

# Error processing and the rostral anterior cingulate: An event-related fMRI study

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## Abstract

The anterior cingulate is believed to play a crucial role in the regulation of thought and action. Recent evidence suggests that the anterior cingulate may play a role in the detection of inappropriate responses. We used event-related functional magnetic resonance imaging techniques to examine the neural responses to appropriate (correct rejections and correct hits) and inappropriate (errors of commission) behavioral responses during a go/no-go task. Analyses of the inappropriate responses revealed extensive activation in the rostral anterior cingulate cortex and in the left lateral frontal cortex. These areas were not activated for correctly classified trials (correct rejections and correct hits). These data suggest that the rostral anterior cingulate and left lateral frontal cortex are integral components of the brain's error checking system.

**Descriptors:** Error checking, Anterior cingulate, Error processing, fMRI, Event-related fMRI, Executive function

Theories of executive control of cognitive function have suggested that the anterior cingulate cortex may be the center of a system that coordinates mental activity to effectively regulate behavior (Logan, 1985; Shallice, 1988; Stuss, Alexander, & Benson, 1997). Evidence for this view comes from animal and human experimentation that has shown the anterior cingulate cortex is involved in response selection, motivation, goal-directed behavior, selective attention, and language generation (see Devinsky, Morrell, & Vogt, 1995, for a review). The neural architecture of the anterior cingulate cortex is as heterogeneous and complex as the functions it serves (Vogt, Finch, & Olson, 1992). This complexity is illustrated in the anterior cingulate's rich afferent and efferent anatomical connections to limbic, association, and motor cortices. Researchers have used the functional architecture of the anterior cingulate to separate the cingulate into two divisions,<sup>1</sup> one cognitive and one affective (also referred to as areas 24' and 24, respectively). The

cognitive division is believed to play a prominent role in visuospatial and memory functions and response selection under high load conditions (e.g., Carter et al., 1998) with little or no involvement in affect. The affective division, which lies rostral to the cognitive division, is believed to play a role in emotional processing, response modulation, and goal-directed behavior (Devinsky et al., 1995).

Some of the best evidence for the role of the anterior cingulate in cognitive function comes from studies that recorded event-related potentials (ERPs) to incorrect behavioral responses. These studies have reported the presence of a response-locked error-related negativity (ERN) appearing 50–150 ms after the execution of an incorrect response (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring, Coles, Meyer, & Donchin, 1990). Results from brain electrical activity source analyses (BESA) have suggested that the ERN has a medial frontal generator (Coles, Scheffers, & Holroyd, 1998; Dehaene, Posner, & Tucker, 1994; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Holroyd, Dien, & Coles, 1998; Miltner, Lemke, Holroyd, Scheffers, & Coles, 1998), possibly originating in the anterior cingulate and/or medial frontal gyrus (e.g., supplementary motor area). It has also been suggested that there is an additional ERN generator in the left lateral frontal cortex (Dehaene et al., 1994). Additional source modeling studies have shown that the generator of the ERN is similar for stimuli presented in the visual, auditory, and somatosensory modalities during a feedback task (Miltner, Braun, & Coles, 1997). The ERN also has a similar source regardless of whether participants generate response errors with either their hands or feet (Holroyd et al., 1998). It must be noted, however, that source modeling of electrical components of the ERP is limited in its spatial resolution because there is no unique solution to the inverse problem.

It has been hypothesized that the ERN reflects a mechanism that monitors and checks, or compares, a representation of the intended correct response to a representation of the actual response

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<sup>1</sup>The cognitive and affective divisions of the anterior cingulate are also known as areas 24' and 24, respectively. In the modified Talairach space used in SPM97, the division between the cognitive and affective regions of the anterior cingulate occurs at approximately  $y = 32$  (see Devinsky et al. [1995], Figure 4, page 287). The cognitive division lies posterior to the affective division, the latter of which extends anteriorly and inferiorly following the genu of the corpus callosum.

(Bernstein, Scheffers & Coles, 1995; Coles et al., 1998; Scheffers & Coles, in press). More generally, it has been argued that the ERN reflects a general error detection mechanism rather than a mechanism involved with error correction (Coles et al., 1998). More recently, it has been hypothesized that the ERN may be related to motivation and/ or the affective processing involved in error detection and correction (Gehring & Fencsik, 1999). This latter interpretation is strengthened by the fact that as motivation to perform accurately is reduced by task instruction, the amplitude of the ERN is reduced, even when controlling for response speed (Gehring, Goss, Coles, Meyer, & Donchin, 1993). A possible explanation for the reduction in the ERN when accuracy is de-emphasized is that the affective/motivational component of error detection and correction is reduced when accuracy is not as important to the subject.

Interestingly, the ERN is present in patients with focal brain damage in the left lateral frontal cortex (Gehring, Himle, & Nisenson, 1998). However, these brain-damaged patients also show large response-locked negativities to correctly classified events (e.g., hits). This finding suggests that the left lateral frontal cortex may also be involved in the generation of, or coordination of, processes that activate the ERN (see also Dehaene et al., 1994).

Disturbances in the processes hypothesized to be involved in the generation of the ERN are believed to contribute to a number of psychiatric illnesses. Obsessive-compulsive disorder (OCD) is believed to be associated with an overactive error-checking system that contributes to excessive self-monitoring leading to obsessional checking (Gehring et al., 1998). Psychopathy, on the other hand, is believed to be associated with a deficient error-checking system leading to a failure in monitoring one's behavior (Allen & Dikman, 1998). Similarly, schizophrenia is putatively associated with a defective or poorly modulated error-checking system (Ford, 1999), possibly resulting from a failure in effective connectivity between the left lateral frontal cortex and the anterior cingulate. Clearly, a better understanding of the neural systems that mediate these functions may help elucidate the cognitive and neurological underpinnings of a number of psychiatric illnesses.

In a recent event-related functional magnetic resonance imaging (fMRI) study of cerebral activity during a continuous performance task (the AX-CPT), Carter et al. (1998) demonstrated that the anterior cingulate (at a location within the cognitive division<sup>2</sup>) is active during error trials and also during correct trials that involved strong response competition, whereas left lateral frontal cortex was selectively active during error trials. This finding suggests that during that task the lateral frontal cortex, rather than anterior cingulate cortex, is associated specifically with error responses. However, it is not clear whether or not that task is associated with a strong ERN. In the AX-CPT the participant must respond to a target stimulus (in this case an "X") that has been preceded (9.5 s) by a cue stimulus (in this case an "A"). Participants must make an alternate response to "X" targets that were not preceded by the appropriate cue. Because the AX-CPT task normally has a very low error rate, Carter et al. enhanced the degree of task difficulty by degrading the stimuli to the point at which subjects performed at a level just significantly greater than chance. Carter et al. observed that activation in the anterior cingulate was stronger with degraded than with nondegraded stimuli. Scheffers

and Coles (in press) have shown that as the participant's confidence in making an error is decreased (induced by degrading the quality of the stimulus) a concomitant decrease in the amplitude of the ERN also occurs (see also Gehring & Knight, 1993). One could argue however, as Carter et al. did, that as task difficulty is increased, response competition will also increase. Thus, we believe that they have elegantly shown that response competition is related to neural activity in the cognitive division of the anterior cingulate. However, the exact relevance of this neural activity to error processing in general, and the ERN is particular, is still poorly understood.

The purpose of the present study was to use whole-brain event-related fMRI techniques to examine the neural responses to appropriate (correct rejects and correct hits) and inappropriate behavioral responses (errors of commission) during a go/no-go task, which we have shown gives rise to a robust ERN (Kiehl, Bates, & Liddle, in preparation). In the principal task (Task 1) participants had to respond on the majority of trials (80%) and inhibit responding on infrequent trials. This task permitted a comparison of cerebral activity during errors of commission with that during correct rejects. In addition, to compare activity during errors of commission with correct hits in response to low probability stimuli, we administered a second task (Task 2), in which participants had to inhibit responding on the majority of trials (80%) and respond to the infrequent trials (20%). Analyses were performed on the correctly classified infrequent trials in which the participant appropriately inhibited their actions (from Task 1), trials with errors of commission (from Task 1), and trials in which participants correctly classified target stimuli (i.e., hits, from Task 2). We hypothesized that errors of commission would be associated with activation of the affective division of the anterior cingulate, consistent with the hypothesis that errors are associated with affective and/or motivational processing. We also hypothesized that the left lateral frontal cortex would be activated during error processing, consistent with recent research from brain-damaged patients (Gehring et al., 1998) and other event-related fMRI studies of error processing (Carter et al., 1998). Furthermore, we hypothesized that the cognitive division of the anterior cingulate would be activated during correctly classified events and during errors of commission consistent with recent research indicating that this division is involved in coordination of response processes in tasks that evoke strong response competition (Carter et al., 1998).

## Methods

### Participants

Fourteen healthy individuals with normal vision (7 men; mean age 28.4 years) volunteered for the study. Participants provided written informed consent and were screened for MRI compatibility. All procedures met with University and Hospital ethical approval.

### Tasks 1 and 2

Stimuli were presented to the participant using a custom visual and auditory presentation package via a computer-controlled projection system that delivered a visual stimulus to a rear-projection screen located at the entrance to the magnet bore. Participants viewed this screen using a system of mirrors attached to the top of the head coil. Participants were instructed to respond as quickly and accurately as possible with their right index finger every time the "X" (.80 probability for Task 1 and .20 probability for Task 2) appeared and not to respond to the "K" (.20 probability for Task 1 and .80 probability for Task 2). The order of presentation of Task

<sup>2</sup>Carter et al. (1998) reported that the anterior cingulate activation in their study corresponded to Talairach coordinates 4, 25, and 43 in X, Y, and Z, respectively. Using the conversion algorithm of Meyer-Lindenberg (1998), these coordinates would correspond to coordinates 5, 29, and 51 (X, Y, and Z) in the modified Talairach space used in SPM97.

1 and 2 were counterbalanced across individuals. The stimuli were approximately  $3 \times 5$  visual degrees and were presented for 50 ms. In Task 1, the interstimulus interval between “X” stimuli (“go” stimuli) varied pseudorandomly between 1,000, 2,000, and 3,000 ms, subject to the constraint that in each consecutive 6-s period, there were three “X” stimuli presented. Because hemodynamic activity associated with processing a single stimulus typically occurs on a time scale of 6–20 s, the “X” stimuli would be expected to generate a sustained, relatively constant hemodynamic response. The “K” stimuli were interspersed among the “X” stimuli in a pseudo-random manner subject to three constraints: the minimum interval between an “X” and a “K” was 1,000 ms; the intervals between K stimuli were in the range 10–15 s; and these stimuli had equal probability of occurring at 0, 1, and 2 s after the beginning of a 3-s image acquisition period. By varying the phase of the stimulus presentation relative to the acquisition time, we were able to effectively sample the hemodynamic response to the stimuli of interest uniformly at 1-s intervals. Thus, the hemodynamic responses to “K” stimuli would be expected to occur as identifiable perturbations set against the relatively constant hemodynamic response to “X” stimuli. The sequence of stimuli for Task 2 was derived from the Task 1 sequence by exchanging the “X” and “K” stimuli. This latter task was included as a control condition to assess whether activity observed in Task 1 for errors of commission (i.e., trials with motor processing) could be related to processes related to motor control. A commercially available MRI compatible fiberoptic response device (Lightwave Medical, Inc., Vancouver, B.C., Canada) was used to acquire behavioral responses. Reaction times were computed on trials for which the participant responded correctly within 1,000 ms poststimulus. Before entry into the scanning room, each participant performed a practice block of 10 trials to ensure understanding of the instructions.

### Imaging

Imaging was implemented on a standard clinical GE 1.5 T whole body system fitted with a Horizon echo-speed upgrade. The participant's head was firmly secured using a custom head holder. Conventional spin-echo T1-weighted sagittal localizers were acquired to confirm positioning. Functional image volumes were collected with a gradient-echo sequence (TR/TE 3000/40 ms, flip angle  $90^\circ$ , field of view  $24 \times 24$  cm,  $64 \times 64$  matrix,  $3.75 \times 3.75$  mm in-plane resolution, 5-mm slice thickness, 29 slices) covering the entire brain (145 mm). Each stimulus run lasted for 423 s, during which 141 images of the entire brain were collected. Before each stimulus run, four brain volumes were collected over 12 s, to allow T1 effects to stabilize. These images were not included in any subsequent analyses.

### Image Processing

Functional images were reconstructed offline and the image volumes were realigned and motion corrected using the procedure by Friston et al. (1995b) as implemented in Statistical Parametric Mapping (SPM97). Translation and rotation corrections did not exceed 2.0 mm and 2.0 degrees, respectively, for any of the participants. A mean functional image volume was constructed for each participant for each run from the realigned image volumes. This mean image volume was then used to determine parameters for spatial normalization into the modified Talairach space used in SPM97 (Talairach & Tournoux, 1988) using the procedure of Friston et al. (1995a). In this space, coordinates are expressed relative to a rectangular coordinate frame with the origin at the midpoint of the anterior commissure and the y-axis passing through the poste-

rior and anterior commissures. All coordinates are reported in this modified Talairach space unless otherwise noted. These parameters were then applied to the corresponding functional image volumes for each participant. The normalized functional images were then smoothed with an 8-mm full width at half-maximum Gaussian filter. For each type of event, the hemodynamic response was modeled using a synthetic hemodynamic response function composed of two gamma functions and their respective temporal derivatives (see Josephs, Turner, & Friston, 1997, for mathematical model; Friston et al., 1998, for illustration). The first gamma function modeled the initial increase in perfusion using a peak latency of 6 s. A term proportional to the temporal derivative of this gamma function was included to allow for small variations in peak latency. The second gamma function and associated derivative were used to model the small “overshoot” of the hemodynamic response on recovery. For Task 1, the modeled composite hemodynamic response for the entire run was derived by constructing a sequence of appropriately located synthetic responses for correctly rejected “K” stimuli and for errors of commission for “K” stimuli. Because “X” stimuli were presented at the rate of 3 per 6 s with the object of maintaining a sustained hemodynamic response that did not vary substantially throughout the task, the response to the “X” stimuli was treated as the baseline and therefore not included in the model. For Task 2, event-related responses were modeled to correctly classified target stimuli (e.g., hits). For each voxel, the probability of activation during each type of event was determined by comparing the amplitude of the fitted response for that type of event with an estimate of the noise variance estimated from the discrepancies between the observed and modeled hemodynamic response. Variations in global signal intensity were removed using analyses of covariance. Low frequency noise was removed using a 0.1 Hz high-pass filter (Holmes, Josephs, Büchel, & Friston, in press). Because multiple voxels were examined, a correction for multiple comparisons based on the theory of Gaussian fields was used (Worsley, 1994). Reported significance levels were all greater than  $p < .05$  corrected for multiple comparisons unless otherwise noted.

## Results

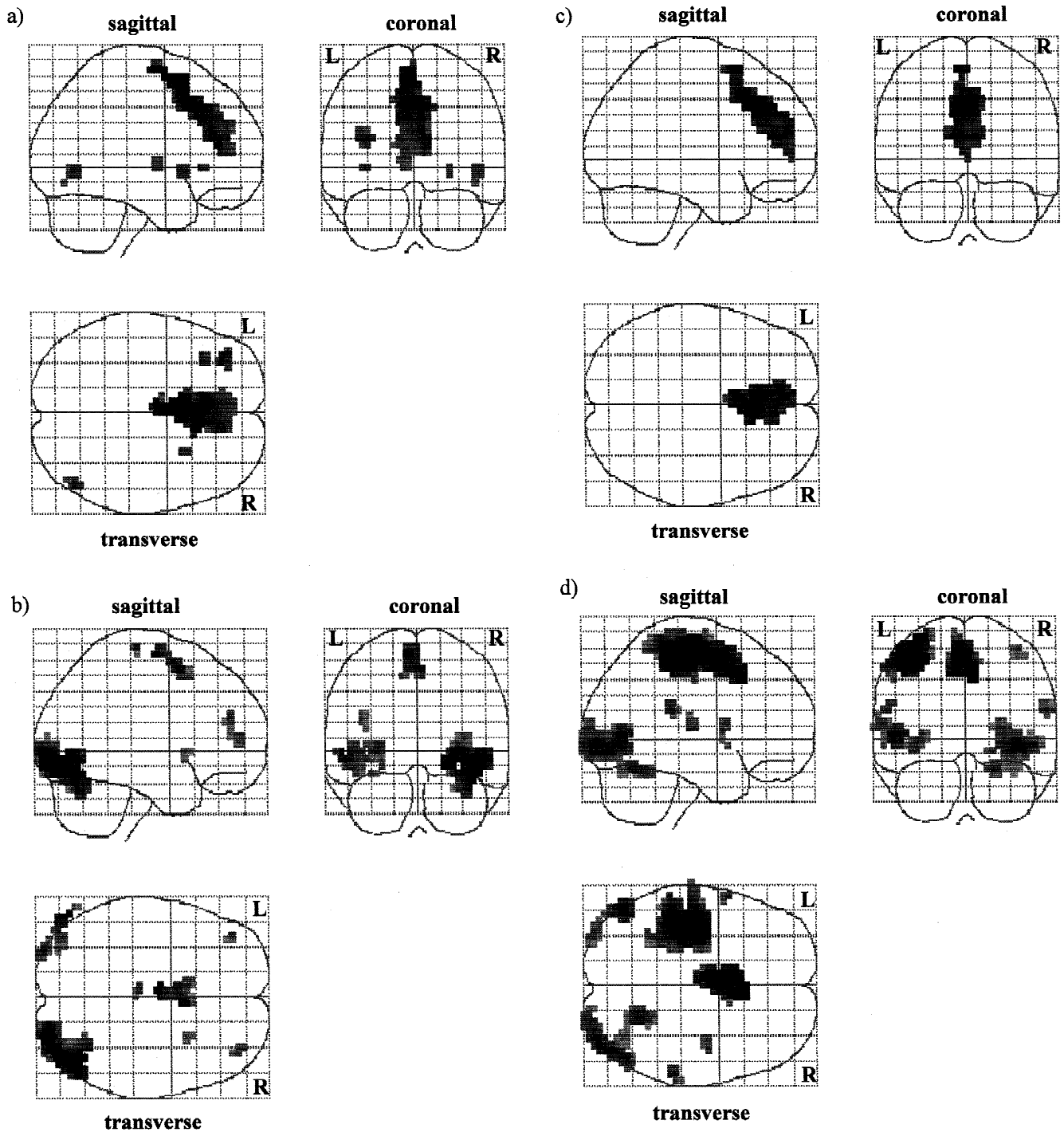
### Behavioral Data

*Task 1.* Participants missed relatively few target stimuli (97% correct) and responded with an average response time of 432 ms ( $SD$  40 ms). Errors of commission occurred on 23.7% of nontarget trials, giving an average of 9.43 ( $SD$  5.46) false alarms per participant.

*Task 2.* Participants correctly responded to 99% of trials with a mean reaction time of 445 ms ( $SD$  55 ms). Errors were rare for Task 2, occurring for only 1.2% of trials.

*Imaging data.* The analyses of the hemodynamic response to trials in which participants failed to modulate their actions appropriately (i.e., errors of commission) revealed an extensive area of activation in the rostral anterior cingulate that extended superiorly through the caudal anterior cingulate and into the medial frontal gyrus (see Figure 1a). The analyses also revealed a significant area of activation in the left middle frontal gyrus (see Table 1).

The analyses of the hemodynamic response for the correctly rejected trials failed to reveal any activation in the rostral anterior cingulate (Figure 1b). Activation was observed in the medial frontal gyrus (supplementary motor area), extending into the superior aspects of the anterior cingulate caudal to the site of



**Figure 1.** SPM(Z)s for the areas of activation for the (a) errors of commission (EOC), (b) correct rejects (CR), and (c) the direct comparison of the EOC vs. CR for Task 1. Also shown is the SPM(Z) for the (d) areas of activation for the correctly classified events (hits) for Task 2. The data are presented as a maximum intensity projection (MIP) on a standard template brain. In the MIP, the three views are presented: sagittal, coronal, and transverse (R = right hemisphere; L = left hemisphere). The gray scale is arbitrary and all SPM(Z)s are set at an uncorrected height threshold of  $p < .001$  with an extent threshold of 4 contiguous voxels.

activation associated with errors of commission. Activation also occurred bilaterally in the occipital/temporal junction with specific peaks of activation occurring in the middle and inferior occipital gyrus, fusiform gyrus, and right cerebellum (see Table 1, Figure 1b).

The results of a direct comparison of the errors of commission with the correctly rejected trials revealed a significant area of activation in the rostral anterior cingulate, indicating significantly greater activation in this region for errors than for correct rejects (see Figures 1 and 2).

**Table 1.** Summary of the Significant Areas of Activation for the Errors of Commission (EOC), Correct Rejects (CR), and the Direct Comparison of the EOC vs. CR for Task 1. Also Included Are Summaries of the Significant Areas of Activation for Correct Hits for Task 2. L = Left; R = Right.

Region	Talairach coordinates			z-score
	x	y	z	
<b>Task 1</b>				
Errors of commission				
1. Caudal anterior cingulate	4	22	40	6.50***
2. Medial frontal gyrus	-4	4	60	6.31***
3. Rostral anterior cingulate	12	36	12	4.90**
4. L middle frontal gyrus	-34	41	20	4.83*
Correct rejects				
1. R middle occipital gyrus	45	-75	-10	7.32***
2. R inferior occipital gyrus	22	-60	-10	6.97***
3. L middle occipital gyrus	-52	-79	-5	6.46***
4. Medial frontal gyrus	-8	-8	60	6.19***
5. R temporal lobe	48	-68	-16	5.69***
6. R cerebellum	38	-70	-24	5.63***
7. Anterior cingulate/medial frontal gyrus	4	8	45	5.51***
8. R fusiform gyrus	30	-88	-16	5.45***
Errors of commission vs correct rejects				
1. Caudal anterior cingulate	4	22	40	5.60***
2. Rostral anterior cingulate	-8	45	15	4.73*
<b>Task 2</b>				
Correct hits				
1. L precentral gyrus	-36	-24	52	7.70***
2. L precentral gyrus	-32	-16	64	6.98***
3. L medial frontal gyrus	-4	4	55	6.83***
4. L middle occipital gyrus	-52	-72	4	6.54***
5. R inferior occipital gyrus	44	-80	-8	6.25***
6. Anterior cingulate/medial frontal gyrus	6	20	40	5.98***
7. R lateral globus pallidus	-36	20	0	5.65***
8. R middle occipital gyrus	48	-72	-4	5.57***
9. R cerebellum	20	-60	-20	5.47**
10. R superior temporal gyrus	60	-32	20	4.82*
11. L inferior parietal lobule	-56	-32	24	4.80*
12. L fusiform gyrus	-44	-56	-12	4.79*

\*\*\* $p \leq .001$ , \*\* $p \leq .01$ , \* $p \leq .05$  corrected for multiple comparisons.

Analyses of the hemodynamic response for the correctly classified target stimuli from Task 2 revealed activation in left motor cortex, medial frontal gyrus extending into the superior aspects of the caudal anterior cingulate, right cerebellum, and bilaterally in occipital cortex (see Table 1; Figure 1d). No activation was observed in the rostral anterior cingulate for this task, suggesting that the observed neural activity in the rostral anterior cingulate for errors of commission (Task 1) is selective to error-related processes and is not due to processes related to motor control.

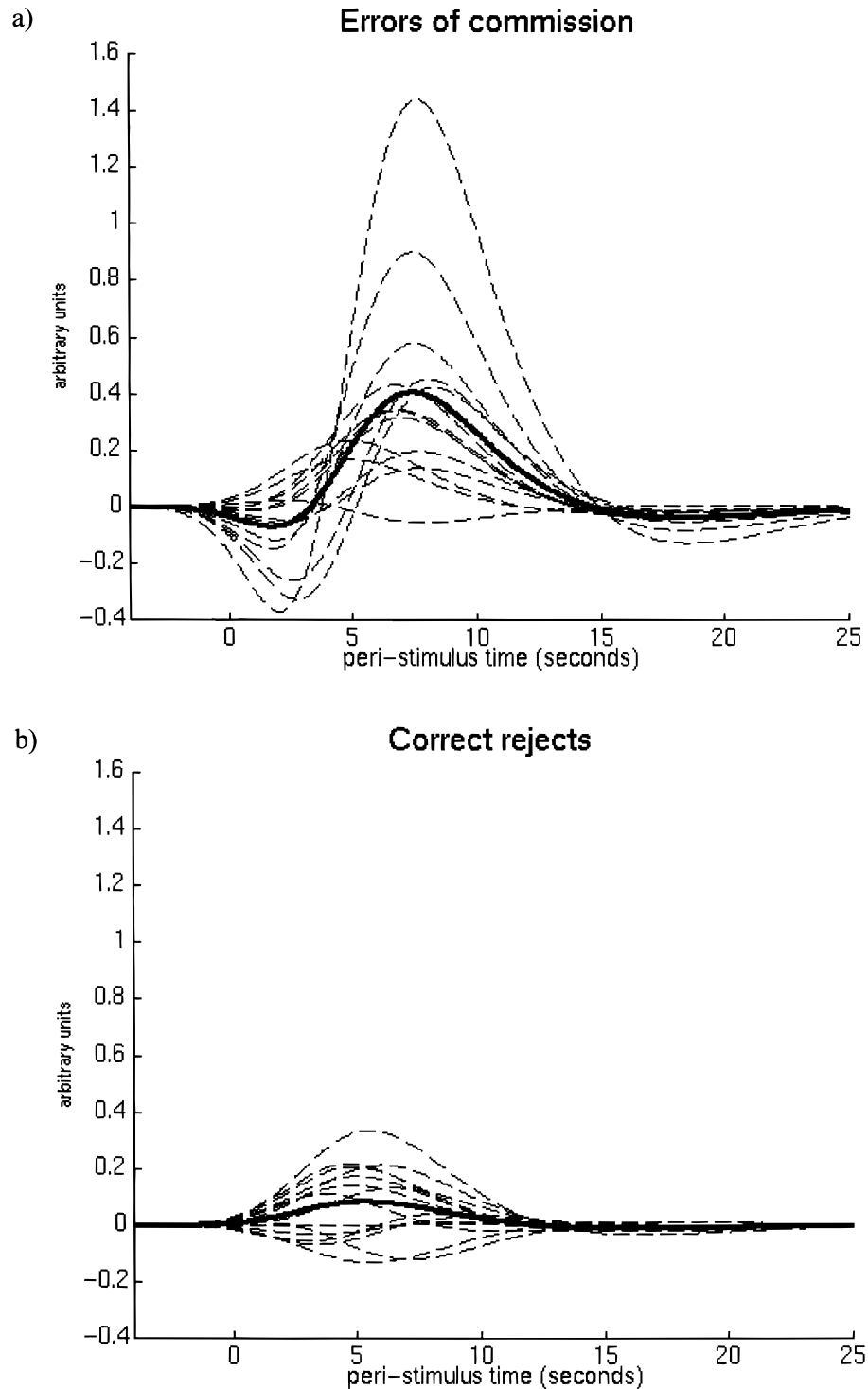
## Discussion

Analyses of the inappropriate responses revealed extensive activation in the rostral anterior cingulate and in the left lateral frontal cortex. These areas were not activated during appropriate responses (i.e., correct rejects or correct hits). These data support the hypothesis that the rostral anterior cingulate and left lateral frontal cortex are involved in the brain's error checking system. These data are consistent with the results from BESA source modeling of the ERN (Tucker, 1998) and with patient data showing that the left lateral frontal cortex is involved in error processing (Coles et al., 1998). The finding that rostral anterior cingulate is activated selectively during error processing is consistent with data from

go/no-go ERN studies in humans (Gemba & Sasaki, 1989; Schefers, Coles, Bernstein, & Gehring, 1996), and monkeys (Gemba, Sasaki, & Brooks, 1986; Sasaki & Gemba, 1986). The latter studies have demonstrated the presence of a sharp surface negative electrical potential in the anterior cingulate occurring approximately 100 ms after the onset of an inappropriate response (i.e., an error).

The location of the rostral anterior cingulate activation for error processing in this study was similar to the location at which Liddle, Friston, Frith, and Hirsch (1992) found a correlation between blood perfusion and severity of disorganization symptoms in patients with schizophrenia (Liddle et al., 1992). Disorganization symptoms reflect impaired ability to suppress inappropriate responses. Recently, Ford (1999) reported that schizophrenic patients show ERNs similar to those of controls for inappropriate responses. However, schizophrenic patients also show large response-locked negativities during processing of correct trials, suggesting that the anterior cingulate is active during all trials in these patients. A better understanding of the role this structure plays in the brain's error checking system may lead to a better understanding of the role this structure plays in schizophrenia and other psychiatric illnesses.

Comparison of our findings with those obtained by Carter et al. (1998) in their study of the AX-CPT task reveals important simi-



**Figure 2.** Single subject (dotted lines) and grand mean (thick solid line) event-related hemodynamic response function (amplitude in arbitrary units vs. peri-stimulus time) from a voxel located in rostral anterior cingulate ( $x, y, z = -8, 45, 15$ ) for (a) errors of commission and (b) correct rejections for Task 1. The amplitude of the hemodynamic response was significantly larger for errors of commission than for correct rejections ( $z$ -score = 4.73,  $p < .05$  corrected for multiple comparisons).

larities and differences. Carter et al. had shown that the anterior cingulate was active not only during error trials but also during trials in which correct responses were made under conditions involving strong response competition. The location of the activation in the anterior cingulate reported in their study<sup>2</sup> overlaps with the

area we observed to be activated during correct hits (peak located 9 mm posterior and 5 mm inferior to that observed by Carter et al.), correct rejections (peak 20 mm posterior and 6 mm inferior), and errors of commission (peak identical in  $x$  and  $y$  coordinates, only 10 mm inferior in the  $z$  plane)—all conditions that involve strong

response competition. However, the error-related activity from the present study, but not the activity associated with correct rejections (Task 1) or correct hits (Task 2), extended nearly 10 mm anterior and 40 mm inferior to that reported by Carter et al. Therefore, the present results provide evidence dissociating the affective division of the cingulate from regions of the cingulate previously found to be involved in response competition. We also confirmed Carter et al.'s observation that the left lateral frontal cortex was selectively activated for error processing, although we were unable to confirm their finding that the right lateral frontal cortex was selectively activated for error processing. Overall, our results support Carter et al.'s conclusion that a high level of response competition engages a region in the anterior cingulate (in the vicinity of Talairach coordinates 4, 29, and 45 in  $x$ ,  $y$ , and  $z$ , respectively), which lies within the cognitive division. However, during our task, which has been shown to produce a strong ERN (Kiehl et al., in preparation), there was also activation of the affective division of the anterior cingulate, that was not observed by Carter et al. in a task during which a weaker ERN might be anticipated. As mentioned earlier, the AX-CPT task used by Carter et al. might be expected to produce a lesser ERN because the ERN is reduced when stimuli are degraded so that recognition of error is less certain (Gehring & Knight, 1993; Scheffers & Coles, in press).

In an fMRI study of cerebral activity during a go/no-go task, Konishi, Nakajima, Uchida, Sekihara, and Miyashita (1998) ob-

served activation of right lateral frontal cortex during no-go trials. Although we did not observe activation at this site that was significant after stringent correction for multiple comparisons, if we apply the criteria for significance used by Konishi et al. (two tailed  $p < .005$  in at least four contiguous voxels), we observe activation in both right and left lateral prefrontal cortex during correct no-go responses (see Figure 1b: right middle frontal gyrus,  $x$ ,  $y$ ,  $z = 34, 52, 10$ ; peak  $z$ -score = 4.14,  $p = .00004$ , two tailed; number of voxels = 7; left middle frontal gyrus,  $x$ ,  $y$ ,  $z = -41, 45, 20$ ; peak  $z$ -score = 4.08,  $p = .00005$ , two tailed; number of voxels = 7). Thus, our findings are consistent with those reported by Konishi et al. Although they do not report the proportion of correct responses, Konishi et al. stated that participants were able to perform their task easily. Therefore, the fact that Konishi et al. did not observe activation of anterior cingulate cortex is consistent with our conclusion that caudal anterior cingulate is active under conditions of strong response competition, while rostral anterior cingulate is engaged when errors are made.

In conclusion, we have shown that the rostral anterior cingulate and left lateral frontal cortex are selectively activated during trials in which there are errors of commission, consistent with data from studies in monkeys, and with source modeling studies of the ERN in human subjects. These findings suggest that the rostral anterior cingulate and left lateral frontal cortex are involved in the brain's error checking system and that activity in these areas may generate the ERN recorded at the scalp following response errors.

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