

# Anterior Cingulate Cortex: An fMRI Analysis of Conflict Specificity and Functional Differentiation

Michael P. Milham<sup>1\*</sup> and Marie T. Banich<sup>1,2</sup>

<sup>1</sup>The Beckman Institute, University of Illinois at Urbana-Champaign, Urbana, Illinois

<sup>2</sup>Department of Psychology, University of Colorado at Boulder, Boulder, Colorado

---

**Abstract:** In this event-related functional magnetic resonance imaging (fMRI) study, we provide evidence that the role of the anterior cingulate cortex (ACC) in cognitive control may not be unitary, as the responses of different ACC subregions vary depending upon the nature of task-irrelevant information. More specifically, using the color-word Stroop task (congruent, incongruent, and neutral trial types), we examined the degree to which increases in neural activity within ACC are specific to conditions of conflict, as posited by the conflict monitoring theory (Botvinick et al. [1999]: *Rev Neurosci* 10:49–57; Carter et al. [1998]: *Science* 280:747–749). Although incongruent and congruent trials both involve two competing sources of color information (color word and ink color), only incongruent trials involve a direct conflict between task-relevant and task-irrelevant information. Although the anterior division of the ACC rostral zone exhibited conflict specific increases in neural activity (i.e., incongruent > congruent = neutral), the posterior division exhibited a more generalized pattern, increasing whenever the task-irrelevant information was color related, regardless of whether it was conflicting (i.e., incongruent and congruent > neutral). Our data thus suggest a possible functional differentiation within the ACC. As such, it is unlikely that the role of the ACC in cognitive control will be able to be accommodated by a single unifying theory. *Hum Brain Mapp* 25:328–335, 2005. © 2005 Wiley-Liss, Inc.

**Key words:** attentional control; anterior cingulate; prefrontal; conflict; Stroop; perceptual integration

---

## INTRODUCTION

Despite more than a decade of neuroimaging studies of human cognition, a comprehensive understanding of the contributions of the anterior cingulate cortex (ACC) to cognitive control remains elusive. During this time, increases in

ACC activity have been implicated in a variety of processes ranging from word reading to response selection to error processing [Paus, 2001]. In attempting to explain the seemingly widespread involvement of ACC in cognition, several authors have attempted to identify the lowest common denominator. Of these efforts, the conflict monitoring theory has proven to be amongst the most prominent and enduring [Botvinick et al., 2004; Carter et al., 1998]. Proposed by Carter et al. [1998], this theory asserts that ACC works to detect the occurrence of conflict capable of creating a potential for erroneous task performance. In response to the occurrence of such conflict, ACC is posited to send a signal to areas involved in top-down control (e.g., dorsolateral prefrontal cortex [DLPFC]) to increase their involvement in task performance.

Of note, a recent study by our laboratory suggests that the involvement of the ACC in attentional control may extend beyond conditions of conflict [Milham et al., 2002]. Using the

---

Contract grant sponsor: Beckman Institute for Advanced Science and Technology, University of Illinois; Contract grant sponsor: NIMH; Contract grant number: MH12415-01.

\*Correspondence to: Michael P. Milham, NYU Child Study Center, 14th Floor, 215 Lexington Avenue, New York, NY 10016.  
E-mail: milhamol@med.nyu.edu

Received for publication 13 April 2004; Accepted 1 November 2004

DOI: 10.1002/hbm.20110

Published online 15 April 2005 in Wiley InterScience (www.interscience.wiley.com).

color–word Stroop task, we detected increases in ACC activity for older individuals (age 60–75 years) whenever task-irrelevant information was related to task demands, not just when it conflicted with task-relevant information. More specifically, in older subjects we found increases in neural activity for both congruent (e.g., the word “red” in red ink) and incongruent (e.g., the word “blue” in red ink) trial types of the Stroop task when compared to that for neutral trials (e.g., the word “lot” in red ink). In contrast, younger participants (age 20–35 years) only exhibited increased activity in the ACC for incongruent trials relative to the neutral trial baseline. Although these findings may suggest some functional change in ACC associated with aging, we suggest they provide a hint that the role of the ACC in attentional control is not restricted to conflict monitoring.

The primary goal of the present work is to reexamine the validity of the hypothesis that ACC activity is specific to conditions of conflict. In doing so, we will entertain an alternative hypothesis, namely, that ACC is a complex brain region with functionally distinct subregions. As such, it is possible that the conflict monitoring theory may explain the functional contributions of a portion of ACC to cognitive control, but not the ACC as a whole. Several authors have already suggested that ACC contains functionally distinct subregions, typically focusing on rostral regions of ACC, which seem to be involved in error-related processing [Braver et al., 2001; Kiehl et al., 2000].

To accomplish our goals, we once again made use of the color–word Stroop task, although with an event-related fMRI design that we expected would increase attentional demands relative to the blocked design employed in our prior work. We expected that such an approach would enhance our ability to detect increases in neural activity within ACC. Our analyses were designed to identify regions of ACC sensitive to: (1) the presence of task-irrelevant information related to the task concept (i.e., color) regardless of conflict (incongruent and congruent > neutral); and (2) those specifically sensitive to the presence of conflicting task-irrelevant information (incongruent > congruent = neutral).

Given the frequent usage of Stroop or Stroop-like stimuli in studies of top-down attentional control, we also took the opportunity to examine the impact of the spatial characteristics of Stroop stimuli on top-down control. More specifically, behavioral studies have shown that physically separating the sources of task-relevant information and task-irrelevant information produces a marked decrease in Stroop interference and facilitation effects [e.g., Dyer, 1973; Flowers and Stoup, 1977; Glaser and Glaser, 1982]. We thus included a manipulation of whether or not the sources of task-relevant and task-irrelevant information were integrated physically. To do so, we compared two conditions, one in which the ink color appeared on the word (integrated stimulus) and one in which the ink color appeared on a rectangle surrounding the word, which was printed in gray (nonintegrated stimulus). Given prior studies of spatial attention and binding [Shafritz et al., 2002], we predicted that

posterior regions (i.e., extrastriate and parietal regions) may play a larger role in selection for physically separated stimulus, thereby decreasing the need for the contributions of frontal regions such as DLPFC and ACC.

## SUBJECTS AND METHODS

### Participants

Eighteen right-handed, native English speakers recruited from the Champaign-Urbana community (age range, 18–40 years) participated in the study. All participants were screened to ensure that they did not have a history of neurologic damage or color blindness and gave informed consent before participation.

### Stimuli and Design

Similar to the standard color–word Stroop task, we presented a series of trials on which participants are required to identify a color (blue, orange, green, or red) in the presence of a word. We varied whether or not the ink color to be identified was physically separate from the word. For each trial, the stimulus display consisted of a word and a rectangle; such that the rectangle surrounded the word without any overlap, keeping the two items distinct. There were two trial types: (1) *integrated* trials, in which the word was printed in the to-be-identified ink color whereas the rectangle was printed in gray; and (2) *nonintegrated* trials, in which the rectangle was printed in the to-be-identified ink color whereas the word was printed in gray. Of note, for any given trial, the task-relevant color information had an equal probability of appearing on the word or on the rectangle surrounding the word. Participants thus could not anticipate either the spatial location of the task-relevant information or the object that would introduce the task-relevant information. Such a design prevented both space-based and object-based attention from modulating selection of task-relevant information.

To examine the impact of introducing a task-irrelevant source of color information, we included the following color–word types: (1) *incongruent* words that name a color incongruent with the to-be-identified ink color (e.g., for integrated stimuli, the word RED printed in green with the rectangle printed in gray; for nonintegrated stimuli, the rectangle printed in green with the word RED printed in gray); (2) *congruent* words that name the to-be-identified ink color (e.g., for integrated stimuli, the word RED printed in red with the rectangle printed in gray; for nonintegrated stimuli, the rectangle printed in red with the word RED printed in gray); (3) *neutral* words that are unrelated to color (e.g., for integrated stimuli, the word LOT printed in red with the rectangle printed in gray; for nonintegrated stimuli, the rectangle printed in red with the word LOT printed in gray). The neutral words were matched with the color words for word frequency and length.

Our study made use of a rapid-presentation event-related design. Functional data for each participant was acquired

during a single session consisting of three runs. Each run consisted of 72 trials (12 trials/condition) presented at a rate of 7 s/condition. First-order counterbalancing was used such that each trial type was preceded by each of the six trial types an equal number of times. Each trial consisted of a 300-ms fixation cross followed by a 1,200 ms presentation of the stimulus (word and rectangle) and 5,500-ms intertrial interval. All stimuli were programmed using Mel v2.0 and presented using an IBM-PC compatible computer.

### Data Acquisition

A GE Signa (1.5-T) MRI system equipped for echo-planar imaging (EPI) was used for data acquisition. For each run, a total of 261 EPI images was acquired (repetition time [TR] = 2,000 ms; echo time [TE] = 40 ms; flip angle = 90 degrees), each consisting of 13 contiguous slices (thickness = 7 mm, gap = 1 mm, and in-plane resolution = 3.75 mm), parallel to the anterior commissure–posterior commissure (AC–PC) line. A high-resolution 3-D anatomic set was collected for each participant, as well as T1-weighted images of our functional acquisition slices. The head coil was fitted with a bite bar to minimize head motion during the session. Stimuli were presented on a goggle system designed by Magnetic Resonance Technologies. A four-button response pad was used to obtain behavioral measures of task-performance.

### Image Processing

Image processing and within-subject statistical analyses were carried out using FMRIB Easy Analysis Tool (FEAT; <http://www.fmrib.ox.ac.uk/fsl/index.html>). The first five volumes of each run's time series were discarded to allow the MR signal to reach steady state. Before statistical tests, images were motion corrected using Motion Correction using FMRIB's Linear Image Registration Tool (MCFLIRT) [Jenkinson and Smith, 2001]. The following prestatistics processing was applied: (1) spatial smoothing using a Gaussian kernel of full-width half-maximum (FWHM) = 8 mm; (2) mean-based intensity normalization of all volumes by the same factor; and (3) nonlinear high-pass temporal filtering (Gaussian-weighted LSF straight line fitting, with  $\sigma = 35.0$  s).

### Statistical Analyses

Statistical analysis was carried out for each participant using FMRIB's improved linear model (FILM) with local autocorrelation correction [Woolrich et al., 2001]. Event-related responses for each condition were modeled using the statistical parametric mapping (SPM99) hemodynamic response. Temporal derivatives for each predictor were included in the model as well, to account for possible differences in phase between the stimulus functions and observed data. Trials on which individuals made an error were excluded from our analyses. Our comparisons of interest included the following: competition (when the task-irrelevant attribute, the word, acts as a source of color information

capable of competing with task-relevant color information; incongruent and congruent > neutral); conflict (incongruent > congruent); stimulus integration (integrated > nonintegrated); Competition  $\times$  Integration; and Conflict  $\times$  Integration.

FLIRT was used to transform parameter estimate (PE) maps into a common stereotaxic space [Talairach and Tournoux, 1988]. For each contrast, group random-effects analyses were used to test if the individual participants' PE values were reliably greater than 0 ( $P < 0.0025$ ; contiguity threshold = 20 voxels) [Forman et al., 1995].

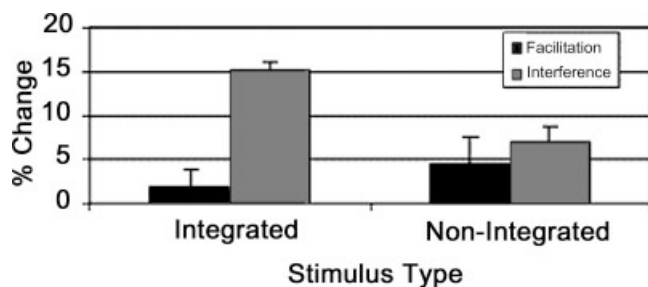
### Confirmatory Overlay Analysis: Regions Active for Both Integrated and Nonintegrated Stimuli

To confirm that the increases in activity during attentionally demanding conditions are present for both integrated and nonintegrated stimuli, we carried out an overlay analysis in addition to the standard approach of testing for possible interactions with stimulus integration. More specifically, at each voxel we tested for the presence of significant increases in activity associated with our comparisons of interest (i.e., competition; conflict) for integrated and nonintegrated stimuli separately, and then overlaid the two (using a threshold of  $P < 0.05$  each). Any voxel not passing the overlay analysis of integrated and nonintegrated stimuli was considered insignificant.

### Confirmatory Analysis: Competition and Conflict Specificity

To confirm that the increases in neural activity identified by our contrast testing for regions sensitive to competing color information regardless of conflict (congruent and incongruent > neutral) are present for both congruent and incongruent stimuli, we carried out an overlay (logical AND) analysis. More specifically, for each voxel identified as significant in our primary analysis, we tested for the presence of significant increases in neural activity for congruent and incongruent trial types (relative to neutral) individually and then overlaid the two (i.e., congruent > neutral at  $P < 0.05$  and incongruent > neutral at  $P < 0.05$ ).

To test for regions that are activated specifically during conditions of conflict, we carried out a disjunction test. First, we excluded any voxels found to be significant ( $P < 0.0025$ ) when we tested for the impact of competing color information regardless of conflict (congruent and incongruent > neutral). Among the remaining voxels, we next took those found to be sensitive to conflict (incongruent > congruent) at a level of  $P < 0.0025$  and ensured that no increases in activity were noted for the comparison of congruent > neutral at  $P < 0.05$ . Finally, to be conservative, we also excluded any voxels that were found to be sensitive to both congruent and incongruent trial types in our prior study [Milham et al., 2002].



**Figure 1.**

Behavioral findings. Note: For clusters in which two or more peaks were detected, each individual peak is reported listed.

## RESULTS

### Behavioral Findings

Consistent with the findings of prior studies, behavioral measures of performance were influenced by whether or not the sources of task-relevant and task-irrelevant information were perceptually conjoined. Because the reaction time for neutral trials differed for integrated (mean  $\pm$  standard error of the mean [SEM]: neutral,  $679 \pm 12$  ms; congruent,  $671 \pm 14$  ms; incongruent,  $775 \pm 20$  ms) and nonintegrated trials (neutral,  $699 \pm 15$  ms; congruent,  $672 \pm 15$  ms; incongruent,  $742 \pm 17$  ms), we converted reaction time measure of performance for congruent and incongruent trial types into the percentage facilitation and percentage interference, respectively (Fig. 1). We then carried out a repeated-measures analysis of variance (ANOVA) with the factors of INTEGRATION (integrated; nonintegrated) and STROOP EFFECT TYPE (interference; facilitation). We found a marginally significant main effect of INTEGRATION ( $F[1,17] = 3.96$ ;  $P < 0.063$ ), and a significant main effect of STROOP EFFECT TYPE ( $F[1,17] = 6.338$ ;  $P < 0.022$ ). More important was a significant interaction between INTEGRATION and STROOP EFFECT TYPE ( $F[1,17] = 6.338$ ;  $P < 0.022$ ). The Stroop interference effect noted for integrated stimuli was approximately twice as large as that noted for nonintegrated stimuli ( $F[1,17] = 7.54$ ;  $P < 0.014$ ), but facilitation effects noted for nonintegrated and integrated stimuli did not differ significantly ( $F[1,17] = 1.566$ ;  $P < 0.228$ ). The greater impact of integration on the interference effect than the facilitation effect is consistent with variability across studies regarding the influence of integration on the facilitation effect [MacLeod, 1991].

### fMRI Findings

#### **Conjunction analysis: Regions sensitive to competing task-related information regardless of conflict**

Regression analyses indicate the presence of ACC subregions sensitive to the presence of competing task-related information, regardless of conflict. More specifically, our contrast of congruent and incongruent trials with neutral trials detected increases in activity within a portion of ante-

rior cingulate cortex commonly activated in tasks requiring attentional control, referred to by Barch et al. [2001] as the posterior division of the rostral zone. These increases extended into nearby portions of pre-supplementary motor area (SMA). Confirmatory analyses verified the presence of increases for both congruent and incongruent trial types, indicating that activity within the posterior rostral zone is greater whenever there are two competing source of task-related information on which one could base a response, a finding that can be viewed as inconsistent with the conflict monitoring theory [Botvinick et al., 2004].

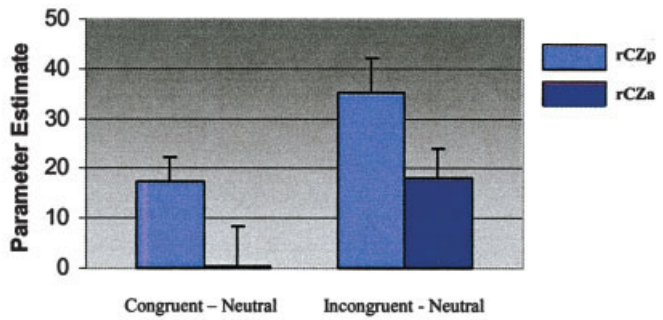
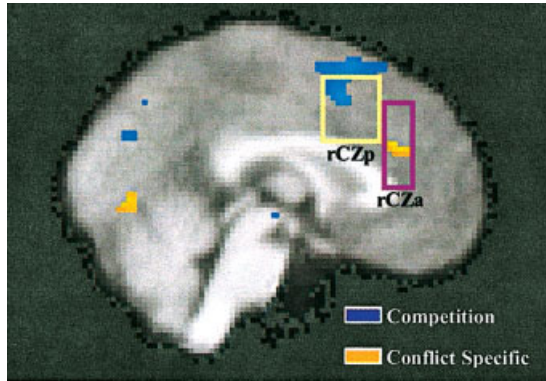
#### **Disjunction analysis: Regions specifically sensitive to competing task-related information that conflicts**

Our disjunction analyses (described in the methods section) identified regions that were active for incongruent trials but not congruent trials relative to the baseline of neutral trials. In contrast to the posterior portion of the rostral zone of the ACC, the anterior portion of the rostral zone (Brodmann area [BA] 24; center of intensity:  $x = 0$ ;  $y = 30$ ;  $z = 22$ ; cluster size = 112) was sensitive solely to the occurrence of conflict (incongruent but not congruent) (Fig. 2). This functional differentiation within anterior cingulate was confirmed by a paired  $t$  test, which found that increases in neural activity associated with congruent trial types were greater in the posterior portion of the rostral zone than the anterior portion ( $n = 18$ ;  $P < 0.05$ ). These findings are consistent with the assertion by Botvinick et al. [2004] that this region is associated with conflict monitoring. Of note, this same portion of ACC has been implicated in error-related processing by others [e.g., Braver et al., 2001; Kiehl, 2001]. Consistent with the suggestions of Carter et al. [e.g., Carter et al., 1998], our findings suggest a role for this ACC subregion in handling conflict, of which error processing is a special case.

#### **Stimulus integration**

Consistent with prior studies of the color–word Stroop task, we found increases in neural activity throughout the frontoparietal network when competing or conflicting color information was present (Fig. 3; Table 1 and 2) [Banich et al., 2000; Carter et al., 2000; Milham et al., 2002]. Despite our predictions, neural activity within neither prefrontal nor parietal regions was dependent upon sources of task-relevant and task-irrelevant information. Stimulus integration interacted with neither the presence of competing color information (congruent and incongruent  $>$  neutral) nor conflicting color information (incongruent  $>$  congruent), even at a more liberal threshold of  $P < 0.01$ .

The only portion of the frontal lobes that showed any reliable changes in activity with respect to stimulus integration was located within anterior inferior prefrontal cortex (BA44), with neural activity being greater for integrated than for nonintegrated stimuli, regardless of competition or conflict. Given that this region was not an a priori region of interest, we believe this finding should be taken with some caution.



**Figure 2.**

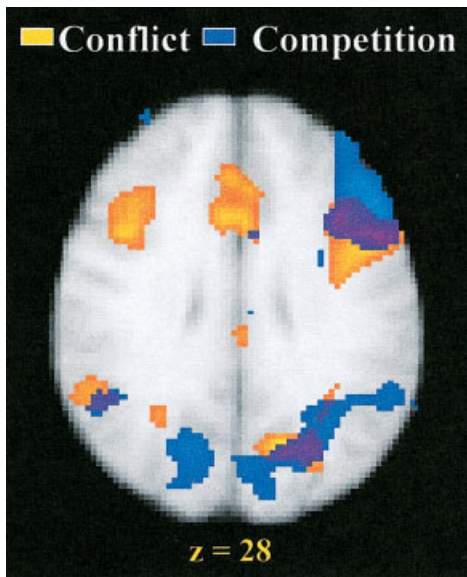
Functional differentiation within ACC as shown by confirmatory analyses. Our overlay analysis identified regions within the posterior rostral zone of ACC and nearby pre-SMA sensitive to the presence of competing color information, regardless of whether it conflicted with task-relevant information (i.e., congruent > neutral and incongruent > neutral). In contrast, our disjunction anal-

ysis identified a conflict-specific region within the anterior rostral zone, only increasing in activity when competing color information conflicted ( i.e., incongruent > congruent = neutral). Note: for clusters in which two or more peaks were detected, each individual is reported listed. (Image displayed on radiological orientation.)

### DISCUSSION

The present work tested a crucial component of the conflict monitoring theory, namely the hypothesis that the involvement of the anterior cingulate cortex in cognitive control is limited to situations involving conflict. Consistent with this hypothesis, the anterior division of the rostral zone exhibited conflict specific increases in neural activity (i.e., incongruent > congruent = neutral). In contrast, the posterior division exhibited increases in neural activity whenever the task-irrelevant information was color related, regardless of whether it was conflicting (i.e., incongruent and congruent > neutral). Only the anterior division of the rostral zone thus seems to exhibit the conflict specificity posited by the conflict monitoring theory.

The pattern of activity within the posterior zone may be better explained by theories of ACC function that suggest its involvement in response selection, facilitating infrequent or novel responses, and inhibiting pre-potent responses [Paus et al., 1993; Paus, 2001]. On both incongruent and congruent trials, the response must be based on the stimulus dimension for which processing is less automatic (i.e., ink color) rather than the stimulus dimension for which processing is more automatic (i.e., word reading), thereby increasing the attentional demands including those associated with response selection. As such, increases in neural activity would be predicted for both trial types. The posterior division exhibited such a pattern of activity, suggesting its involvement in response selection. Such a finding is consistent with our prior work indicating that this region of the ACC is only activated when the word names a potential response [Milham et al., 2001]. In that study, we found that this region was activated by response-eligible trials in which the word names a possible response (e.g., the word “blue” in yellow ink when blue, green, and yellow are possible responses) but



**Figure 3.**

Impact of competition and conflict on frontal and parietal regions. Voxel-wise analyses ( $P < 0.0025$ ) identified frontal and parietal regions sensitive to (1) the mere presence competing color information, regardless of whether it conflicted with task-relevant information (congruent and incongruent > neutral) (blue), (2) whether competing color information conflicted with task-relevant information (orange), and (3) both the presence of competing color information and whether it conflicted (incongruent > congruent neutral) (purple). Note: for clusters in which two or more peaks were detected, each individual peak is reported listed. (Image displayed in radiological orientation.)

**TABLE I. Regions sensitive to the presence of competing color information**

Region	BA	x	y	z	-Log(prob)	Cluster size*
Cerebellum	—	38	-68	-22	4.14	462
Superior colliculus	—	12	-28	-6	4.12	825
Recticular nucleus	—	4	-12	-2	2.95	—
Thalamus	—	-14	-28	-2	4.99	—
Thalamus	—	14	6	-2	4.55	65
Fusiform gyrus	19	-22	-56	-6	3.09	159
Lingual gyrus	18	-6	-86	0	4.31	129
	18	-34	14	-14	3.83	34
Inferior occipital gyrus	18	-38	-72	0	5.1	325
Middle occipital gyrus	18/19	-30	-80	8	3.45	—
Middle occipital gyrus	18/19	38	-82	14	3.91	263
Cuneus	17	10	-78	10	2.85	16
Middle temporal gyrus	21	66	-50	10	6.35	211
Superior temporal gyrus	22	50	-50	22	3.46	79
Precuneus	19	18	-68	28	3.71	353
AIPS	40	28	-62	46	3.54	164
Superior temporal gyrus	22	-54	-48	22	3.43	2,934
Middle temporal gyrus	39	-34	-54	22	3.69	—
Precuneus	7	-16	-68	28	3.57	—
AIPS	40	-30	-62	40	4.78	—
Superior parietal lobule	7	-14	-68	54	2.88	—
Inferior parietal lobule	40	-46	-30	40	3.78	—
Insula	—	-32	22	2	4.18	2,650
Middle frontal gyrus	46	-44	46	22	5.15	—
Inferior frontal gyrus	44	-46	18	26	5.34	—
Middle frontal gyrus	8	-30	26	54	5.36	—
Middle frontal gyrus	6	-44	6	52	3.87	49
Middle frontal gyrus	10	-28	42	2	4.04	75
Insula	—	30	22	2	3.21	318
Middle frontal gyrus	9	34	18	18	3.9	—
Middle frontal gyrus	10	32	38	20	3.72	959
Middle frontal gyrus	9	36	58	30	3.53	—
Middle frontal gyrus	8	28	46	44	4.19	—
Middle frontal gyrus	8	44	24	48	4.11	—
Anterior cingulate cortex	32	-2	32	36	2.7	590
Anterior cingulate cortex	32	-2	14	38	4.22	—
Pre-SMA	6	0	14	54	4.06	—
Anterior cingulate cortex	32	12	22	36	2.97	24

For clusters in which two or more peaks were detected, each individual peak is reported listed.

\*Cluster size given in number of voxels.

BA, Brodmann area.

not on response-ineligible trials in which the word does not name a possible response (e.g., the word “purple” in yellow ink when blue, green, and yellow are possible responses). In the present study, both congruent and incongruent trials produced increases in ACC activity (relative to neutral), as both trial types introduce task-irrelevant information that is associated with a valid response.

Some concern may arise as to whether the more generalized pattern of neural activity noted within the posterior division is truly inconsistent with the conflict monitoring theory. At face value, the conflict monitoring theory would predict no increases in ACC activity for congruent trials, as the color word and ink color are in clear agreement. Only if a more broad definition of conflict is employed can these

results be viewed as consistent, namely one in which conflict is construed to be any situation in which there are two or more competing sources of information upon which a response can be based. Even with such a definition, a single hypothesis would be unable to explain the differential patterns of activity noted between the anterior and posterior divisions of the rostral zone.

Although the pattern of neural activity of the anterior division is consistent with the conflict-monitoring hypothesis, an alternative explanation exists. Activity in this subregion may reflect its involvement with the affective processing associated with the occurrence of conflict. Such an assertion would be consistent with models proposing that the more rostral portion of ACC is involved in emotional

**TABLE II. Regions sensitive to the presence of conflicting color information**

Region	BA	x	y	z	-Log(prob)	Cluster size
Cerebellum	—	34	-32	-24	3.76	43
Thalamus	—	-12	-24	16	3.57	111
Reticular nucleus	—	8	-16	-4	4.12	237
Fusiform gyrus	37	-40	-50	-12	3.78	188
Fusiform gyrus	19	-26	-78	-12	3.3	75
Lingual gyrus	19	-18	-54	-8	3.58	35
Fusiform gyrus	18	34	-78	-8	4.29	109
Fusiform gyrus	37	50	-50	-16	3.21	42
Middle temporal gyrus	21	56	-38	-4	3.26	33
Lingual gyrus	18	2	-70	2	3.42	197
Lingual gyrus	18	24	-64	6	3.02	37
AIPS	—	-26	-66	34	6.4	3,275
AIPS	39	-32	-48	38	5.9	—
Precuneus	7	2	-54	36	3.33	—
Inferior parietal lobule	40	54	-46	26	3.79	945
AIPS	39	34	-50	36	5.13	—
Superior frontal gyrus	10	-30	56	2	4.08	27
Superior frontal gyrus	10	-36	16	6	4.18	1,817
Middle frontal gyrus	9	-42	6	32	5.86	—
Inferior frontal gyrus	47	36	28	-6	4	100
Inferior frontal gyrus	44	40	14	26	5.25	675
Anterior cingulate cortex	24	6	20	28	4.86	1,653
Anterior cingulate cortex	32	-4	14	48	3.97	—

rather than cognitive processes. This same subregion has been implicated in error-related processing by both Braver et al. [2001] and Kiehl et al. [2001]. Similar to conflict, error-related processing has a clear affective component. Findings of increased neural activity within this subregion for both error-related and conflict-related processing are thus consistent with a role in affective processing as well [Gehring and Knight, 2000].

In summary, the present study suggests that no one theory may be sufficient to explain ACC's contributions to control, as it seems to be functionally differentiated. Although the anterior division of the rostral zone exhibited a pattern of activity consistent with the conflict-monitoring theory, the posterior division exhibited a more generalized pattern of activity more compatible with theories that posit a role for ACC in response facilitation/inhibition. Future studies using higher strength magnets (the present study employed a 1.5-Tesla GE Signa) may show even further sub-differentiation than our results indicate. At a minimum, our findings emphasize the need to take into account the specific locations within ACC at which changes in activity are observed in studies of ACC function, rather than treating ACC as a whole.

**ACKNOWLEDGMENTS**

This work was supported by the Beckman Institute for Advanced Science and Technology at the University of Illinois (Urbana-Champaign, Carle Clinic, Urbana, Illinois), NIMH (MD/PhD pre-doctoral National Research Service

Award MH12415-01 to the principal investigator, Michael P. Milham). This research was carried out in part to fulfill the requirements for the doctoral degree in neurosciences at the University of Illinois at Urbana-Champaign. We thank S. Colcombe and K. Erickson.

**REFERENCES**

Banich MT, Milham MP, Atchley R, Cohen NJ, Webb A, Wszalek T, Kramer AF, Liang ZP, Wright A, Shenker J, Magin R (2000): fMRI Studies of Stroop tasks reveal unique roles of anterior and posterior brain systems in attentional selection. *J Cogn Neurosci* 12:988-1000.

Barch DM, Braver TS, Akbudak E, Conturo T, Ollinger J, Snyder A (2001): Anterior cingulate cortex and response conflict: effects of response modality and processing domain. *Cereb Cortex* 11:837-848.

Botvinick MM, Cohen JD, Carter CS (2004): Conflict monitoring and anterior angulate cortex: an update. *Trends Cogn Sci* 8:539-546.

Braver TS, Barch DM, Gray JR, Molfese DL, Snyder A (2001): Anterior cingulate cortex and response conflict: effects of frequency, inhibition and errors. *Cereb Cortex* 11:825-836.

Carter CS, Braver TS, Barch DM, Botvinick MM, Noll D, Cohen JD (1998): Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* 280:747-749.

Carter CS, Macdonald AM, Botvinick M, Ross LL, Stenger VA, Noll D, Cohen JD (2000): Parsing executive processes: strategic vs. evaluative functions of the anterior cingulate cortex. *Proc Natl Acad Sci USA* 97:1944-1948.

Dyer FN (1973): Interference and facilitation for color naming with separate bilateral presentations of the word and color. *J Exp Psychol* 99:314-317.

- Flowers JH, Stoup CM (1977): Selective attention between words, shapes and colors in speeded classification and vocalization tasks. *Mem Cognit* 5:299–307.
- Forman S, Cohen J, Fitzgerald M, Eddy W, Mintun M, Noll D (1995): Improved assessment of significant activation in functional MRI: use of a cluster-size threshold. *Magn Reson Med* 33:636–647.
- Gehring WJ, Knight RT (2000): Prefrontal-cingulate interactions in action monitoring. *Nat Neurosci* 3:516–520.
- Glaser MO, Glaser WR (1982): Time course analysis of the Stroop Phenomenon. *J Exp Psychol* 76:413–418.
- Jenkinson M, Smith SM (2001): A global optimisation method for robust affine registration of brain images. *Med Image Anal* 2:143–156.
- Kiehl KA, Liddle PF, Hopfinger JB (2000): Error processing and the rostral anterior cingulate: an event-related fMRI study. *Psychophysiology* 37:216–223.
- MacLeod CM (1991): Half a century of research on the Stroop effect: an integrative review. *Psychol Bull* 109:163–203.
- Milham MP, Banich MT, Webb A, Barad V, Cohen NJ, Wszalek T, Kramer AF (2001): The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Brain Res Cogn Brain Res* 12:467–473.
- Milham MP, Erickson KI, Banich MT, Kramer AF, Webb A, Wszalek T, Cohen NJ (2002): Attentional control in the aging brain: insights from an fMRI study of the Stroop task. *Brain Cogn* 49: 277–296.
- Mintun M, Fox P, Raichle M (1989): Highly accurate method of localizing regions of neuronal activation in the human brain with positron emission tomography. *J Cereb Blood Flow Metabol* 1:96–103.
- Paus T (2001): Primate anterior cingulate cortex: where motor control, drive and cognition interface. *Nat Rev Neurosci* 2:417–424.
- Paus T, Petrides M, Evans AC, Meyer E (1993): Role of the human anterior cingulate cortex in the control of oculomotor, manual, and speech responses: a positron emission tomography study. *J Neurophysiol* 70:453–469.
- Shafritz KM, Gore JC, Marois R (2002): The role of the parietal cortex in visual feature binding. *Proc Natl Acad Sci USA* 16:10917–10922.
- Talairach J, Tournoux P (1988): Co-planar stereotaxic atlas of the human brain: 3-D proportional system: an approach to cerebral imaging. Stuttgart: Thieme.
- Woolrich MW, Ripley BD, Brady JM, Smith SM (2001): Temporal autocorrelation in univariate linear modelling of fMRI Data. *Neuroimage* 14:1370.