

The Role of the Anterior Cingulate Cortex in Conflict Processing: Evidence from Reverse Stroop Interference

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A recent theoretical account delineated the role of the anterior cingulate cortex (ACC) in cognitive control as the detection of conflict between competing information streams. Using functional magnetic resonance imaging, we examined the activity of this brain structure during different forms and degrees of conflict between the word and the color dimensions of Stroop stimuli. Overall, our results showed a dissociation between the degree of conflict and ACC activation. More specifically, although ACC activation was very extensive when print color interfered with word reading performance, the level of conflict, as measured by reaction time costs, was only moderate compared to other conditions. These results suggest that either the ACC is differentially sensitive to various types of conflict or its function should be extended to include other cognitive constructs, such as resolution of prior inhibition. © 2001 Academic Press

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INTRODUCTION

A currently controversial topic in cognitive neuroscience is the role of the anterior cingulate cortex (ACC) in the higher order control of cognitive activity. A number of neuroimaging studies have found an increase in the activity of a dorsal part of the ACC during the performance of tasks which necessitate the processing of conflict between information streams. The nature of this conflict has included overriding a dominant response tendency (Bush *et al.*, 1998; Evans and Meyer, 1993; Pardo *et al.*, 1990; Paus *et al.*, 1994), dividing attention between competing tasks (Corbetta *et al.*, 1991; D'Esposito *et al.*, 1995), initiating the selection of an appropriate novel response among several alternatives (Liddle *et al.*, 2001; Frith *et al.*, 1991; Petersen *et al.*, 1988; Raichle *et al.*, 1994), or modifying behavior according to error-related feedback (Carter *et al.*, 1998; Kiehl *et al.*, 2000; Menon *et al.*, 2001). It is

thus empirically well established that the ACC is crucially involved in processing conflicting information (Bush *et al.*, 2000; Carter *et al.*, 1999; Posner and DiGirolamo, 1998).

Traditionally, the cognitive role ascribed to the ACC in these "conflict" situations has been that of *conflict resolution* (Posner and Rothbart, 1998; Peterson *et al.*, 1999). For example, Peterson *et al.* (1999) concluded that "anterior cingulate subregions modulate neural pathway strengths within attentional subsystems" and that the ACC carries out "higher order coordination and organization of activity in distributed attentional networks" (p. 1253). However, this widely held notion has recently been displaced by the hypothesis that the ACC is involved in the *detection* of the *degree* of a conflict. According to this hypothesis, the ACC has the evaluative function of monitoring performance for processing conflict, while the strategic processes resolving conflict are mediated by other brain structures such as the prefrontal cortex (Carter *et al.*, 1999, 2000; Cohen *et al.*, 2000; MacDonald *et al.*, 2000).

Many of the investigations of ACC function have employed classical Stroop paradigms, in which participants are asked to name the print color of color words with an incongruent (RED printed in blue, answer blue), neutral (XXXX printed in blue, answer blue), or congruent (RED printed in red, answer red) word dimension (MacLeod, 1991; Stroop, 1935). The degree of conflict between word meaning and print color is usually referred to as the *Stroop effect* and is computed as the reaction time (RT) difference between the incongruent and the neutral color-naming trials. Note that a slowing of *word reading* due to conflict with incongruent print color (the *reverse Stroop effect*) is normally not observed (i.e., word reading, the dominant response, is not affected by conflicting information in the nondominant color dimension of the stimulus) (Glaser and Glaser, 1982; MacLeod, 1991). Thus, while ACC activation is expected to be present comparing incongruent to neutral *color naming*, ACC activation is expected to be absent comparing incongruent to neutral *word reading*

(the neutral word reading stimulus is a color word written in black "ink").

In direct contrast to the traditional view of the respective presence and absence of Stroop and reverse Stroop conflict, it has now been clearly demonstrated that substantial reverse Stroop conflict (i.e., interference from the conflicting print color during word reading) can be elicited when subjects are required to switch between color naming and word reading (Allport *et al.*, 1994; Allport and Wylie, 1999). This suggests that the study of conflict evaluation/resolution in response to Stroop stimuli need not be restricted to the task of color naming, but may be extended to word reading. Moreover, because the Stroop and reverse Stroop effects are considered symmetrical in terms of size within the context of task switching (Allport *et al.*, 1994; Allport and Wylie, 1999), they can be considered approximately equivalent indices of conflict. Thus, within specific experimental contexts (such as task switching), the involvement of the ACC in processing conflicting information streams can be studied *across* tasks (color naming and word reading) in response to the same Stroop stimuli.

If the ACC's main function in conflict processing is the detection of the degree of any given conflict (as predicted by the conflict detection account), roughly equivalent ACC activation should be observed for both the Stroop and the reverse Stroop conditions, in the context of task switching. However, if the ACC activation does not correspond to the degree of behavioral conflict present in the reverse Stroop condition, we must formulate new hypotheses regarding the involvement of this brain structure in conflict detection. For example, if we fail to observe ACC activation in the reverse Stroop condition, we may conclude that the involvement of this brain structure in processing word-color interference does not extend to the task of word reading. Alternatively, if we observe disproportionately increased ACC activation in the reverse Stroop condition, we may conclude either that the ACC subserves additional executive processes other than conflict detection for incongruent word reading, or that the ACC is differentially sensitive to qualitatively distinct types of conflict, resulting in a lack of correspondence to the behavioral indices of conflict.

We employed event-related fMRI in four distinct stimulus runs. For all runs, conflict was quantified as the RT difference between incongruent and neutral trials. These runs were as follows: (1) repeated word reading (no conflict expected), (2) repeated color naming (Stroop interference expected), (3) switching from color naming to word reading (reverse Stroop interference expected), and (4) switching from word reading to color naming (Stroop interference expected). The degree of ACC activation was quantified in a similar fashion, by comparing the magnitude of the hemodynamic response to incongruent stimuli with that for

neutral stimuli. The "conflict detection" account outlined above would predict ACC activation in comparable anatomical locations, and of comparable magnitude, for both Stroop and reverse Stroop conflict conditions. Moreover, no conflict or ACC activation would be predicted for word reading in the repeated block.

MATERIALS AND METHODS

Subjects and Tasks

Subjects were 12 right handed, healthy, native English speakers with normal or corrected to normal vision (mean age 23.08, SD 2.48 years, 6 women). Participants underwent screening for MRI compatibility and gave their written consent. The procedures administered complied with both University and Hospital ethical approval.

Prior to entering the scanning room, subjects were trained to read color words using a manual response. The words RED, GREEN, BLUE, and YELLOW were presented using SuperLab software (SuperLab Experimental Lab Software 2.01, 1999), and subjects responded with the following scheme: left index finger RED, left middle finger GREEN, right index finger YELLOW, and right middle finger BLUE. Stimuli were randomly selected, and 50% were printed in black "ink," while the other 50% were printed in one of the three incongruent print colors. Each stimulus remained on the screen until the subject responded, and the interstimulus interval (ISI) was 3–5 s (randomly determined). Feedback for errors ("Incorrect") or slow responses exceeding 1200 ms ("Too slow") appeared on the screen for 1 s before the next stimulus was presented. Two runs of 180 trials each were administered, and all subjects had extinguished incorrect and slow responses on completion of these runs.

For scanning trials, in the darkened room, a custom visual presentation package projected the stimuli on a rear projection screen mounted at the entrance to the magnet bore. Participants viewed the screen by means of a mirror system attached to the head coil. Two commercially available MRI-compatible fiber-optic response devices with two buttons each were used for the subjects' responses according to the pattern described above. Each of the four conditions (color-naming repeated, color-naming switch, word-reading repeated, and word-reading switch) was administered in one distinct stimulus run of 495 s. Timing scales and displays of the stimuli used in these blocks are given in Fig. 1.

In each of these recording blocks, 60 pairs of Stroop stimuli (font Helvetica 38, visual angle approximately $3 \times 7^\circ$) were sequentially presented, articulated into pairs, against a grey background image. Each stimulus of a pair stayed on the screen for 2 s, with no delay between the completion of the presentation of the first

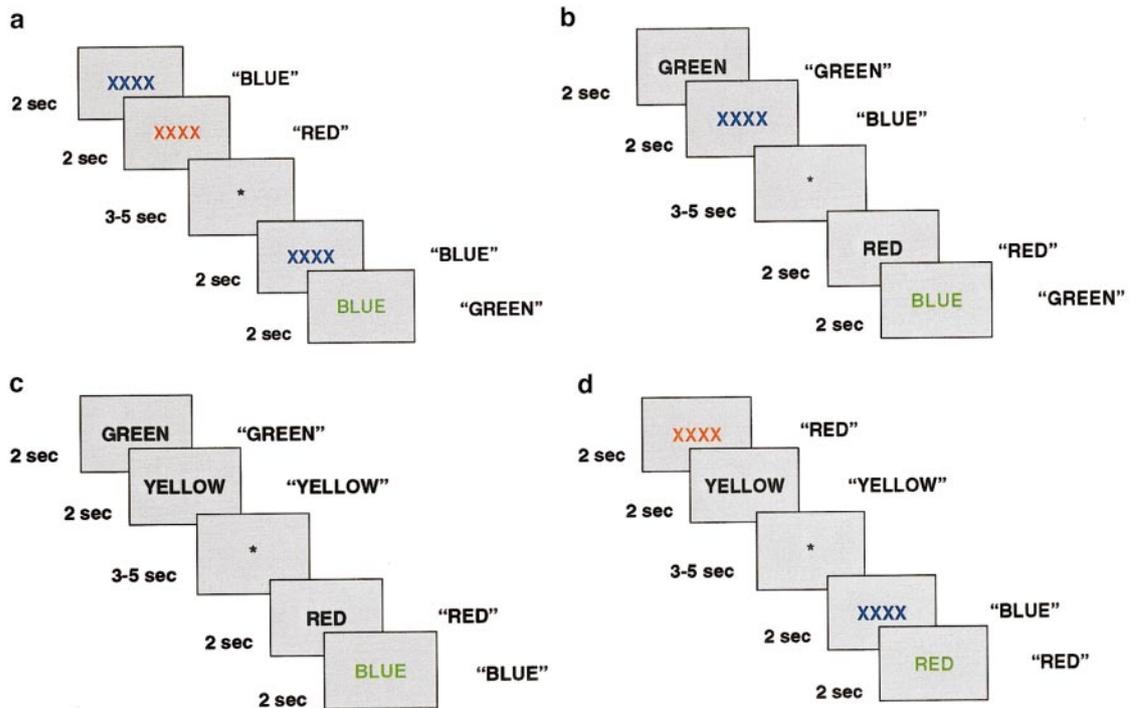


FIG. 1. Experimental design of the four conditions. (a) Repeated color naming, (b) switching color naming, (c) repeated word reading, and (d) switching word reading. Designated responses are given at the right of each screen symbol. Stimuli were presented in pairs, with a presentation time of 2 s per stimulus and an ISI of 7–9 s between the stimuli of interest (second stimulus of the pairs). One image per 3 s was acquired, allowing the sampling of the hemodynamic response at 1-s intervals.

stimulus and the onset of the second stimulus. A randomly determined interval of 3–5 s showing a fixation cross in the center of the screen was included between stimulus pairs. Thus, stimuli of interest had an equal probability of occurring at 0, 1, or 2 s after the beginning of a 3-s image acquisition period, allowing sampling of the hemodynamic response uniformly in 1-s intervals.

Prior to each of the four scan series, the participants were informed which features of the paired stimuli that they should respond to throughout that series (“always word,” “always color,” “first color, then word,” “first word, then color”). The first stimulus of a pair was always a neutral Stroop stimulus and served to establish a repeated or switching response to the second stimulus. The second stimulus of a pair was the stimulus of interest and was either a neutral or an incongruent Stroop stimulus (30 of both types). Neutral stimuli for color-naming responses were always the letters XXXX printed in one of the four colors. Neutral stimuli for word-reading responses were always one of the color words RED, GREEN, BLUE, or YELLOW printed in black “ink.” Stimuli and stimulus combinations within pairs were completely randomized.

Both color-naming blocks (indicating that responses to the stimuli of interest consisted of color naming) comprised 30 neutral and 30 incongruent stimuli of interest each. (Recall that the “stimulus of interest”

was always the second member of the pair.) The repeated and switching color-naming blocks differed only with respect to the task carried out in position 1 of the response pair. Participants were instructed to respond either by color naming or by word reading in response to the first stimulus of the pair. (Recall that the response to the second member of the pair was always color naming.)

Both word-reading blocks (indicating that responses to the stimuli of interest consisted of word reading) comprised 30 neutral and the 30 incongruent stimuli of interest, with the only difference being whether the subjects performed word reading or color naming in response to the first stimulus of the pairs. As reading of incongruent color words has been demonstrated to be slowed by interference effects from previous incongruent color-naming responses (Allport *et al.*, 1994; Allport and Wylie, 1999), all participants completed repeated word-reading blocks first, followed by repeated color-naming blocks. The two switching blocks were completed next, and the order of the switching blocks was counterbalanced across subjects.

Imaging and Image Processing

Imaging was performed with a clinical GE 1.5-T whole-body MRI system fitted with a Horizon echo speed upgrade. The participant’s head was firmly se-

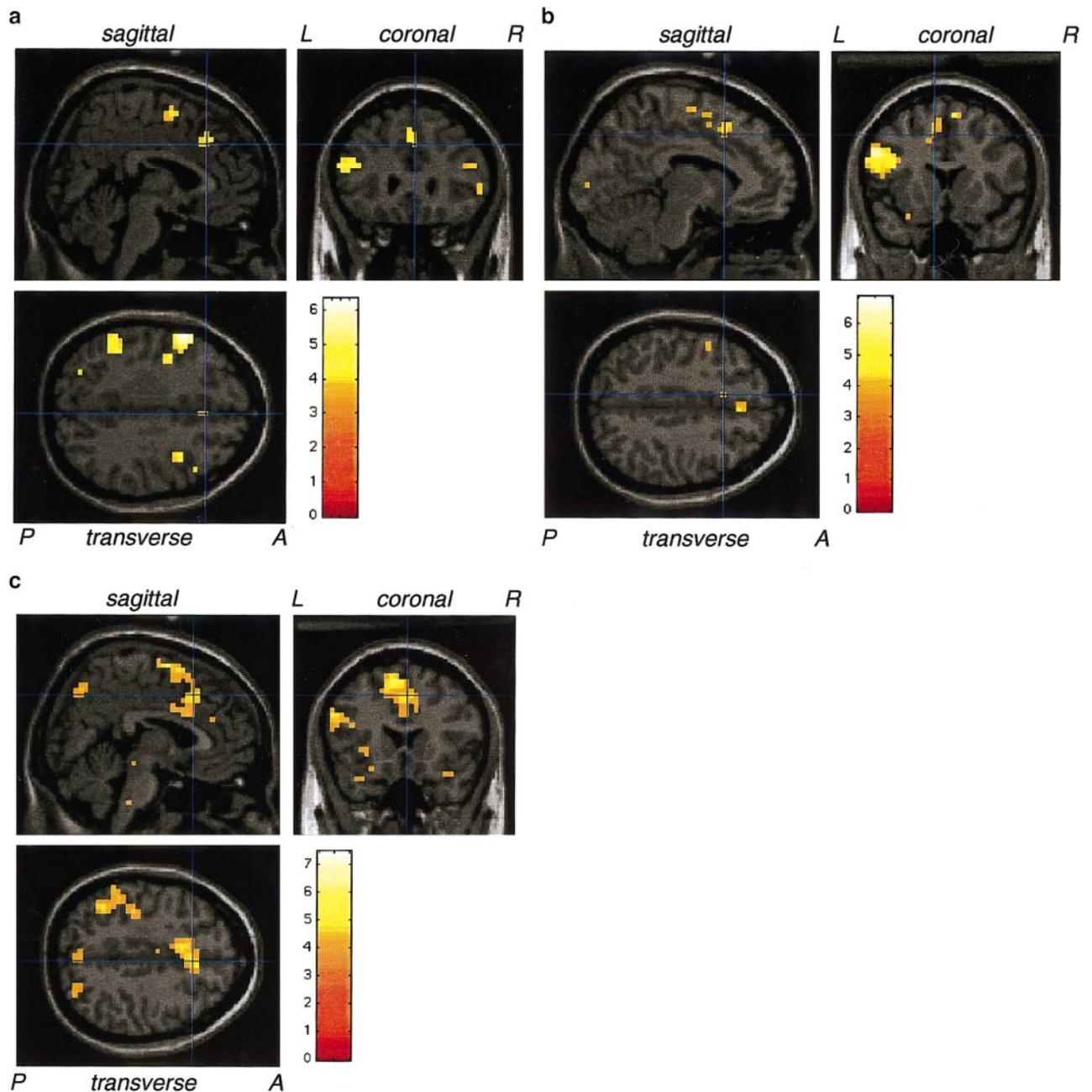


FIG. 2. ACC activation for incongruent compared to neutral stimuli. (a) Repeated color naming, (b) switching color naming, and (c) switching word reading. No activation differences were found for repeated word reading. Z values are plotted on sagittal, coronal, and transverse sections of a standard template brain according to the color scale given at the right of each transverse section (L, left hemisphere; R, right hemisphere; A, anterior end; P, posterior end). Note the scaling differences of these three color bars. Slices chosen for the different conditions are not in the exact same anatomical location, as they were chosen to display the maximum ACC activation present in the respective condition. All Z values are significant on the level of $P < 0.05$ corrected for multiple comparisons only within the anterior cingulate.

cured using a custom head holder. Conventional spin echo T1-weighted sagittal localizers confirmed this positioning. Functional image volumes were collected with a gradient echo sequence (TR/TE = 3000/40 ms, flip angle 90° , FOV 24×24 cm, 64×64 matrix, 62.5-kHz bandwidth, 3.75×3.75 mm in-plane resolution, 5-mm slice thickness, 29 slices) effectively covering the

whole brain (145 mm axial extent). During each stimulus run, a total of 165 images of the entire brain were collected in a period of 495 s. Each of these stimulus runs was preceded by a 12-s rest condition allowing T1 effects to stabilize. The four brain volumes collected during this period were not included in any subsequent analyses.

Functional images were reconstructed offline, and the four scan series were independently realigned and motion corrected using the method implemented in SPM99 (Statistical Parametrical Mapping 99, 1999). Translation and rotation corrections did not exceed 2.0 mm and 2.2° for any of the participants. Parameters for spatial normalization into the modified Talairach space used in SPM99 (Statistical Parametrical Mapping 99, 1999) were determined using mean functional images constructed from the realigned images of each participant and scan series. Note that all coordinates given in this article refer to this modified Talairach space. The normalized functional images were smoothed with an 8-mm full width at half-maximum Gaussian filter. Low-frequency noise was removed using a 0.1-Hz high-pass filter. Variations in global signal intensity were not removed because of the danger of producing spurious local changes in the direction opposite to any change in global signal. The event-related responses to all events were modeled using a synthetic hemodynamic response function composed of two γ functions, including their temporal derivatives (Josephs *et al.*, 1997). For each of the scan series, the model of the composite hemodynamic response for the entire run comprised a sequence of appropriately placed synthetic responses to three different events: the 60 neutral stimuli presented as the first members of the stimulus pairs, the 30 neutral stimuli of interest, and the 30 incongruent stimuli of interest. The general linear model approach implemented in SPM99 (Statistical Parametrical Mapping 99, 1999) thus allowed us to estimate, and statistically test, the influence of each of these event conditions on the hemodynamic response in each voxel under consideration. By specifying and calculating contrasts between incongruent and neutral event conditions *within* each of the runs (e.g., incongruent repeated word reading vs neutral repeated word reading), we thus obtained an estimate of (and statistical values for) the additional increase of ACC activation in response to incongruent compared to neutral stimuli. The error variance for this procedure was estimated from the residuals within each subject, with the method implemented in SPM99 (Statistical Parametrical Mapping 99, 1999).

In addition, a region of interest (ROI) analysis was performed to test the hypothesis that the magnitude of the difference in hemodynamic response between incongruent and neutral stimuli was greatest during the word-reading reverse Stroop condition in the context of switching, compared to the color-naming Stroop conditions, in the vicinity of the cingulate site implicated in conflict detection in previous studies. We defined a 27-voxel cubic ROI ($3 \times 3 \times 3$ voxels) whose central voxel contained the location ($x = 0, y = 15, z = 41$) at which Carter *et al.* (2000) reported peak activation during conflict detection using Stroop stimuli. We chose this theoretically derived location, as performing

the analysis in the voxels demonstrating peak activations for the different conditions in our study would lead to a bias toward the respective condition. For each voxel in the ROI, the difference between the regression weights fitting the hemodynamic response for the incongruent stimuli and those for the neutral stimuli was taken as a measure of the magnitude of the difference in hemodynamic response between the incongruent and the neutral stimuli, for each of the four conditions. Using SPSS for Windows release 8.0, a two-way repeated-measures ANOVA, treating word naming/color naming and switching/nonswitching as the two factors, was performed, together with a planned comparison contrasting the effect for reverse Stroop in the context of switching with the mean of the two Stroop conditions.

RESULTS

In congruence with our hypotheses and previous findings, substantial behavioral conflict was observed in both the repeated (235 ms, $t(11) = 9.09, P < 0.001$) and the switching (126 ms, $t(11) = 6.21, P < 0.001$) color naming conditions (Stroop interference) and in the switching word reading condition (148 ms, $t(11) = 12.52, P < 0.001$) (reverse Stroop interference). For repeated word reading, a small but significant reverse Stroop effect was found (26 ms, $t(11) = 3.53, P < 0.01$). Error rates were low, with over 90% correct responses for all conditions (see Table 1)¹.

To analyze the ACC activation associated with these interference effects, we specified contrasts (for the comparison of incongruent versus neutral stimuli of interest, see above) within each of the four stimulus runs, with the method implemented in SPM99 (Statistical Parametrical Mapping 99, 1999). A fixed-effects analysis was employed to compare these within-subjects conditions. To examine our a priori hypotheses regarding activation in the ACC, a small-volume correction for multiple comparisons within this brain structure only was applied to the threshold for statistical significance ($P = 0.05$), with a method based on the theory of Gaussian fields (Worsley *et al.*, 1996). As reported previously for repeated color naming (Carter *et al.*, 2000; Macdonald *et al.*, 2000; Pardo *et al.*, 1990; Peterson *et al.*, 1999; Posner and DiGirolamo, 1998; Posner and Rothbart, 1998) areas of increased activation in the ACC were found for Stroop interference (peak: $x = 4, y = 28, z = 36, Z$ score 4.30). We found strikingly similar activation (in terms of both level and location) for Stroop interference in the switching condition (peak: $x = -12, y = 16, z = 40, Z$ score 4.02). These clusters were of comparable size (2 and 3 contiguous

¹ Due to equipment failure, the RT for one key (GREEN) was not recorded for two subjects.

TABLE 1

Mean Reaction Times and Percentage of Correct Responses for the Stimuli of Interest in the Four Conditions

	Repeated response		Switching response	
	Reaction time	Correct response	Reaction time	Correct response
Color naming				
Color neutral	691 ms (137 ms)	97.11% (9.10%)	748 ms (142 ms)	98.88% (12.88%)
Color incongruent	926 ms (189 ms)	92.15% (11.59%)	874 ms (188 ms)	96.62% (12.13%)
Stroop effect	235 ms***		126 ms***	
Word reading				
Word neutral	639 ms (97 ms)	98.53% (11.05%)	757 ms (131 ms)	97.52% (8.99%)
Word incongruent	665 ms (95 ms)	96.29% (13.06%)	905 ms (136 ms)	91.58% (13.55%)
Reverse Stroop effect	26 ms**		148 ms***	

Note. Standard deviations are given in parentheses. Reaction time differences for incongruent and neutral stimuli were tested for significance with paired *t* tests (*df* = 11) and are marked according to the scheme *** *P* ≤ 0.001 and ** *P* ≤ 0.01.

voxels, respectively, within the ACC) and extended into the pre-SMA. For the comparison of the hemodynamic response associated with reverse Stroop interference, we found an extensive cluster of increased activation in the ACC for the switching condition (55 voxels), extending into the pre-SMA, with peaks located bilaterally at *x* = 4, *y* = 20, *z* = 44 (*Z* score 5.18) and at *x* = -4, *y* = 12, *z* = 40 (*Z* score 5.18). No ACC activation was detected for the contrast of incongruent and neutral trials in the condition of repeated word reading (Fig. 2).

To counter the possibility that differences in variances in the four conditions may have contributed to the differences in activation detected in our within-condition contrasts, we directly compared the ACC activation associated with incongruent word reading in the switching condition with the mean ACC activation during incongruent color naming in the two color-naming conditions. In both ACC peak voxels detected in the switching word-reading condition (*x* = -4, *y* = 12, *z* = 40, and *x* = 4, *y* = 20, *z* = 44), this comparison revealed significantly higher activation for incongruent word reading compared to incongruent color naming (*Z* = 5.00 and *Z* = 6.46, respectively, both *P* < 0.000001 uncorrected for multiple comparisons). The disproportionately high and extensive ACC activation detected for reverse Stroop interference can thus not be considered an artifact of differences in the variability of the hemodynamic response in the different conditions.

An exploratory examination of activations in the whole brain revealed highly significant areas of increased activation in left lateral prefrontal cortex for both repeated (*x* = -56, *y* = 12, *z* = 36, *Z* score 6.30) and switching (*x* = -56, *y* = 12, *z* = 32, *Z* score 6.84) color-naming conditions. (Note that the peak of activation for repeated color naming was only 4 mm superior to that of switching color naming.) In contrast, the strongest activation for both word-reading conditions was found in occipital areas, which was expected, given

the presence of color in the incongruent condition only (see Tables 2 and 3).

Our pattern of results was not affected by an additional analysis at an uncorrected height threshold for significance (*P* = 0.001), which revealed the same, yet

TABLE 2

Color Naming: Significant Areas of Higher Activation for the Response to Incongruent than for Neutral Stimuli

Region of interest	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>Z</i> score
Repeated color naming				
Frontal				
L superior frontal gyrus	-8	16	52	4.76*
L middle frontal gyrus	-40	0	56	6.09***
R middle frontal gyrus	32	0	64	4.99*
L inferior frontal gyrus	-56	12	36	6.30***
R inferior frontal gyrus	36	4	32	5.38**
L precentral gyrus	-36	-4	40	4.81*
Parietal				
L supramarginal gyrus	-44	-44	36	4.86*
L inferior parietal lobule	-48	-56	48	4.73*
Temporal				
L fusiform gyrus	-44	-60	-20	5.06**
Cerebellar				
R uvula	36	-72	-36	4.96*
Switching color naming				
Frontal				
L superior frontal gyrus	-4	4	60	5.30**
R superior frontal gyrus	8	16	60	4.76*
L middle frontal gyrus	-48	44	-8	4.76*
L middle frontal gyrus	-40	0	56	4.68*
L inferior frontal gyrus	-56	12	32	6.84***
L medial frontal gyrus	-8	16	48	4.76*
Cerebellar				
R pyramis	12	-84	-40	5.70***

Note. L, left; R, right. Significance levels of *Z* scores are marked according to the scheme *** *P* ≤ 0.001, ** *P* ≤ 0.01, * *P* ≤ 0.05, corrected for multiple comparisons within the whole brain.

TABLE 3

Word Reading: Significant Areas of Higher Activation for the Response to Incongruent than for Neutral Stimuli

Region of interest	X	Y	Z	Z score
Repeated word reading				
Frontal				
L inferior frontal gyrus	-52	8	36	5.37**
R inferior frontal gyrus	48	4	24	5.55***
L precentral gyrus	-36	-24	52	4.93*
Parietal				
L inferior parietal lobule	-36	-44	40	4.67*
Occipital				
L middle occipital gyrus	-28	-96	0	5.77***
R lingual gyrus	24	-84	-12	8.29***
Cerebellar				
L declive	-40	-60	-24	6.12***
Switching word reading				
Frontal				
L superior frontal gyrus	-4	20	56	6.06***
R middle frontal gyrus	48	28	20	4.76*
L inferior frontal gyrus	-52	24	24	5.23**
L inferior frontal gyrus	-48	32	8	4.85*
L precentral gyrus	-36	-28	68	5.78***
Parietal				
L postcentral gyrus	-24	-36	68	4.71*
L postcentral gyrus	-32	-24	48	5.01*
L inferior parietal lobule	-40	-52	48	5.39**
Occipital				
L inferior occipital gyrus	-36	-92	-12	5.14**
R inferior occipital gyrus	24	-88	-16	7.45***
L lingual gyrus	-24	-100	-12	5.45***
R lingual gyrus	28	-72	-12	5.64***
R cuneus	20	-100	0	6.06***
Cerebellar				
L anterior lobe	-8	-56	-32	5.56***
R anterior lobe	16	-44	-32	5.08**
R pyramid	28	-56	-36	5.88***

Note. L, left; R, right. Significance levels of Z scores are marked according to the scheme *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, corrected for multiple comparisons within the whole brain.

more extensive clusters of ACC activation for both color-naming conditions and for word reading when switching response only. No regions of *deactivation* for incongruent compared to neutral stimuli were found in any of the four conditions. To counter the possibility that differential error rates produced the observed pattern of ACC activation, we repeated the analysis excluding functional images associated with error trials. This did not significantly change the pattern of results.

For the ROI analysis, a 2×2 ANOVA revealed no significant main effect of word reading/color naming ($F(1,11) = 1.44$, $P = 0.25$) or switching/nonswitching ($F(1,11) = 3.37$, $P = 0.09$) nor any significant interac-

tion between these effects ($F(1,11) = 1.78$, $P = 0.21$). However, the planned comparison revealed that the mean value of the difference in regression weights between incongruent and neutral stimuli for the reverse Stroop condition in the context of switching, in the 27-voxel cubic ROI, was 10.68 (SD = 9.51) while the mean of the two Stroop conditions combined was 4.20 (SD = 8.16). A paired t test demonstrated that this difference was significant ($t(11) = 1.72$, $P = 0.056$, one-tailed). In addition, a less conservative fixed-effects contrast of the activation in this ROI associated with incongruent word reading in the switching condition and incongruent color naming in both color-naming conditions revealed significantly higher activation for incongruent word reading ($Z = 5.26$, $P < 0.000001$ uncorrected for multiple comparisons). Taken together, both analyses thus revealed that reverse Stroop interference is associated with higher activation in a theoretically derived, and thus unbiased, location of the ACC.

DISCUSSION

In the present study, we replicated the commonly observed finding of ACC activation for Stroop interference in task repetition. In congruence with the results and predictions of prior research (Carter *et al.*, 2000; Macdonald *et al.*, 2000; Pardo *et al.*, 1990; Peterson *et al.*, 1999; Posner and DiGirolamo, 1998; Posner and Rothbart, 1998), the peak of this activation was located in the so-called "cognitive division" of the ACC, situated posterior to the genu and superior to the corpus callosum (dorsal parts of BA 24 and/or 32, see Bush *et al.*, 2000). Interestingly, an essentially identical pattern of ACC activation was observed for Stroop interference within the context of task switching. However, the most striking result was observed in the reverse Stroop condition within the context of switching. Although stronger and more extensive ACC activation was observed for the reverse Stroop comparison, behavioral conflict, as measured by RT costs, was of intermediate size. Finally, no significant ACC activation was observed for the reverse Stroop comparison in the repeated condition. Correspondingly, conflict, as measured by RT, was decidedly minor in this condition.

The role of the ACC in *detecting conflict* is well established and has been reported in a number of fMRI studies investigating Stroop interference and other paradigms involving response conflict (Bush *et al.*, 1998; Carter *et al.*, 1998, 1999, 2000; Cohen *et al.*, 2000; Corbetta *et al.*, 1991; D'Esposito *et al.*, 1995; Evans and Meyer, 1993; Frith *et al.*, 1991; Kiehl *et al.*, 2000; MacDonald *et al.*, 2000; Pardo *et al.*, 1990; Paus *et al.*, 1988; Peterson *et al.*, 1999; Posner and DiGirolamo, 1998; Posner and Rothbart, 1998; Raichle *et al.*, 1994). Our interpretation of the present set of results does not take issue with this account. However, the

extensive ACC activation observed during a rarely examined task associated with only moderate levels of behavioral conflict (switching reverse Stroop) suggests that either (a) in some instances of conflict processing, the ACC plays a distinct role, over and above conflict detection, or (b) the ACC is differentially sensitive to qualitatively different sources of conflict.

Considering the competing conflict resolution accounts of ACC function, one could presume that an additional function of the ACC might be related to the participation in executive task switching processes, such as modulating attention between stimulus dimensions (Peterson *et al.*, 1999). However, our experimental design excludes this possibility, as this process should be present in both task-switching conditions (color naming and word reading). Therefore, while our results do not exclude the possibility that the ACC may be involved in operations such as modulating attention between stimulus dimensions, this account cannot easily explain the difference in ACC activation between the word-reading (reverse Stroop) and the color-naming (Stroop) switching conditions. The pattern of activation seems instead better explained by an account focusing on between-task differences in the nature of conflict and on the cognitive differences in conflict processing elicited by them.

One possibility for an additional executive process involving the ACC is resolution of prior inhibition. Previous investigations have demonstrated that task switching involves inhibition of the now-irrelevant task (Arbuthnott and Frank, 2000; Mayr and Keele, 2000) and that marked long-term suppression of the dominant stimulus–response (S-R) mappings is a consequence of executing the nondominant task in response to multidimensional stimuli (Allport *et al.*, 1994; Allport and Wylie, 1999). Moreover, it has been demonstrated that this marked suppression may persist for an extended period of time (e.g., between testing blocks) (Allport *et al.*, 1994; Allport and Wylie, 1999) and may be more pronounced when the to-be-processed stimulus is identical to the stimulus on which suppression took place (Allport and Wylie, 1999). Thus, because incongruent color naming always preceded the switching trials in the present experimental session (see Materials and Methods), resolution of the suppressed, dominant S-R mappings may have been more pronounced on incongruent word reading than on neutral word-reading trials within the context of switching.

As was mentioned above, another interpretation of these results is that the ACC is preferentially sensitive to qualitatively distinct types of conflict, resulting in a lack of correspondence with the behavioral indices of conflict. For example, the conflict associated with reverse Stroop interference may be based on the impact of suppression, as discussed above, and/or enhanced competition between the color and the word responses

(Allport and Wylie, 1999). This can be contrasted with the conflict associated with traditional Stroop interference, which is based in interference from the dominant link between reading the word and the response (producing a color word). If the former type of conflict elicits more activation in the ACC than the latter, we would expect a dissociation between the behavioral index of conflict and the activation of ACC, which appears similar to the pattern of results found in our study.

In concordance with this position is the fact that the strategic processes involved in resolving the traditional Stroop interference are thought to be mediated by the lateral prefrontal cortex (Carter *et al.*, 2000; Cohen *et al.*, 2000; MacDonald *et al.*, 2000). We observed substantial activation of left lateral frontal cortex only during the color-naming Stroop comparisons and not during the word-reading reverse Stroop comparisons. This provides additional support for the hypothesis that the conflict associated with these conditions is qualitatively different. Whereas the left lateral frontal cortex seems to be engaged in the suppression of the dominant response to the word dimension (necessary during incongruent color naming), this strategic response is not required to resolve the conflict associated with reverse-Stroop interference.

In summary, the main finding of the present study was that the role of the ACC in conflict processing appears more complex than is postulated by the conflict detection account. Our data suggest that the nature of the conflict under consideration either may demand unique cognitive processes, which are also mediated by the ACC, or may elicit increased or decreased ACC activation depending on the nature of the conflict, which does not correspond to the magnitude of conflict as measured by RT differences. If the ACC does mediate additional cognitive processes over and above conflict detection, it can currently be hypothesized that these processes may be related to the resolution of prior inhibition of dominant S-R mappings. This hypothesis may be tested by future investigations in a variety of ways. Using the same task-switching Stroop paradigm, it could be determined whether switching word reading leads to disproportionately strong ACC activation only after previous incongruent color naming. No inhibition of the dominant word dimension should be present if switching word reading is performed as the first task of an experimental series. In addition, the study of other paradigms focusing on resolving inhibition (e.g., negative priming tasks) may provide converging evidence for the proposed function of the ACC. Only through such detailed investigations of conflict between stimulus dimensions will we increase our understanding of the role of the ACC in conflict processing.

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