Anterior Cingulate and the Monitoring of Response Conflict: Evidence from an fMRI Study of Overt Verb Generation

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Abstract

■ Studies of a range of higher cognitive functions consistently activate a region of anterior cingulate cortex (ACC), typically posterior to the genu and superior to the corpus collosum. In particular, this ACC region appears to be active in task situations where there is a need to override a prepotent response tendency, when responding is underdetermined, and when errors are made. We have hypothesized that the function of this ACC region is to monitor for the presence of "crosstalk" or competition between incompatible responses. In prior work, we provided initial support for this hypothesis, demonstrating ACC activity in the same region both during error trials and during correct trials in task conditions designed to elicit greater response competition. In the present study, we extend our testing of this hypothesis to task situations involving underdetermined responding. Specifically, 14 healthy control subjects performed a verb-generation task during event-related functional magnetic resonance imaging (fMRI), with the on-line acquisition of overt verbal responses. The results demonstrated that the ACC, and only the ACC, was more active in a series of task conditions that elicited competition among alternative responses. These conditions included a greater ACC response to: (1) Nouns categorized as low vs. high constraint (i.e., during a norming study, multiple verbs were produced with equal frequency vs. a single verb that produced much more frequently than any other); (2) the production of verbs that were weak associates, rather than, strong associates of particular nouns; and (3) the production of verbs that were weak associates for nouns categorized as high constraint. We discuss the implication of these results for understanding the role that the ACC plays in human cognition. ■

INTRODUCTION

Studies of a variety of higher cognitive functions, including working memory, language production, and inhibition, consistently activate a region of anterior cingulate cortex (ACC), typically situated posterior to the genu and superior to the corpus collosum. In terms of the anatomical divisions of the ACC proposed by researchers such as Picard and Strick (1996), the region of ACC on which we are focusing falls within the rostral cingulate zone, in front of the anterior commisure line. In particular, this ACC region appears to be active in at least three different task situations (Botvinick, Braver, Carter, Barch, & Cohen, submitted). First, this ACC region is active in task conditions in which a prepotent response tendency has to be overcome, such as in studies of the Stroop task and the Go-No/GO task (e.g., Casey et al., 1997; Kawashima et al., 1996; Carter, Mintun, & Cohen, 1995; George et al., 1994; Taylor, Kornblum, Minoshima, Oliver, & Koeppe, 1994; Bench et al., 1993; Paus, Petrides, Evans, & Meyer, 1993; Pardo, Pardo, Janer, & Raichle, 1990). Second, the ACC is active in task conditions when the response to be made is not fully constrained by the task context, such as in studies of verb generation, verbal fluency, and stem completion (e.g., Buckner et al., 1995; Yetkin et al., 1995; Friston, Frith, Liddle, & Frackowiak, 1993; Frith, Friston, Liddle, & Frackowiak, 1991; Frith, Friston, Liddle, & Frackowiak, 1993; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Petersen, Snyder, & Raichle, 1990). Lastly, ACC activity is also commonly found in association with the commission of errors. Specifically, the term "error-related negativity" (ERN) has been

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used to describe an event-related potential that appears to accompany the commission of errors in speeded response tasks (Gehring, Coles, Meyer, & Donchin, 1990; Hohnsbein, Falkenstein, & Hoorman, 1989). A number of studies have localized the generator of this ERN to a medial-frontal region, with the ACC being the most likely candidate generator within this region (Dahaene, Posner, & Tucker, 1994). The ERN usually starts with the onset of response-related electromyographic activity, peaking 100–150 msec later, and is observed most clearly in response-aligned ERP average over error trials.

We have recently proposed an hypothesis about the function of the ACC that we believe can account for its activation under all of the task conditions described above. Specifically, we have hypothesized that the ACC serves to evaluate the demand or need for cognitive control by monitoring for the occurrence of conflict or crosstalk in information processing (Botvinick et al., submitted; Carter et al., 1998). By crosstalk we mean interference or interaction in the processing of two stimuli or responses that occurs when the pathways for this processing overlap. According to this hypothesis, the ACC should be active when there is a high degree of competition between two incompatible motor responses. One example of this would be a task where a subject needs to respond "yes" with one finger or "no" with another finger, and both responses are activated simultaneously.

In previous research, to explicitly test our hypothesis about the function of ACC, we conducted an event-related functional magnetic resonance imaging (fMRI) study with an AX version of the Continuous Performance Test (CPT-AX., Carter et al., 1998). This task was designed to examine the pattern of ACC activity under two of the task situations described above: (1) when subjects make errors, and (2) when subjects make correct responses, but must overcome interference from prepotent, but incorrect, response tendencies. Our hypothesis predicted that ACC activity should occur in response to errors because in many error situations, both the correct and incorrect response are simultaneously active for at least some period of time, creating crosstalk in processing pathways (e.g., Falkenstein, Hohnsbein, & Hoorman, 1995; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). However, our hypothesis also predicted that we should see ACC activity on *correct* trials, if a prepotent but inappropriate response tendency must be overcome. This is a classic situation that elicits crosstalk between processing pathways, as two incompatible responses are activated at the same time, one of which needs to be suppressed in order for a correct response to be made. Consistent with prior research, we found event-related ACC activity in response to the commission of errors in our CPT-AX task. However, more importantly, we also found that ACC activity was greater during task conditions that required subjects to overcome prepotent response tendencies, even when only correct trials were examined.

The current study was designed to extend the testing of our specific hypothesis about the function of the ACC to the domain of tasks involving underconstrained responding. As noted above, several previous studies have found activation of ACC in tasks such as verbal fluency, verb generation, and stem completion (e.g., Buckner et al., 1995; Yetkin et al., 1995; Friston et al., 1993; Frith et al., 1991; Frith et al., 1993; Petersen et al., 1989; Petersen et al., 1990). These are all tasks in which the response to be made is not fully constrained by the task context, but which do not necessarily require prepotent response tendencies to be overcome. Nonetheless, the finding that the ACC is active during performance of these tasks is a very robust one. However, the specific functional interpretation of the role that the ACC plays during verb generation, verbal fluency or word stem completion has been somewhat of a puzzle. The most common interpretation of ACC activation in these tasks is that it is somehow related to selection among competing, complex contingencies (e.g., Buckner et al., 1995; Frith et al., 1991; Petersen et al., 1989), and that this ACC activity reflects its critical role in an "anterior attentional system" (e.g., Raichle et al., 1994).

Our hypothesis allows us to make a very specific interpretation of the functional role of ACC activity during verb generation, verbal fluency, and word stem completion tasks. We would argue that the ACC activation in these tasks reflects the fact that multiple responses are likely to be activated simultaneously by the cue, creating crosstalk in the pathways responsible for the selection and/or production of these responses. This hypothesis allows us to make several specific predictions about the patterns of ACC activity that should be elicited by particular conditions of tasks such as verb generation. In verb generation, subjects are presented with a noun and asked to produce a verb that is a use of or an action associated with the noun. Our first prediction is that the degree of ACC activity during verb generation should be modulated by the number of verb alternatives typically associated with a particular noun. Nouns that tend to elicit several different verbs with equal strength should elicit a high degree of ACC activity, as such nouns are likely to simultaneously activate multiple responses, creating competition among these responses in pathways responsible for the selection and/or production of these responses. In contrast, nouns that tend to activate a single verb across subjects should not elicit much ACC activity, as such nouns are likely to activate only this single response, precluding competition in selection/production pathways.

A prior fMRI study by Thompson-Schill et al. (Thompson-Schill, D'Esposito, Aguire, & Farah, 1997) provides initial support for this hypothesis. Thompson-Schill et al. used a covert verb-generation paradigm to examine activity that varied according to whether the noun was one that provided high constraint for the verb choice (i.e., during norming studies, a single verb was produced much more frequently than any other verb) or a low constraint for the verb choice (multiple verbs were produced with equal frequency during norming studies). Thompson-Schill et al. were interested in studying selection processes, and argued that the low-constraint nouns should lead to a greater need for selection, as they required choosing among several equally prepotent associated verbs. However, in light of our hypothesis, one could also posit that the low constraint nouns lead to greater response competition or crosstalk, since multiple possible responses are likely to be active at the same time. Thompson-Schill et al. (1997) found that two regions consistently demonstrated greater activity for low- vs. high-constraint nouns. The first region was the left-inferior-frontal cortex (LIFC; Brodmann's area 44), the activity of which they interpreted as reflecting the need to select a relevant feature of semantic knowledge from a set of competing alternatives. In addition, and relevant to our hypothesis, these researchers also found a supplementary motor area/ACC region that was more active for low- than high-constraint nouns. This latter finding is consistent with our hypothesis that the ACC is monitoring for the presence of conflict among incompatible representations, which is more like to occur for low- than high-response strength nouns.

Our hypothesis about the function of ACC makes a second prediction about the pattern of ACC activity during verb-generation tasks. We would predict that the degree of ACC activity should also be modulated by the type of verb produced by subjects on a trial-by-trial basis. Specifically, our hypothesis predicts that the ACC should *not* be active during the production of verbs that are the most common or strongest response for a noun, based on the hypothesis that such verbs are the prepotent response, and thus, should not elicit much conflict. However, our hypothesis would predict that the ACC should be active during the production of less common or weaker responses for a noun, based on the hypothesis that the production of such verbs should elicit greater response conflict because the activation of a more strongly associated verb may have to be overcome.

Lastly, our hypothesis about the function of the ACC makes a third, even more specific prediction about the pattern of ACC activity during verb generation. As described above, our hypothesis predicts that ACC activity should be modulated both by the type of noun presented to subjects (high vs. low constraint) and by the type of verb produced by the subject (weak vs. strong associate). However, our hypothesis also predicts that the degree of ACC activity should be further modulated by the interaction between noun type and verb type. Specifically, we would argue that the degree of conflict elicited by the production of a weak-verb associate should be modulated by the degree of constraint provided by the noun. In other words, the conflict or crosstalk arising from the production of a weak-verb associate for a noun with high constraint should be great, as a much more strongly associated or prepotent verb choice may need to be inhibited. However, the conflict arising from the production of a weak-verb associate for a noun with low constraint should not be as great, as the various verbs associated with such nouns should be more equally prepotent.

The goal of the current study was to test these predictions of our hypothesis about the function of ACC by both replicating and extending the findings of Thompson-Schill et al.. To do so, we used event-related fMRI and an overt-verb-generation paradigm. To replicate the findings of Thompson-Schill et al., we normed a series of nouns during a verb-generation task, and divided them into high- and low-constraint nouns. We then analyzed the data by comparing brain activity in response to nouns associated with high vs. low constraint. As described above, we predicted that there should be a greater ACC response to low-constraint nouns, based on the hypothesis that such nouns activate several, potentially competing responses. For example, in our study, the noun "bell" was categorized as a high-constraint noun because the vast majority of norming subjects (83%) produced the same verb "ring" as a response. In contrast, the noun "ball" was categorized as a low-constraint noun because the norming subjects produced a range or verbs as responses (i.e., throw, 34%; play, 27%; bounce, 18%; hit, 10%). Thus, we predicted that we would see greater ACC activity associated with the processing of nouns such as "ball" as compared to nouns such as "bell."

To extend Thompson-Schill et al.'s findings and to test our predictions about the relationship between ACC activity and verb type, we also used the data from the norming study to determine the relative association strength for verb responses to each noun. Specifically, we determined whether the response (i.e., the verbs rather than the nouns) produced by subjects on each trial was the verb most strongly associated with the noun (strong-verb associate), or one of the less strongly associated verbs for that noun (weak-verb associates). In the context of the example described above, the verb "ring" was categorized as the strong-verb associate for the noun "bell," while all other responses were categorized as weak-verb associates for "bell" (e.g., hear, hit). We then analyzed the data according to the relative association strength of the verbs actually produced by subjects on each trial. As described above, we predicted that the ACC would not be active for the production of strong-verb associates, based on the hypothesis that such verbs should not elicit much conflict. However, we predicted that the ACC would be more active during the production of weak-verb associates (e.g., the verb "hear" for the noun "bell"), based on the hypothesis that the production of such verbs should elicit greater response conflict because the activation of a more strongly associated verb (e.g., the verb "ring" for the noun "bell") has to be overcome. Further, we predicted that ACC activity would be modulated by the interaction between noun type and verb type, such that the degree of ACC activity would be greatest for weak-verb associate responses to high-constraint nouns. In other words, we predicted that producing a weak-verb associate to a high-constraint noun such as "bell," should elicit more ACC activity than producing a weak-verb associate to a low-constraint noun such as "ball." This prediction is based on the hypothesis that to produce a weak-verb associate to a high-constraint noun such as "bell," the much more strongly associated or prepotent verb choice (e.g., "ring") may need to be inhibited. However, with a low-constraint noun such as "ball," the various verb choices (e.g., "throw," "play," "bounce") should be more equally prepotent.

RESULTS

Estimated Movement Data

A potential concern in studies using overt verbal responses is that speaking will induce an increased, and potentially unacceptable, level of movement into fMRI images. To explore this possibility, we examined the estimated movement data obtained from AIR to examine the degree of movement associated with producing overt verbal responses. Movement associated with generating verbal responses should primarily be apparent in the first one to two scans of each trial, the scans acquired while subjects were producing their overt responses. We used one-factor ANOVAs, with scan (1–5) as the within-subject factor, and the six movement parameters (Pitch, Roll, Yaw, *X*, *Y*, *Z*) as the dependent variables. For absolute movement from the reference image, there was only one significant main effect of condition, yaw ($F(4,52) = 3.811$, $p < .01$), with higher yaw scores for the later scans. This result is consistent with our prior research

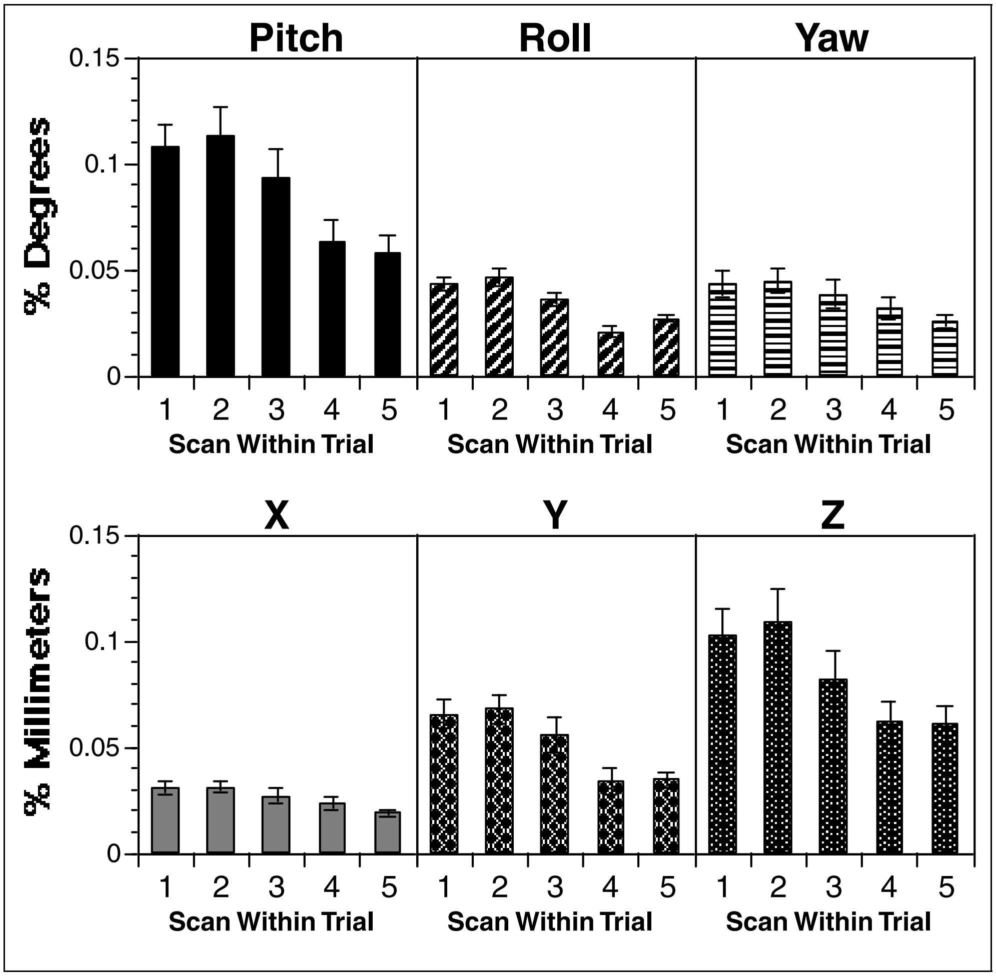

Figure 1. Graph illustrating the magnitude of estimated incremental movement across the five scans within each trial.

demonstrating no increase in absolute movement during overt as compared to covert verbal responding (Barch et al., in press). For incremental movement (see Figure 1), the ANOVAs demonstrated main effects of scan for all six parameters (all *p*'s<.05, see Figure 1). For all six parameters, the first two scans had greater incremental movement than the later scans. However, as can be seen in Figure 1, the magnitude of incremental movement during the first two scans of each trial is still relatively small, again consistent with the results of our prior research on overt verbal responding (Barch et al., 1999). We also compared the amount of movement across the task conditions of interest described below (e.g., high- vs. low-constraint nouns, strong- vs. weak-verb associates) and found no significant differences in any of the estimated movement parameters.

Quality of Response Recording

The audio tapes containing the participants' responses were transcribed by a research assistant and checked for accuracy by the first author. For all 14 subjects, almost all responses were recorded clearly, and were able to be transcribed. The content of a response was ambiguous for only two participants, and for each of these participants, the ambiguity only occurred on two trials. All subjects performed the task appropriately (producing verbs that were action of or uses of the noun). However, 11 out of 14 subjects failed to generate a verb on a few trials. The use of event-related fMRI imaging methods enabled these trials to be eliminated in all analyses reported below. For those subjects who missed trials, the average number of trials without a response was 2.3 (range 0–11).

Low- vs. High-Constraint Nouns

We began by comparing responses to low- and high-constraint nouns. To do so, we used voxel-wise two-factor ANOVAs, with noun type (low vs. high constraint) and scan (1 through 5) as within-subject factors. The inclusion of scan as a factor allowed us to look for regions showing event-related responses to the onset of each trial. This analysis identified two regions that displayed a significant noun type by scan interaction, with a greater response to low- than high-constraint nouns. One region was in LIFC (centroid of activation: *X*: −50(L), *Y*: 15, *Z*: 20) and one region was within the ACC (centroid of activation: BA 32/24; *X*: 2(R), *Y*: 30, *Z*: 14). The LIFC activation contained 19 contiguous voxels and the ACC activation contained 18 contiguous voxels. As predicted, this ACC activation falls within the rostral cingulate zone (Picard & Strick, 1996). This result replicates the findings of Thompson-Schill et al., as they found the same two regions to be active in the identical comparison, although our ACC region was somewhat more inferior than the one they identified.

Weak- vs. Strong-Verb Associates

As noted above, the previous analyses only used information about the nouns gained from the norming study, and did not take into account the actual verb response produced by the subjects on each trial. Thus, our next set of analyses used the overt verbal response data we

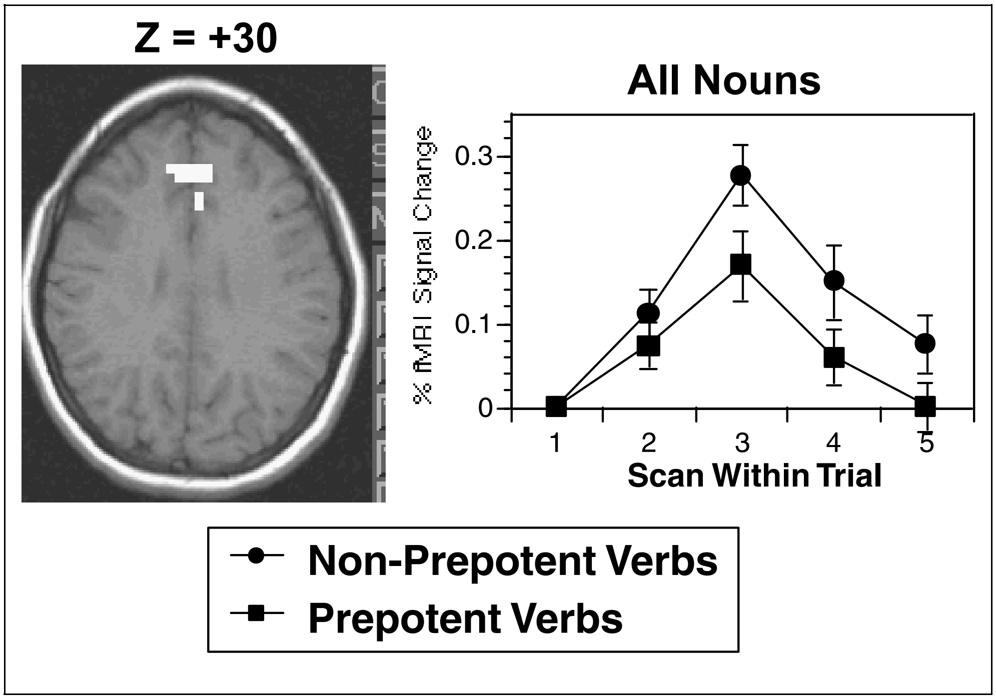

Figure 2. Anterior cingulate region demonstrating a significantly greater event-related response to weak- vs. strong-verb associates. Image is displayed in radiological convention, with the right side of the image corresponding to the participant's left. The graph plots the signal as a percent change from first scan of each trial, and reflects the average of all voxels in this region, averaged across all participants.

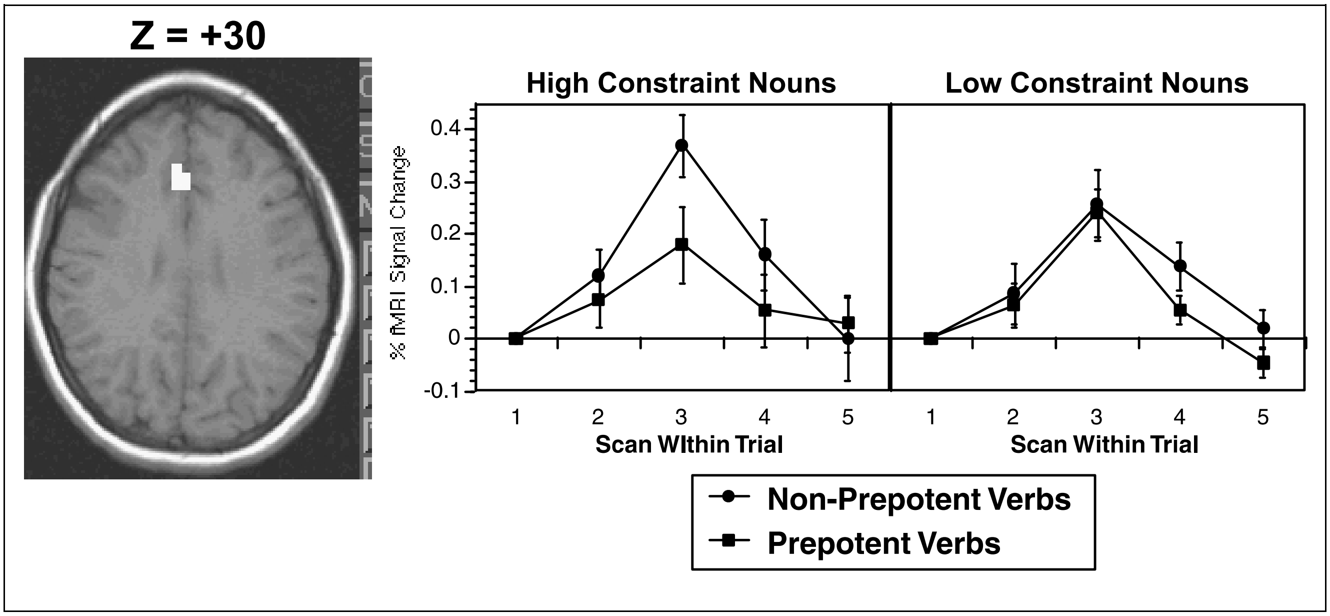

Figure 3. Anterior cingulate region demonstrating an interaction between noun type (high vs. low constraint) and verb type (weak vs. strong verb associate). Graphs plot the signal as a percent change from first scan of each trial, and reflects the average of all voxels in this region, averaged across all participants.

were able to acquire on-line. We compared activation responses to verbs produced by subjects that were categorized as either the strong- or weak-verb associate for a particular noun. To do so, we used voxel-wise two-factor ANOVAs, with verb type (weak vs. strong associate) and scan (scan 1 through 5) as within-subject factors. Again, the inclusion of scan as a factor allowed us to look for regions showing event-related responses to the onset of each trial. This analysis identified only one region, an area of 93 contiguous voxels within the ACC (centroid of activation: *X*: 3(R), *Y*:28, *Z*:29) that displayed a significantly greater event-related response to weak- as compared to strong-verb associates. Again, this ACC region falls within the rostral cingulate zone (Picard & Strick, 1996). As shown in Figure 2, this greater response to weak- as compared to strong-verb associates, included both a higher peak and a longer time to return to baseline. This result is consistent with the hypothesis that the ACC is monitoring for response conflict, as one would predict that there would be more crosstalk among competing responses for weak- than for strong-verb associates.

Interaction Between Noun Type and Verb Type

We next examined the production of weak- and strong-verb associates separately for nouns that had been classified as high or low constraint. As described in the Introduction, the logic behind this analysis was that the degree of conflict elicited by the production of weak-verb associates should be modulated by the relative constraint provided by the noun to which it is associated. In other words, the conflict or crosstalk arising from the production of a weak-verb associate for a noun with high constraint should be great, as a much more strongly associated verb choice may need to be inhibited. However, the conflict arising from the production of a weak-verb associate for a noun with low constraint should not be as great, as the various verbs associated with such nouns should be more equally prepotent. To test this hypothesis, we conducted voxel-wise three-factor ANOVAs, with noun type (high vs. low constraint), verb type (weak- vs. strong-verb associate) and scan (scan 1–5) as within-subject factors. Again, this analysis identified only one region, an area of 21 contiguous voxels within the ACC (centroid of activation: *X*: 4(R), *Y*:24, *Z*:30) that displayed the predicted interaction. Once again, this ACC region falls within the rostral cingulate zone (Picard & Strick, 1996). Planned contrasts indicated that the two-way interactions between verb type and scan was significant for the high-constraint nouns ($F(4,52)=6.09$, $p<.001$), but was only marginally significant for the low-constraint nouns ($F(4,52)=2.31$, $p=.07$). As shown in Figure 3, there was a very striking difference between the ACC activity for weak- vs. strong-*verb* associates produced for *nouns* categorized as high constraint. In contrast, the difference in ACC activity for weak- vs. strong-verb associates produced for low-constraint nouns was not nearly as large.

DISCUSSION

The results of this study are consistent with our hypothesis regarding the functional significance of ACC activity: Namely that the ACC serves to monitor for the presence of crosstalk or competition among incompatible responses. Further, the results of our study are consistent with findings of ACC activity in prior studies of verb generation, verbal fluency, and word stem completion (e.g., Buckner et al., 1995; Yetkin et al., 1995; Friston et al., 1993; Frith et al., 1991; Frith et al., 1993; Petersen et al., 1989; Petersen et al., 1990). However, our results go beyond those of previous studies by specifically demonstrating that the ACC, and only the ACC, was more active in a series of task conditions during a verb-generation paradigm that elicited competition or crosstalk among competing responses.

First, we replicated the findings of Thompson-Schill et al. by demonstrating that the ACC displayed a greater response to nouns categorized as low compared to high constraint. As noted above, we predicted this result based on the hypothesis that responding to low-, as compared to high-, constraint nouns activated a greater number of alternative responses, creating greater competition in the pathways responsible for selecting and producing these responses. Second, we demonstrated greater ACC activation during the production of verbs that were weak- rather than strong-verb associates of particular nouns. We predicted this result based on the hypothesis that the production of weak-verb associates, should elicit greater response conflict because the activation of more strongly associated verbs may have to be overcome. Lastly, we also demonstrated that the degree of ACC activation elicited by weak- vs. strong-verb associates was further modulated by whether the noun had been categorized as low- or high-constraint. Specifically, the magnitude of the ACC response across the various conditions seemed to match the degree of response conflict one would expect. The greatest ACC response occurred to the production of weak-verb associates for high-constraint nouns, the condition *most* likely to elicit conflict. The smallest ACC response occurred to strong-verb associates produced for high-constraint nouns, the condition *least* likely to elicit cross talk or conflict. The degree of ACC activity, to both weak- and strong-verb associates for the low-constraint nouns, fell in between these two extremes. This is to be expected, as these conditions should both elicit some conflict, since there is no highly prepotent response to be made or overcome, and several equally associated verbs are likely competing for production.

Overt Verbal Responses in fMRI

To our knowledge, this is the first fMRI study to use the content of subjects overt verbal responses as a basis for analyzing the fMRI data. We found that overt verbal responding did not increase absolute movement from a reference image, but did increase incremental, scan-to-scan movement. Consistent with our prior research (Barch et al., in press), this result suggests that during overt verbal responses, participants were exhibiting small movements to and from their original head position, but were not progressively shifting away from their initial head position. Further, the relatively small magnitude of the increased incremental movement during overt responding, combined with the fact that we obtained clearly interpretable data, suggest that the use of overt verbal response during fMRI scanning is a very feasible experimental methodology. The acquisition of these overt verbal responses allowed us to validate that subjects were performing the task accurately and as instructed. More importantly, our results demonstrate the importance and power of being able to acquire the content of subjects overt verbal responses, allowing us to use these responses as the basis for a set of analyses that would not have been possible otherwise. We believe that the ability to use paradigms employing, or even requiring, overt verbal responses opens up a whole new avenue of potential questions that can now be addressed using fMRI.

Left-Inferior-Frontal Cortex

Like Thompson-Schill et al., we found activation of LIFC in the comparison of high- and low-constraint nouns. As such, our results are consistent with the hypothesis that LIFC is involved in the selection of a relevant feature of semantic knowledge from a set of competing alternatives. However, we did not find activation of LIFC in the comparison of weak- vs. strong-verb associates This lack of an effect is also consistent with Thompson-Schill et al's hypothesis that LIFC is involved in the selection of semantic information, for the following reasons: We hypothesized that the production of a weak- over a strong-verb associate elicits more competition between alternative responses, due to differences in response strength for weak- vs. strong-verb associates. However, it is not clear that the production of a weak- over a strong-verb associate creates a greater demand for *selection* of a particular semantic feature. It may be that LIFC responds more to the number of semantic alternatives from which a response needs to be selected, rather than the relatives strengths of the various alternatives. If so, then one would not expect activation of LIFC in situations where there are only a few semantic alternatives, even if there are strong prepotency differences among the alternatives. Thus, the production of weak-verb associate, particularly for a high constraint, may not activate LIFC because this task situation does not necessarily increase the number of semantic alternatives. In contrast, processing low-constraint nouns may activate LIFC because this task situation does increase the number of semantic alternatives when compared to the processing of high-constraint nouns.

Comparison to Other Theories of ACC Function

Our current findings also go beyond our prior research in allowing us to more specifically rule out at least one alternative interpretation of the functional significance of ACC activity. As discussed in the Introduction, the ACC is commonly active during the commission of errors. To account for this, Gehring and Falkenstein have hypothesized that the ACC is involved in monitoring and compensating for errors (Falkenstein et al., 1995; Gehring et al., 1993). More specifically, it has been proposed that the ERN (the ERP component thought to index ACC activity) reflects a comparator process, which involves comparing a representation of the intended, correct response, to a representation of what response the person actually made (Gehring et al., 1993). In our prior research, we found ACC activity during task conditions that required subjects to overcome prepotent response tendencies, even when only correct trials were examined. On the surface, these findings would seem to rule out the comparator interpretation of ACC activity that the ACC is specifically responding to the production of errors. However, one might still be able to interpret the results of this prior study as also being consistent with the comparator hypothesis. This is because in the CPT-AX, the conditions with the highest response conflict, were also those the produced the most errors. Thus, even though we examined only correct trials, one could argue that the ACC activity on these trials reflected the fact that on at least some trials, subjects may have started to make an incorrect response, which they then overcame in order to produce the correct response. However, in the verb generation paradigm used in the current study, there were no correct or incorrect responses to be made by the participant. Thus, it is not possible to interpret the ACC activity as potentially reflecting a response to errors during performance of a cognitive task.

In many ways, our hypothesis is similar to at least two other theories about the functional significance of the ACC. First, Posner and Dahaene (1994) have suggested that the ACC is critically involved in cognitive control, suggesting that the ACC is involved in attention to action and the recruitment and control of brain areas needed to carry out complex cognitive tasks. This hypothesis would give the ACC a central role in a wide variety of cognitive domains that require the involvement of other brain areas. In a similar vein, Pardo et al. (1990) has suggested that the ACC plays a selection role, serving to arbitrate between alternative processing possibilities according to some type of internally represented plan. Like our hypothesis, both of these theories suggest that the ACC should be active in a wide variety of task situations that may potentially require cognitive control (Posner & Dahaene, 1994; Posner & DiGirolamo, 1998). However, Posner's and Pardo's hypotheses imply that the ACC itself is supplying or regulating the control functions. In contrast, our hypothesis suggests that the ACC plays more of an evaluative role in cognitive control, serving to monitor or evaluate the degree of response competition (Botvinick et al., submitted). In a recent work, Botvinick and colleagues (Botvinick, Nystrom, Fissel, Carter, & Cohen, in press) have provided evidence that suggests that the ACC is indeed monitoring for response conflict rather than providing control itself. Specifically, these researchers used an Eriksen flanker paradigm to demonstrate that, across subjects, the degree of ACC activity was strongly correlated with a measure of response conflict, but was not correlated with a behavioral measure of cognitive control. Although further research on this issue is clearly needed, such results suggest that the ACC may be playing more of an evaluative role rather than a regulative role in cognitive control.

One other possible alternative interpretation of our data is that the region of ACC upon which we are focusing does not serve specifically to monitor for response competition. Instead, it is possible that situations eliciting response competition simply place a stronger demand on some other function, such as initiation or generation of responses, that might be subserved by this region of ACC. If this were true, one would expect that the some index of the difficulty of generation or initiation, such as reaction time, would more clearly predict ACC activity than would the presence of response competition. However, studies using the Eriksen flanker task and either ERPs or fMRI provide data inconsistent with the hypothesis that the ACC is simply active whenever response generation is more difficult, at least as indexed by reaction times. Specifically, these studies have found evidence for ACC activation in response to errors in the Eriksen task, even though the error responses are typically faster than correct responses (Botvinick et al., in press; Gehring et al., 1993; Gratton et al., 1988). Errors in speeded response tasks often represent premature responses delivered before stimulus analysis is complete (Gratton et al., 1988). However, even as these "premature" error responses are executed, stimulus evaluation can continue, leading to activation of the correct response, and some level of conflict between incompatible responses (Botvinick et al., submitted). Thus, findings from these studies with the Eriksen flanker task are more consistent with the hypothesis that the ACC monitors for response conflict, rather than the hypothesis that the ACC is involved in some other function (such as generation or initiation of responses) that is simply more strongly tapped under conditions of conflict.

ACC and Cognitive Control

We believe that our functional interpretation of the significance of ACC activity during a range of cognitive paradigms helps further our understanding of the precise contribution that this brain region makes to cognitive processing. However, the argument that the ACC serves to monitor for the presence of response competition begs two additional questions: Why does the ACC perform such a function? And what does the ACC do with this information? One hypothesis is that by monitoring for the presence of response competition, the ACC serves to index the demand for additional cognitive control functions that may be carried out by other brain regions or systems, such as the prefrontal cortex (Botvinick et al., submitted). In other words, the ACC may monitor for the presence of crosstalk or competition in order to determine when other brain regions need to be recruited to help with processing. For example, the ACC is commonly found to be active in tasks that also engage the dorsolateral-prefrontal cortex, such as tasks tapping working memory (Braver et al., 1997; Cohen et al., 1997), inhibition (e.g., Carter et al., 1995), and attention switching (e.g., Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991). One hypothesis about the function of dorsolateral-prefrontal cortex is that it serves to actively maintain and represent context information that can be used to bias processing in task-relevant pathways, particularly when task irrelevant, but prepotent information is present (Braver, Barch, & Cohen, submitted; Cohen & Servan-Schreiber, 1992). Thus, it may be that the ACC serves to help determine when the dorsolateral-prefrontal cortex needs to come on line to provide needed biasing in favor of task relevant processing. If this hypothesis was correct, it would predict that the ACC and the dorsolateral prefrontal should show a strong but time-lagged correlation in tasks, in which the intervention of the dorsolateral-prefrontal cortex would be helpful. In such tasks, the degree of ACC activity on a given trial should be able to predict the degree of dorsolateral-prefrontal cortex activity on subsequent trials. This is a hypothesis that will need to be tested in future research.

METHODS

Subjects

Informed consent was obtained from 14 neurologically-normal right-handed subjects. Subjects were six males and eight females, with a mean age of 27.2 (a range of 18–46 years). All subjects were given a pretesting session, in which they briefly practiced the task.

Cognitive Tasks

Subjects performed a verb-generation task, in which they were shown nouns one at a time, and asked to generate a verb that was either an action of the noun, a use of the noun, or something one could do with the noun. The stimuli consisted of 192 high-frequency concrete nouns, which varied in length from three to six letters. Each subject saw half of the 192 nouns during the experiment, with the stimulus list counterbalanced across subjects, such that all words were used equally often across subjects. Subjects observed the stimuli on a visual display controlled by a Macintosh computer in the scanner control room running PsyScope software (Cohen, MacWhinney, Flatt, & Provost, 1993). Subjects performed the task continuously within each 96-sec block, blocks contained six trials each, and there was a total of 16 blocks. Each trial lasted 16 sec, allowing the acquisition of five scans per trial.

Acquisition of Verbal Responses

We used a novel albeit relatively simple method to acquire participants' overt verbal responses during fMRI scanning (Barch et al., 1999). Participants' overt verbal responses were acquired through the use of a funnel, a plastic tube, and a condensor microphone attached to a standard taperecorder. For each participant, an appropriately-sized plastic funnel was placed over the region of their mouth and taped to the top of the headcoil. The use of this funnel helped isolate the participants' voices from the background noise of the scanner. We created several different sizes of funnels to accommodate the differences in the size of participants' heads and the closeness of their faces to the top of the head coil. The size of the funnel used for an individual participant was chosen based on which was most comfortable to them and which provided the best fit. A plastic tube was then attached to the small end of the funnel, and led out to approximately knee level on each participant. A condensor microphone was taped into the end of the plastic tube, and the microphone was attached to a standard taperecorder within the scanner room. The plastic tube was used to allow placement of the microphone outside the bore of the scanner. In pilot testing, we found that placement of the microphone within the bore of the scanner caused an unacceptable level of interference with the quality of the acquired responses. To reduce the amount of head movement during overt response production, participants were trained on how to speak without moving their head before entering the scanner.

Scanning Procedures

Images were acquired with a conventional 1.5-T GE Signa whole body scanner. Twenty oblique axial slices (3.75 mm^3 isotropic voxels) were acquired parallel to the AC-PC line, with the middle of the third slice on the AC-PC line. Functional scans were acquired with a two-interleave spiral-scan pulse sequence (TR=1600 ms, TE=35 ms, FOV=24 cm, flip=60°) (Noll, Cohen, Meyer, & Schneider, 1995). Scanning was synchronized with stimulus presentation by means of a TTL pulse generated by the PsyScope software, which triggered the start of the scanner. Five scans of all 20 slice locations were acquired during the course of each 16-sec trial. Anatomical scans were acquired at the same locations as the functional images, using a standard T1-weighted pulse sequence.

Movement Estimation and Correction

Functional images were corrected for movement using a 6 parameter 3D automated algorithm (AIR, Woods, Cherry, & Mazziotta, 1992; Woods, Mazziotta, & Cherry, 1993). Two sets of estimated movement parameters (Pitch, Roll, Yaw, *X*, *Y*, *Z*) were obtained from AIR. The first set was the difference of the current image from the immediately preceding image, which will be referred to as incremental movement. The second set was the difference of the current image from the reference image (the first image acquired), which will be referred to as absolute movement. For Pitch, Roll and Yaw, the parameters are expressed in degrees. For *X*, *Y*, and *Z* the parameters are expressed in millimeters. The absolute values of these parameter estimates were used as the dependent measures in the analyses presented below.

Image Processing Procedures

Images were coregistered and pooled across participants using the following procedures (Barch et al., 1997; Braver et al., 1997; Cohen et al., 1997). Participants' structural images were aligned to a reference brain using a 12-parameter 3D algorithm AIR (Woods et al., 1992). The functional images were then scaled to a common mean (to reduce the effect of scanner drift or instability). The functional images were then registered to the reference brain using the alignment parameters derived for the structural scans, and smoothed using an 8-mm FWHM Gaussian filter (to reduce effects of anatomic variability across participants). The imaging data, pooled across participants, were then analyzed using voxel-wise ANOVAs, looking for a priori predicted interactions between particular factors (e.g., noun type or verb type) and scan within trial, as described in more detail in the Results section. In all ANOVAs, subjects were treated as random effects and a Huynh–Feldt correction for nonindependence of repeated measures was used to adjust for temporal autocorrelations in the data. Voxel-wise statistical maps were generated for each of these interactions, and then thresholded for significance using a cluster-size algorithm (Forman et al., 1995) that protects against an inflation of the false-positive rate with multiple comparisons. A cluster-size threshold of 8 voxels and a per-voxel alpha of .01 was chosen, corresponding to a corrected image-wise false positive rate of .01. These regions were overlaid onto the reference structural image, which was transformed to Talairach atlas (Talairach & Tournoux, 1988) standard stereotactic space using AFNI software (Cox, 1996).

Behavioral and Imaging Data Analysis Procedures

Seventy-one norming subjects performed the verb-generation task without fMRI scanning, which provided norming data for the 192 nouns used in the fMRI study. Using this norming data, we calculated a measure of constraint that was designed to distinguish among nouns with a single strong-verb associate and those nouns with multiple-verb associates. Thompson-Schill et al. (1997) computed the ratio of the relative frequency of the most common verb completion to the second-most common verb completion as their measure of constraint. However, this measure only takes into account information about the two most commonly produced verbs. Thus, we used a different measure that would allow us to take into account the five most frequently produced verbs. Specifically, for each noun we computed the kurtosis of the frequency distribution for the five most commonly produced verbs during the norming session (all nouns elicited at least five different verbs). Kurtosis is the characteristic of a distribution that measures its peakedness. Nouns for which one verb was produced much more frequently than any other verb demonstrated the most peaked distributions. We then did a median split on kurtosis scores to designate nouns as either high or low constraint. The high- and low-constraint nouns differed in kurtosis ($t(190)=282.94$, $p<.001$), but not in frequency ($t(190)=.07$, $p>.15$), or word length ($t(190)=1.9$, $p>.15$). We also compared the verbs most commonly produced to high- and low-constraint nouns during the norming session, and again found no differences in either frequency ($t(190)=.08$, $p>.15$), or word length ($t(190)=.17$, $p>.15$). We then conducted a second set of analyses using information about the actual verbs produced by subjects during fMRI scanning. Specifically, we used the norming data to categorize verb responses as either weak- or strong-verb associates of a particular noun. If the verb was the most commonly produced verb in response to a noun in the norming data, it was classified as the strong-verb associate. All other verbs for a particular noun were categorized as weak-verb associates. We then compared trials on which the fMRI subjects produced a weak- vs. a strong-verb associate. It is possible that the length of the verbs actually produced by subjects during the fMRI session may have varied across constraint or association strength, which could confound interpretation of our results. Thus, we conducted a two-way ANOVA for verb length, with constraint (high vs. low) and verb associate strength (weak vs. strong) as within-subject factors. This analysis indicated no main effects of either constraint ($F(1,13)=.43$, $p>.20$), verb-associate strength

($F(1,13)=1.38$, $p>.20$) and no interaction between these two factors ($F(1,13)=3.13$, $p>.10$).

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