance on congruent trials but impairs performance on incongruent trials. Such a manipulation also leads to a larger ACC response for incongruent trials during mostly congruent blocks (Carter *et al.*, 2000). Conversely, during mostly incongruent blocks, the subject's attention is likely to be highly engaged, resulting in less RT interference and a small ACC response. In the present experiment, we expected that using a majority of CO trials would induce subjects to rely more heavily on the flankers. This manipulation should increase the effects of both stimulus conflict and response conflict, which would maximize our ability to detect any effects of stimulus conflict.

## MATERIALS AND METHODS

### Research Participants

Subjects were 12 right-handed healthy adults (mean age 27.25, SD = 4.73; 6 females) recruited by advertisements. Subjects received a small monetary fee for participating. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Pittsburgh.

### Procedure

The task, presented on a visual display controlled by a Macintosh computer in the scanner control room running PsyScope (Cohen *et al.*, 1993), consisted of six blocks of 16 trials each. Trials were randomized within a block. Within a block, 50% of trials were CO, 25% of trials were SI, and 25% of trials were RI. At the start of each block, a fixation point was presented for 4 s. At each stimulus presentation, five letters were presented simultaneously, the middle of which (referred to as target) was in the same location as the fixation point. In addition, a small arrow below the central letter indicated the target. The flankers always consisted of identical letters, two presented on each side of the target. After 300 ms, the stimulus was replaced again by the fixation point. The interstimulus interval was 11,700 ms, to allow time for the hemodynamic response to resolve. Subjects were instructed to respond to the central letter and to ignore the surrounding letters. Subjects were instructed to respond with the index finger of the right hand if the central letter was an S or M and with the middle finger if the letter was an H or P, and to respond fast but accurately. CO stimuli consisted of a target flanked by letters that were identical to the target (e.g., SSSSS or HHHHH). For SI stimuli, the flankers were different from the target, but mapped onto the same response finger (e.g., MMSMM

or PPHPP). For RI stimuli, the flankers mapped onto the opposite response finger (e.g., PPSPP or SSHSS). A priori, trials with error responses, null responses, or responses with RTs below 200 ms or above 1000 ms were omitted from analysis. Prior to the task, subjects received a practice session consisting of one block of trials.

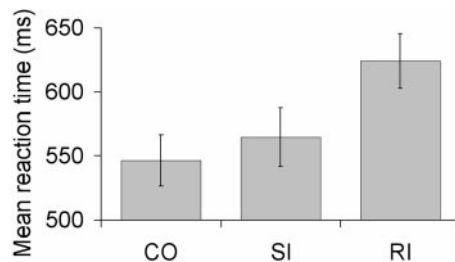
### MRI Scanning Procedures

Images were acquired with a conventional 1.5-T GE Signa whole body scanner (General Electric Company) and a standard RF head coil. Nineteen oblique axial slices (3.75 mm<sup>3</sup> voxels) were acquired parallel to the AC-PC line, with the middle of the 3rd slice from the bottom through the AC-PC line (a total of 71.25 mm of brain coverage). Functional scans were acquired using a two-shot T2\*-weighted spiral-scan pulse sequence (TR = 1500 ms, TE = 35 ms, FOV 24 cm, flip angle 60°) (Noll *et al.*, 1995). Scanning was event-related, with image acquisition synchronized to stimulus presentation, such that four scans, each containing all 19 slices, were acquired during each 12-s trial. Anatomical scans (36 slices) were acquired using a standard T1-weighted pulse sequence, with the middle of the 10th slice from the bottom through the AC-PC line. Data from individual subjects were subjected to a voxel-wise within-block linear detrending and between-block, subtractive mean normalization. Images were then coregistered to a common reference structural MRI scan by means of a 12-parameter automatic algorithm AIR (Woods *et al.*, 1992), and smoothed with an 8-mm, full width at half-maximum, three-dimensional Gaussian filter to accommodate individual differences in anatomy. Finally, data were pooled across subjects to increase the signal-to-noise ratio. To identify areas showing an effect of condition, analyses of variance were conducted on each voxel, using subject as a random effect and condition (CO, SI, RI) and within-trial scan (1–4) as factors, and using a voxel clustering threshold (Forman *et al.*, 1995) of 8 to correct for multiple comparisons. Voxel clusters that showed a significant condition by scan interaction at  $P < 0.005$  were selected for further, post hoc analysis. The signal was normed to scan 1, and post hoc tests were carried out between SI and CO, and between RI and CO, individually for each functional base-normed scan time point. Only voxel clusters that survived these post hoc tests were considered.

## RESULTS

### Behavioral Data

Subjects were highly accurate, the total number of errors per subject ranging from 0 to 5 (95–100%). Average reaction times were 546 ms (SD = 69) for the CO condition, 565 ms (SD = 74) for the SI condition, and



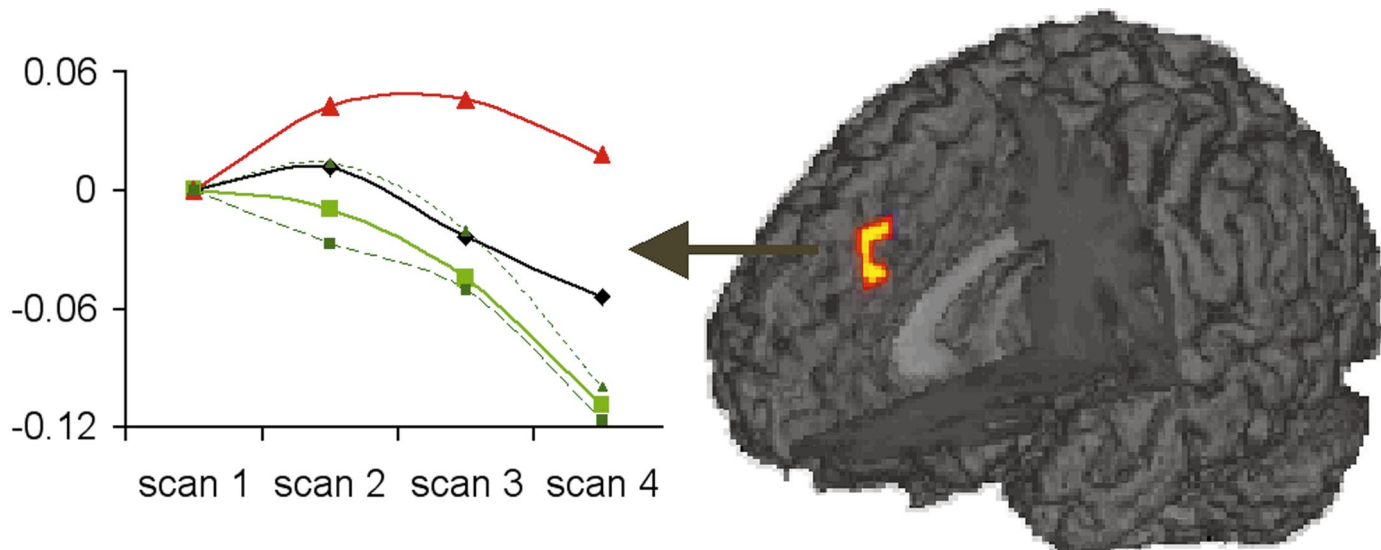
**FIG. 1.** Reaction time data to congruent (CO), stimulus-incongruent (SI), and response-incongruent (RI) stimuli. SI stimuli elicit longer RTs than CO stimuli, indicating stimulus conflict; RI stimuli elicit longer RTs than SI stimuli, indicating response conflict. Error bars represent  $\pm 1$  standard error of the mean.

624 ms (SD = 79) for the RI condition. A repeated-measures ANOVA indicated that these were significantly different ( $F(2,22) = 43.17$ ,  $P < 0.000$ ). Specifically, paired  $t$  tests indicated that the difference between CO and SI was significant ( $t = 3.30$ ,  $P < 0.01$ ), and so were the differences between CO and RI ( $t = 8.42$ ,  $P < 0.0001$ ) and SI and RI ( $t = 5.57$ ,  $P < 0.0005$ ). Thus, reaction times increased with the degree of conflict (see Fig. 1).

### fMRI Data

As hypothesized, a region was found in the ACC that showed a significant interaction between scan and condition (BA 32; 24 contiguous voxels, peak activation  $x$ , -3;  $y$ , 32;  $z$ , 31). This region showed the largest BOLD response to RI stimuli. However, SI stimuli elicited a signal that was smaller than the signal to CO stimuli (see Fig. 2). Post hoc testing indicated that the difference between CO and SI was not significant, at any scan time point ( $F$  range 0.884–3.796, all  $P > 0.05$ ), whereas RI was significantly larger than CO at scan 3 ( $F = 7.712$ ,  $P < 0.05$ ) and scan 4 ( $F = 5.836$ ,  $P < 0.05$ ). The correlation between peak activity in the RI condition and reaction time interference was not significant ( $r = -0.031$ , NS).

Thus, the present data appear to indicate that the ACC is selectively responsive to response conflict. However, because the behavioral effect of stimulus conflict was relatively small (19 ms) compared to the effect of response conflict, the possibility exists that the ACC is responsive to *strong* general conflict rather than response conflict. We tested this possibility by analyzing high and low stimulus conflict by using a median split on the RTs for that condition. This resulted in a fast SI (mean RT = 493 ms; SD = 74) and a slow SI (mean RT = 634 ms, SD = 87) condition for each subject. Thus, RTs in the slow SI condition were *slower* than RTs in the RI condition (624 ms), although this difference was not significant ( $t = 0.88$ , NS). The RTs in these two conditions can therefore be considered roughly equal. We can thus assume that the amount of



**FIG. 2.** The BOLD response of the anterior cingulate cortex in each condition (% MR change from baseline). Activity was increased in response to RI stimuli, but did not differ between CO and SI stimuli. CO, black; SI, green; RI, red; fast SI, dashed dark green; slow SI, dotted dark green.

general conflict was similar for the slow SI and the RI conditions. If the ACC were responsive to strong general conflict rather than response conflict, its signal should therefore be equal for these two conditions. However, paired *t* tests carried out for each scan showed that the signals for both fast SI and slow SI were still significantly lower than the RI signal for scans 3 and 4 (*t* range 2.88–3.80, all *P* < 0.05), while there was a trend toward significance at scan 2 (*t* range 1.87–2.12, all *P* < 0.1). At no scan were there any significant differences between the fast SI and slow SI signals and the CO or the total SI signal. Thus, although there was no reliable RT difference between the RI and the slow SI conditions, the ACC response was still significantly larger to RI stimuli. It should, however, be noted that a median split carried out for the RI condition did not result in a significant difference between the BOLD responses to the slow and fast conditions either, which is consistent with the lack of between-subject correlation observed between the BOLD response for the RI trials and the RT interference in the present study.

Several other regions showed a significant interaction between scan and condition (see Table 1). The BOLD responses of several regions mirrored the BOLD response of the ACC, in that the activation to RI stimuli was highest, without a significant difference between the response to CO and SI stimuli. These regions are the bilateral superior DLPFC (BA 9), the right posterior parietal cortex (BA 40), and the precuneus. A number of other regions showed a pattern in which the BOLD response elicited by SI stimuli was lowest and the response to RI stimuli was highest. These areas are

the left polar frontal cortex (BA 9), the bilateral mid-DLPFC (BA 46), and the posterior cingulate (BA 23). Only one region, located in the left inferior frontal cortex (BA 44; 8 contiguous voxels; peak activation *x*, -44; *y*, 16; *z*, 13), showed a BOLD response that was larger to SI stimuli than to CO stimuli (at scan 2, *F* = 7.463, *P* < 0.05). The BOLD response to RI stimuli was larger than to SI stimuli at scan 3 (*F* = 6.690, *P* < 0.05). Thus, the amplitude of the BOLD response of this region reflected RT data.

## DISCUSSION

In the present study, we sought to determine what levels of processing may be monitored by the ACC for the presence of conflict. Analysis of the behavioral data confirmed that subjects showed evidence for conflict at both earlier and later processing levels. SI stimuli elicited longer RTs than CO stimuli (indicating earlier or stimulus conflict), and RI stimuli elicited longer reaction times than SI stimuli (indicating later or response conflict). These results replicate earlier findings using the flanker task (Eriksen and Eriksen, 1974; Eriksen and Schultz, 1979). Analyses of the functional MRI data revealed a region in the ACC (BA 32) that responded strongest to RI stimuli, as expected; however, its activation to SI stimuli was the same as its activation to CO stimuli. To address the possibility that the ACC is responsive to the *degree* of conflict rather than the *type* of conflict, we analyzed the data using a subject-wise median split based on RTs for the SI condition. Although the RTs were not significantly different between the slow SI and the RI conditions, the ACC

**TABLE 1**  
Regions Showing Differential Activity to Different Experimental Conditions

Area	No. voxels	<i>x</i>	<i>y</i>	<i>z</i>	Avg. <i>F</i>	Max. <i>F</i>	Pattern
ACC (BA 32)	24	-3	32	31	4.08	4.97	(CO = SI) < RI
Left IFC (BA 44)	8	-44	16	13	4	4.54	CO < SI < RI
Left DLPFC (BA 9)	11	-38	16	39	4.12	4.93	(CO = SI) < RI
Right DLPFC (BA 9)	10	36	13	40	4.28	5.02	(CO = SI) < RI
Right DLPFC (BA 46)	31	46	42	16	4.38	6.35	SI < (CO = RI)
Left DLPFC (BA 46/45)	8	-34	33	15	4.49	5.82	SI < (CO = RI)
Right parietal (BA 40)	9	37	-46	41	3.74	4.25	(CO = SI) < RI
Left precuneus (BA 7/31)	36	2	-64	28	3.83	4.52	(CO = SI) < RI
Posterior cingulate gyrus (BA 23)	42	3	-15	32	4.32	5.9	SI < CO < RI
Left polar frontal (BA 10/9)	118	-1	57	23	4.57	10.15	SI < CO < RI

*Note.* Overview of regions showing a significant scan by condition interaction. Shown are the number of pixels; the *x*, *y*, and *z* coordinates in Talairach space; the maximum and average *F* values of the interaction term; and the overall pattern of the BOLD responses.

response was still significantly higher in the RI than in the slow SI condition. This ruled out the possibility that the ACC is responsive to strong general conflict independent of the processing level at which it occurs. Moreover, if the ACC were responsive to conflict at a stimulus encoding or target detection level, we would have expected the BOLD response to SI to be higher than to CO stimuli. Thus, these results suggest that the ACC detects conflict only at later or response-related processing levels.

The finding that the ACC is activated to response conflict rather than stimulus conflict is consistent with the close relationship between the ACC and the motor system (Picard and Strick, 1996). There exists a rich interconnectivity between the motor areas and the ACC; the ventral and dorsal banks of the cingulate sulcus are proposed to contain motor areas (Picard and Strick, 1996). The ACC region identified in this study (*x*, -3; *y*, 32; *z*, 31) is remarkably close to the region identified in our earlier study using the Eriksen flanker task (*x*, -2; *y*, 28; *z*, 31) (Botvinick *et al.*, 1999) and fairly close to another recent study that used the Eriksen task (*x*, -8; *y*, 22; *z*, 32) (Casey *et al.*, 2000). The area identified in these three studies falls into what Picard and Strick (1996) call the rostral cingulate motor zone, which they observe is activated during complex motor acts. Our results unite the view that the ACC is part of the motor system (Picard and Strick, 1996) with the view that the ACC plays a role in attention and performance monitoring (Carter *et al.*, 1998). In this view, the ACC contributes to executive functions by evaluating the level of conflict at the level of action planning or execution and indicating the degree to which top-down control needs to be engaged (Botvinick *et al.*, 2001).

It should be pointed out that, in addition to response conflict detection, the observed pattern of ACC activity to the three types of stimuli is also consistent with the

notion that the ACC is involved in response inhibition (George *et al.*, 1994; Kopp *et al.*, 1996; Smith and Jonides, 1999). Assuming that the flankers "prime" the associated response, only in the RI condition would one inhibit an incorrectly primed response. However, this hypothesis can be ruled out on the basis of previous findings. Although in the present study, no relationship was found between ACC activity and RT interference in the RI condition, previous studies have consistently found a positive correlation (Botvinick *et al.*, 1999; Carter *et al.*, 2000; Casey *et al.*, 2000; MacDonald *et al.*, 2000). Such results are inconsistent with the response inhibition hypothesis: larger inhibitory effort should result in more effective suppression of the erroneous response, thus in a shorter RT. The response inhibition hypothesis would thus predict a larger ACC response to shorter reaction times in the RI condition. The conflict hypothesis, in contrast, predicts a larger ACC signal with a larger amount of response conflict, thus with longer reaction times in the response-incongruent condition, which is mostly what has been found previously.

As can be seen in Table 1, a number of other regions activated differentially to the various trial types. These include several patterns of activity similar to that seen in the ACC. Although it is beyond the scope of the present paper, it is likely that this activity in these regions represents the detection and subsequent resolution of conflict by regions forming a distributed network in the service of executive control. Although the present data do not directly address the nature of the interactions among these regions, several theoretical accounts have recently been put forward to address the possible dynamics of monitoring and control functions within the human brain (Botvinick *et al.*, 2001; Cohen *et al.*, 2000; Gehring and Knight, 2000; MacDonald *et al.*, 2000).

The present results, taken together with those reviewed, argue against the notions that the ACC is directly involved in the top-down control of attention (Posner and Petersen, 1990) or that it responds to general difficulty (Paus *et al.*, 1998). These theories would have predicted an increase in ACC activity that mirrored the differences in the reaction times. The current study provides evidence that the ACC is mostly responsive to response-based conflict, rather than stimulus-based or general conflict, which has important implications for theories regarding performance monitoring and its implementation in the brain and makes strong predictions regarding the type of situations in which ACC activity should be observed in future studies. However, it should be emphasized that the present study was limited to conflict at stimulus and response levels. This leaves open the possibility that in addition to response conflict, the ACC is responsive to conflict occurring between different goal states, plans, rewards, semantic or syntactic representations, activity associated with early sensory processes, decisions which occur at intermediate levels between stimulus processing and action planning, and so on. Future studies are needed to address these issues.

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**REFERENCES**

Barch, D. M., *et al.* 2000. Anterior cingulate and the monitoring of response conflict: Evidence from an fMRI study of overt word generation. *J. Cognit. Neurosci.* **12**: 298–309.

Bench, C. J., *et al.* 1993. Investigations of the functional anatomy of attention using the Stroop test. *Neuropsychologia* **31**: 907–922.

Botvinick, M. M., *et al.* 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature* **402**: 179–181.

Botvinick, M. M., *et al.* 2001. Conflict monitoring and cognitive control. *Psychol. Rev.* **108**: 624–652.

Bush, G., *et al.* 2000. Cognitive and emotional influences in anterior cingulate cortex. *Trends Cognit. Sci.* **4**: 215–222.

Carter, C. S., *et al.* 1998. Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* **280**: 747–749.

Carter, C. S., *et al.* 2000. Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *Proc. Natl. Acad. Sci. USA* **97**: 1944–1948.

Casey, B. J., *et al.* 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., *et al.* 1993. PsyScope: An interactive graphic system for designing and controlling experiments in the psychology laboratory using Macintosh computers. *Behav. Res. Methods Instrum. Comput.* **25**: 257–271.

Cohen, J. D., *et al.* 1996. A computational approach to prefrontal cortex, cognitive control and schizophrenia: Recent developments and current challenges. *Philos. Trans. R. Soc. London Biol.* **351**: 1515–1527.

Cohen, J. D., *et al.* 2000. Anterior cingulate and prefrontal cortex: Who's in control? *Nat. Neurosci.* **3**: 421–423.

Crosson, B., *et al.* 1999. Activity in the parcingulate and cingulate sulci during word generation: An fMRI study of functional anatomy. *Cereb. Cortex* **9**: 307–316.

D'Esposito, M., *et al.* 1995. The neural basis of the central executive system of working memory. *Nature* **378**: 279–281.

Dehaene, S., *et al.* 1994. Localization of a neural system for error detection and compensation. *Psychol. Sci.* **5**: 303–305.

Desimone, R., and Duncan, J. 1995. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18**: 193–222.

Devinsky, O., *et al.* 1995. Contributions of anterior cingulate cortex to behaviour. *Brain* **118**: 279–306.

Eriksen, B. A., and Eriksen, C. W. 1974. Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept. Psychophys.* **16**: 143–149.

Eriksen, C. W., and Schultz, D. W. 1979. Information processing in visual search: A continuous flow conception and experimental results. *Percept. Psychophys.* **25**: 249–263.

Forman, S. D., *et al.* 1995. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magn. Reson. Med.* **33**: 636–647.

Gehring, W. J., and Knight, R. T. 2000. Prefrontal-cingulate interactions in action monitoring. *Nat. Neurosci.* **3**: 516–520.

George, M. S., *et al.* 1994. Regional brain activity when selecting a response despite interference: An H<sub>2</sub><sup>15</sup>O PET study of the Stroop and an emotional Stroop. *Hum. Brain Mapp.* **1**: 194–209.

Kiehl, K. A., *et al.* 2000. Error processing and the rostral anterior cingulate: An event-related fMRI study. *Psychophysiology* **37**: 216–223.

Kopp, B., *et al.* 1996. N200 in the flanker task as a neurobehavioral tool for investigating executive control. *Psychophysiology* **33**: 282–294.

Kornblum, S. 1994. The way irrelevant dimensions are processed depends on what they overlap with: The case of Stroop- and Simon-like stimuli. *Psychol. Res./Psychol. Forsch.* **56**: 130–135.

Kornblum, S., *et al.* 1990. Dimensional overlap: Cognitive basis for stimulus-response compatibility: A model and taxonomy. *Psychol. Rev.* **97**: 253–270.

Kornblum, S., *et al.* 1999. The effects of irrelevant stimuli. 1. The time course of stimulus-stimulus and stimulus-response consistency effects with Stroop-like stimuli, Simon-like tasks, and their factorial combinations. *J. Exp. Psychol. Hum. Percept. Perform.* **25**: 688–714.

Lindsay, D. S., and Jacoby, L. L. 1994. Stroop process dissociations: The relationship between facilitation and interference. *J. Exp. Psychol. Hum. Percept. Perform.* **20**: 219–234.

Logan, G. D., and Zbrodoff, N. J. 1979. When it helps to be misled: Facilitative effects of increasing the frequency of conflicting stimuli in a Stroop-like task. *Memory Cognit.* **7**: 166–174.

MacDonald, A. M., *et al.* 2000. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* **288**: 1835–1838.

Miller, E. K. 2000. The prefrontal cortex and cognitive control. *Nat. Rev. Neurosci.* **1**: 59–65.

Noll, D. C., *et al.* 1995. Spiral K-space MR imaging of cortical activation. *J. Magn. Reson. Imaging* **5**: 49–56.

Pardo, J. V., *et al.* 1990. The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proc. Natl. Acad. Sci. USA* **87**: 256–259.

Paus, T., *et al.* 1998. Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex: A review of 107 PET activation studies. *NeuroReport* **9**: R37–R47.

- Petersen, S. E., *et al.* 1988. Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* **331**: 585–589.
- Picard, N., and Strick, P. L. 1996. Motor areas of the medial wall: A review of their location and functional activation. *Cereb. Cortex* **6**: 342–353.
- Posner, M. I., and Petersen, S. E. 1990. The attention system of the human brain. *Annu. Rev. Neurosci.* **13**: 25–42.
- Smith, E. E., and Jonides, J. 1999. Storage and executive processes in the frontal lobes. *Science* **283**: 1657–1661.
- Taylor, S. F., *et al.* 1997. Isolation of specific interference processing in the Stroop task: PET activation studies. *NeuroImage* **6**: 81–92.
- Tzelgov, J., *et al.* 1992. Controlling Stroop effects by manipulating expectations for color words. *Memory Cognit.* **20**: 727–735.
- Woods, R. P., *et al.* 1992. Rapid automated algorithm for aligning and reslicing PET images. *J. Comput. Assisted Tomogr.* **17**: 536–546.
- Zhang, H., *et al.* 1999. A parallel distributed processing model of stimulus–stimulus and stimulus–response compatibility. *Cognit. Psychol.* **38**: 386–432.