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Conflict monitoring in the human anterior cingulate cortex during selective attention to global and local object features

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Abstract

Parallel processing affords the brain many advantages, but processing multiple bits of information simultaneously presents formidable challenges. For example, while one is listening to a speaker at a noisy social gathering, processing irrelevant conversations may lead to the activation of irrelevant perceptual, semantic, and response representations that conflict with those evoked by the speaker. In these situations, specialized brain systems may be recruited to detect and resolve conflict before it leads to incorrect perception and/or behavior. Consistent with this view, recent findings indicate that dorsal/caudal anterior cingulate cortex (dACC), on the medial walls of the frontal lobes, detects conflict between competing motor responses primed by relevant versus irrelevant stimuli. Here, we used a cued global/local selective attention task to investigate whether the dACC plays a general role in conflict detection that includes monitoring for conflicting perceptual or semantic representations. Using event-related functional magnetic resonance imaging (fMRI), we found that the dACC was activated by response conflict in both the global and the local task, consistent with results from prior studies. However, dACC was also activated by perceptual and semantic conflict arising from global distracters during the local task. The results from the local task have implications for recent theories of attentional control in which the dACC's contribution to conflict monitoring is limited to response stages of processing, as well as for our understanding of clinical disorders in which disruptions of attention are associated with dACC dysfunction.

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Introduction

The anterior cingulate cortex (ACC) is one of the most widely activated brain regions in functional neuroimaging studies of attention and working memory. As a consequence, it has been difficult to pinpoint its exact contributions to attentional processing. In recent years, some progress has been made by realizing that the ACC is both functionally and anatomically heterogeneous. For example, there is now growing evidence that rostral areas of the ACC are involved in emotional processing (Whalen et al., 1998), possibly including emotional aspects of error monitoring (Braver et al., 2001; Kiehl et al., 2000; Menon et al., 2001).

There is considerable debate, however, as to the role played by more dorsal/caudal regions of the ACC (dACC).

There are two distinct theories of the dACC's contribution to attentional processing. Some data suggest that the ACC contributes rather broadly to attentional control (Posner and Petersen, 1990). These data are consistent with a role for the dACC in shifting the focus of visual selective spatial attention (Corbetta et al., 1993), boosting the activation of behaviorally relevant sensory inputs (Posner and DiGirolamo, 1998), and participating in the generation of visual imagery (Kosslyn et al., 1993). Other findings, however, suggest that the dACC's contribution is limited to detecting processing conflicts at response stages of processing (Banich et al., 2000a,b; Botvinick et al., 1999, 2001; Braver et al., 2001; Carter et al., 1999, 2000; MacDonald et al., 2000; Milham et al., 2001). According to the conflict monitoring account of dACC functioning, the dACC signals lateral prefrontal regions when the activation of competing

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response tendencies increases the probability of making an incorrect response. Lateral prefrontal areas then further bias attention toward task-relevant processing to ensure correct behavior (Botvinick et al., 2001; MacDonald et al., 2000). In this framework, both lateral prefrontal areas and the dACC contribute to attentional control, but they do so in different ways. Lateral prefrontal areas, through their interaction with parietal and sensory cortices, regulate the current focus of attention. In contrast, the dACC plays a role in signaling the need for greater control (e.g., the need for greater focusing of attention) when conflict arises.

Although there continues to be debate concerning the functional contributions of the dACC to attentional control, support for the conflict monitoring view has grown considerably in recent years. For example, a recent functional magnetic resonance imaging (fMRI) study (MacDonald et al., 2000) provided evidence for a double dissociation between the dorsolateral prefrontal cortex (DLPFC) and the dACC in a cued selective attention task, which was highly consistent with the conflict monitoring view. This dissociation indicated that the DLPFC selectively contributes to establishing an attentional set for task-relevant information during cue processing, while the dACC selectively contributes to detecting conflict evoked by distracter stimuli during target processing. These and similar findings (Banich et al., 2000b) have provided key support for the response conflict monitoring view.

Whether the dACC also monitors for conflict at pre-response stages of processing is less clear, however. Pre-response conflict arising from irrelevant perceptual and semantic representations often impairs performance in selective attention tasks (MacLeod, 1991). For example, in each trial of the Eriksen flanker task (Eriksen and Eriksen, 1974), participants identify a central target letter while ignoring two flanker letters. Participants are sometimes (Eriksen and Schultz, 1979), though not always (Eriksen and Eriksen, 1974), slower to respond when the flanker letters activate different perceptual and semantic representations than the target (e.g., E H E) than when all three letters are identical (e.g., H H H), even though, in both types of trials, the target and flankers are mapped to the same response. A broader role for the dACC in conflict monitoring, which includes monitoring for conflict at pre-response levels, might therefore be useful for ensuring correct behavior. The dACC is interconnected with parietal and temporal regions that perform high-level perceptual processing (Van Hoesen et al., 1993), as well as frontal regions that participate in response selection (Paus, 2001). As previously argued (Botvinick et al., 2001), these characteristics make the dACC an ideal structure for detecting processing conflict at multiple stages of processing.

Findings from two recent fMRI studies, however, suggest that the dACC contributes to conflict monitoring exclusively at response stages of processing. Nonetheless, the designs of these experiments may not have been ideal for identifying a role for the dACC in monitoring for pre-

response level conflict. In a study of the Eriksen flanker task (Van Veen et al., 2001), distracters that evoked only perceptual and semantic conflict failed to activate the dACC, relative to distracters that evoked no conflict. In this study, however, the task trials were presented at extremely slow rates of presentation, which are believed to reduce overall attentional demands and, hence, the role of the dACC in attentional tasks (Bench et al., 1993; Posner and DiGirolamo, 1998). For example, the degree to which task stimuli in one trial prime, or increase behavioral interference from, a conflicting distracter presented in the next trial is likely far greater when the next trial occurs relatively quickly (e.g., 3 s later) than when it occurs much more slowly (e.g., 12 s later) (see MacLeod, 1991, for a review).

A slightly different issue complicates the interpretation of findings from a block-design study of the Stroop effect (Milham et al., 2001). In this study, participants were instructed to identify the ink color (i.e., green, blue, or yellow) of the word that was presented in each trial. However, distracter words that evoked both semantic and response conflict (e.g., blue) with a target ink color (e.g., green) were likely more primed, or activated, by the task set than were distracter words that evoked only semantic conflict (e.g., red). This is because the semantic distracters (e.g., red) were less related to the task set (i.e., identify the ink color on each trial—green, blue, or yellow) than were the distracters that evoked both semantic and response conflict (e.g., green). The relatively low level of activation for distracters evoking only semantic conflict may have led to a lack of dACC activity for these items, in contrast to the robust activity that was associated with more highly activated distracters evoking both semantic and response conflict.

In the present study, we therefore investigated whether the dACC monitors for processing conflict at pre-response stages of processing using an experimental design in which trials were presented at fast rates and all of the distracter stimuli were task relevant. Similar to a prior fMRI study (Van Veen et al., 2001), we reasoned that dACC activity in response to three types of conflict situations—no conflict (NC), pre-response conflict (PC), and response conflict (RC)—would reveal the stage(s) of processing at which the dACC monitors for conflict. If the dACC monitors exclusively at response stages, then RC trials should evoke greater activity than either PC or NC trials, which, in turn, should not differ from one another. On the other hand, if the dACC monitors for conflict at pre-response as well as response stages, then both PC and RC trials should evoke greater dACC activity than NC trials.

Materials and methods

Participants and task

Fifteen right-handed participants with normal or corrected-to-normal vision were paid \$20 per hour to participate in the

study (10 males, 5 females; age range, 22 to 45 years; mean age, 26 years). All gave informed written consent in accordance with the procedures of the Duke University Internal Review Board.

Participants performed a cued global/local attention task (Navon, 1977) while neural activity was recorded by using a recently developed, event-related fMRI approach (Shulman et al., 1999; Woldorff et al., 2001, 2003). In each 3-s trial, an attention-directing cue (G, L, or P; $1.6 \times 1.0^\circ$ of visual angle; duration, 200 ms) instructed participants to attend to and identify either the global (“G”) or the local (“L”) aspect of an upcoming hierarchical stimulus (Global letter, $3.3 \times 2.1^\circ$; Local letters, $0.6 \times 0.4^\circ$; duration, 200 ms), or a single (“P”) nonhierarchical letter ($1.6 \times 1.0^\circ$; duration, 200 ms). Participants were instructed to press one button with the index finger of their right hand if the target was an H or S and a different button with the middle finger of the same hand if the target was an X or O. The single-letter task was not crucial for testing the present hypotheses and, therefore, will not be discussed further.

We included several types of trials to determine the nature of conflict monitoring performed by the dACC (Fig. 1). In cue-plus-target trials (75%), a target stimulus that required a response followed the presentation of each cue after a 1300-ms interstimulus interval (ISI). For global-task and local-task trials, the target stimulus was a hierarchical letter. Within each hierarchical stimulus, the identities of the distracter (e.g., global letter) and target (e.g., local letter) could evoke one of the following conflict situations: (1) no conflict, NC trials (e.g., a global H made of local Hs), (2) perceptual and semantic conflict, PC trials (e.g., a global H made of local Ss), or (3) perceptual, semantic, and response conflict, RC trials (e.g., a global H made of local Xs). Each of these three trial types appeared in one-third of cue-plus-target trials. For single-letter-task trials, the target was always a single nonhierarchical letter. In all cue-plus-target trials, there was a 1300-ms ISI before the next trial began. Cue-only trials (25%) were identical to cue-plus-target trials with the exception that only a fixation dot was presented during the target period. The presence of cue-only trials allowed isolation of target-related neural activity in cue-plus-target trials as described below.

During the cued global/local attention task, the different trial types were presented such that each one was preceded equally often by every trial type in the design. Such counterbalancing allows subtraction of response overlap from adjacent trials when comparing the average time course of hemodynamic activity for different trial types (Burock et al., 1998; Dale and Buckner, 1997; Woldorff, 1993) because the adjacent-response overlap will be the same on average for the different types. For the global and local tasks, there were 72 trials per condition.

We extracted target-related neural activity by contrasting the time-locked average responses to cue-plus-target trials with those to cue-only trials (Woldorff et al., 2001, 2003). To ensure attention-directing cues evoked pretarget atten-

tion-biasing processes of similar duration in these trial types, the fixation dot changed color in all trials, from white to red, 1500 ms after cue presentation (i.e., coincident with target presentation in cue-plus-target trials) (Corbetta et al., 2000). Participants were told that they should cease attending if a target did not appear at this point on cue-only trials.

Data acquisition and analysis

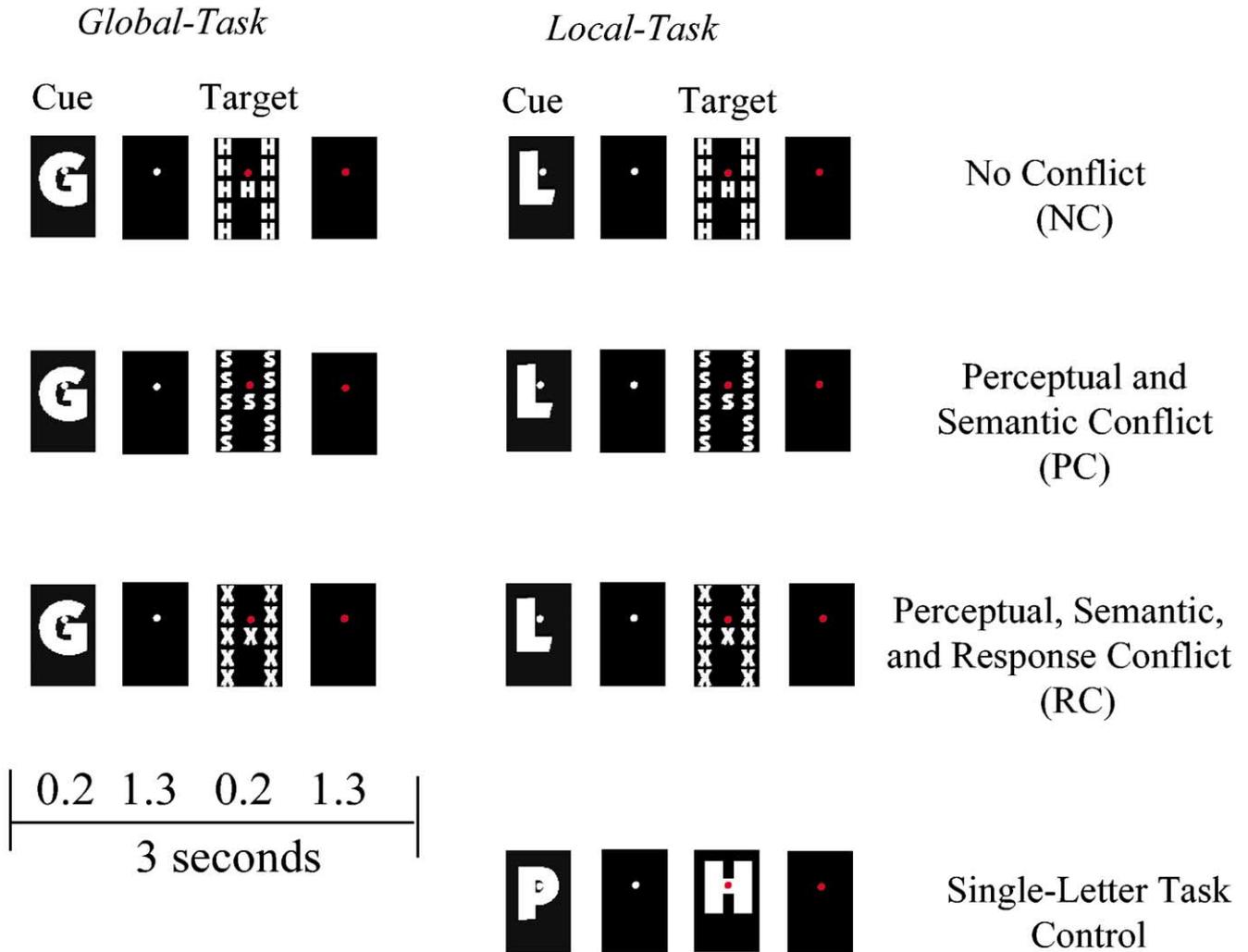
A PC running customized software was used to present stimuli and to record participants' responses. Stimuli were projected onto a screen at the back of the magnet's bore that participants viewed through a mirror. Responses were made by using the index and middle fingers of the right hand and were recorded with a magnetic resonance (MR) compatible response box. Behavioral data were analyzed separately for the global and local tasks using planned *t* contrasts.

The blood oxygenation level dependent (BOLD) signal was measured with an echo-planar imaging sequence (TR = 1.5 s, TE = 40 ms, flip angle = 90° , 18 contiguous 7-mm-thick slices, in-plane resolution = 3.75×3.75 mm, voxel size = $3.75 \times 3.75 \times 7$ mm) during the collection of functional images on a 1.5-T GE whole-body scanner. Each participant completed six runs (one completed only four). During each run, 306 brain volumes were collected. The first six functional images contained no trials and were discarded. Structural images for each participant were also collected by using a T1-weighted spin-echo sequence (TR = 600 ms, TE = 14 ms, flip angle = 90° , 18 contiguous 7-mm-thick slices, in-plane resolution = 0.94×0.94 mm).

The software analysis package SPM'99 (Friston et al., 1995) was used to correct functional images for temporally asynchronous slice acquisition and head motion, to warp the functional images to MNI (Montreal Neurological Institute) standard space, and to spatially smooth the functional images with a Gaussian filter (FWHM = 8 mm in the *x*, *y*, and *z* dimensions). Data from one participant were discarded due to excessive motion. We performed selective averaging in each voxel to extract the average time course of hemodynamic activity that was evoked by each trial type. Then, for every participant, we converted the average time course for each trial type to units of percent change from baseline, which was defined as the time point that immediately preceded trial onset.

To functionally define a region of interest that included the dACC, we first averaged the time courses for (1) global and local cue-plus-target trials, and (2) global and local cue-only trials for each participant. Contrasting the average BOLD signal for cue-plus-target versus cue-only trials allowed us to define target-related activity in a way that would not bias results from subsequent contrasts of neural activity associated with distinct types of target stimuli (i.e., NC, PC, and RC targets). One might wonder whether the inclusion of NC trials, in which no conflict was present, limited our ability to identify a dACC region of interest. We do not think so for two main reasons. First, as described below, our

Cue-Plus-Target Trials



Cue-Only Trials

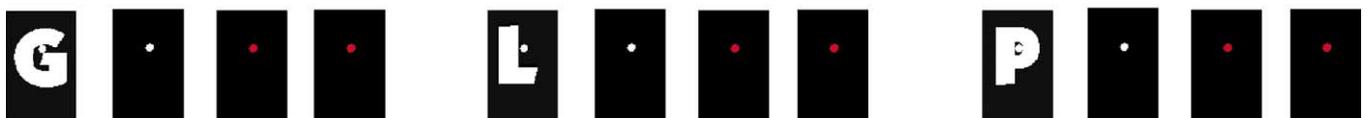


Fig. 1. Timing and sequence of events for sample cue-plus-target and cue-only trials in the cued attention task. In each 3-s trial, an attention-directing cue instructed participants to attend for and identify an upcoming target stimulus. In both global-task and local-task cue-plus-target trials (75%), the distracter could evoke no conflict (NC), perceptual and semantic conflict (PC), or perceptual, semantic, and response conflict (RC) with the target. Cue-only trials (25%) allowed isolation of target-related activity in cue-plus-target trials.

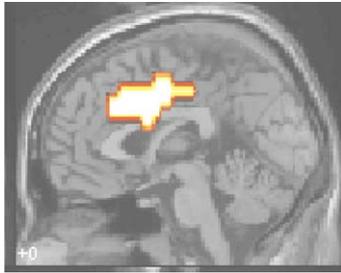


Fig. 2. Targets activated a relatively large region of dorsal/caudal anterior cingulate cortex as shown on a midsagittal slice of the SPM (statistical parametric mapping) normalized anatomical brain. Subsequent region of interest (ROI) analyses were performed by averaging functional magnetic resonance imaging data across all voxels within this region.

dACC region contained 255 voxels (Fig. 2), which is a relatively large number. Second, the ACC is known to play a role in general aspects of motor processing (Paus, 2001), which may lead to target-related activity (since participants pressed a button for each target) even when no conflict from distracters is present. Third, even when a distracter does not conflict with a target, as in our no-conflict cue-plus-target trials, it may be detected and filtered as a general strategy since, in most (i.e., 66%) of our trials, the distracter did conflict with the target (Posner and DiGirolamo, 1998). Consistent with these arguments, no-conflict cue-plus-target

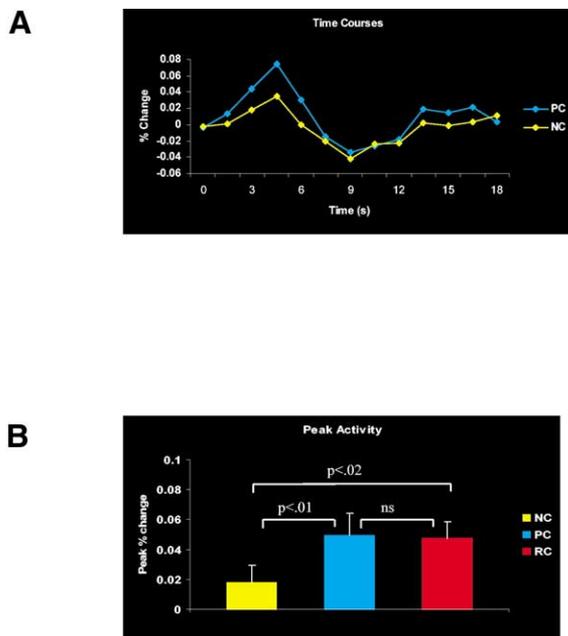


Fig. 3. Conflict-related activity in dorsal/caudal anterior cingulate cortex (dACC) for the local task. (A) The hemodynamic time course of activity for trials with perceptual and semantic conflict (PC trials) and no conflict (NC trials). (B) PC trials evoked significantly greater peak activity than NC trials, $t(13) = 2.80$, $P < 0.008$. In addition, perceptual, semantic, and response conflict (RC trials) also activated the dACC significantly more than NC trials, $t(13) = 2.52$, $P < 0.02$, but not more than PC trials, $P > 0.44$.

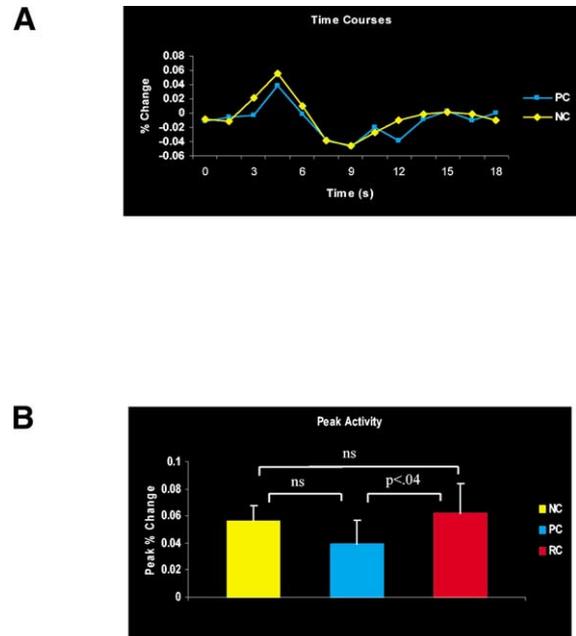


Fig. 4. Conflict-related activity in dorsal/caudal anterior cingulate cortex (dACC) for the global task. (A) The hemodynamic time course of activity for trials with perceptual and semantic conflict (PC trials) and no conflict (NC trials). (B) PC trials did not evoke significantly greater peak activity than NC trials, $P > 0.21$, but trials that evoked perceptual, semantic, and response conflict (RC trials) activated the dACC significantly more than PC trials, $t(13) = 1.98$, $P < 0.035$, and marginally more than NC trials, $t(13) = 1.49$, $P < 0.08$.

trials activated the dACC in the present study as can be seen in Fig. 3 and 4. Hence, the inclusion of NC trials appeared not to pose major limitations in our ability to functionally define a region of interest in the dACC.

We entered these averaged cue-plus-target and cue-only time courses into a random effects, two-way repeated measures analysis of variance, in which we tested for an interaction between Trial Type (cue-only trials, cue-plus target trials) and Time Point (12 time points; 0–18 s following trial onset) to isolate voxels activated more when a target was present (i.e., cue-plus-target trials) than when a target was absent (i.e., cue-only trials). This analysis revealed a large area of activation in the midline frontal cortex that included a bilateral region of the dACC. Using the atlas of Talarach and Tournoux (1988), we isolated 255 dACC voxels within this activated region, each of which was reliably activated by targets, $F(11,143) = 3.06$, $P < 0.001$, and part of a cluster consisting of 10 or more activated voxels (Forman et al., 1995; Xiong et al., 1995). These voxels were distributed across Brodmann areas (BAs) 24, 32, and 33 (geographic center of mass in Talarach space: $x = 2$, $y = 7$, $z = 34$), which have been implicated in conflict monitoring (Banich et al., 2000a; Botvinick et al., 1999; MacDonald et al., 2000; Milham et al., 2001).

Regions of interest in the left prefrontal cortex were defined in an analogous fashion. These included two regions of the middle frontal gyrus, i.e., Region 1 (48 voxels:

geographic center of mass in Talaraich space: $x = -44$, $y = 32$, $z = 21$: BA 46) and Region 2 (80 voxels: geographic center of mass in Talaraich space: $x = -44$, $y = 19$, $z = 32$: BA 9). They also included a third region in the inferior frontal gyrus (73 voxels: geographic center of mass in Talaraich space: $x = -47$, $y = 16$, $z = 20$: BA 9).

To determine the nature of conflict that activated this region of the dACC, we computed the time-locked average response to each trial type averaged across all voxels in the region. For each task (i.e., global and local), we tested whether the dACC was activated more by (1) PC versus NC trials, (2) RC versus NC trials, and (3) RC versus PC trials. Each random effects t test compared the peak amplitude (i.e., the average of three peak time points, 3 to 7.5 s after trial onset) for two trial types (e.g., PC versus NC trials). Since we had only a single region of interest, P values of less than 0.05 were considered significant. Region of interest analyses for the left prefrontal cortex were performed in a similar way, except that only the peak time point (4.5–6 s poststimulus onset) was used for t tests because peak activity was more sharply defined in these regions.

Results

Dorsal/caudal anterior cingulate cortex

Local task

fMRI data confirmed that perceptual and semantic conflict from global distracters during the local task was sufficient to activate a region of interest in the dACC (Fig. 2). Consistent with prior studies (MacDonald et al., 2000; Milham et al., 2001), targets in both the global and local tasks evoked a hemodynamic (i.e., blood flow) response in the dACC that peaked and returned to baseline over a 12–14-s period. For the local task (Fig. 3), the time course of hemodynamic activity within the dACC reached a higher peak value for PC trials than for NC trials (Fig. 3A). Contrasting peak activity (see materials and methods section) for these two trial types (Fig. 3B) confirmed that this difference was highly significant, $t(13) = 2.80$, $P < 0.008$. Further tests of peak activity revealed that RC trials also activated the dACC significantly more than NC trials, $t(13) = 2.52$, $P < 0.02$, but, importantly, not more than PC trials, $P > 0.44$. Thus, the presence of perceptual and semantic conflict from global distracters was sufficient to fully engage the dACC during the local task.

Behavioral data from the local task indicated that response times for RC trials (809 ms) were significantly slower than response times to either NC trials (751 ms), $t(13) = 4.77$, $P < 0.0005$, or PC trials (754 ms), $t(13) = 5.42$, $P < 0.0001$, which, in turn, did not significantly differ from each other, $t(13) = 0.39$, $P > 0.34$. Similarly, error rates for RC (8.9%) trials were significantly greater than for either NC (4.8%), $t(13) = 3.59$, $P < 0.001$, or PC (6.1%)

trials, $t(13) = 1.82$, $P < 0.053$ which, in turn, did not significantly differ from each other, $t(13) = 1.08$, $P > 0.15$.

Global task

Consistent with prior findings demonstrating global advantage, conflict-related ACC activity was less robust for the global task than for the local task (Fig. 4A and B). Specifically, and in contrast to the findings from the local task, PC trials did not activate the ACC significantly more than NC trials, $P > 0.21$. RC trials, however, activated the dACC significantly more than PC trials, $t(13) = 1.98$, $P < 0.035$, and there was a nonsignificant trend for RC trials to activate the dACC more than NC trials, $t(13) = 1.49$, $P < 0.08$. Thus, during the global task, local distracters did not activate the ACC unless they engendered response conflict. These results are consistent with the finding that local aspects of an object's shape typically evoke less conflict than global aspects (Kimchi, 1992; Navon, 1977). Local distracters may therefore need to evoke multiple forms of conflict (i.e., perceptual, semantic, and response) to activate the dACC relative to NC trials.

Behavioral data from the global task indicated that response times for RC trials (782 ms) were significantly slower than response times to either NC trials (728 ms), $t(13) = 4.36$, $P < 0.001$, or PC trials (743 ms), $t(13) = 2.92$, $P < 0.01$, which, in turn, did not significantly differ from each other, $t(13) = 1.20$, $P > 0.14$. Similarly, error rates for RC (9.0%) trials were significantly greater than for either NC (4.7%), $t(13) = 5.23$, $P < 0.001$, or PC (5.0%) trials, $t(13) = 1.82$, $P < 0.053$ which, in turn, did not significantly differ from each other, $t(13) = 0.28$, $P > 0.39$.

Lateral prefrontal regions

Although not the primary focus of the present article, the view that dACC signals the presence of conflict to lateral prefrontal regions (Botvinick et al., 2001) might be interpreted as predicting conflict-related activity in prefrontal regions. As described earlier in the materials and methods section, there were three left prefrontal regions of interest, i.e., (1) middle frontal gyrus (BA 46), (2) middle frontal gyrus (BA 9), and (3) inferior frontal gyrus (BA 9). Contrary to some recent findings (MacDonald et al., 2000), but consistent with others (Milham et al., 2001), planned t contrasts of peak activity during the local task revealed that RC trials produced greater activity than NC trials ($P < 0.05$) in all three prefrontal regions of interest. For the global task, RC trials produced significantly more activity than NC trials in two of the three regions of interest ($P < 0.05$), the middle frontal gyrus (BA 46) and inferior frontal gyrus ($P < 0.05$). PC trials produced reliably greater activity than NC trials in just one middle frontal region (BA 9) and only for the local task. Thus, similar to what was observed for dACC, neural activity in prefrontal areas was sensitive to the presence of response conflict for both tasks and to the presence of prereponse conflict for only the local task.

Discussion

The present findings indicate that the dACC plays a broader role in conflict monitoring than has been suggested by recent data (Milham et al., 2001; Van Veen et al., 2001), but are still highly consistent with the view that the ACC monitors for processing conflict (Botvinick et al., 2001). Specifically, our results indicate that the dACC detects preresponse level as well as response-level conflict. The dACC may therefore serve as a general conflict detection system, which signals lateral prefrontal areas to increase attention toward task-relevant processing whenever there are processing conflicts that could impair performance (Botvinick et al., 2001). Future studies will be necessary to fully define the generality of the dACC's contributions to conflict monitoring.

An interesting characteristic of the present findings is that they varied with the task being performed. For the local task, the presence of preresponse level conflict was sufficient to fully engage the dACC. For the global task, however, conflict at response levels was necessary to activate the dACC, relative to NC trials. Given that global forms often evoke more conflict than local forms in selective attention tasks (Kimchi, 1992; Navon, 1977), we speculate that local forms may need to evoke conflict at multiple levels (both preresponse and response) to elicit dACC activity, whereas global forms may be able to evoke dACC activity even when conflict is present only at preresponse levels. Since dACC activity in response to conflict increased incrementally, rather than gradually, in both the global and the local tasks, our findings indicate some nonlinearity in dACC activity associated with conflict. This result may indicate that the dACC responds in an "all-or-none" fashion to conflict, once a certain threshold is met. Future studies are necessary, however, to assess the viability of this hypothesis.

Exploratory analyses revealed similar patterns of conflict-related activity in left prefrontal regions. Response conflict activated regions of both the middle and the inferior frontal gyri. Preresponse level conflict activated only the middle frontal gyrus and, similar to the dACC, only for the local task. These findings are highly consistent with the view that dACC signals lateral prefrontal regions to bias more attention toward target processing when the presence of conflicting distracters makes selection more difficult. Interestingly, these results are in general agreement with recent findings from a fast-rate event-related fMRI study (Milham et al., 2001), but do not concur with results from an fMRI study in which extremely slow rates of stimulus presentation (1 stimulus every 12.5 s were used (MacDonald et al., 2000). Thus, as we suggested might be the case in the introduction, stimulus presentation rates appear to play an important role in determining the nature of conflict-related activity that is observed.

Importantly, the behavioral data indicate that the greater dACC and left middle frontal gyrus activation we observed

for PC trials than for NC trials during the local task is unlikely to be accounted for by differences in task difficulty between these two conditions. This is because behavior was virtually identical for situations in which there was perceptual and semantic conflict (PC trials) and situations in which there was no conflict (NC trials). Although the lack of a significant behavioral difference between PC and NC trials may seem surprising given some findings (Eriksen and Schultz, 1979), such differences are typically small and sometimes not even found (Eriksen and Eriksen, 1974). In the present experiment, we speculate that the dACC detected the presence of preresponse level conflict arising from global distracters during the local task and signaled left middle frontal regions to resolve that conflict before it impacted behavior. This account is highly consistent with the conflict monitoring view of the dACC (Botvinick et al., 2001).

Our findings may also be relevant to understanding the neural bases of certain clinical syndromes in which increased distractibility is associated with dysfunction of the dACC, such as schizophrenia and attention-deficit and hyperactivity disorder (Bush et al., 1999; Carter et al., 1997). The present data suggest that dysfunction of the dACC in these syndromes may increase distraction from irrelevant perceptual and semantic representations as well as competing response alternatives. Our results therefore inform both theoretical and clinical models of attentional control.

In sum, the present findings broaden our understanding of the ACC and its role in conflict monitoring. Specifically, they indicate that dorsal/caudal regions of the ACC monitor for conflict at preresponse as well as response levels of processing. Given that rostral regions of the ACC contribute to error monitoring (Braver et al., 2001; Kiehl et al., 2000; Menon et al., 2001), the present results suggest that distinct functional subregions within the ACC monitor different aspects of performance (e.g., errors versus processing conflicts). Communication between these subregions of ACC and other regions (e.g., lateral prefrontal areas) may underlie dynamic changes in behavior under conditions of conflict (Botvinick et al., 2001).

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