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Mechanisms of Conflict Resolution in Prefrontal Cortex

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Executive processes in humans are a central feature of human cognition. While there is no widespread agreement about a taxonomy of executive processes, it is generally recognized that selectively attending to one source of information to the exclusion of others is either a separate executive process or a critical feature of many executive processes (Smith & Jonides, 1999). For example, scheduling consecutive processes in complex tasks, planning a sequence of tasks, and monitoring ongoing performance all depend on control over attention, and these are generally considered examples of executive processes necessary for higher cognitive function. Consequently, an understanding of executive processing requires an understanding of the mechanisms that control the allocation of attention.

The allocation of attention is critical when there are multiple sources of information competing for processing. Of course, many everyday and laboratory tasks have this feature. In the laboratory, the Stroop task is perhaps the best-studied paradigm in which two sources of information compete for control over responses, and thus attentional allocation is demanded (Stroop, 1935). In the Stroop task, participants are presented color names that are themselves printed in ink colors. When the task is to name the color of the ink,

subjects are hindered in producing a correct response if the color name differs from the ink being named compared to a control condition in which the underlying word is not color related. For example, it takes longer to say "green" to the word "blue" printed in green ink than to say "green" to the word "bell" printed in green ink. The most frequent account of the conflict in this task is that naming words (in this case color words) is a skill better learned than naming ink colors, and so the color responses from the two sources of information (lexical and hue) conflict with one another. To resolve this conflict, there must be a mechanism that allocates attention to one response (or inhibits attention from the other). The mechanism by which this conflict resolution occurs remains an open matter, but the fact that the conflict is caused by competing sources of information vying for control is undisputed.

There are many experimental effects that depend on the resolution of interference in addition to the Stroop effect. One example is the stimulus–response compatibility effect: stimuli that are naturally and compatibly associated with some response yield faster and more accurate responses than stimuli that are arbitrarily associated with a response (Kornblum et al., 1990; Kornblum & Lee, 1995).

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For example, responding with a right key press to a stimulus presented on the right of a screen and with a left key press to a stimulus on the left yields faster and more accurate responses than if the mapping is crossed. Another example is the flanker effect (Eriksen & Eriksen, 1974). When subjects are required to respond to a stimulus presented foveally, they display poorer performance if that stimulus is surrounded by stimuli that are associated with a different response. Yet other examples can be found in the large literature concerned with proactive interference on memory. In these cases, a previous association between a stimulus and a response intrudes on the encoding or retrieval of a new association. Beyond these examples, there are still other tasks, such as the go/no-go task, which can be construed as having two sources of information, one of which competes against the other (e.g., Chao & Knight, 1995; Carter et al., 1998). In a popular version of the go/no-go task, subjects are required to produce a response to a stimulus in one context, but to withhold a response to that same stimulus in another context.

What all these tasks share in common is that each features a competition between two or more sources of information that vie for control over responses. In the Stroop task, the two sources are the hue and lexical value of the stimulus. In the flanker task, they are the stimulus–response association of the central item and the stimulus–response association of the flankers. In the go/no-go task, they are the trained tendency to respond to a stimulus and the need to withhold that response when the context is inappropriate. In proactive interference situations, the two sources are the previously established association of a stimulus and a response and the current association of a stimulus with a different response.

This similarity among tasks leads naturally to the hypothesis that all these tasks share some commonality in the source of conflict resolution, a hypothesis that is largely untested. The little behavioral research that has investigated this issue has not been particularly encouraging. For example, research by Kramer et al. (1994) has revealed that correlations in performance among several tasks

that all putatively involve conflict and its resolution are quite low.

Nevertheless, there have been proposals suggesting a common theoretical tie among conflict-resolution mechanisms in tasks of this sort. Perhaps the leading such proposal comes from the work of Botvinick et al. (1999), Carter et al. (1995, 1998), and MacDonald et al. (2000). Consider the experiment reported by MacDonald et al. (2000). Subjects were given a Stroop task on some trials in which they had to report the hue in which a word was printed and on other trials in which they had to report the word itself. Each trial began with an instruction to either read the word or name the color. Following an 11-second delay, the target stimulus was presented, and subjects gave their response. Subjects were slower in naming the color when word and color were incongruent, consistent with the classic effect documented by Stroop (1935). Brain activations in this task were examined with event-related functional magnetic resonance imaging (fMRI) during two periods of the experiment: during five scanning sequences (each 2.5 seconds in duration) after the presentation of the task instruction and during five scanning sequences after presentation of the target stimulus. When monitoring activation after the target stimulus was presented, activation in the anterior cingulate cortex (ACC) was greater for incongruent than for congruent trials, but there was no difference in activation on these two types of trials in the dorsolateral prefrontal cortex (DLPFC). By contrast, the instruction-related fMRI activations in the ACC (Brodmann's areas 24 and 32) showed no differentiation between trials when subjects were instructed to name the hue or to read the word. But activation in the DLPFC during the instruction period (Brodmann's area 9) became increasingly larger with successive scans during the instruction period when subjects were instructed to read the hue, compared to when they read the word. Not only did activation in the DLPFC differentiate between hue-naming versus word-reading trials, individuals with more activation in the DLPFC after the color-naming instruction showed lower Stroop interfer-

ence. These and other results have led these investigators to conclude that there are two fundamentally different mechanisms involved in the allocation of attention in tasks that require conflict resolution. One, lodged in the ACC, is responsible for the detection and monitoring of conflicting representations, and so this mechanism is activated once a stimulus is presented for processing. The other, lodged in DLPFC, is responsible for "representing and maintaining the attentional demands of the task" (MacDonald et al., 2000), and so it is increasingly activated when instructions indicate that the color must be named, a task that requires increased attentional resources. It is this mechanism that putatively resolves the conflict in the task.

A question that arises from this model is whether it generalizes to the larger variety of tasks that involve conflict resolution. Is there a common network of brain regions involved in resolving interference in various task contexts, and is conflict detection by ACC necessary for the enabling of prefrontal interference-resolution mechanisms? By now, there have been several imaging studies of tasks that involve conflict resolution, and so we conducted a meta-analysis of these tasks to discover whether they share a common circuitry.

META-ANALYSIS OF CONFLICT-RESOLUTION TASKS

We conducted a search of the published literature for neuroimaging experiments in which conflict-resolution tasks had been used. In these studies, the following tasks were the subject of imaging: the Stroop task, the flanker task, various stimulus–response compatibility tasks, go/no-go tasks, and the AX continuous performance task. Our criteria for including findings in the meta-analysis were the following. First, the studies had to be published in refereed venues and they had to be full archival presentations, not abstracts. Second, they had to make use of either positron emission tomography (PET) or fMRI methods tested on healthy, young participants. Third,

activations· from the respective experiments had to be reported for either the subtraction of a neutral condition from an incompatible condition or a compatible condition from an incompatible condition. Fourth, the coordinates of peak activation in each region had to be reported, and these activations had to pass a relatively generous statistical criterion of $z = 2.5$ to be included in the analysis. The application of these criteria yielded the inclusion of 15 published reports in the meta-analysis, shown in Table 15–1.

The purpose of the meta-analysis was to discover whether certain common regions of the brain were activated in these studies or whether the activations were strewn throughout the brain in a haphazard manner. To discover this, we developed an iterative chi-squared technique to determine whether the foci of activation from interference-resolution tasks were distributed randomly in the brain or were clustered in certain areas greater than would be expected by chance. We describe this method only briefly here.

Activation foci were grouped by Brodmann's areas (BA), and the number of such foci represented our observed values. If there was no clustering in foci, they should be spread nonsystematically among all the areas, which became our expected values, correcting for the fact that BAs differ in volume from one to another, so the expected number of activations by chance alone would differ from one to another.

Having established expected and observed values for each BA, we computed a chi-squared statistic for the comparison of observed and expected frequencies of foci. This was reliable ($P < 0.001$). This test does not reveal the regions in which the clustering deviates from a random distribution. To locate specific regions of nonrandom clustering, we deleted each BA one at a time (by collapsing each deleted area with others) and recomputed chi-squared to determine if the significance of the model changed. Comparison of each new model with the original is possible because the difference between the chi-squared value for the original model and the chi-squared for a new model is itself distributed as chi-squared. This procedure can be

Table 15–1. Experiments included in the meta-analysis of interference-resolution tasks

| Study	Experimental Condition A	Experimental Condition B	Control Condition A	Control Condition B	Imaging Modality	Num. Foci (Z > 2.5)
Bench et al., 1993	Stroop		Crosses		PET	13
Botvinick et al., 1999	°Event-related flanker				fMRI	2
Carter et al., 1995	Stroop incongruent		Congruent	Neutral	PET	10
Derbyshire et al., 1998	Stroop incongruent		Congruent		PET	2
George et al., 1997	Stroop incongruent		Color naming		PET	4
Hager et al., 1998	°Event-related CPT				fMRI	10
Humberstone et al., 1997	°Event-related go/no-go				fMRI	3
Kawashima et al., 1996	Go/no-go	Response selection	Response selection	Go/no-go	PET	46
Klingberg et al., 1997	GO/no-go		Baseline		PET	11
Konishi et al., 1998	°Event-related GO/no-go				fMRI	5
Konishi et al., 1999	°Event-related GO/no-go				fMRI	5
Paus et al., 1993	Response selection	Anti-stimulus	Baseline	Pro-stimulus	PET	30
Sweeney et al., 1996	Antisaccade		Visually guided saccade		PET	5
Taylor et al., 1994	S-R incompatible		S-R compatible		PET	2
Taylor et al., 1997	Stroop incongruent		Neutral	False fonts	PET	18

°Involved event-related comparison between incompatible and compatible trials.

repeated in an iterative fashion until it is not possible to remove any BAs without causing a significant decline in the predictability of the remaining model. The resulting BAs can then be considered the sites of nonrandom clustering in the brain.

Very few BAs contained clusters greater than would be expected by chance (Fig. 15–1 shows the areas of common activation among the various studies). The ACC was prominent among these. Brodmann's area 24 was reliably present on the left and BA 32 was reliable in both hemispheres. Brodmann's area 6, a region that mingles with anterior cingulate cortex at its most ventral extent medially, contained a cluster in the left hemisphere. There was also a cluster in right DLPFC (BA 9).

This analysis reveals a striking consistency across studies of interference-resolution tasks with respect to activation in three regions: the ACC, DLPFC, and a region of the supplementary motor area that may be continuous with the activation in the ACC. Thus, the areas of overlap among these studies are in part consistent with the prediction by Botvinick et al. (1999), Carter et al. (1998, 1995), and MacDonald et al. (2000). Tasks in which conflict is present should recruit mechanisms of ACC to detect and monitor that conflict, and they should recruit mechanisms of DLPFC in the service of controlling attention to resolve that conflict. These earlier studies are silent about activations in area 6, at least to the extent that activation in this area is separable from that in ACC.

Figure 15-1. Axial view (*top*) and sagittal view (*bottom*) of a schematic of the brain. Each of these is a "glass" view, in that all activations in the axial view, regardless of z-coordinate, are shown, and all activations in the sagittal view, regardless of x-coordinate, are shown. The plotted points represent the areas of activation that survived the iterative chi-squared analysis procedure discussed in the text, thus they show the areas of common activation across the studies included in our meta-analysis. BA, Brodmann's area.
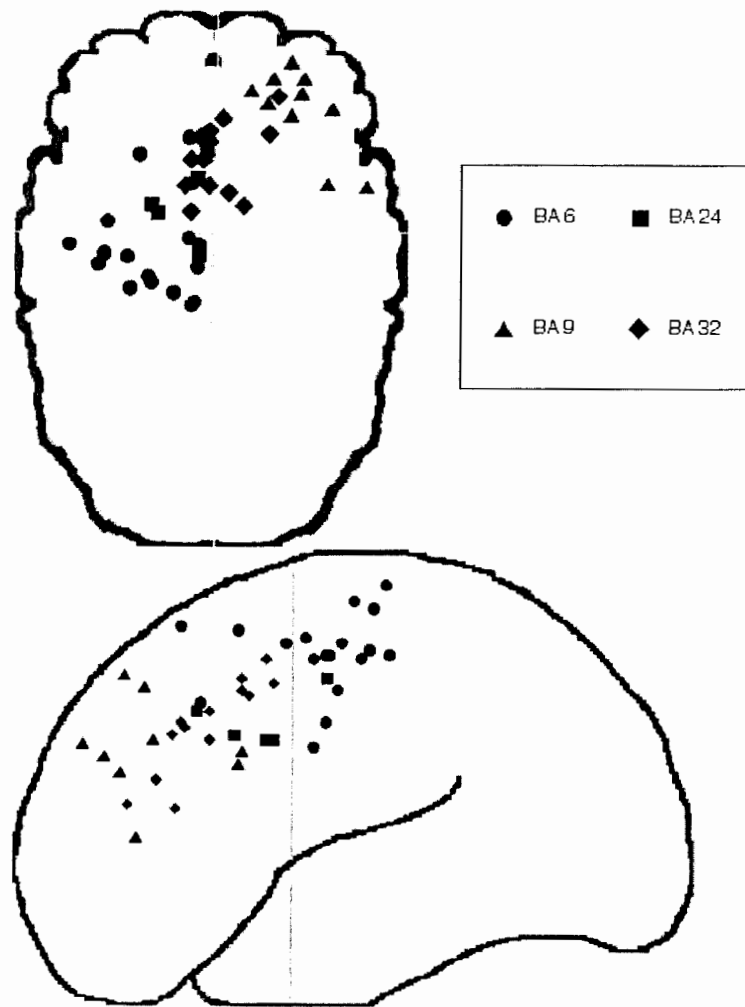
RESOLUTION OF PROACTIVE INTERFERENCE

The studies reviewed above share in common the feature that one response is prepotent— that is, one response tends to be more automatic than another. This response must be inhibited in favor of an alternative, correct response. Knowing this, it is natural to ask whether the activations that are shared in common are a direct consequence of resolving conflict in the face of a prepotent response or whether they are a result of resolving conflict in the face of possible competition somewhere earlier in the processing stream.

A striking commonality among all of the tasks included in our meta-analysis is that the conflict that is resolved can be attributed to processes near the response end of the stream. This is certainly apt for the go/no-go and stimulus–response compatibility tasks, as these have been modeled commonly (Kornblum et al., 1990). Interference in response selection has also been implicated in the flanker task (see, e.g., Cohen et al., 1995; Cohen & Shoup, 1997). One way to show this is to compare flanker tasks in both of which the flankers differ in form from the central target item, but in one of them the flanker is associated with the same response as the target and in the other with a different response. Flankers associated with a different response

yield a larger flanker effect than those associated with the same response, suggesting that interference associated with response selection is a component of the flanker effect. Similarly, the Stroop effect has also been shown to be due in part to conflict at the time of response selection. If the ensemble of colors represented in the color words is different from the ensemble of colors represented in the inks, the size of the Stroop effect is diminished, compared to a condition in which the two ensembles are identical (Klein, 1964). So, for example, if the ink colors and words are all chosen from the set "pink, green, yellow," there is a larger Stroop effect than if the inks are chosen from this set, but the color words are chosen from the set "blue, orange, red." Thus, it may be the reliance on a common stage of conflict resolution at the time of response selection that causes the activations that are revealed in our meta-analysis.

This construal of the results of the meta-analysis raises two questions: Is conflict among responses necessary to recruit processes of conflict resolution? Do processes of conflict resolution inevitably present themselves as a

network that includes the structures found in our meta-analysis regardless of whether the conflict occurs at the time of response or earlier? To address these issues, we have conducted a program of research on a conflict-resolution task that involves interference in a working memory paradigm (Jonides et al., 1998).

The paradigm is an adaptation of the classic item-recognition task devised by Sternberg (1966), and its two critical conditions are shown in Figure 15–2. The high-conflict condition is a standard item-recognition task in which a contingency is created between successive trials to create conflict that must be resolved. On each trial, subjects are presented with four randomly selected letters that serve as targets for that trial. Subjects have to store these targets during a retention interval of 3 seconds, following which a single probe-letter is presented, and subjects must decide positively or negatively whether this letter matches one of the targets. The critical feature of this high-conflict condition is that on half of the trials when the probe letter does not match any of the target items, it *does* match one of the targets from the previous trial. Thus, there
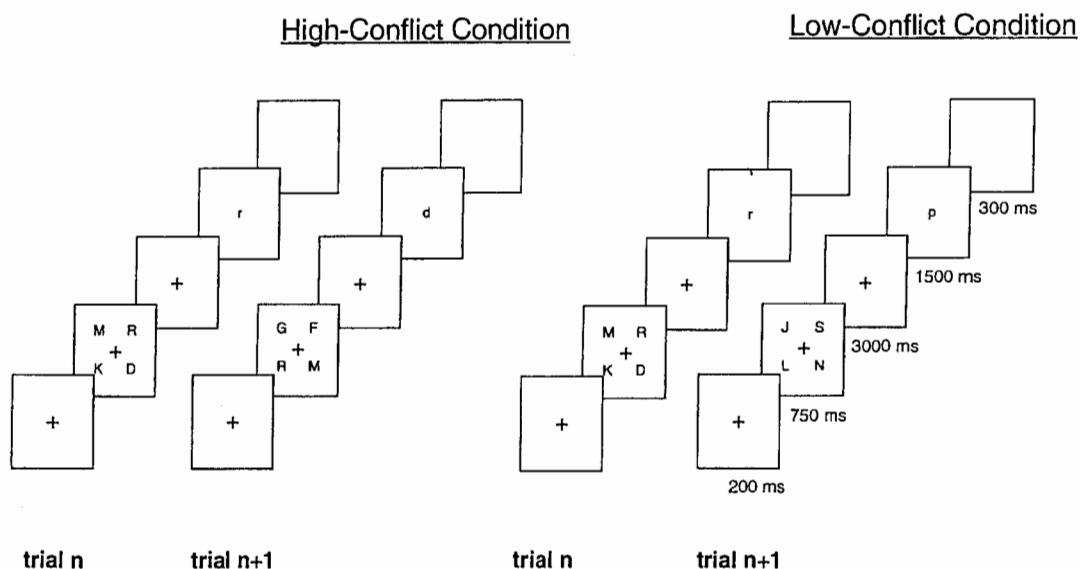

High-Conflict Condition   **Low-Conflict Condition**

trial n   trial n+1   trial n   trial n+1

Figure 15–2. Schematic of the two critical conditions that were compared to show an effect of interference resolution. In the high-conflict condition, a probe on some trials that required a negative response because it was not a member of the target set of letters had been a member of the target set on the previous trial. In the low-conflict conditions, this sort of overlap between successive trials was not permitted. See text for further elaboration.

is a relatively high familiarity value for that probe, creating a tendency to respond positively to it; this tendency interferes with the proper response on that trial in that the probe does not match a target item. The control (low conflict) condition does not have this contingency between successive trials. In this condition, each probe that requires a negative response does not match any of the targets from the immediately preceding three trials, so little interference is created.

Behaviorally, the contrast between these conditions produced a reliable interference effect such that responses on high-conflict trials were longer in latency than responses on low-conflict trials. For example, in a practice session of this experiment, response time was 757 ms in the high-conflict condition vs. 695 ms in the low-conflict condition, and accuracies were consistent with this difference at 91% vs. 96% respectively. After these behavioral data were collected, subjects were PET scanned while they performed in the two conditions again. A subtraction of the activations of the high-conflict condition minus the low-conflict condition revealed a single region of reliable activation in left lateral prefrontal cortex (the peak voxel was at $x = -48$, $y = 21$, $z = 9$, and the region extended in superior and posterior directions; BA 45). So, this experiment showed an association between a behavioral effect and a brain activation: increased interference between the familiarity of a negative probe and its lack of membership in the current target set was associated with increased brain activation in lateral prefrontal cortex in the left hemisphere.

The fact that this outcome was realized in a PET experiment has its limitations. Of particular interest is the fact that the temporal stage of prefrontal activation in comparing the high- and low-conflict conditions cannot be surmised from the PET data. For example, if the difference in activation between these conditions is a result of brain activation during the retention interval, one might conclude that there are processes at work to heighten the trace of the current target set that is being rehearsed against the backdrop of previous target sets. This might be an effective mechanism to fight the effects of interference from

previous items. Alternatively, if the activation difference occurs at the time of encoding of each target set, then one might argue that enhanced perceptual processes were required to encode each target set in the face of competing prior alternatives. Finally, if the activation difference was due to processes at the time the probe was presented, it might be due to one of two effects. One possibility is that two responses are elicited at the time the probe is presented, and an inhibitory mechanism is activated to defeat the incorrect response. The other possibility is that at the time the probe is presented, it elicits two competing internal codes: one is a result of its familiarity from the previous trial, and the other is a result of the item's episodic code indicating that it is not a member of the present target set.

To test among these possibilities, we conducted a very similar experiment with fMRI as the imaging vehicle. This experiment had a trial structure that permitted us to examine whether the activation difference between the high- and low-conflict conditions was largely a function of encoding, retention, or retrieval differences (D'Esposito et al., 1999). The experiment included high- and low-conflict trials presented in an intermixed fashion. Each trial was stretched in length, such that target sets were presented for 1 second, following which there was a 7-second retention interval, followed by a probe presented for 2 seconds. An intertrial interval of 14 seconds permitted an examination of the activations of each trial individually. Behaviorally, the subjects in this experiment also showed a reliable difference between high-and low-Conflict trials (850ms vs. 818 ms). We then examined activation in the same left lateral prefrontal region (BA 45) that had revealed itself in a comparison of the high- and low-conflict conditions in the PET experiment. The only difference in activation between the high- and low-conflict trials in this region appeared at the time the probe letter was presented. We ruled out the possibility that this difference was somehow due to global differences between conditions by examining a different left frontal area that showed no activation differences for the two types of trials during any epoch of the experiment.

Taken together, the results of the PET and fMRI experiments using this conflict-resolution paradigm show a behavioral interference effect coupled with an activation difference in left inferior prefrontal cortex. The fMRI experiment establishes that the temporal locus of this activation is at the time of processing of the probe item. Of course, what these experiments establish is an association between brain activation and a behavioral effect; they do not establish that the brain activation is causally linked to the behavioral outcome. To examine whether there is a causal link, we undertook two further explorations.

The first involved testing normal older adults in the PET version of the task. It is by now well established that older adults have more difficulty resolving conflict between competing tasks than younger adults (e.g., Hasher & Zacks, 1988; Connelly et al., 1991; Tipper, 1991); Thus, it seemed likely that older adults would have even more difficulty than younger adults with probe items on high-conflict trials than on low-conflict trials. This failure to resolve interference on the high-conflict trials should be accompanied by a lower level of brain activation in the left lateral prefrontal site that the earlier experiments had implicated in this task, indicating that this site was causally involved in mediating conflict-resolution processes (Jonides et al., 2000).

This proved to be so. Jonides et al. (2000) compared the performance of younger and older adults on this task and found that the older adults showed a larger performance difference (combining accuracy and response time) between high-and low-conflict trials. When we compared activation between age groups in BA 45, we found that younger subjects showed reliably more activation. In fact, the older subjects themselves did not have statistically reliable activation at this site when examined individually.

The second test of causal involvement of BA 45 in conflict resolution for this task involved a patient with damage to this region (Thompson-Schill et al., 1999). The patient, R.C., was a 51-year old right-handed man who had an arteriovenous malformation resected in 1981. As a result of the procedure, he had a 53 cc lesion in the left prefrontal cortex, in-

cluding area 45. R.C.'s performance on high- and low-conflict trials was compared to that of three control groups of subjects: other patients with frontal lesions, normal age-matched older adults, and normal younger adults. The lesion locations for R.C. and the control patients are shown in Figure 15–3. Figure 15–4 shows the performance difference between high- and low-conflict trials for R.C. and the three control groups. What is stunningly obvious from the figure is that R.C. showed massively greater interference on the task than any of the control groups.

All told, then, the following picture has emerged from these investigations of conflict resolution in a working memory task. First, there is a quite reliable and robust interference effect as a result of memory codes that
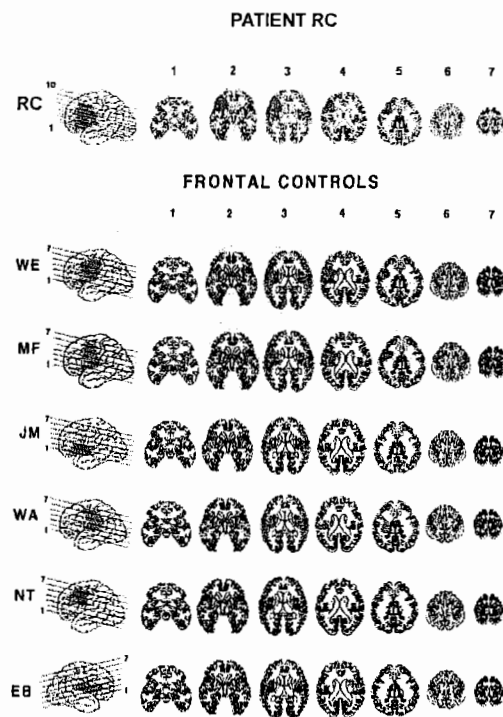

PATIENT RC

FRONTAL CONTROLS

Figure 15–3. Locations of the lesions for patient R.C. and for the patients in a control group. Patient R.C., as described in the text, has a left lateral lesion that includes Brodmann's area 45. Three of the patient-controls have left frontal lesions that are centered more posteriorly; one has a left frontal lesion that is centered more inferiorly; one has a left frontal lesion that is centered more superiorly; and the final one has a right frontal lesion that includes inferior frontal gyrus.
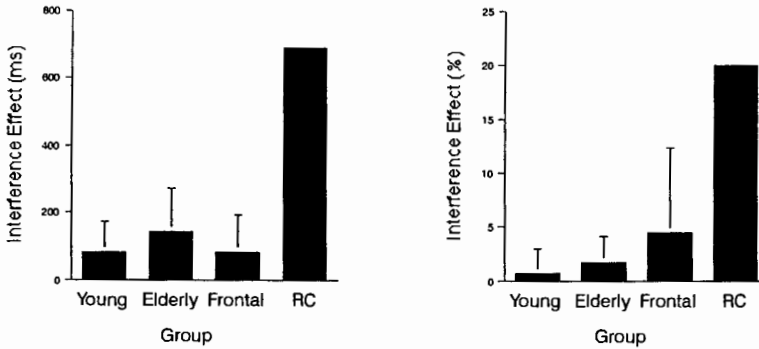
Figure 15–4. Magnitude of interference effect for patient R.C. compared to that of young and elderly normal adults and of patient-controls with frontal lesions during a working memory interference task described in the text. *Left:* Effects on response times. *Right:* Effects on error rates.

present a conflict between familiarity and episodic context. Second, there is a brain region associated with this interference effect in the inferior frontal gyrus of the left hemisphere. Third, this brain region is functionally involved in producing the resolution of conflict. This picture tightly ties the left inferior frontal gyrus to conflict resolution in this task; but how is it related to other demonstrations of conflict resolution that have emerged from the study of tasks included in our meta-analysis?

RELATIONSHIP AMONG STUDIES OF CONFLICT RESOLUTION

One might ask first whether the site of activation in our working memory task matches the sites of activation found in the meta-analysis of other tasks. It does not, in two important ways. First, the site of lateral activation in inferior left prefrontal cortex is not consistent with the sites of activation shown in Figure 15–1 for the various studies of interference-resolution tasks. The hemisphere of predominant activation differs, and beyond this, the peak of the site found in the working memory studies is inferior and posterior to the sites found in studies of the Stroop task, stimulus–response compatibility, and so on.

A second kind of mismatch concerns activations in the ACC. As we documented, this is a region that is activated commonly in tasks such as the Stroop. We did not find reliable activation in this region in our direct comparison of high- and low-conflict trials in the original report (D'Esposito et al., 1999).

We tested this further by conducting two types of region of interest (ROI) analyses. First, structural ROIs were drawn for each subject $(n = 7)$ that included all of the supracallosal anterior cingulate regions. These structural ROIs included the regions that were reported reliable in the studies by Botvinick et al. (1999), Carter et al., (1998), and MacDonald et al. (2000). For each subject, activation in the ROI during the probe phase for the high-conflict trials was compared to that during low-conflict trials. Neither the average magnitude of activation $(t \ [6] = 1.12, P = 0.15$, one-tailed test) nor the number of active suprathreshold voxels $(t \ [6] = 0.49, P = 0.33$, one-tailed test) within the ROI was significantly different between the high- and low-conflict trials. Next, a functional ROI analysis was conducted by identifying all voxels within the anterior cingulate ROI that were active during the response phase for both high- and low-conflict trials combined. One subject was not included in this analysis because he showed no significant activation in the anterior cingulate ROI during the high- or low-conflict trials. Within these functionally defined ROIs, no difference in activation was found when comparing high- and low-conflict trials $(t \ [5] = 1.59, P = 0.09$, one-tailed test). However, it is not the case that the anterior cingulate was not active at the time of response (6/7 subjects showed many suprathreshold voxels, mean $= 38.4$, SD $= 27.5$); rather, the anterior cingulate was *equally* active during high- and low-conflict trials. Thus, within the context of the verbal item-recognition paradigm, the conflict induced by interference is unrelated to anterior cingulate activation.

Of course, a failure to find activation when

comparing high- and low-conflict conditions must be taken with caution in that it is a null result. In this case, however, there is corroboration of this null result by a report from another laboratory. Bunge et al. (submitted) conducted an fMRI experiment using the verbal item-recognition task in which they manipulated two variables. One was the very same comparison of high- and low-conflict conditions reported by Jonides et al. (1998, 2000) and D'Esposito et al. (1999). The other variable was a manipulation of the size of the memory load that subjects had to store in working memory. In this report, there was reliable activation in the ACC elicited by both variables, with the greater effect depending on the load variable. Furthermore, increased activation in the ACC due to greater memory load was associated with slowed response times, but no association was found between ACC activation and the effect that interference had on response times. The authors concluded that the activation in this region was more closely linked to working memory load than to interference resolution.

Yet another report using a different task also casts doubt on the generality of activation in the ACC as a function of conflict detection and resolution. Hazeltine and colleagues (in press) conducted an fMRI study of the flanker task. They recorded fMRI images as subjects performed congruent and incongruent trials on a flanker task involving colored stimuli, where two colors (red, green) indicated a right button-press and two other colors (blue, yellow) indicated a left button-press. When the response indicated by the central stimulus matched the response indicated by flanking stimuli, the trial was congruent (e.g., a red central target circle flanked by green distracter circles). When the flanking stimuli indicated a different response from the target, the trial was incongruent (e.g., a red central target circle flanked by blue distracter circles). They found no evidence of ACC activation when comparing the congruent and incongruent conditions.

This is an interesting contrast to the report of Botvinick et al. (1999), who did find anterior cingulate activation in this task. However, it is important to note that the activation re-

ported by Botvinick et al. (1999) on incongruent trials appeared in a task in which there was a heavy stimulus–response compatibility component; furthermore, the activation appeared only when incompatible trials followed compatible ones. In this task, the imperative stimulus was an arrow embedded among surrounding arrows that were either compatible or incompatible. For example, the stimulus "<<<<<" would be a left-facing arrow surrounded by other left-facing arrows, whereas the stimulus "<<><<" would be a right-facing arrow surrounded by left-facing arrows. This task resulted in a flanker effect that was larger by a factor of 5 or more than that of the standard task studied by Hazeltine et al. (in press) and many others. The larger magnitude may signal that there are other factors at work in this task, such as facilitation in response due to the natural association of arrows with directions and the homogeneity of compatible stimuli on this dimension compared to incompatible stimuli. As such, the activation in the ACC may be a function in part of the jarring effect of switching from a uniform stimulus such as the former to a heterogeneous one such as the latter, an effect that would occur only on trials in which an incompatible stimulus follows a compatible one.

Overall, then, we are led to two conclusions: First, there is a noticeable similarity among activations in certain studies of conflict resolution in regions of DLPFC and ACC. Second, these similarities do not describe the activation pattern we have documented for a working memory task and that Hazeltine et al. (in press) have described for the flanker task. What might be the root of the discrepancy?

Several possibilities suggest themselves. First, consider the sheer sizes of the interference effects in question. The reports included in our meta-analysis are of phenomena that are substantial in size behaviorally. For example, the Stroop interference effect is often measured in hundreds of milliseconds. By contrast, the interference effects found for working memory and for the flanker task are substantially smaller, typically 50 ms or so in magnitude. Perhaps this difference in magnitude reveals a fundamental property of conflict-resolution mechanisms. It may be that

conflict must be substantial in size to recruit a detection mechanism in the ACC and an attention-allocation mechanism in the DLPFC. Conflict that is smaller in magnitude may be handled by other mechanisms, and it may be earlier in the processing sequence as well, distinct from the later processing stages when tasks such as the Stroop have their effect. Possibly related to this is the fact that subjects performing tasks such as the Stroop are quite distinctly aware of the conflict that is present on incongruent trials, while subjects performing the working memory task and flanker tasks often have little or no awareness of the difference between high- and low-conflict trials. Awareness may be a function of the sheer size of the interference effect or whether it occurs late in the processing sequence, and it may take awareness to trigger the detection of conflict by the ACC and the allocation of attention by the DLPFC.

Another possibility is that the activation found in the ACC for some conflict tasks represents not so much detection of conflict as response to conflict after it has been detected. By this account, tasks in which the effect of conflict is sufficiently substantial to give subjects awareness of it may trigger an affective response that is a consequence of either the conflict directly or the perceived difficulty of the task in the face of conflict. This affective response may be the source of the signal in the ACC that is found in tasks such as the Stroop task or other tasks in which conflict is substantial (such as the flanker task, when it is performed under conditions of response compatibility or incompatibility, as in the report by Botvinick et al., [1999]). By this account, the activation in ACC represents not a detection of conflict for later resolution by other mechanisms, but rather a response to conflict that has elicited awareness and been detected in some other way. One piece of evidence relevant to this position comes from an event-related potential study that measured error-related negativity (ERN) in a flanker task (Gehring & Fencsik, 1999). The ERN signal is an event-related brain potential that is found when subjects produce a response in tasks that involve conflicting response possibilities. Although there is still controversy

about the brain mechanisms that produce this signal, there are source-localization studies suggesting that it emanates from medial frontal structures, possibly the ACC. So, the ERN may well be a measure of the ACC signal that is measured in fMRI neuroimaging studies of conflict-resolution tasks such as those reviewed in our meta-analysis. Gehring and Fencsik (1999) found that the ERN in the flanker task began after the agonist muscle in their task showed evidence of suppressing an error in the task, and that it peaked after the onset of agonist electromyogram activity that was associated with error correction. Thus, the ERN cannot reflect a mechanism of error detection, rather, it must reflect a response to an error. If the ERN, in turn, is the temporal signal of anterior cingulate activation, this casts doubt on the view that the ACC is acting to detect errors for later correction.

There is much yet to learn about processes of conflict resolution. What we know at present is that anterior cingulate and dorsolateral prefrontal cortical regions are activated among some tasks that require processes to resolve among competing responses. We also know that these brain regions are not necessarily involved in all such tasks, but that other regions may be recruited instead. What differentiates the constellation of tasks in which these regions are recruited from those in which they are not is as yet undetermined. To make substantial progress on these issues, we will need both a better taxonomy of tasks and their psychological processes, and we will need a better corpus of brain activations that tasks may share in common.

The next several years are going to be very exciting ones for study of the role that the frontal lobe and other brain structures play in implementing executive processes of cognition. What we are discovering at this stage is that executive functioning seems best characterized in terms of a number of identifiably different processes. That this discovery is relatively new, is, of course, understandable, as there is much to learn about the range of executive processes, about the relationship of one to another, about the brain implementation of these processes, and about models that might capture the essence of how these pro-

cesses work individually and in collaboration with each other. Research about all these issues is just beginning and promises to lead to rich theories of the processes that in many ways make human intelligence intelligent.

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