Conflict Monitoring and Cognitive Control

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A neglected question regarding cognitive control is how control processes might detect situations calling for their involvement. The authors propose here that the demand for control may be evaluated in part by monitoring for conflicts in information processing. This hypothesis is supported by data concerning the anterior cingulate cortex, a brain area involved in cognitive control, which also appears to respond to the occurrence of conflict. The present article reports two computational modeling studies, serving to articulate the conflict monitoring hypothesis and examine its implications. The first study tests the sufficiency of the hypothesis to account for brain activation data, applying a measure of conflict to existing models of tasks shown to engage the anterior cingulate. The second study implements a feedback loop connecting conflict monitoring to cognitive control, using this to simulate a number of important behavioral phenomena.

A remarkable feature of the human cognitive system is its ability to configure itself for the performance of specific tasks through appropriate adjustments in perceptual selection, response biasing, and the on-line maintenance of contextual information. The processes behind such adaptability, referred to collectively as *cognitive control*, have been the focus of a growing research program within cognitive psychology. A number of theoretical models have been proposed for how the control of cognition is achieved (Baddeley & Della Sala, 1996; Cohen, Dunbar, & McClelland, 1990; Norman & Shallice, 1986), and progress has been made toward identifying its neuroanatomical substrates (Cohen, Braver, & O'Reilly, 1996; Cohen & Servan-Schreiber, 1992; Desimone & Duncan, 1995; Goldman-Rakic, 1996; Luria, 1973; Posner & Petersen, 1990).

Despite the importance of these efforts to characterize the function of cognitive control, most of them share an important limitation in scope. Most current theories focus nearly exclusively on the nature of the influence exerted by control. In contrast, very little is yet known about how the intervention of control processes is itself brought about. Existing theories portray the relevant mechanisms as coming into play when their participation is required, but without an account of how the need for intervention is detected or how the intervention itself is triggered. The lack of such an account is problematic, for without it control remains a sort of homunculus that "just knows" when to intercede.

For any theory of cognitive control to be complete, it will need to offer an account of how the system determines when control is required. Specifically, it will need to provide answers to the following three questions:

- 1. On what basis is control recruited? It cannot be the case that one always knows before beginning to act whether a given task will require high levels of control. Kahneman (1973) has argued, to the contrary, that it is often the actual attempt to perform a difficult task that leads to the recruitment of cognitive resources. This appears consistent, for instance, with the finding that participants performing the Stroop task show greater interference on the initial one or two trials in each block than on subsequent trials in the series (Henik, Bibi, Yanai, & Tzelgov, 1997).
- 2. Once the relevant control processes are engaged in guiding task performance, how is their influence modulated or optimized? There is evidence that adjustments in control do occur on-line, in response to variations in performance. For instance, it is well-established that, in speeded response tasks, reaction time and accuracy tend to rise following errors (e.g., Laming, 1968; Rabbitt, 1966). Even in the absence of errors, control appears to adjust to task demands. To take another example from the Stroop literature, participants tend to show less interference on incongruent trials if these are frequent relative to congruent trials than if they are rare (Lindsay & Jacoby, 1994; Logan & Zbrodoff, 1979). What is it that triggers these adjustments?
 - 3. What processes govern how and when control is withdrawn?

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With practice on some initially difficult tasks performance becomes increasingly automatic (e.g., Anderson, 1982; Shiffrin & Schneider, 1977). As this happens, the need for control diminishes. How do control processes evaluate the rate at which their top-down influence can be withdrawn without causing a deterioration in performance?

Clearly, in order for the recruitment, modulation, and disengagement of control to occur, control processes need access to information about the functioning of the systems that they modulate. That is, in addition to the *regulative* dimension of control, by which its top-down influence is exerted, there must also exist an *evaluative* component that monitors information processing, making an assessment of current demands. If one is to expunge the homunculus from theories of cognitive control, it will be necessary to develop an account of this evaluative function.

The Conflict Monitoring Hypothesis

In this article we take an initial step toward characterizing the evaluative side of cognitive control, proposing one mechanism by which the demand for control might be gauged. Specifically, we will argue that there exists a system that monitors for the occurrence of conflicts in information processing, a function we refer to as *conflict monitoring*. By the overall account we will put forth, conflict monitoring serves to translate the occurrence of conflict into compensatory adjustments in control: The conflict monitoring system first evaluates current levels of conflict, then passes this information on to centers responsible for control, triggering them to adjust the strength of their influence on processing.

A first goal of the present work is to draw together evidence for the occurrence of conflict monitoring. In particular, we will consider data suggesting that the detection of conflict may be among the functions of a particular area of the human frontal lobe, the anterior cingulate cortex (ACC). Our second objective is to articulate the hypothesis that conflict monitoring serves as a basis for the regulation of control, showing how this idea can be used to explain a set of interesting empirical phenomena.

We begin, in the next section, with some theoretical considerations, deriving an initial motivation for the idea of conflict monitoring from current theories of cognitive control. After this, the article is divided into two main sections, corresponding to the objectives identified above. Part 1 examines the possibility that a conflict monitoring function might be reflected in the behavior of the ACC. The section begins by reviewing recent brain activation studies, which together encourage the idea that the ACC may respond specifically to the occurrence of conflict. We then present the results of a first computational modeling study, which serves to articulate our interpretation of the brain activation data and to demonstrate the sufficiency of the theory to account for them. With Part 1 as a foundation, Part 2 turns to the issue of how conflict monitoring might play a role in modulating cognitive control. The section focuses on three behavioral phenomena, quite different from one another in their details, but each involving on-line shifts in control. In a second computational modeling study, we show how linking conflict monitoring to the modulation of control leads naturally to a unifying, mechanistic explanation for these phenomena.

Theoretical Background

We have suggested that the systems subserving cognitive control are likely to include an evaluative system, which keeps tabs on current demands. This raises the question, what precisely might such a system measure? That is, how does a need for increased control manifest itself within the processing system? One potential answer can be derived directly from current theories of cognitive control, which portray it as serving to prevent the occurrence of conflicts in information processing.

Control as Conflict Prevention

Given the highly parallel and distributed character of cognitive processing, one of its inherent hazards is *crosstalk interference* between concurrent processes. A succinct description of the problem is provided by Mozer and Sitton (1998):

One can conceive of processing . . . as occurring along a certain neural pathway. If the processing pathways for two stimuli are nonoverlapping, then processing can take place in parallel. But if the pathways cross—i.e., they share common resources or hardware—the stimuli will interact or interfere with one another. (p. 342)

This sort of interference is perhaps easiest to illustrate in the setting of dual-task performance. According to Navon and Miller (1987), concurrently performed tasks interfere with one another when "each produces outputs, throughputs, or side effects that are harmful to the processing of the other one, in that they change the state of some variable that is relevant for the performance of the concurrent task" (p. 435). A concrete example is provided by Shaffer (1975), who showed that dramatic decrements in performance occur in both typing to dictation and reading aloud when an attempt is made to perform these two tasks simultaneously. The difficulty of this combination can be understood as deriving from crosstalk between the processing pathways activated by auditory and visual inputs, leading to conflicting responses at the level of both speech and typing. The result is a slowing of response times and an increase in the frequency of errors, including so-called crosstalk errors where the participant produces a response in one modality that should have been delivered in the other.

Conflict between concurrent processes has been understood as affecting performance in an extremely wide variety of domains. Indeed, it has been credited with placing a central limitation on human information-processing capacity: Allport (1987), in agreement with a number of other researchers (e.g., Cohen et al., 1990; Duncan, 1996; Mozer, 1991; Mozer & Sitton, 1998; Navon, 1985; Navon & Miller, 1987; Schneider & Detweiler, 1987), has argued that "the behavioral phenomena attributed in the past to the limited capacity of a central processor are more appropriately conceptualized . . . as the expression of crosstalk interference between parallel processes" (p. 411).

This recognition of crosstalk as a ubiquitous pitfall of parallel processing has led to a particular view of cognitive control, according to which one of its central functions is to prevent conflicts. As Allport (1980) put it, "for any distributed system, fundamental issues are raised by the demands of conflict resolution and of controlling undesirable interactions: of keeping separate processes separate" (p. 38). The job of dealing with these problems falls to cognitive control. This view can be discerned in much work on visual search, where the top-down control of visual attention has

been portrayed as helping to prevent the interference that can occur when multiple objects are processed in parallel (e.g., Mozer & Sitton, 1998; Treisman, 1988). It also informs accounts that portray attention as serving to regulate the flow of information through the processing system, favoring flow into selected processing streams while helping to gate off others (Cohen et al., 1990; Desimone & Duncan, 1995; Norman & Shallice, 1986).

The idea that control serves to prevent conflicts suggests one answer to the question of how a need for increased control might manifest itself in the processing system. It implies that a need for greater control will typically be indicated by the occurrence of conflict itself.

Using Conflict as a Basis for Modulating Control

The potential usefulness of conflict as a basis for the regulation of control was recognized early on by Berlyne (e.g., 1960). Working within an information—theoretic framework, Berlyne proposed that the occurrence of conflict often leads to compensatory adjustments in perceptual selection, which in turn serve to alleviate conflict.

In the years since Berlyne (1960) made this suggestion, the idea that conflict might be linked to the regulation of cognitive control has resurfaced intermittently, usually in the context of highly theory-driven work. For example, the production system architecture known as Soar (Laird, Newell, & Rosenbloom, 1987) proposes that problem-solving algorithms are triggered by the occurrence of impasses, one important class of which involves conflicts between simultaneously selected but incompatible productions.

Conflict appears to play a similar role in the theory of control put forth by Norman and Shallice (1986). Here, a supervisory attentional system (SAS) is understood as monitoring the processes by which action schemas are routinely selected, intervening when these contention-scheduling processes prove inadequate. Although the theory does not explicitly indicate what particular events within contention scheduling serve to trigger SAS intervention, it is emphasized that contention scheduling serves primarily to prevent conflict among potentially relevant schemas (Norman & Shallice, 1986). Thus, the theory seems to imply that control is recruited when conflicts occur that contention-scheduling processes are not able to resolve efficiently.

A more explicit instance is provided by the work of Schneider and Detweiler (1987, 1988). This specifies a connectionist-control framework within which a central control module regulates the exchange of information among a number of domain-specific processing modules. In this scheme, input from control is recruited when conflict occurs between messages converging on a single module.

In most of this earlier work, conflict monitoring has been adopted as a background assumption, rather than a direct object of scientific inquiry. Moreover, its motivation has typically been almost entirely theoretical; conflict monitoring has been incorporated primarily because it makes sense or because it solves computational problems, rather than because of experimental evidence pointing to its occurrence. However, recent work from cognitive neuroscience has begun to provide evidence that conflict monitoring may in fact play a role in human cognition. Specifically, this work indicates that the occurrence

of conflict may trigger activation in a specific area of the brain, the ACC.

Part 1: Cognitive Neuroscientific Evidence for the Detection of Conflict

Anterior Cingulate Cortex

The ACC, situated adjacent to the corpus callosum on the medial surface of the frontal lobe, 1 is widely believed to play a role in cognitive control (e.g., D'Esposito et al., 1995; LaBerge, 1990; Mesulam, 1981; Posner & DiGirolamo, 1998). Beyond this general claim, however, no consensus exists as to its specific contribution to cognitive processing. ACC engagement has been reported in a remarkably wide variety of cognitive settings, including tasks that involve language, learning and memory, perceptual target detection, imagery, motor control, and dual-task performance, among other capacities (Cabeza & Nyberg, 1997; Paus, Koski, Caramanos, & Westbury, 1998), making it difficult to discern a meaningful common factor that might explain ACC engagement across studies. The notion of conflict monitoring opens up a new possibility here, for the vast majority of data from ACC activation studies appears consistent with the idea that the ACC responds to the occurrence of conflict.²

In the following section, we present an overview of ACC activation studies, dividing them into three categories and suggesting how ACC activation in each of these can be interpreted as reflecting a response to the presence of conflict. In order to make this idea explicit and support its validity, we conducted computer simulations using models of specific tasks drawn from each of the three basic areas of the ACC literature. These studies, presented here as Simulation Study 1, test the consistency of our hypotheses with existing accounts of information processing in these three domains, applying a quantitative measure of conflict to simulate findings from the ACC activation literature.

Cognitive Activation of the ACC: Review of Major Findings

Empirical research on the role of the ACC in cognition has been conducted using a variety of methodologies, including neuropsychological techniques (e.g., Janer & Pardo, 1991; Turken & Swick, 1999), single-unit recording (e.g., Gabriel, 1993; Niki & Watanabe, 1979), and brain activation techniques including functional neuroimaging and event-related potentials. Although neuropsychological and neurophysiological data have inspired some influential theories of ACC function (e.g., Mesulam, 1981; Vogt, Finch, & Olson, 1992), the vast majority of recent findings and some of

¹ Anatomically, the anterior cingulate cortex begins above the callosum, extending forward to wrap around the genu and end inferiorly to it. However, the vast majority of the studies with which we will be concerned involve activation of the portion of the ACC posterior to the genu and superior to the callosum (cf. Bush et al., 1998; Paus et al., 1998, for discussions of functional heterogeneity in the human ACC).

² As specified in the general discussion, the idea that the ACC responds to conflict is here viewed as part of a more general monitoring function, according to which the ACC responds to a variety of events, all indicating that attentional adjustments are needed to optimize performance or avoid negative outcomes.

the most consistent results derive from brain activation studies. In what follows, we focus on this literature; however, our conclusions can in many instances be viewed as consistent with established findings from lesion and single-unit recording studies.

Although brain activation studies have reported ACC engagement in a wide variety of task settings, the bulk of these studies can be organized into three general types. In one set of experiments, ACC activation has been associated with tasks calling for the overriding of prepotent but task-irrelevant responses; in a second group, it has been associated with tasks requiring the participant to choose among a set of equally permissible responses; and in a third, with tasks that lead to the commission of errors. Here we discuss these three domains in detail, suggesting how in each case ACC activation can be seen as accompanying the occurrence of conflict.

Response override. A large number of studies have reported ACC activation in tasks requiring the participant to override relatively automatic but task-inappropriate responses. The most frequently studied of these has been the classic Stroop conflict paradigm (Stroop, 1935; for a review see MacCleod, 1991), in which the participant is asked to name the color in which a color word is displayed. Response times are greater if there is a mismatch between the color the word refers to and the color in which the word is displayed (e.g., red displayed in green) than if the two colors are the same (red displayed in red) or if the stimulus consists of a noncolor word, a series of colored Xs, or merely a color bar. The explanation usually offered for the difficulty of the incongruent condition is that word reading, a strongly automatic process, interferes with color naming. The challenge for the participant is to overcome the word-reading response.

ACC activation on the Stroop task was first observed by Pardo, Pardo, Janer, and Raichle (1990). Using positron emission tomography (PET), this study demonstrated increased ACC activation during performance of the incongruent condition when compared with the congruent condition. Increased ACC activation was also shown by Carter, Mintun, and Cohen (1995) in a similar comparison. Several studies have also reported greater ACC activation in association with the incongruent condition when compared with the neutral condition (Bench et al., 1993; Carter et al., 1995; George et al., 1994). The finding of greater ACC activation with incongruent stimuli has been found in variants of the Stroop task as well; Bush et al. (1998) observed ACC activation in a numeric version of the task.

Other tasks requiring the overriding of prepotent responses have also been shown to engage the ACC. Taylor, Kornblum, Minoshima, Oliver, and Koeppe, 1994, for example, asked participants in one condition to name the individually displayed letters B, J, Q, and Y. In a second condition, participants were asked to respond with the name of a different letter in the group according to a simple set of rules (e.g., if J is displayed, respond with "Y"). The latter task required them to overcome the temptation to read the letter in order to recover the less stimulus-compatible response dictated by the instructions. In agreement with the Stroop studies, increased ACC activity was observed on the conflict task.

A multipart PET study by Paus, Petrides, Evans, and Meyer (1993) showed that the need to override prepotent responses will activate ACC across tasks involving a range of input and output modalities. In one set of experiments, participants first performed according to extensively practiced stimulus—response pairings and later according to a novel mapping. In one version of the experi-

ment, participants were trained to respond to each of three simple visual stimuli with a direction-specific saccade. In the reversal condition, the pairing between the three stimuli and the three saccade responses was changed. Two other versions of the experiment involved mappings from visual stimuli to buttons to be pressed and from heard words to spoken words. In each version, the reversal condition elicited greater ACC activation than the overlearned condition.

In a second set of experiments, Paus et al. (1993) asked participants first to produce stimulus-compatible responses, and later to produce responses less congruent with the stimulus. In one version, participants first lifted whichever of two fingers was touched by the experimenter. Later, participants were instructed to raise the opposite finger. In a second version, participants performed a saccade in the direction of either a left-sided or right-sided visual cue, and then later were asked to respond with a saccade in the direction opposite the cue. In a third version, participants responded to the two heard letters "A" and "L" by naming the letter coming next in the alphabet. In the reversal condition, participants responded to "A" with "M" and to "L" with "B." In each version of the experiment, greater ACC activation was once again observed on the task requiring the participant to overcome an ingrained response in favor of a less familiar one.

Another instance of ACC activation associated with response override is provided by studies of go/no-go tasks. Using functional magnetic resonance imaging (fMRI), Casey et al. (1997; see also Kawashima et al., 1996) had participants view a series of individually presented letters, pressing a button with each presentation but omitting this response if the presented letter was an X. The majority of trials involved non-X letters, leading the button-press response to be prepotent. In control conditions, the presented letter series contained no Xs. Greater ACC activation was observed in the go/no-go condition. As in other response override tasks, ACC activation is here associated with conditions that require the participant to overcome a prepotent response in order to perform successfully.

The finding of ACC engagement in response override tasks provides a first piece of evidence for the view that this brain area responds to the occurrence of conflict. In each of the studies we have reviewed, the strongest ACC activation was observed under conditions where it was necessary for the participant to overcome interference from prepotent but task-irrelevant responses. These circumstances can be understood as involving conflict between processing pathways leading to correct (but otherwise weaker) and incorrect (but prepotent) responses. The mechanisms responsible for this form of crosstalk are considered further in Simulation 1A.

Underdetermined responding. In a second group of studies, ACC activation occurs under conditions requiring the participant to choose from a set of responses, none of which is more obvious or compelling than the others. We describe these tasks as involving underdetermined responding, because the stimulus presented to the participant does not uniquely specify the appropriate response.

The first studies to examine brain activation under such task circumstances were reported by Petersen, Fox, Posner, Mintun, and Raichle (1988, 1989). In a series of PET studies, the group asked participants to generate a verb in response to a seen or heard noun, identifying a use for the object named by the stimulus. When activation patterns for this task were compared with those for a condition in which the participant simply repeated or read the presented word, the ACC was found to be consistently engaged.

The finding has been replicated in a number of studies from other laboratories (e.g., Andreason et al., 1995; Barch, Sabb, Braver, & Noll, 2000; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997), in some cases with verb generation carried out silently (Warburton et al., 1996; Wise et al., 1991).

In the related letter fluency (or FAS) task, participants are asked to list words beginning with a given letter (Spreen & Benton, 1969). Here again, the participant selects freely among a number of potential responses. Letter fluency has been repeatedly shown to activate ACC, in comparisons with simply repeating the lettername cue (Friston, Frith, Liddle, & Frackowiak, 1993), repeating heard words (Frith, Friston, Liddle, & Frackowiak, 1991a), or performing a lexical decision task (Frith, Friston, Liddle, & Frackowiak, 1991b). Yetkin et al. (1995), using fMRI, found ACC activation even if participants generated letter fluency responses without voicing them aloud. Semantic fluency, in which the task is to name members of a given category, also activates ACC (Yetkin et al., 1995), as has stem completion, another task involving underdetermined responding (Buckner et al., 1995).

Activation of ACC under conditions of underdetermined responding is not limited to verbal tasks. Frith and colleagues found it when participants were asked to lift either of two fingers, chosen at random, when one of the fingers was tapped, in comparison with a condition where participants were instructed to lift the tapped finger (Frith, Friston, Liddle, & Frackowiak, 1991a). Deiber et al. (1991) compared PET activation patterns when participants were asked to move a joystick randomly in any of four directions with a condition in which they moved it repeatedly in only one specified direction, finding relative ACC activation in the free selection condition, a finding replicated by Playford et al. (1992) and (with button presses) Jeuptner, Frith, Brooks, Frackowiak, and Passingham (1997).

As in response override tasks, ACC activation in underdetermined responding is consistent with the view that the ACC is engaged by the occurrence of conflict. Because the stimuli involved in underdetermined responding tasks are each associated with a number of legal responses, stimulus presentation may lead to the parallel activation of multiple incompatible response pathways, resulting in crosstalk during the period between stimulus presentation and response delivery.

In support of this interpretation (examined more critically in Simulation 1B below), Raichle et al. (1994) showed that the verb generation task no longer produced detectable ACC activation once participants had encountered the same list of nouns several times and their responses had become well rehearsed. Activation was restored when a new list of nouns was later presented, once again placing the participant in the position of generating underdetermined responses. Similarly, in the Deiber et al. (1991) joystick movement study, no difference in ACC activation was observed between the single-direction condition and conditions where participants moved the joystick according to a previously learned sequence or on the basis of a direction-specifying tone. Again, increased ACC activation was noted only when the stimulus is likely to have activated pathways to multiple, mutually interfering response representations.

Error commission. In a third group of studies, ACC activity has been observed in association with the commission of errors. In contrast to the work discussed so far, using PET or fMRI, indications of a connection between ACC activity and errors comes

primarily from studies of event-related potentials in electroencephalographic (EEG) recordings (Rugg & Coles, 1995).

The term *error-related negativity* (ERN) refers to a discrete event-related potential that has been described as accompanying the commission of errors in a number of speeded response tasks (e.g., Falkenstein, Hohnsbein, & Hoorman, 1995). The potential, independently discovered by two laboratories in 1989 and 1990 (Gehring, Coles, Meyer, & Donchin, 1990; Hohnsbein, Falkenstein, & Hoorman, 1989), is best seen in response-aligned averages over error trials, where it usually appears with the onset of response-related electromyographic (EMG) activity, peaking 100—150 msec later.

The ERN (also designated as N_e) has been demonstrated in a variety of task settings. Gehring and colleagues (Gehring et al., 1990; Gehring, Coles, Meyer, & Donchin, 1995; Gehring, Goss, Coles, Meyer, & Donchin, 1993) used versions of the Eriksen flanker and Sternberg memory search tasks and a category judgment task requiring participants to indicate whether one of two displayed words represented an exemplar of the class named by the other. Falkenstein and colleagues used two- (Falkenstein, Hohnsbein, Hoorman, & Blanke, 1991) and four-way (Falkenstein et al., 1995) forced-choice letter discrimination tasks (cf. Bernstein, Scheffers, & Coles, 1995). Dahaene, Posner, and Tucker (1994) have also observed the ERN in a task requiring participants to indicate with a rapid keypress whether viewed numbers (displayed either as an Arabic numeral or in word form) were greater or less than 5, and in another task whether viewed words denoted animals. The ERN has also been observed in association with errors of commission in go/no-go tasks of varying design (Falkenstein et al., 1995; Scheffers, Coles, Bernstein, Gehring, & Donchin, 1996).

The generator of the ERN has consistently been localized to a medial frontal region. Dahaene et al. (1994), applying a dipole localization technique to EEG data, judged the source of the potential to lie in the ACC. Given the limited spatial resolution of the technique, however, a localization in supplementary motor cortex could not be ruled out. Carter et al. (1998), in a study discussed in more detail below, used fMRI to evaluate regional activity associated with incorrect versus correct responses in a version of the Continuous Performance Test, confirming that error responses were accompanied by temporally and anatomically specific activation of ACC.

As discussed in Simulation Study 1C, it appears likely that errors are associated with conflict due to interference between the pathways leading to correct and incorrect responses. Behavioral data indicates that errors in speeded response tasks frequently represent premature responses delivered while stimulus analysis is still incomplete (Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). Even as such impulsive errors are executed, stimulus evaluation can continue, leading to activation of the correct response (Rabbitt & Vyas, 1981). The very short latency of error-correcting movements confirms that activation of the correct pathway can take place even while an incorrect response is being delivered (Cooke & Diggles, 1984; Rabbitt & Rodgers, 1977). This makes it seem likely that errors will frequently be associated with conflict between the coactivated pathways leading to correct and incorrect responses.

More direct evidence for this idea is provided by a recent study by Gehring and Fencsik (1999). Participants in this study performed the flanker task, responding using the left hand for one target and the right hand for the other. EMG was used to measure the strength of the response made with each hand. Participants very frequently reversed errors, and the EMG results indicated clearly that when this occurred, there was typically temporal overlap between the error and error-correcting responses. This same study provides evidence consistent with the idea that this transient response conflict is a critical factor in the generation of the ERN; EEG data indicated that the ERN coincided with the period of response overlap on error trials.

A number of other findings corroborate the connection between response conflict and the ERN. First, error trials associated with the largest ERN amplitudes more frequently involve response reversals than do trials with smaller ERNs (Gehring et al., 1993). Thus, the largest ERNs are associated with error trials where there is the strongest evidence for belated activation of the correct response. Second, an ERN appears, even in association with correct responses, if these are subsequently reversed (Gehring et al., 1993).3 Third, in a study where participants were asked to withhold their responses until 2 s after stimulus presentation, no ERN was observed in association with errors (Dahaene et al., 1994). Given such a delay, any transient competition between processing pathways is likely to have resolved by the time of response delivery. Thus, incorrect responding in the Dahaene et al. study is unlikely to have been accompanied by the sort of crosstalk to which we attribute the ERN.

Residual studies. The close association between conflict and ACC activation in the studies we have reviewed is reinforced by the fact that conflict also appears to play a role in ACC activation studies that do not fall into any of the three categories we laid out above.

For example, D'Esposito et al. (1995) used fMRI to compare ACC activity during two simple tasks performed either singly or concurrently, observing greater activation in the latter condition. On the basis of the earlier discussion of the role of crosstalk in dual-task performance, it is clear how ACC activation in this study can be explained as a response to conflict.

In another divided attention study, Corbetta, Miezin, Dobmeyer, Shulman, and Petersen (1991) measured brain activity with PET while participants monitored forms in a visual display for subtle changes along the dimensions of color, shape, and direction of movement. In a focused attention condition, participants monitored only one of these dimensions. In a divided attention condition, participants searched for changes in any of the three dimensions. Greater ACC activation was associated with the divided attention condition. Participants made more errors in this condition, and so it may be possible to attribute ACC activation in this study to errors. However, another interesting (and closely related) possibility is that the parallel evaluation of different stimulus dimensions led on some trials to crosstalk between pathways supporting "same" and "different" responses. Although the published data do not allow a conclusive evaluation of this possibility, it is consistent with the reported higher frequency of misses (incorrect "same" judgments) in the divided attention condition.

In another study, Baker et al. (1996) found ACC activation in association with performance of the Tower of London task. Because the solution to this task is rarely immediately apparent to the unpracticed participant, competition or conflict among alternative actions seems likely to be involved. As we have already noted, certain computational models accord such competition a pivotal functional role in triggering problem-solving behavior (e.g., Laird et al., 1987), a point to which we will return in later discussion.

Finally, Grasby et al. (1993) had participants listen to and immediately repeat word lists from 2 to 13 items long. Using PET, they found that ACC activation increased with list length. As in the Corbetta et al. (1991) study, one option is to attribute this finding to errors, for the frequency of errors rose along with list length. However, there are again other potential explanations that involve conflict. One is that, as list length grew, greater response competition occurred during the retrieval process. Even more intriguing is the possibility that ACC activation may have been related to interference among lexical representations being maintained in working memory. One way of examining this latter possibility is provided by the phonological similarity effect, the fact that participants asked to repeat a list of words shows relatively poor memory for the list if it is composed of similar-sounding entries (Baddeley, 1966). If, as appears reasonable, this phenomenon can be assumed to derive from interference among representations being held in working memory, then a potentially informative experiment might be to measure ACC activity during retention of short word lists, comparing activity levels during maintenance of phonologically similar and dissimilar items. If the ACC is responsive to conflict among representations in working memory, then greater activation should be seen in the condition using phonologically similar words.

Accounting for ACC Activation: Simulation Study 1

In connection with each group of studies reviewed above, we briefly proposed how ACC activation can be understood as a response to the occurrence of conflicts in information processing. In the present section, we describe a set of three computer simulations in which this interpretation of the ACC literature is more fully articulated.

The objectives of these modeling studies were threefold. A first goal was to make the account we have presented so far more explicit, providing a precise indication of what we intend by such terms as crosstalk, conflict, top-down control, and conflict monitoring. A second goal was to confirm the sufficiency of these constructs, as we have used them in the conflict monitoring hypothesis, to account for the results of ACC activation experiments. The third goal was to lay the groundwork for further modeling work, reported in Part 2, that examines the entire feedback loop running from conflict monitoring to cognitive control.

Each of the present simulations makes use of a previously and independently implemented computational model of a single task from one of the three primary domains in which ACC activation has been reported. To examine the role of conflict in response override, we consider a model of the Stroop task (Cohen & Huston, 1994); for underdetermined responding, a model of stem completion (McClelland & Rumelhart, 1981); and to evaluate the relation between conflict and error commission, we examine a model of the Eriksen task (Servan-Schreiber, 1990), the task most frequently used in studies of the ERN.

To each of these models, we apply a quantitative measure of conflict, allowing the models to be used in simulations of the

³ Although trials involving overt reversals are likely to involve the strongest coactivation of correct and incorrect responses, the account we are proposing does not require that any actual reversal occur, only that activation of the correct pathway occur while activation of the incorrect pathway is still present.

behavior of the ACC as it has been observed in brain activation experiments. Each study provides an explicit account of the mechanisms that give rise to conflict, comparing their role across task conditions that have been shown to engage the ACC to different degrees.

General Methods

Selection of models. Although the models we consider are examined in a novel context, they are not themselves new. Each has been drawn from the published literature and is considered here in its original form. The fact that these models were formulated independently of present hypotheses allows us to approach them quasi-empirically, using them to test the consistency of the conflict monitoring hypothesis with current theories of information processing in specific tasks known to engage the ACC. Leaving the models' original parameters intact and using the same simple computation to determine conflict across all three studies reduces the number of free parameters associated with our simulation of ACC activation to zero.

Of course, these points should not be taken to imply that the models used were selected in a disinterested or theory-neutral fashion. On the contrary, the three models implement a shared set of basic assumptions about information processing that also form part of the background for the conflict monitoring hypothesis. Specifically, they assume that information processing is parallel, distributed, and interactive. These assumptions are captured in the connectionist framework, within which all three models were conceived (McClelland, 1992; Rumelhart & McClelland, 1986).

Like other connectionist models, the ones we will consider here are composed of identical processing units, each carrying a real-valued activity level, which excite and inhibit one another through weighted connections. When external input is applied to a subset of the units, information propagates through the network, resulting in a final output activation pattern. Information processing relies upon the strength of the network's connections, which can either be set by hand or by a number of training algorithms. Again, these values were set in previous studies and used unmodified in our current simulations.

Implementing conflict monitoring. In each simulation, the underlying model adopted from the literature is extended by the addition of a single conflict-monitoring unit (see Figures 1–3). This unit takes input from the basic network and computes the current amount of conflict prevailing there.

This component of the simulations raises the important question of how conflict might be measured. As a first step toward defining a method for accomplishing this, conflict may be operationally defined as the simultaneous activation of incompatible representations. In the models we will consider here, incompatible representations (e.g., representations of alternative responses) correspond to units interconnected by inhibitory weights. Thus, conflict can here be defined as the simultaneous activation of mutually inhibiting units.

Although this makes it clear what conflict involves at a qualitative level, it is a more difficult question how conflict should be quantified. Berlyne (1957, 1960), who discusses this issue at length, offers a list of desiderata for a measure of conflict: (a) It should increase with the absolute activation of the competing representations; (b) it should increase with the number of competing representations; and (c) it should be maximal when the acti-

vations of competing representations are equal. Although it is an empirical question how conflict might be measured by the brain (a point we consider further in the General Discussion), Berlyne's criteria provide a reasonable starting point for considering alternative possibilities. Berlyne noted that there are many potential measures of conflict that would meet his specifications. He himself adopted one based on the information-theoretic expression for entropy (specifically, this involves multiplying entropy by the average activation in the set of competing representations). In the present context, this approach carries the technical disadvantage that it requires activation levels to be translated into probability values, a step that in turn requires peripheral assumptions. In the present studies, we chose a different measure of conflict—Hopfield energy—which satisfies Berlyne's criteria while being based on values specified directly by the models we examine.

Hopfield (1982) defined the energy in a recurrent neural network as

$$-\sum \sum a_i a_i \mathbf{w}_{ii},\tag{1}$$

where a indicates unit activity and both subscripts are indexed over all units in the set of interest (related measures are discussed by Rumelhart, Smolensky, McClelland, & Hinton, 1986, and Smolensky, 1986).

To see how energy reflects conflict, consider a single pair of mutually inhibiting (incompatible) units. When both are inactive, energy is zero, consistent with the absence of conflict. Energy remains at zero if only one of the units becomes active, once again mirroring the level of conflict. Energy rises above this level only if both units are active. The particular value for energy then depends on the activation values of the two units, becoming largest when both units are maximally active and thus most strongly in conflict.⁴ Note that his implementation of conflict does not involve any additional parameters, and this preserves the zero-parameter nature of our simulations.

As in the cognitive system, conflicts between representations in connectionist networks can occur at a variety of levels of processing, including stimulus evaluation, memory and set representation, and response selection. In the simulation studies presented here, we focus exclusively on the role of response conflict, measuring energy over units in the output layer of each model. We were motivated in this choice by the commonality of response selection processes among tasks that involve response override, underdetermined responding, and error commission, which led us to hypothesize that ACC activation in these domains might be accounted for in terms of conflict at this level of processing. Although this is the hypothesis addressed in the simulation studies, there are reasons for leaving open the possibility that conflict at other levels of processing might also be relevant to ACC activation, a point to which we return in later discussion.

Simulation procedure. In each study, the underlying model is used to simulate information processing in conditions that have been reported to engage the ACC to different degrees. In the

⁴ For completeness, it is worth noting that concurrent activation of units interconnected by excitatory links causes a reduction in energy. In this regard, energy is more than a measure of conflict; it measures compatibility or consistency. This interesting aspect of Hopfield's (1982) formula does not come into play in the simulations to be reported here, where units share only inhibitory connections.

Stroop model, congruent, neutral, and incongruent trial conditions are compared; in the stem completion model, the stem completion task is compared with word reading; and in the Eriksen model, correct responses are compared with errors. Except where explicitly noted, simulations are run according to the procedure originally used for each of the basic models as reported in the literature.

With each step of processing, the conflict monitoring unit assumes an activity equal to the current level of energy in the output layer of the underlying model. In each study, the activity of this unit is compared across conditions, with the prediction that the greatest activity will be observed in the condition associated with the strongest ACC activation.

Simulation 1A: The Stroop Task

In this first simulation study, we introduce the basic elements of the proposed framework by considering the origins of ACC activation—and, by implication, the role of conflict monitoring—in a response override task.

Method. Stroop performance was simulated using a model proposed by Cohen and Huston (1994), shown in Figure 1 (left). This model is based on an earlier feed-forward model (Cohen et al., 1990), revised to include recurrent connections and interactive processing (both of which are amenable to our measurement of conflict).

The model includes input units for display color and word identity. The appropriate units in each group connect reciprocally via excitatory weights to an output layer with units representing potential responses. In addition, the model includes a task demand layer with units standing for word reading and color naming, respectively. The task demand units serve to bias activation in the model so that either word or color inputs may dominate response activation. As shown in Figure 1, units within every layer are interconnected by symmetrical negative weights.

The procedure used in simulating a trial is detailed in Cohen and Huston (1994). Briefly, one of the task units is activated during an initial priming interval, during which the output units are inhibited to prevent premature responses. The input pattern is then applied and the response-layer inhibition removed.

As illustrated in Figure 1, the current simulation added a conflict monitoring unit that takes inputs from the response layer of the underlying model, taking on an activation level equal to the energy in that layer on the current cycle of processing. In order to account for the findings regarding ACC activation in neuroimaging studies of the Stroop task, the activation of the conflict monitoring unit was evaluated during simulation of incongruent, congruent, and neutral conditions in the color-naming task.

Results. Results are shown in Figure 1 (right). As with ACC activation in neuroimaging studies of the Stroop task, activation of the conflict monitoring unit was higher in the incongruent condition than in the congruent or neutral conditions. As shown in the figure, activation rose rapidly in all three conditions; this is because both output units move toward their (nonzero) resting activity levels once the inhibition they receive prior to stimulus presentation is removed. Differences in energy across conditions soon appeared, however, with incongruent trials associated with the highest degree of energy.

The increased activity of the conflict monitoring unit on incongruent trials reflects the occurrence of crosstalk within the Cohen and Huston (1994) model. On incongruent trials, word and color inputs each activate a different set of units in their corresponding pathways. The intersection of these two pathways in the output layer (in addition to the other sectors of the model) causes conflict between the response units, and this in turn raises the activity of the conflict monitoring unit.

Discussion. Response override tasks have been repeatedly observed to engage the ACC. This first simulation provides an

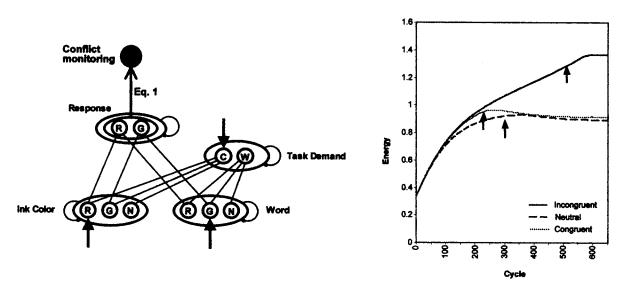


Figure 1. Left panel: Illustration of the Stroop model discussed in Simulation Study 1. From "Progress in the Use of Interactive Models for Understanding Attention and Performance," by J. D. Cohen and T. A. Huston, 1994, in C. Umilta and M. Moscovitch, Attention and Performance XV (Figure 18.8, p. 462), by J. D. Cohen and T. A. Huston, 1994, Cambridge, MA: MIT Press. Copyright 1994 by MIT Press. Adapted with permission. Eq. = equation; R = red; G = green; C = color-naming; W = word-reading; N = neutral. Right panel: Energy as measured in the response layer of the Cohen and Huston (1994) model during simulation of congruent, neutral, and incongruent trials in the Stroop task. Arrows indicate average response times. Energy was recorded for each cycle of processing, and the data shown are means based on 100 trials in each condition.

illustration of how the idea of conflict monitoring can be used to explain this finding. When an element is added to an existing model of a typical response override task, acting to transform the occurrence of conflict into an activation-based signal, a pattern is observed across conditions that parallels that observed in ACC activation studies.

The color-naming condition of the Stroop task is a classic example of controlled information processing, and in fact, the Cohen and Huston (1994) model was originally proposed as a basic model of control function. Control is implemented here through the color-naming and word-reading units, insofar as these units bias information flow through the rest of the system in accordance with task demands. It is interesting that varying the control signal coming from these units impacts the degree to which conflict occurs during stimulus processing. In simulations of the color-naming task, specifically, weakening the input from the color-naming unit on incompatible trials leads to increasing interference between color and word inputs and, thus, to higher peak energy.⁵ This aspect of the model's behavior fits well with the idea that conflict might serve as an indicator of insufficient control, as it means that conflict is most likely to occur when control is weak. It also translates into a testable prediction: If ACC activation reflects conflict detection, then, on the basis of the model, ACC activation during incongruent trials in the Stroop task should vary inversely with the strength of control, defined as the effort to attend exclusively to color.

We recently tested this prediction in a functional neuroimaging study (Carter et al., 2000). Here, the strength of top-down control was influenced indirectly by manipulating trial-type frequency. As shown by a number of behavioral studies (e.g., Lindsay & Jacoby, 1994; Logan & Zbrodoff, 1979), participants display a smaller Stroop interference effect if incongruent trials are frequent than if they are rare. In our terms, frequent incongruent trials lead to a high-control state (a tight focus on the color-naming task as opposed to the word-reading task). The Carter et al. (2000) study exploited this phenomenon to test for the predicted relationship between control state and ACC activation. Participants performed the Stroop task while undergoing fMRI. Trial-type frequency was varied across blocks; in one half of the blocks, incongruent trials occurred frequently, in the other half, relatively infrequently. Behavioral results confirmed the expected effect of trial-type frequency on control state. Participants were faster on incompatible trials when these were frequent than when they were rare. Eventrelated scan acquisition allowed evaluation of the time course of ACC activation on individual trials. As predicted, peak activation on incongruent trials differed as a function of trial-type frequency, with greater activity occurring during blocks where incompatible trials were rare.

Simulation 1B: Stem Completion

As in response override tasks, we have attributed ACC engagement in underdetermined responding tasks to the engagement of a conflict monitoring function. Using the approach taken in Simulation 1A, this proposal was tested against a relevant model of information processing, in this case a model of the stem completion task.

Method. Stem completion can be simulated using the interactive activation (IA) model of word reading introduced by McClelland and Rumelhart (1981; Rumelhart & McClelland, 1982), illustrated in Figure 2 (left).

The model consists of three interconnected sets of processing units. External input is applied to a layer encoding featural elements—vertical, horizontal, and diagonal line segments—from which individual letters are constructed. Activation feeds forward from this feature layer to a layer of units representing individual letters. This layer connects to a third set of units, each standing for an individual four-letter word. Between layers, compatible units (e.g., the unit for the letter A in the first slot and the word unit for ALSO) are connected by excitatory weights, and incompatible ones by inhibitory weights. There are also symmetrical inhibitory connections between each pair of units in the word layer.

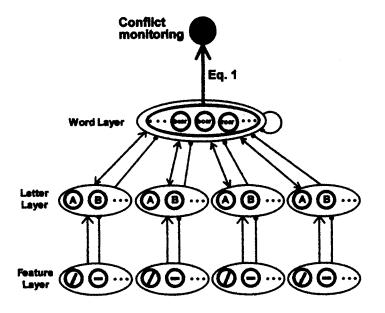
Stem completion can be simulated in the IA model by presenting letters in the first two positions, leaving the third and fourth slots blank. Given such input, the model completes it, settling into a final state dominated by a word unit (and corresponding letter units) representing a word beginning with the two letters presented, similar to what would have resulted had all four letters of the word been present.

As in Simulation 1A, a conflict monitoring element was added to the underlying model. Here, the conflict monitoring unit takes its input from the units in the word layer and assumes an activation equal to the current level of energy in that layer.

In order to account for the finding of ACC activation in association with stem completion, the activity of the conflict monitoring unit was evaluated during simulations of both stem completion (partial input) and word reading (full input). A total of 20 words were chosen at random from the corpus represented in the word-unit layer of the model. In the word-reading condition, each word was presented in full to the feature layer. In the stem-completion condition, only the first two letters of each word were presented, with the last two slots receiving no input. As in Simulation 1A, energy was measured at regular intervals throughout each trial.

Results. Results are shown in Figure 2 (right). Whereas presenting a full word led to only a fleeting rise in energy, stem presentation led to much greater and sustained levels of energy. As in Simulation 1A, these results can be understood as deriving from the different degrees of crosstalk involved in the two task conditions. Although the final outcome in the word layer is similar for full words and word stems, the paths by which the network reaches its final representation entail quite different amounts of crosstalk. For full words, the process is fairly straightforward. The input for each letter activates its corresponding feature units and letter unit. The selected letter units together strongly activate one word unit. Although subgroups of letters might also weakly activate a small set of other words (e.g., the FIS in FISH might activate FIST), the support for the fully specified word is stronger, and this word unit quickly dominates the word layer. The small increase in energy associated with word reading corresponds to the minor conflict among words partially matching the input. For word stems, processing unfolds differently. Initially, the input activates one letter unit in each of the first two letter positions. These two units together activate a wide range of word units (FI_ will activate FISH, FIND, FINE, FIRE, etc.). These word units compete through inhibitory interconnections, also sending activation to the letter units associated with them in the third and fourth positions of the letter layer. Although this conflict is ultimately resolved in

⁵ The effects of varying task—unit input were first explored in an earlier version of the model by Cohen et al. (1990). Usher and Cohen (2000) have replicated and extended these findings in the context of the Cohen and Huston (1994) model. Simulation 2B in the present article also contains relevant findings.



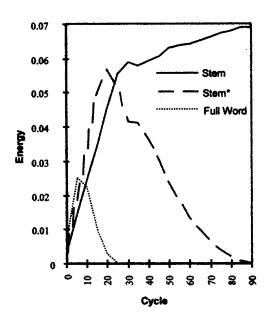


Figure 2. Left panel: Illustration of the IA model. From "An Interactive Activation Model of Context Effects in Letter Perception: Part I. An Account of Basic Findings," by J. L. McClelland and D. E. Rumelhart, 1981, Psychological Review, 88, Figure 3, p. 380. Copyright 1981 by the American Psychological Association. Eq. = equation. Right panel: Energy as measured in the word layer of the IA model during simulation of word reading and stem completion. *Energy during simulation of stem completion with the weight of inhibitory connections in the letter layer set to match those in the word layer, in order to prevent two-way ties between words. Energy was recorded every five cycles of processing.

favor of one word that completes the input pattern,⁶ the degree of crosstalk sustained in the response selection process is much greater than for word reading, giving rise to the greater amount of energy observed.

Discussion. Underdetermined responding tasks make up an important subset of the tasks that have been shown to activate the ACC. The results of the present simulation demonstrate how the engagement of the ACC in this setting can be understood in terms of a conflict monitoring function. This result stems from the same factor that produced the results of Simulation 1A. On the basis of the models we have adopted, conflict in both types of task is the result of crosstalk between processing pathways. Thus, despite the superficial differences between response override and underdetermined responding tasks, the ACC activation associated with both can be understood as a response to precisely the same type of system state.

As in Simulation 1A, consideration of the factors that affect the degree of conflict in the underlying model leads to testable predictions. One example involves the fact that, in the IA model, the degree of crosstalk associated with stem completion depends on the specific stem tested. Energy varies with the degree to which words other than the eventual winner are excited by the stem. Stems that activate one completion much more strongly than any other will be associated with the least conflict, because the preferentially activated word unit quickly suppresses its competitors. Considered in the context of the conflict monitoring hypothesis, this leads to the prediction that stem completion should engage the ACC more strongly when the stem presented is associated with several completions than when the stem is associated with one strongly preferred response.

A finding related to this prediction has been reported in the context of another underdetermined responding task, verb generation. Thompson-Schill et al. (1997) recorded the frequency with which specific responses were elicited in this task by a set of nouns. For each noun, they divided the frequency of the most frequent response by that of the second most frequent, using this response strength ratio as an index of the degree to which each noun was associated with a single predominant response. Using fMRI, the group compared brain activation during completion of stems with high and low response strength ratios. Consistent with the conflict monitoring hypothesis, greater ACC activation was observed for low-response-ratio nouns.

This finding was recently replicated by Barch et al. (2000) in a study that also tested further predictions based directly on the

⁶ In simulations of stem completion using the model's original parameters, the settling process sometimes resulted in a two-way tie between word units. This is reflected in a plateau in the average energy trajectory, as shown in Figure 2. We tested whether the occurrence of these ties might be responsible for the higher levels of energy during stem completion by introducing reciprocal inhibitory weights between each pair letter units, similar to those in the word layer (and equal in strength). This had the effect of eliminating deadlocks, but without otherwise affecting the differences between processing in the word-reading and stem-completion conditions. The resulting energy trajectory, shown as a dashed line in Figure 2 (right), remained significantly greater in amplitude than the baseline condition, confirming that the differences in energy between the two conditions were not due to the incidental occurrence of two-way ties, but instead to the transient competition among processing pathways triggered by presentation of the word-stem input.

conflict monitoring hypothesis. Specifically, Barch and colleagues predicted that ACC activation would vary not only as a function of noun class (high vs. low response strength ratio), but also as a function of the particular verb selected by the participant on any given trial. Activation should be lower with selection of a verb strongly associated with the noun (e.g., ring with bell) than with selection of one more weakly associated (e.g., hear with bell), as selection of the latter verb is more likely to involve sustained competition among multiple candidate responses. This prediction was confirmed; Barch et al. found greater activation during production of weak-associate verbs, an effect that was restricted uniquely to the ACC.

Simulation 1C: Error Commission in the Eriksen Task

As we discussed earlier, the ERN is an event-related potential that has been localized to the ACC and reported to occur in association with errors in a variety of speeded response tasks. In the present study, we explored the origins of this ACC response by examining the dynamics of error commission in the task most frequently used in studies of the ERN, the Eriksen flanker task.

The flanker task, introduced by B. A. Eriksen and Eriksen (1974), requires participants to identify the central letter in a briefly presented five-letter array. For example, they might be instructed to press one button if the central letter is an S, another if it is an H. In stimuli with compatible noise (e.g., SSSSS), the four distractor letters or flankers map to the same response as the central target letter. In stimuli with incompatible noise (e.g., SSHSS), the flankers map to a different response. Analogous to the Stroop task, the basic behavioral finding is that reaction times and error rates are higher on incompatible trials, presumably reflecting the greater degree of conflict in this condition. However, like researchers using the Eriksen task to study the ERN, we were less

concerned with differences between compatible and incompatible trials than with the occurrence of errors in the task.

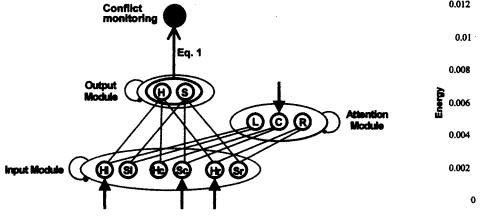
Method. A model of information processing in the Eriksen task has been proposed by Servan-Schreiber and colleagues (Cohen, Servan-Schreiber, & McClelland, 1992; Servan-Schreiber, 1990), as illustrated in Figure 3 (left).

Inputs corresponding to compatible stimuli (SSSSS and HHHHHH) and incompatible stimuli (HHSHH and SSHSS) are represented as patterns of activity across three pairs of position-specific letter units, one pair for the central target and one for the flankers on each side. For example, the input HHSHH is presented to the model by applying input to the left and right H units and to the center S unit. As shown in the diagram, the letter units connect to an array of three spatial attention units and to two output units, one for each letter. Connections between layers are excitatory, and there are reciprocal inhibitory connections between units within each layer.

To simulate an experimental trial, a priming input is first applied to the center spatial attention unit, and the model settles for three cycles. This step simulates participants' allocation of attention to the location where the central target letter will soon appear (similar to the priming step in the Stroop model, which also simulates the assumption of a preparatory set). Next, a pattern representing the stimulus is applied to the letter units as described above. The model cycles until one output unit has reached the activity level defined as the response threshold, simulating the forced choice made by participants performing the task. With each cycle, random noise is applied to each unit's activity level, leading the model to produce responses with a variable latency and, occasionally, to commit errors.

Once again, a conflict monitoring element was added to the model. As in the previous two simulations, this received inputs from each of the response units in the model and assumes an activation value equal to the energy value in the response layer.

In order to simulate the ERN, we evaluated the activity of the conflict monitoring unit as measured during correct and incorrect trials. A total of 500 trials were run, using all four input patterns in equal proportions. Response accuracy was determined on the basis of the first response to cross a specified activity threshold, following the method used by Servan-



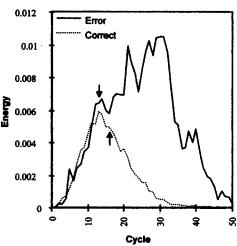


Figure 3. Left panel: Illustration of the Eriksen model proposed by Servan-Schreiber and colleagues. From "A Parallel Distributed Processing Approach to Automaticity," by J. D. Cohen, D. Servan-Schrieber, and J. L. McClelland, 1992, American Journal of Psychology, 105, Figure 8, p. 255. Copyright 1992 by the Board of Trustees of the University of Illinois. Used with the permission of the University of Illinois Press. Eq. = equation; L = left; C = center; R = right; H = H left; S = S left; H = H center; H = H right; H = H right; H = H right; H = H center; H = H right; H = H r

Schreiber (1990). Data from correct and error trials were separated, and the mean cycle-by-cycle energy value for the output layer was calculated for each group. Incompatible and compatible trials were pooled within each accuracy condition, as is the case in studies that have used the Eriksen task to elicit the ERN (e.g., Gehring et al., 1993).

Results. Results are shown in Figure 3 (right). On average, error trials showed greater and more sustained energy than correct trials, a difference that remained even when compatible and incompatible groups were considered separately. Like in the ERN, energy began to increase just before error commission, peaking and resolving shortly thereafter.

Consistent with the proposal made earlier, the increase in energy associated with errors in the Servan-Schreiber model relates to crosstalk between pathways supporting correct and incorrect responses. In order to see the reasons for this, it is useful to consider the mechanisms by which errors occur. In the model, the key factor leading to errors is the random noise added to each unit's activation level with each cycle of processing. Noise may actually benefit performance on some trials by priming units relevant to the correct response during the period prior to stimulus presentation. When this happens the correct response gets a head start, and the time to responding is shorter. On other trials, however, noise may prime pathways relevant to the incorrect response. This can lead to two alternative outcomes. The correct response may manage to override the primed error pathways before they can activate the incorrect response unit above threshold. Here the reaction time will be long, but the response correct. Alternatively, if the early priming of the incorrect pathway strongly enough outweighs the input to the correct pathway, the erroneous response may pass threshold before the correct response can overcome the effects of priming, resulting in an error.

On error trials, even as the incorrect response is being delivered, continued processing of the input leads to activation of the correct response. As a result, there is often a period during which the pathways for correct and incorrect responses are coactivated. On average, the period of overlap occurs just after the delivery of the incorrect response, precisely as in the empirical data reported by Gehring and Fencsik (1999). It is this transient period of crosstalk between correct and incorrect pathways that accounts for the increase in energy—and thus increased activity in the conflict monitoring unit—during error trials.

Discussion. This study provides an account of how ACC engagement during error commission can be understood in terms of conflict monitoring, similar to the account offered for response override and underdetermined responding tasks. As in Simulations 1A and 1B, a comparison of energy across conditions yielded results matching those obtained in ACC activation studies, consistent with the idea that the ACC is responsive to the occurrence of conflicts in information processing.

One important claim of the proposed account is that the ACC response associated with errors is not due to response accuracy itself. Errors are associated with a relatively large ACC response, not because they involve delivery of the incorrect response but rather because they tend to involve conflict between response representations. If this view is accurate, then the ACC response to errors and to high-conflict correct responses should occur in the same anatomical location within the ACC. We have tested this prediction using fMRI (Carter et al., 1998). In this experiment, participants performed the AX version of the Continuous Performance Test (AX-CPT; Rosvold, Mirsky, Sarason, Bransome, &

Beck, 1956). Here, the participant monitors a sequence of individually presented letters for the occurrence of a specific two-letter sequence (an A followed immediately by an X). A target key is to be pressed when the second letter in the specified sequence (X) appears, but only if preceded by the first letter of that sequence (A). On all other trials a second, nontarget key is to be pressed. Conflict in the task derives from an important frequency manipulation, according to which 70% of trials are AX trials. This produces the expectation that any given A will be followed by X, resulting in response conflict on trials where an A is in fact followed by some other letter (AY trials). Similarly, the appearance of an X comes to be associated with the target response, creating conflict on trials where an X follows some letter other than X (BX trials).

The Carter et al. (1998) study tested three predictions of the conflict monitoring hypothesis: first that AY and BX trials would produce more ACC activation than AX and BY trials; second that ACC activation would accompany errors in the AX-CPT; and third—most important for the present discussion—that these two effects would occur within the same area of the ACC. Imaging data confirmed all three of these predictions. Transient ACC activation appeared in conjunction with the second letter in each stimulus pair, and this rose to higher levels on AY and BX trials. An increased ACC response was also observed in association with errors. These two effects were observed in precisely the same area of the ACC, consistent with the claim that the ACC response on errors and high-conflict correct trials represents a common underlying function.

Although the present model predicts these findings, it also predicts differences between the ACC response on error versus high-conflict correct trials. Specifically, it suggests that there should be differences in the timing of the ACC response in these two contexts. According to the model, conflict during errors occurs primarily after the response has been produced (see Figure 3). Conflict on correct trials occurs earlier, peaking before an overt response is emitted. This difference has important implications for our theory's predictions. For example, it is tempting to assume that the theory should predict an ERN-like deflection in the EEG following high-conflict correct responses. However, given what the model suggests about the timing of conflict, response-aligned EEG averages are in fact not predicted to show such a potential. In this regard, it strikes us as potentially significant that studies reporting an ERN-like potential on high-conflict correct trials have used stimulus-aligned averages (e.g., Kopp, Rist, & Mattler, 1996; for more on this set of issues, see Yeung, Botvinick, & Cohen, 2000).

Although we used the Servan-Schreiber (1990) model to examine error commission, it is worth noting that the model also implements a classic response override task. In the Eriksen task, the presence of incompatible flankers leads to early activation of the incorrect response, and this must be overcome in order for the correct response to be ultimately delivered. In the model, this process leads to conflict between the response units. Thus, as in the other model of response override we have considered, the trial type most associated with the need to override a prepotent response tendency is also associated with greater conflict. Like the Cohen and Huston (1994) model, the Servan-Schreiber model also contains a mechanism acting to minimize such conflict. The attention layer in the Servan-Schreiber model acts very much like the task layer in the Stroop model, serving to bias information flow in the rest of the system in accordance with task demands. The input

from the attention layer thus represents another implementation of top-down control. Here, control serves to focus processing on the center input units, partially blocking the influence of the flankers. Note that, once again, weakening the influence of control leads to increased conflict; lower or more evenly distributed activation in the spatial attention layer will result in a less exclusive focus on the center input units and thus to greater conflict at the response level (Servan-Schreiber, 1990). Thus, the Servan-Schreiber model provides another illustration of how the occurrence of conflict might indicate the presence of insufficient control.

As in the Stroop model, this demonstration also leads to a testable prediction concerning ACC activation. If the ACC responds to conflict, then on incompatible trials in the Eriksen task it should respond more strongly when the participant's focus on the center of the stimulus display is weakest. We tested this prediction using fMRI (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). As in Carter et al. (2000), control state was influenced indirectly by way of a task manipulation. It has been shown, for the Eriksen task as for the Stroop, that trial-type frequency affects top-down control, in that when incompatible trials are frequent, participants show a smaller interference effect (Gratton et al., 1992). It is interesting, however, that the same line of research revealed that reactive shifts in attentional strategy also occur on a finer time scale; Gratton et al. found that performance on any given trial depends on the compatibility of the immediately preceding trial. Specifically, they showed on the basis of reaction-time data that the flankers' distracting effect is weaker on trials that follow incompatible trials than on trials that follow compatible ones. In the terms we have been using, control—the mechanism that focuses processing on the central target—is stronger after incompatible trials than after compatible ones. Like trial-type frequency in the Stroop study, this sequential adjustment effect affords a test of the prediction that ACC activation should vary with control state. Specifically, ACC activation on incompatible trials should vary depending on the compatibility of the preceding trial. After compatible trials, control should be relatively lax, conflict should be intense, and therefore ACC activation should be high. After incompatible trials, control should be stronger, conflict should be less severe, and therefore ACC activation should be comparatively weak.

To test this prediction, Botvinick et al. (1999) had participants perform the Eriksen flanker task while undergoing fMRI. Incompatible and compatible trials were intermixed in a pseudo-random fashion. Behavioral results confirmed the presence of the sequential adjustment effect; participants showed less interference after incompatible trials than after compatible ones. As in the companion Stroop study, event-related scan acquisition allowed evaluation of ACC activation on individual trials. As predicted, the degree of ACC activation on incompatible trials varied depending on the compatibility of the preceding trial. Greater activity was observed when the preceding trial was incompatible and, thus, when control was relatively weak.

Simulation Study 1: General Discussion

Together, Simulations 1A-1C serve to demonstrate how ACC activation in disparate domains can be understood in terms of the single function of conflict monitoring. It is interesting that the models we have adopted suggest not only that conflict occurs in all

three settings, but that it shares common origins in all three, stemming from crosstalk among processing pathways.

Two of the models discussed here (A and C) provide a partial account of the relationship between conflict monitoring and cognitive control. Both models include a set of units that play the part of control, serving to bias information flow in the rest of the network. In line with the theories reviewed at the beginning of the article, input from these units helps to minimize conflict. The models thus indicate how the occurrence of conflict might signal a demand for greater control; effectively, activation of the conflict monitoring unit in the models can be interpreted as indicating that current levels of control are insufficient to meet task demands.

This point has important implications for the interpretation of ACC activity. Specifically, it means that the ACC response to conflict may also be viewed as signaling a demand for increased control. This interpretation is consistent with the neuroimaging results of Carter et al. (2000) and Botvinick et al. (1999), where ACC activation was highest when control was relatively weak. Indeed, in the brain activation literature at large, the circumstances in which ACC activation has been observed are almost always ones where the demand for control is likely to be high. For illustration, consider the following list of task circumstances identified by Shallice and Burgess (1993) as involving a high demand for control: (a) situations that require the overcoming of a strong habitual response or resisting of temptation, (b) situations in which the responses are not well learned or that contain novel sequences of actions, (c) situations that involve planning or decision making, (d) situations that involve error correction or troubleshooting, and (e) situations judged to be technically difficult. It is not difficult to see how the ACC activation studies reviewed earlier might be sorted into these categories.7

The data presented so far provide a strong motivation for two basic conclusions: (a) There exists a system in the human brain that responds to the occurrence of conflicts in information processing, and (b) activation of this system occurs under circumstances where input from cognitive control is insufficient given current task demands. In Part 2 we turn to the remaining tenet of the conflict monitoring hypothesis, the idea that information about conflict is used in the modulation of cognitive control.

Part 2: Conflict Monitoring and the Regulation of Cognitive Control

One of our central proposals is that the conflict monitoring system exerts an influence on centers responsible for cognitive control, causing them to intervene more strongly in processing when conflict is occurring. An important motivation for this idea comes from studies demonstrating on-line fluctuations in control, linked to variations in performance and task demands. In this section, we focus on three specific examples of this general phenomenon, with the objective of demonstrating how conflict monitoring can be used to understand them.

Our approach once again involves the use of computational modeling. Building on Simulation Study 1, the modeling work we describe in Part 2 implements the complete feedback loop proposed by the conflict monitoring hypothesis, through which con-

⁷ See Posner and DiGirolamo (1998) for an alternative interpretation of the finding of ACC activation in these settings.

flict detection leads to shifts in top-down control. Adding this mechanism to existing models of specific laboratory tasks yields behavior closely resembling the behavioral data concerning online shifts in control.

On-Line Adjustments in Control: Three Empirical Phenomena

One ex-1. Sequential adjustment effect in the Eriksen task. ample of behavior reflecting on-line adjustments in control is provided by Gratton, Coles, and Donchin (1992). As briefly described earlier, this study reported that participants performing the Eriksen flanker task tend to display less interference after incompatible trials than after compatible ones. The relevant data are shown in Figure 4 (top). In line with previous studies, the study found incompatible trials to be associated with longer reaction times and higher error rates than compatible trials. The key feature of the data, however, lies in an interaction between previous and current trial type. After the occurrence of an incompatible trial, performance becomes faster on incompatible trials but slower on compatible ones. As shown in the figure, effects on error rate run in the same direction as those for reaction time. This pattern of findings is consistent with an interpretation according to which incompatible trials induce a focusing of visual attention, which in turn reduces the influence of the flankers on performance.

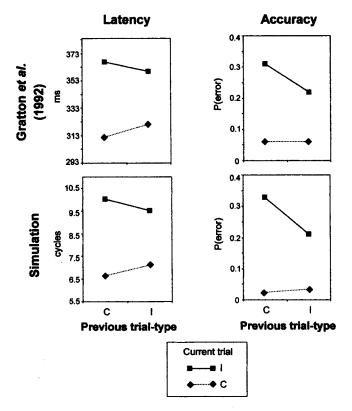


Figure 4. Top panels: Ordinate labels: C = previous trial compatible, I = previous trial incompatible. Data from "Optimizing the Use of Information: Strategic Control of Activation and Responses," by G. Gratton, M. G. H. Coles, and E. Donchin, 1992, Journal of Experimental Psychology: General, 4, Figure 1, p. 485. Copyright 1992 by the American Psychological Association. Bottom panels: Results of Simulation 2A.

To our knowledge, no account has been offered concerning the mechanism by which the occurrence of incompatible trials exerts this effect on behavior. The conflict monitoring theory provides such an account, based on the fact that incompatible trials are associated with a relatively high degree of conflict. As detailed in Simulation Study 2A below, allowing conflict to influence the top-down control of spatial attention leads to a pattern of behavior matching that reported by Gratton et al. (1992).

2. Trial-type frequency effect in the Stroop task. Another striking example of task-induced adjustments in control is the trial-type frequency effect observed in the Stroop task. Here, as will again be familiar from the earlier discussion, the degree of interference from word reading on color naming depends on the frequency of incongruent trials, with less interference occurring when incongruent trials are frequent. This (and similar) effects of trial-type frequency have been reported in a number of experiments using the Stroop task (e.g., Cheesman & Merikle, 1986; Lindsay & Jacoby, 1994; Logan, 1980; Logan & Zbrodoff, 1979). A particularly detailed data set is provided by Tzelgov, Henik, and Berger (1992; Figure 5, left). Here, participants performed blocks of trials with varying proportions of neutral, congruent, and incongruent trials. The researchers adjusted the proportion of incongruent trials by, in effect, diluting them with neutral trials. A frequent-incongruent condition contained 37.5% incongruent trials, 37.5% congruent trials, and 25% neutral trials. An infrequent-incongruent condition contained 12.5% incongruent trials, 12.5% congruent trials, and 75% neutral trials. Finally, an intermediate condition contained 25% incongruent trials, 25% congruent trials, and 50% neutral trials. (The Tzelgov et al. study also included a condition with no neutral trials. We concentrate here exclusively on the conditions that included neutral trials, as it is here that interference and facilitation can be evaluated.)

In line with related studies, Tzelgov et al. (1992) found a larger difference between performance on congruent and incongruent stimuli when incongruent trials were relatively infrequent than when they occurred often. The investigators quantified interference as the reaction-time difference between incongruent and neutral trials and observed that this grew smaller as the proportion of incongruent trials increased, as shown in Figure 5 (left). It is interesting that no statistically reliable effect of frequency was observed on facilitation, measured as the difference between neutral and congruent trials. That is, the increase in the difference between compatible and incompatible trials across conditions could be attributed almost entirely to an increase in interference.

A natural explanation for this pattern of findings is that the occurrence of incongruent trials led participants to focus more effectively on the color-naming task, enhancing their ability to avoid interference from the word-reading response. Once again, existing work provides no indication of the mechanism by which incongruent trials exert this effect. Conflict monitoring offers a potential answer to this question, in view of the fact that incongruent trials involve greater conflict than congruent and neutral trials. Simulation Study 2B demonstrates that allowing conflict to influence top-down control in a model of the Stroop task produces behavior closely resembling the empirical data reported by Tzelgov et al. (1992).

3. Changes in performance following errors. A third behavioral phenomenon indicating reactive adjustments in control is the fact that participants performing forced-choice decision tasks tend

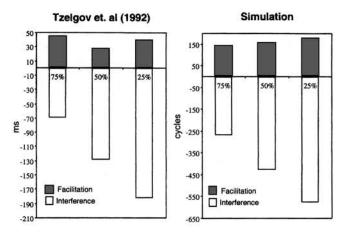


Figure 5. Left panel: Labels indicate percentage of color words (incompatible and compatible stimuli). Data from "Controlling Stroop Effects by Manipulating Expectations for Color Words," by J. Tzelgov, A. Henik, and J. Berger, 1992, Memory & Cognition, 20, Figure 1, p. 730. Copyright 1992 by the Psychonomic Society. Adapted with permission. Right panel: Results of Simulation 2B.

to adopt a more conservative strategy following the occurrence of errors. Although this phenomenon has been observed in a number of studies (most notably Rabbitt, 1966; see Luce, 1986, for a review), the most detailed data come from a set of studies by Laming (1968). Laming had participants perform a task in which they viewed a series of individually presented line segments and were asked to indicate by button press which of two prototypes,

presented at the beginning of the block, each line resembled. His results, based on three slightly different parameterizations of the task, are summarized in Figure 6 (left). In the reaction-time plots presented here, the first column of points represents the average reaction time associated with error trials themselves, expressed as a difference from the overall mean reaction time. As is common in relatively easy discrimination tasks, errors were faster than the average correct trial. The opposite is true of the first few correct trials coming after errors. The following points show average reaction times for these trials. Immediately after errors, reaction times tend to be larger than average, trending back toward the overall mean over the next few trials.

In addition to these changes in response latency following errors, there are also changes in accuracy. This effect is illustrated in the accuracy plots shown in Figure 6. The left-most points in these plots show the average error rate for each study as a whole, the remaining points showing the error rate for trials coming after errors. Here, there is a shift to lower error rates after the occurrence of an error and a slow recovery over the next trials toward the study mean. In summary, performance becomes slower and more accurate after errors, a change that can be understood as a shift along the speed-accuracy tradeoff curve (Luce, 1986).

Conflict monitoring offers a ready explanation for these observations, on the basis of the occurrence of conflict in association with errors. In Simulation 2C, the occurrence of conflict in a model of the forced-choice decision task is allowed to drive shifts in the tradeoff between speed and accuracy, leading to a pattern of behavior closely resembling that reported by Laming (1968).

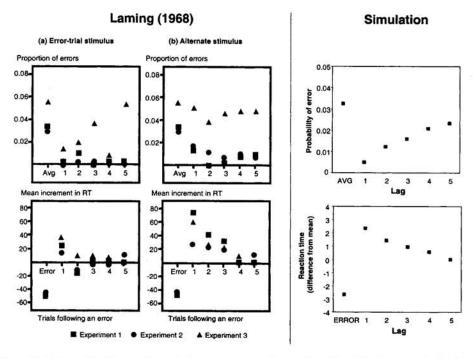


Figure 6. Left panel: Following the original report, separate plots are shown for trials where the stimulus from the error trial was repeated and trials where the alternative stimulus occurred. Reprinted from Acta Psychologica, 43, D. Laming, "Autocorrelation of Choice-Reaction Times," Figure 1, p. 202, copyright 1979 with permission from Elsevier Science. Adapted with permission. Right panel: Results of Simulation 2C showing behavior of the model following errors. Avg = average; RT = reaction time.

Simulation Study 2

As in the previous simulation study, the present study considers three separate models. Once again, models of the underlying tasks are drawn with as little modification as possible from the published literature. The models used for the Eriksen and Stroop tasks are, not surprisingly, the same ones we used in our first set of simulations. Added to these is a model of simple forced choice drawn from work by Usher and McClelland (1995; see also Usher & McClelland, 2001). Again, as in the previous set of studies, conflict is measured in the response layer of each model and quantified in terms of energy. And once again, top-down control is implemented as the input to a separate group of context units (e.g., the spatial attention units in the Eriksen model and the task units in the Stroop model), whose activity serves to bias processing in the rest of the model.

However, unlike the earlier models, where the state of top-down control was determined by the experimenters and was fixed from trial to trial, in the present simulations control was allowed to vary from trial to trial on the basis of conflict monitoring. Specifically, on each trial the input to the control units (henceforth referred to informally as the *control signal*) was based on the degree of conflict incurred on preceding trials, with periods of high conflict leading to an intensification of top-down control (e.g., a focusing of spatial attention or a sharpening of the task representation) and periods of low conflict leading to a shift in the opposite direction. Each model tests the sufficiency of this simple arrangement to account in a quantitative way for data from relevant experiments.

General Methods

Except where explicitly noted, the underlying models were implemented and run as described in the reports from which the models were drawn. As in Simulation Study 1, conflict was calculated using energy in the output layer. A scalar value indicating the amount of energy attached to a given trial was obtained by integrating the activity of the conflict unit across all processing cycles for that trial. This value formed the basis for computing the input to the control units on the next trial. The general approach was to convert energy (E) into a value C (control), according to the expression

$$C(t+1) = \lambda C(t) + (1-\lambda)(\alpha E(t) + \beta), \tag{2}$$

where t indexes trials, and α and β are scaling parameters. λ in this equation is limited to values between zero and one, meaning that the control signal is based on an exponentially weighted average of conflict over multiple preceding trials, rather than only on the immediately preceding trial. To put it another way, on each trial the control value is nudged up or down from its initial state, in proportion to the degree of conflict occurring on the preceding trial. (This aspect of the implementation was motivated by the fact, made clear by the behavioral data discussed below, that shifts in control are gradual, occurring over the course of multiple trials.) It should be noted that given the degree of conflict, control can be either increased or decreased; not only will high conflict lead to a strengthening of control, but low conflict will lead control to become more lax.

Slightly different procedures were followed in each simulation for translating C into a particular set of inputs to the units imple-

menting control. Specifics are discussed in conjunction with each model.

Simulation 2A: Sequential Adjustments in the Eriksen Flanker Task

The goal of Simulation Study 2A was to evaluate whether the pattern of behavior reported by Gratton et al. (1992) could be reproduced by establishing a feedback loop from conflict monitoring to top-down control, thereby allowing the occurrence of conflict on incompatible trials to trigger a focusing of spatial attention on subsequent trials.

Method. The structure of the model is shown in Figure 7. In most respects, the model is identical to that used in Simulation Study 1C. However, a connection has now been established between conflict monitoring and control. As in the previous simulation, control is implemented as a spatial attention layer. Unlike the earlier simulation, the input to this layer is now adjusted from trial to trial on the basis of the output of conflict monitoring, so that high levels of conflict lead to a concentration of input to the center attention unit, and low levels of conflict lead to a more even distribution of input to the attention layer.

Energy was converted into a index of control using Equation 2. The input to the center attention unit was set equal to this value, with a priori maximum and minimum values of 3 and 0 imposed. As suggested by Figure 7, input was also applied to the left and right units in the attention layer. These inputs were computed as left = right = (3 - center)/2. Thus, although the cumulative magnitude of control-signal input to the attention layer was held constant, its distribution across the layer was permitted to vary between an unfocused [1 1 1] and a tightly focused [0 3 0].

The procedure used in simulating individual trials was identical to that used in Study 1C above. As in the Gratton et al. (1992) experiment, compatible and incompatible trials occurred with equal frequency and in a randomized order.

Results and discussion. Average response times and error rates from the simulation are displayed in Figure 4 (bottom). These results were obtained with $\lambda = 0.5$, $\alpha = 4.41$, $\beta = 1.08$. Adjusting the noise parameter of the underlying model from 0.05 to 0.035 optimized the model's fit to the data. However, this change was not necessary to obtain the qualitative pattern of behavior, which proved quite robust.

As is evident from Figure 4, allowing conflict to influence control proved sufficient to reproduce the sequential adjustment effect reported by Gratton et al. (1992). The occurrence of an incompatible trial, tending to be associated with a relatively high degree of conflict, led to a shift in the control signal, so that input to the attention layer was more tightly focused on the center unit for the next trial. This reduced the influence of the flankers on processing, yielding faster, more accurate performance on incompatible trials and slower performance on compatible trials, in line with human performance. Compatible trials, associated with less conflict, had the opposite effect on control, leading to a more evenly distributed input to the attention layer and thus to a greater impact of the flankers.

⁸ This approach was chosen arbitrarily over the alternative approach of using peak energy as the index of conflict on a given trial.

⁹ In the original Servan-Schreiber (1990) model, the pattern of input to the attention layer was [0 1 0]. In choosing the range of inputs for the present simulation, it was necessary to allow for both weaker and stronger emphasis on the center location. In order to implement the latter, inputs stronger than one were required.

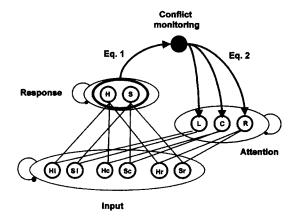


Figure 7. Structure of model used to simulate results of Gratton, Coles, and Donchin (1992). Eq. = equation; L = left; C = center; R = right; Hl = H left; Sl = S left; Hc = H center; Sc = S center; Hc = H right; Hc = H r

The results of this first simulation demonstrate the sufficiency of the conflict monitoring hypothesis to account for a pattern of behavior in a specific laboratory task. Further implications of the simulation and some of its testable predictions are discussed below. First, however, we turn to a second model, which asked whether a similar mechanism might account for the frequency effect observed in the Stroop task.

Simulation 2B: Trial-Type Frequency Effects in the Stroop Task

We have proposed that the effect of trial-type frequency in the Stroop task might be explained in part by a mechanism linking the occurrence of conflict to the recruitment of control. Given such a mechanism, frequent incongruent trials, through the accompanying occurrence of conflict, would lead to a strengthening of top-down control, focusing processing on color naming and reducing the interference produced by incongruent trials. We returned to the Cohen and Huston (1994) Stroop model in order to test the sufficiency of this mechanism to account for the findings of Tzelgov et al. (1992).

Method. The underlying model was identical to that described in Simulation Study 1A, now amended with a link from conflict monitoring to control (Figure 8). This link was implemented as in Simulation 2A, with high conflict leading to an increase in the input to the color-naming task unit. 10 Usher and Cohen (2000) have simulated the results of the Tzelgov et al. (1992) experiment by varying activation in the task-representation layer of a very similar model. The novel contribution of the current model pertains to the fact that here the task representation, rather than being set by the experimenter, adjusts dynamically in response to the occurrence of conflict.

Three conditions were simulated, using the trial-type proportions detailed above. As in the Tzelgov et al. (1992) study, each condition began with a warm-up period of 48 trials, which were excluded from analysis.

Results and discussion. The model's performance is shown in Figure 5 (right). These data were obtained with the parameter settings: $\lambda = 0.95$, $\alpha = 11.24$, and $\beta = 9.46$. Optimal fits were obtained with one minor adjustment to the underlying model (the strength of the weights connecting input to task units was reduced from 4.0 to 3.0), but the qualitative pattern of results did not

depend on this change, holding over a wide region of parameter space.

In the model, as in the Tzelgov et al. (1992) data, reaction times decreased for incongruent trials and increased for congruent and neutral trials as the proportion of incongruent trials increased. As also observed in the behavioral data, changes in the degree of interference across conditions far outweighed any change in facilitation.

The mechanisms responsible for this pattern of behavior are similar to those at work in the Simulation 2A. The occurrence of an incongruent trial, associated with a relatively large degree of conflict, leads to a tightening of control, here a strengthening of the input to the color-naming task unit. This limits the amount of crosstalk induced by incongruent stimuli, making responses on these trials faster. More frequent incongruent trials have a cumulative effect in augmenting the control signal, placing the system in a state highly conducive to color naming. When incongruent trials are less frequent, the control signal becomes less intense, allowing the word input to have a stronger impact on processing.

This second simulation extends the findings of the first, supporting the generality of the relevant mechanisms. Together, the simulations show how a unitary mechanism can account for detailed aspects of behavior in two rather different tasks and under different experimental manipulations. In a third simulation, we examined whether the same mechanism could account for data from a more distant domain, that of error compensation.

Simulation 2C: Shifts in Behavior After Errors

Our goal in Simulation study 2C was to ascertain whether a conflict monitoring mechanism could account for the set of findings reported by Laming (1968). We reasoned that, inasmuch as errors tend to be associated with a high degree of conflict, allowing conflict to shift control might produce the pattern Laming observed.

In addition to the data on post-error performance discussed above, two other, closely related empirical observations provided targets for modeling. The first of these also was also reported by Laming (1968). Here, in addition to the observations concerning behavior after errors, Laming described an interesting pattern of correlation among reaction times on correct trials. As shown in Figure 9 (left), autocorrelation analysis revealed a tendency for nearby trials to have similar reaction times. As the diagram shows, reaction-time correlations were strongest for immediately adjacent trials, weaker for trials separated by one intervening trial, still weaker with two intervening trials, and so on. The curve yielded by this analysis appears to have roughly exponential form, with an initial steep drop leading into an asymptotic approach to zero.

The interest of this finding in the context of our modeling project was twofold. First, the finding suggests that the parameters affecting reaction time shift not only after errors, but continuously throughout the entire stream of performance. Laming (1968) offered separate explanations for post-error phenomena and the slow shifts in reaction time he observed among correct trials; we de-

 $^{^{10}}$ In this simulation, the degree of conflict attaching to an individual trial was quantified as the degree of energy present at response. The task-unit input was based directly on the value C from Equation 2, with a priori maximum and minimum values of 1 and 0.5 imposed.

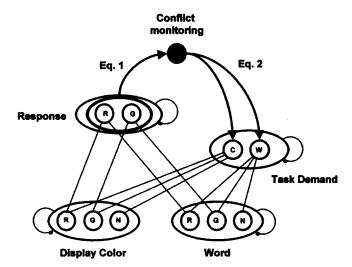


Figure 8. Structure of model used to simulate results of Tzelgov, Henik, and Berger (1992). Eq. = equation; R = red; G = green; C = colornaming; W = word-naming; N = neutral.

cided to ask whether both sets of phenomena could be accounted for by a single mechanism, a continuous adjustment of control based on the occurrence of conflict. Second, Laming's autocorrelation findings provide a useful constraint on a specific parameter of our general model. In the two previous models, the parameter λ determined the gradualness of changes in the control signal, a value close to one meaning that control could change only very slowly from trial to trial, and a value close to zero meaning that large shifts could occur rapidly. Laming's autocorrelation data provide an empirical constraint on this parameter, inasmuch as they provide information about the time scale on which shifts in control actually occur. It was a substantive challenge to the model, then, to see if both the post-error and autocorrelation data could be fit using a single mechanism and one set of parameters.

A final target for modeling came from work on the ERN. As noted in an earlier section, Gehring et al. (1993) asked whether there might be a relationship between ERN magnitude and the magnitude of the post-error slowdown that Laming (1968) and others had reported. It is interesting that they did find a correlation. Error trials with large ERNs tended to be followed by trials with

relatively large reaction times (Figure 10, left). In the context of the present modeling project, this finding provided an important additional constraint. If, as claimed in Simulation Study 1C, the ERN reflects a response to conflict, then in the present model errors associated with larger amounts of conflict should be followed by trials with larger reaction times.

Method. As in earlier simulations, a model of the underlying task was drawn directly from the literature. Usher and McClelland (1995) have put forth a connectionist model of simple choice tasks, extremely similar in structure to those we have been considering. The two-choice version of this model is shown in Figure 11. The model includes two input units, each representing one of the two stimuli involved in the task paradigm. Each of these connects with one of two output units, corresponding to the two potential responses (button presses in the Laming experiments). As in the other models we have adopted, the response units here are placed in competition by reciprocal inhibitory connections.

Simulation of a trial begins with a response preparation period, which precedes application of the stimulus input. During this interval (20 cycles in the current simulations), two factors influence the state of the output units. First, there is a weak, excitatory input from a response priming unit (see Figure 11). This serves to raise the activity of the response units above baseline, moving it closer to the response threshold. Second, random noise is added to the activation of each response unit on each cycle. At the end of the foreperiod, the input units are activated, eventually causing one of the response units to cross the response threshold. The degree of stimulus ambiguity is encoded in the input pattern. Absolutely unambiguous stimuli are represented with inputs of [0 1] and [1 0], and indiscriminable stimuli with the input [0.5 0.5]. Following one of the simulations described by Usher and McClelland (1995), we used the inputs [0.85 0.15] and [0.15 0.85]. (The values for a number of other parameters were drawn directly from Usher & McClelland: inhibitory weights, 0.75; standard deviation of noise, 0.5; response threshold, 1.057; and cascade rate, 0.1.)

As in the previous simulations, mechanisms for monitoring conflict and translating this into a control signal were added to the underlying model of task processing, as shown in Figure 11. Conflict was once again measured as energy in the response layer, integrated across processing cycles. The resulting value was once again transformed into a control signal according to Equation 2, with the value C directly dictating the input to the (linear) response priming unit. Parameters were chosen ($\alpha < 0$) so that high conflict tended to decrease the input to this unit. In keeping with the previous simulations, maximum and minimum values were imposed on this input (0 and 0.5).

The functional implications of the response priming unit may be less obvious than those of the task units in the Stroop model or the spatial attention layer in the Eriksen model. In effect, changing the activation of this unit moves the system to a new point on the speed–accuracy tradeoff

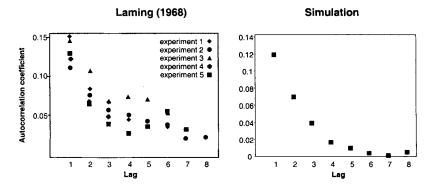
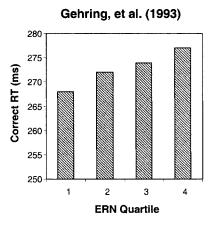


Figure 9. Left panel: Autocorrelation data from Laming (1968). From "Choice Reaction Performance Following an Error," by D. Laming, 1979, Acta Psychologica, 43, Figure 1, p. 395, copyright 1979 with permission from Elsevier Science. Adapted with permission. Right panel: Simulation of autocorrelation data from study 2C.



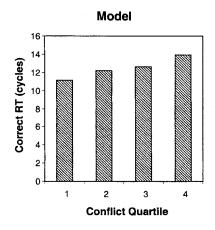


Figure 10. Left: Data from "A Neural System for Error Detection and Compensation," by W. J. Gehring, B. Goss, M. G. H. Coles, D. E. Meyer, and E. Donchin, 1993, *Psychological Science*, 4, Figure 3, p. 388. Copyright 1993 by the American Psychological Society. Adapted with permission. Right panel: Results of Simulation 2C. RT = reaction time; ERN = error-related negativity.

curve. Raising its activity has the effect of moving the output units closer to their response thresholds prior to stimulus presentation. This leads to shorter reaction times, as there is less time required for the buildup of activation. However, because strong input from the priming unit may drive the incorrect response unit hazardously close to threshold prior to stimulus presentation, it also leads to an increased error rate. With weaker activity in the response priming unit, both response units tend to be far from threshold at stimulus onset, making for longer response times but lower error rates. These effects are of immediate applicability in simulating post-error shifts in behavior, considering that these shifts have been described as reflecting a speed–accuracy tradeoff (Luce, 1986).

Results and discussion. Simulation results are displayed in Figures 6, 9, and 10. Parameter settings for the data shown included $\lambda = 0.75$, $\alpha = -0.05$, and $\beta = 0.5$. As in the previous two simulations, the qualitative pattern of results was not highly parameter dependent.

The behavior of the model following errors is shown in Figure 6 (right). As in human performance, errors are faster than the average correct response. More important, there is a transient slowdown after errors, with reaction times returning gradually to the

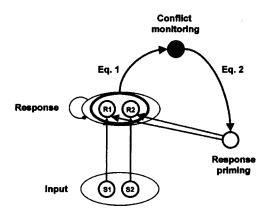


Figure 11. Structure of Usher and McClelland (1995) model, with conflict monitoring and control signal elements superimposed as in Simulation 2C. R1 = Response Alternative 1; R2 = Response Alternative 2; S1 = Stimulus 1; S2 = Stimulus 2; Eq. = equation.

mean over the following few trials. The same pattern appears for response accuracy, which rises after errors, as in Laming (1968). At the same parameter settings, the reaction times of the model displayed a pattern of autocorrelation very closely resembling those reported by Laming (Figure 9, right). Finally, as in Gehring et al. (1993), the reaction time of correct trials following errors was affected by the degree of conflict occurring with the error, with greater conflict resulting in larger subsequent reaction times (Figure 10, right).

The single mechanism underlying all of these patterns is the feedback loop from conflict through control. On the basis of this loop, periods of high conflict lead to a reduction in response priming, resulting in slower but more accurate responding. Periods of low conflict lead to an increase in response priming and, thus, to faster but less accurate responses. Because errors tend to be associated with a relatively high degree of conflict, they tend to induce a shift toward slower, more accurate behavior. Because the change in the control signal is proportional to the degree of conflict, the size of the slowdown after errors varies with the amount of conflict associated with the error. The autocorrelation data reflect the fact that shifts induced by conflict are not limited to those occurring after errors. Because the degree of conflict also varies among correct trials, there is a continuous fluctuation in the system's control state, with periods of high conflict leading to slower responses and periods of low conflict leading to faster ones. Because the control state varies gradually, trials that are near to one another tend to have more similar reaction times than trials that are widely separated.

Participants in reaction-time tasks must adjust their performance to achieve an appropriate balance between speed and accuracy (Wickelgren, 1977). Although it may be possible to arrive at a roughly appropriate strategy prior to beginning the task, it seems clear that adjustments must also be made on-line, on the basis of an ongoing evaluation of one's own performance. Rabbitt (1979) proposed that this fine-tuning process was based on the occurrence of errors. By adjusting the size of the slowdown induced by errors, participants could increase the spacing between errors, thereby reducing their overall error rate. The model we have proposed suggests a revision of this account. Here, it is not error per se, but

conflict that induces changes in control. Adjustments in the tradeoff between speed and accuracy are therefore associated not just with errors, but with every response, on the basis of the degree of associated conflict. Although this account is consistent with the autocorrelation data from Laming (1968), it also makes a number of interesting and potentially testable predictions. One of these is that slowdowns in responding should occur not only after errors, but also after correct trials involving a high degree of conflict. Thus, for example, if participants were asked to perform a discrimination task such as that used by Laming (1968), but under conditions of randomly varying stimulus degradation, reaction times should be slower and more accurate after severely degraded than mildly degraded targets (assuming the preceding sequences of stimuli are comparable in the two cases). Other predictions of the account require us to integrate the role of the ACC. These are discussed in the next section, alongside predictions based on the other two models we have presented.

Simulation Study 2: General Discussion

The three effects we investigated in this series of simulations the sequential adjustment effect occurring in the Eriksen flanker task, the effect of trial-type frequency in the Stroop task, and the effect of errors in simple forced-choice decision tasks-all have the flavor of strategic behavior. In each case, participants appear to adjust their behavior in response to their own performance; difficulty in the task results in a more focused, conservative approach, ease in performance to a slackening of cautiousness or effort. A basic account of the mechanisms involved in focused, conservative, or effortful behavior is inherent in the models we drew from the literature, where efficient performance is supported by representations of context, whose activity serves to bias information processing. The simulations we performed extend this account, adding to it an indication of how these biasing inputs are themselves regulated, through a mechanism that monitors for the occurrence of conflict. The simulations demonstrate the sufficiency of the resulting control loop to account at a detailed level for the strategic behaviors we have considered, revealing a potential unifying account for phenomena from diverse settings.

To this point, our discussion of these simulations has been framed in strictly behavioral terms. However, the simulations have clear implications for the cognitive role of the ACC. Specifically, they entail the proposal that ACC activation leads to shifts in cognitive control. This has some interesting consequences. First, note that it should make it possible to predict aspects of future behavior based on ACC activation. For example, in the Eriksen task, periods of high ACC activation should be followed by a reduction in the influence of the flankers, whereas periods of low ACC activation should be followed by an increase. Thus, in principle, it should be possible to predict how much interference participants will display on the basis of the level of ACC activation associated with preceding trials. Similar predictions should be possible in the Stroop task; high levels of ACC activation should predict relatively fast responses on incongruent trials and relatively slow responses on compatible ones, and low levels of ACC activation should predict the opposite.

The case of the simple forced-choice identification task is particularly interesting here. According to the model presented above, ACC activation is linked to processes responsible for controlling the speed-accuracy tradeoff. This predicts that it should be possi-

ble to determine where a participant currently lies on the tradeoff curve by looking at the degree of recent ACC activation, as illustrated in Figure 12 (on the basis of data from Simulation 2C). In a way, the findings reported in Gehring et al. (1993) already give us this result. Here, high ACC activation (a large ERN) predicts slower reaction times on succeeding trials than does low ACC activation. The account we have put forth suggests that it should be possible to predict reaction times (and accuracy) based on ACC activation associated with all trials, not just errors.

Another important prediction of our overall theory is that any disruption of ACC function should also disrupt the behaviors we have been discussing. Thus, acute lesions to the ACC should reduce the sequential adjustment effect in the Eriksen task, frequency effects in the Stroop task, and post-error shifts in forced-choice decision tasks. It would be reasonably straightforward to test at least two of these predictions in nonhuman primates, which can be trained to perform versions of the Eriksen and forced-choice decision tasks.

The theory also suggests that it might be possible to induce shifts in behavior by stimulating cells in the ACC. Groh, Born, and Newsome (1997) found that microstimulation of motion-sensitive neurons in area MT affected monkeys' visual tracking, reflecting a distortion of perceptual information. Analogously, microstimulation of conflict-responsive cells in the ACC, by artificially intensifying activation representing conflict, might be expected to result in shifts toward more focused or conservative behavior, reflected as a reduction of interference in the Eriksen task and as a shift toward slower, more accurate responding in forced-choice decision tasks.

General Discussion

The current literature on cognitive control offers no clear account of what triggers control to intervene in processing. We have argued, on the basis of several converging lines of evidence, that the demand for control might be evaluated through monitoring for conflict. We have presented conflict monitoring as a theoretical construct and related this to empirical findings from cognitive

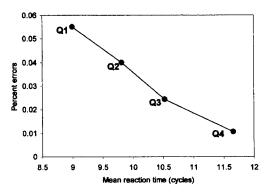


Figure 12. Relationship between conflict and the speed-accuracy tradeoff in Simulation 2C. The model was run for a total of 50,000 trials, and for each trial reaction time and response accuracy were recorded. Also recorded was the degree of energy over preceding trials, using a weighted average as suggested by Equation 2. Trials were separated into four groups based on the quartiles of the energy value (Q1-4). Trials after periods of low conflict (Q1) showed smaller average reaction times and lower accuracy than trials after periods of high conflict (Q4).

neuroscience. An analysis of three connectionist models demonstrated the sufficiency of the hypothesis to account for basic findings concerning the behavior of the ACC, a medial frontal brain region that has been previously implicated in cognitive control. Recent neuroimaging results have confirmed predictions of the conflict monitoring hypothesis concerning the relationship between ACC activation and the state of cognitive control. Finally, models implementing the proposed feedback loop connecting conflict monitoring and control provide a unifying explanation for a complex set of strategic behavioral phenomena.

In what follows, we identify a number of questions that the theory poses for future investigation and consider the relation of the present proposals about ACC function to existing accounts.

Questions for Future Investigation

Does the ACC influence control state? The present account entails two claims concerning the ACC: (a) The ACC responds to the occurrence of conflict, and (b) its activity impacts cognitive control. We have reviewed a wide range of data in support of the first of these points. Existing support for the second is more indirect. An immediate challenge for further research is to confirm the presence of this functional link.

As we have tried to indicate, the existing data provide ample reason to suspect that such an effort will be successful. Across disparate tasks, strong ACC activation is observed just preceding shifts toward more conservative behavior. In the Stroop task, for example, high ACC activation is seen in conjunction with incompatible trials, and these trials have been shown behaviorally to induce a stronger focus on the color-naming task. Analogously, in the Eriksen task, greater ACC activation is seen on incompatible trials, and a stronger focus on the central target is seen after these trials. Finally, as Gehring et al. (1993) have shown, the magnitude of ACC activation during errors is correlated with the size of the slowdown on subsequent trials. Simulation Study 2 suggested how all of these effects can be explained in terms of a causal relationship between conflict detection (a function we have attributed to the ACC) and adjustments in control.

Convergent—though still indirect—evidence for an influence of the ACC on control comes from this area's connectivity. Anatomically, the ACC connects strongly with brain regions thought to play a crucial role in cognitive control. Specifically, it shares extensive connections with prefrontal cortex (Goldman-Rakic, 1987), regions of which have been implicated in executive processes (Cohen et al., 1996; Duncan, 1986; Fuster, 1980; Gathercole, 1994; Stuss & Benson, 1984). In a wide variety of studies using functional neuroimaging, activation of prefrontal cortex and the ACC has been found to co-occur, indicating a tight functional link between the two areas (e.g., Braver et al., 1997; Carter et al., 1995; Frith et al., 1991a,b; Posner, Peterson, Fox, & Raichle, 1988; Raichle et al., 1994).

Another route by which the ACC might impact control processes is through its influence on brainstem neuromodulatory centers, including the ventral tegmental area (VTA) and locus coeruleus (LC). The VTA is believed to play an important role in regulating attentional state and working memory function (Cohen & Servan-Schreiber, 1992; Goldman-Rakic, 1998; Oades, 1985). In the rat, electrical stimulation of ACC leads to burst firing in this brainstem nucleus (Gariano & Groves, 1988), a pattern of discharge that has been proposed to play a role in the updating of

goal-related information (Braver, 1997). Stimulation of the ACC has also been shown to lead to changes in activity in the LC (e.g., Jodo, Chiang, & Aston-Jones, 1998). This nucleus, which sends noradrenergic projections to large portions of the thalamus and cortex, has been reported to play a role in regulating attentional focus and task engagement (Usher, Cohen, Servan-Schreiber, Rajkowski, & Aston-Jones, 1999).

Convergent evidence from functional and anatomical domains thus encourages the idea that the ACC influences cognitive control. Further research to confirm this influence is clearly indicated, however. A number of methods for accomplishing this, including lesion and microstimulation approaches, are discussed in conjunction with Simulation Study 2.

Assuming the basic claims of the conflict monitoring theory are borne out by further investigation, a number of more detailed questions arise. Several of the most important of these were raised by the effort to implement the theory in computational models: How can conflict be measured? At what levels of processing is conflict monitored? How rich is the information that conflict monitoring provides to control? We discuss these questions in the following sections.

How might conflict be measured? In each of our simulation studies, we quantified conflict by measuring the degree to which incompatible units were simultaneously active. Hopfield's (1982) energy expression provided a convenient means for accomplishing this. Unlike most discussions of energy, which treat it purely as an analytical device, we have suggested that the dimension of information processing measured by energy might in fact be actively monitored as a normal function of cognition.

It is interesting that there is a precedent for this proposal, appearing in work on lexical decision. Borowsky and Masson (1996) measured energy in a model of single word reading after presentation of inputs representing words and nonwords, showing that higher levels were associated with nonwords (cf. Joordens & Becker, 1997). They proposed that an evaluation of energy might serve as a basis for judgments of stimulus familiarity, suggesting, as we have, that energy might pick out a dimension of information processing that is evaluated by mechanisms operating within cognition.

Although in our simulation studies energy provided a convenient means for quantifying conflict, energy represents only one of many ways that this can be measured. Examples of alternative methods are provided by Schneider and Detweiler (1987, 1988) and Pomerleau (1992).

Schneider and Detweiler (1987, 1988), in their model of cognitive control, dealt with conflict among distributed representations, in contrast to the models we studied, which use a localist coding scheme. In their work, the activities of the units forming any single representation are interpreted as components of a multidimensional vector, and conflict is detected by determining this vector's length. To see how this works, consider the case where two signals converge on a single processing module. In the Schneider and Detweiler scheme, the output of the module is determined by adding these inputs together. If the inputs are conflicting (i.e., very different from one another), the resulting output vector will be very short, and this shortness—as a reflection of interference—provides a basis upon which to recruit the intervention of control structures.

Pomerleau (1992) used a different method for detecting conflict. In his work, a neural network was used to steer a vehicle based on information conveyed by a video camera mounted on the top. Although this was fairly straightforward, as long as the vehicle traveled down a road without intersections, special mechanisms were required when the vehicle reached a fork in the road, in order to determine the correct way to turn. Pomerleau enabled the system to determine when it had reached an intersection by allowing it to detect conflict in the network responsible for routine steering decisions. This was accomplished by capitalizing on the fact that the outputs of the steering network in the absence of an intersection (or other problematic setting) always conformed to a specific pattern, involving a Gaussian distribution of activation across the output layer. This made it possible to detect conflict by comparing each output from the steering network with the nearest "ideal" (Gaussian) output. Pomerleau defined a quantitative measure of the difference between these two representations, calling it the appearance error. When the vehicle encountered an intersection, crosstalk between the pathways activated by each of the available paths led to an output representation that differed from the nearest ideal output, resulting in a high appearance error, which in turn was used to signal the need for extrinsic steering guidance.

These examples suggest the range of techniques that can be used to detect and quantify conflict. The question arises, What algorithm might the brain use? Although current data are insufficient to constrain theorizing on this point, it does appear reasonable to regard conflict monitoring as a biologically plausible proposition. The results we obtained by measuring energy show that the information necessary for quantifying conflict is present in the instantaneous activation values of units in the network, and is thus available in a form that could plausibly be used by a neural monitoring system. Although we have not attempted to model the relevant mechanisms, there do not appear to exist any in principle barriers to doing so. On the contrary, a number of plausible approaches present themselves almost immediately. One could, for example, allow the co-activation of incompatible units to activate single units in a conflict monitoring layer. Summing activity over this layer would provide a measure similar to energy. Quite a different method, which would also appear to be less computationally demanding, is suggested by models where incompatible units feed into a common pool of inhibitory units, so-called pooled inhibition (see, e.g., Usher & Niebur, 1996). In such a scheme, the simultaneous activation of incompatible units will lead to a greater peak in activity in the inhibitory group than activation of only compatible units. As a result, the occurrence of conflict can be detected by simply monitoring the level of inhibitory activity. This, in turn, might be accomplished through connections linking inhibitory units to a central structure responsible for conflict monitoring, in our theory the ACC. An interesting aspect of this possibility is that much of the work of conflict monitoring would be accomplished at a local level, within the regions where conflict actually occurs.

Even simpler solutions are possible, depending on the assumptions that can be made about the constraints on representational form. For example, under certain conditions, the activation of each output unit in a standard feed-forward connectionist network can be interpreted as representing the posterior probability that the present input should be interpreted as belonging to a particular category. In these circumstances, conflict can be detected by simply determining the activity level of the most strongly activated unit, which reflects the confidence with which the system is able to interpret the current input (Bishop, 1995).

One factor that differentiates various potential measures of conflict is the amount of information each conveys about which particular conflicts are being detected. The question of how conflict is measured thus relates closely to the question of how much information conflict monitoring might convey to cognitive control, as discussed in the next section.

How rich is the information conveyed by conflict monitoring? In Simulation 2, top-down control was implemented in each model in the form of a special set of units, whose outputs served to bias information processing in the rest of the system. At one level of abstraction, the role of these units was identical across the three simulations. However, in each model, the specific content ascribed to the input from control was particular to the task being considered. In the Stroop model, control influenced the relative weight given to color-naming and word-reading pathways. In the Eriksen model, control biased processing toward the center position of the input array, and in the forced-choice decision model, control influenced response preparation. It was assumed that the specific domain addressed by control in each setting would be determined prior to task performance, for example on the basis of task instructions (Noelle & Cottrell, 1995). The role of conflict monitoring was to influence the strength of top-down control, not the particular area of information processing toward which it was directed; conflict monitoring influenced control in a quantitative but not qualitative fashion.

Underlying this approach was the assumption that conflict monitoring conveys only a very nonspecific type of information, indicating that conflict has occurred in some unspecified form at some unspecified point in the system. Given this assumption, conflict monitoring can convey information about when control processes are needed, but not about the particular content of the situation that calls for their intervention. However, the role of conflict monitoring need not be limited in this way. If it is assumed that conflict monitoring conveys specific information about the location and content of conflict, then it becomes theoretically possible for conflict monitoring to influence the content of control, as well as its intensity.

Whether conflict monitoring is able to convey this sort of information depends, in turn, on how conflict is measured. As noted above, different algorithms for measuring conflict preserve differing amounts of information about the conflicting representations. At one end of the logical spectrum, there is the case where each of the units involved in conflict monitoring is sensitive to conflict among a specific set of representations. This would make it possible for conflict monitoring to provide very specific information about what sort of intervention is called for. At the other end of the spectrum is the case where conflict is evaluated on the basis of peak activation across a large population of units. Here, no information is transmitted other than that conflict of some kind is present. An intermediate case might involve a set of units each monitoring the activity of pooled inhibition at different levels of processing. Here, conflict monitoring could convey information about the general domain where conflict is occurring, but not the specific representations coming into conflict.

Once again, current data are insufficient to guide the construction of specific hypotheses in this area. The important theoretical point is that the potential role of conflict monitoring in regulating cognitive control depends on the richness of the information this function is able to convey. Ascertaining this is thus an important project for further investigation.

What levels of processing are monitored? As in the Borowsky and Masson (1996) study of lexical decision, we, in our simulations, measured energy only within each model's response layer. This concentration was based on the centrality of response selection processes to the task domains considered in the simulation studies. Our results for these tasks were consistent with the idea that the qualitative behavior of the ACC can be successfully accounted for by considering energy in the response layer alone.

If conflict monitoring were restricted to only one component of the information-processing stream, the activation of responses would be a good candidate. According to continuous flow models of response selection (C. W. Eriksen & Schultz, 1979; Gratton et al., 1988; Cohen et al., 1992), stimulus evaluation processes feed activation to relevant response channels in an ongoing fashion, even from their early stages. By this account, conflicts occurring at any number of points in processing are likely to be reflected at the level of response activation.

Furthermore, the connectivity of the ACC indicates that it is in close communication with areas involved in response-selection processes. Some of the largest projections to the ACC run from primary motor, supplementary motor, and premotor areas (Van Hoesen, Morecraft, & Vogt, 1993).

However, conflict monitoring could in theory involve the detection of conflict at any number of points in processing. It is thus important to note that existing evidence does not rule out that the ACC might be responsive to conflict at levels other than response selection. The connectivity of the ACC in fact makes this seem very plausible. Although the area has strong connections to brain areas typically associated with response selection and execution, it also connects richly with parietal and temporal areas involved with high-level perceptual processing (Van Hoesen et al., 1993). In fact, it has previously been speculated that the ACC might also be responsive to stimulus–stimulus incompatibility (Taylor et al., 1994).

If the ACC does respond to stimulus conflicts, one might expect this area to become active under conditions of binocular rivalry or in viewing ambiguous figures. Although some imaging studies suggest the ACC may be activated under these circumstances, the currently available data is not entirely conclusive (e.g., Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998).

One way of further testing the relevance of stimulus-stimulus conflicts might be to measure ACC activity during performance of a modified flankers task described by C. W. Eriksen and Schultz (1979). In this version of the task, stimuli with compatible and incompatible flankers are used as in the B. A. Eriksen and Eriksen (1974) study, but now a third sort of stimulus is included, in which the distracter letters differ from the central target, but map to the same response (e.g., TWT, where both T and W call for movement of a response lever to the left). C. W. Eriksen and Schultz found that reaction times were slower for this type of stimulus than for the standard compatible stimuli (e.g., TTT). This effect cannot be attributed to response conflict; it would instead seem to reflect interference occurring at a point in processing upstream of response selection, closer to stimulus evaluation. It would be interesting to compare the ACC activation evoked by these two kinds of stimuli. If ACC activation were greater for the stimuli introduced by C. W. Eriksen and Schultz, this would provide evidence in favor of monitoring for conflicts prior to the response level. (For a very recent study taking the approach we have described here, see van Veen, Cohen, Botvinick, Stenger, & Carter, 2000.)

Another potentially relevant form of conflict is that between representations of the task being performed. The possibility that such conflicts might lead to ACC activation may help to explain an otherwise puzzling finding in cognitive activation studies of the Stroop task. Several studies have reported a greater ACC response associated with congruent stimuli than neutral stimuli in the Stroop (e.g., Bench et al., 1993; Carter et al., 1995) task. As Carter et al. (1995) pointed out, in congruent but not neutral stimuli the stimulus word belongs to the response set. As a result of this, on congruent trials attention may be more likely to be drawn toward word reading. Because the participant is instructed to perform the color-naming task, processing of congruent trials could lead to conflict between task representations that, although not slowing response, might nonetheless involve conflict at the level of task selection.

Experimental tools for testing whether conflict in task representations are associated with ACC engagement might be drawn from research on task alternation. Rogers and Monsell (1995) have studied a task in which participants are required to alternate between categorizing numbers as odd or even and categorizing letters as consonants or vowels, using the same two buttons in each task. Some (neutral) stimuli contain one letter or one number plus a task-irrelevant character (e.g., #). Others contain both one number and one letter (crosstalk stimuli); here the participant must keep track of which task is to be performed. On the basis of reaction-time data from this task, Rogers and Monsell argued that crosstalk stimuli led to interference between task representations, even when both characters led to the same response (congruent crosstalk stimuli). If this analysis is correct, then measuring ACC activation during performance of the Rogers and Monsell task might be one way of testing whether the ACC is sensitive to task-set conflicts. If this is the case, then greater ACC activation should be observed in response to congruent crosstalk stimuli than to neutral stimuli.

Relation to Existing Theories of ACC Function

Although our primary purpose has been to articulate a psychological theory, we have in the process made a novel interpretation of data related to a specific area of the brain, the ACC. It is important to emphasize from the outset that the conflict monitoring hypothesis is not intended as a exhaustive account of ACC function. Our general view, detailed at the end of this section, is that conflict monitoring may represent one of a set of closely interrelated functions performed by the ACC. Nonetheless, our interpretation of existing data often differs from existing accounts in important ways. In what follows, we compare the conflict monitoring theory with three influential views of ACC function.

Error detection. One interpretation of ACC function has been suggested by work on the ERN. As discussed in Part 1, the ERN is believed to have a midline frontal generator, generally thought to lie in the ACC. Several studies of the ERN have interpreted it as reflecting a mechanism dedicated specifically to the detection of errors (Coles, Sheffers, & Fournier, 1995; Falkenstein et al., 1991, 1995; Gehring et al., 1993). It has been proposed that the ERN reflects the outcome of a comparison process, by which the response actually produced is compared with a representation of the correct response (e.g., Coles et al., 1995; Falkenstein et al., 1995).

One question raised by the comparator hypothesis is how the system gains access to a representation of the correct response, even as an error is being committed. One possible answer might be that this representation is provided directly by activation of the correct response itself, occurring alongside the prematurely activated error response. If the comparator theory is understood in this way, then it can be viewed as quite closely related to the conflict monitoring view. Under this interpretation, the one remaining difference between the proposals would be that, whereas one posits an explicit comparison process between coactivated responses, the other suggests that this coactivation itself suffices to trigger a response in the ACC. This difference is important, as it allows only the conflict monitoring account to explain ACC activation in settings other than error commission, such as response override and underdetermined responding tasks.

One finding that calls for special consideration is that an ERN-like potential can occur when participants receive a signal indicating that they have just committed an error (Miltner, Braun, & Coles, 1997). It is not obvious how, in this instance, activation of the ACC might be interpreted as a response to conflict. ¹¹ Indeed, this is one finding (along with the response of the ACC to pain) that has prompted us to adopt the view that conflict monitoring may be one of a set of closely interrelated functions performed by the ACC (see *Conflict monitoring in the larger context of ACC function*, below).

However, it is important to consider carefully the implications of the Miltner et al. (1997) finding for our interpretation of the ERN when it occurs during error commission, in the absence of external feedback. Independent of ACC activation in other settings, an explanation is needed for how the ACC is able to detect errors on-line, as they are being committed. At present, there appear to be two available explanations for how such error detection occurs, the comparator account and the conflict monitoring account, between which the latter appears to provide a more comprehensive account of existing data. Thus, despite the farreaching implications of the Miltner et al. results, the conflict monitoring account continues to provide a much-needed explanation for phenomena related to the ERN, one that also accounts well for ACC activation in settings not involving errors.

Task difficulty. Another interpretation of ACC activation is that it reflects a response to task difficulty (e.g., Paus et al., 1998). The main difference between this account and the one we have put forth lies in our theory's specificity. The notion of task difficulty on its own is rather vague. Although it is true that Paus et al. (1998) operationally define difficulty, identifying it with the presence of relatively long reaction time and high error rates, ACC activation does not appear to be a specific response to either of these features. It cannot be characterized as a specific response to errors, as the area also activates during some correct trials. Nor can it be viewed as a specific response to long reaction times, as the area does become active during errors, which tend to have relatively short reaction times. The difficulty hypothesis thus leaves open the question of what it is about difficult tasks that leads to ACC activation. 12 The conflict monitoring theory provides a precise answer to this question. As a consequence, the theory is also able to provide a more detailed account of the data. For example, the conflict monitoring theory explains why ACC activation occurs just after errors. Task difficulty alone does not explain this, as it is not obvious in what (noncircular) sense error trials are more difficult than other trials. Furthermore, the conflict monitoring account makes numerous predictions that do not obviously follow from the difficulty account. For example, as described earlier, we predicted on the basis of the conflict monitoring account that during verb generation ACC activation would be greater when participants happened to select a verb weakly associated with the cue noun than when they selected a strong associate, and confirmed this prediction using fMRI (Barch et al., 2000). It is not clear how this result might have been predicted on the basis of a task difficulty account.

Regulative accounts. According to the account most prevalent in previous work, the ACC is tied to what we have called the regulative component of control (e.g., D'Esposito et al., 1995; Grossman, Crino, Reinich, Stern, & Hurtig, 1992; Vogt et al., 1992). For example, Posner and Dahaene (1994) have described the ACC as "involved in the attentional recruitment and control of brain areas to perform complex cognitive tasks" (p. 76), and Pardo et al. (1990) described the ACC as selecting between processing alternatives on the basis of some preexisting internal, conscious plan. In order to refer to this function, a number of investigators have adopted the term attention (or selection) for action (e.g., Frith et al., 1991b; Petersen et al., 1988, 1989). According to Posner et al. (1988), the term "is used to summarize the idea that attention seems to be involved in selecting those operations that will gain control of output systems" (p. 1628). Others, viewing the role of the ACC in a similar way, have identified it with Baddeley's (1986) central executive (e.g., D'Esposito et al., 1995) or Norman & Shallice's (1986) SAS (Grossman et al., 1992; Posner & Di-Girolamo, 1998). Although the notion of conflict has been invoked by several theorists (e.g., Pardo et al., 1990; Posner & DiGirolamo, 1998; Taylor et al., 1994), in each case the ACC has again been cast in a regulative role, with an emphasis on conflict resolution rather than conflict detection.

One drawback of regulative accounts is that they do not explain ACC engagement associated with errors. ¹³ In contrast, the conflict monitoring hypothesis provides a detailed account for such engagement, also indicating how it relates to ACC activation unassociated with errors.

A further difficulty for regulative accounts is posed by the fMRI data reported by Botvinick et al. (1999) and Carter et al. (2000; see also MacDonald, Cohen, Stenger, & Carter, 2000). As described earlier, both of these studies examined tasks where the strength of control varied from trial to trial, comparing ACC activation between high- and low-control trials. In contradiction to regulative

¹¹ However, it is possible to speculate that the response to symbolic feedback may in fact occur precisely because errors are typically associated with conflict, just as areas of cortex responsive to color can be engaged by monochromatic stimuli with strong associations to colors (e.g., Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995).

¹² Paus et al. (1998) do speculate that ACC activation during difficult tasks may be a response to arousal, driven by increased dopaminergic and noradrenergic input to the ACC. Although this proposal does not attempt to specify the nature of information processing carried out within the ACC itself, it does have the merit—unlike the more general version of the difficulty account—of being relatively easy to test empirically.

¹³ A regulative view might attempt to explain error-associated ACC activity as reflecting the engagement of mechanisms mediating either error-suppression/correction or compensatory shifts in subsequent behavior. An argument against the first of these possibilities has been offered by Scheffers et al. (1996). The second does not appear to offer a parsimonious explanation for the time course of the ACC response, in particular its return to baseline prior to the subsequent trials where compensatory shifts in behavior are observed.

accounts, both studies found greater ACC activation on trials where control was weakest. The data fit more closely with a conflict monitoring view; in both studies, greater ACC activation was observed on trials involving high conflict.

One way of preserving the regulative account in the face of these findings might be to interpret ACC activation on highconflict trials as reflecting a rapid, within-trial compensatory mobilization of top-down control. It is true that the fMRI data themselves do not prohibit this interpretation. However, this last-minute view has two problems. First, because ACC activation in the Botvinick et al. (1999) and Carter et al. (2000) studies was not elevated on high-control trials, the last-minute account requires the assumption that two control systems exist: (a) a system coming into play in anticipation of demanding activities and sustained through the course of such activities (as in the frequentincongruent condition of the Carter et al. [2000] study), and (b) a system, involving the ACC, that is responsible only for last-minute conflict resolution. Current data provide little independent support for this division of labor; indeed, we are aware of no databehavioral, physiological, or otherwise—to indicate that compensatory shifts in control actually occur on the time scale that this modified version of the regulative account would require. Until such evidence emerges, the conflict monitoring theory appears to offer a more parsimonious account of the data.

Conflict monitoring in the larger context of ACC function. Although the goals of the present research have led us to focus on the potential role of the ACC in conflict monitoring, we do not intend to imply that conflict monitoring is the only function of the ACC. Our more general view is that the ACC may monitor for the demand for control in multiple ways. This view is motivated by evidence suggesting that the ACC is responsive to indicators of a need for control other than conflict. For example, a number of attention-demanding sensory inputs have been shown to activate the area, including pain and itch (Hsieh et al., 1994; Jones, Brown, Friston, Qi, & Frackowiak, 1991). 14 Furthermore, as noted earlier, explicit feedback about performance may also activate the ACC (Miltner et al., 1997). Note that these stimuli, like the occurrence of conflict, indicate that adaptive behavior calls for a shift in the allocation of attention. The occurrence of pain and feedback indicating error commission fall into the same class of signals as conflict, all of which indicate that the current distribution of attention is failing to prevent negative outcomes.

These considerations suggest an account of ACC function by which the region evaluates attentional demands based both on an assessment of environmental inputs and, through conflict monitoring, on an evaluation of how the processing system is dealing with them. Although, by this account, conflict would provide just one among several potential signs of trouble, conflict has properties that make it rather special. For whereas signals such as pain or negative feedback indicate that something has already gone wrong, conflict has the potential to act as an early warning system, indicating a high risk of problems before they actually occur. Because conflict is an identifying feature of situations predisposing to failures in performance—and therefore likely to precede them—conflict monitoring could enable the system to anticipate and avert problems, rather than responding only to their actual occurrence.

Conclusion

If the homunculus is to be eliminated from theories of cognitive control, an account is needed of how the demand for control is evaluated. The work we have presented takes a step in this direction, pointing to conflict as one possible basis for the assessment of demand and providing evidence from several domains that a mechanism exists for monitoring conflict. The theory that conflict monitoring is reflected in the activity of the ACC is consistent with a large body of existing data and is supported by both computational modeling and empirical work using fMRI. The theory relates in interesting ways to existing ideas about attention, interactive computation, and ACC function, and makes predictions productive of further research.

The account we have presented brings together material from cognitive psychology and cognitive neuroscience, using each to help answer questions posed by the other. We found that neuroscientific data allowed an advance in psychological theory by providing evidence for the existence of a system serving to monitor for conflict. In return, ideas from cognitive psychology allowed us to interpret studies of the ACC in a new light, leading us to see a common basis for seemingly disparate findings. Connectionist simulations played a special role, allowing us to specify explicitly the computations under discussion and in such a way as to give them equal relevance to psychological and neuroscientific spheres.

The interdisciplinary nature of the work we have presented is mirrored in the diversity of the questions it raises for future research. Further investigation is called for to firmly establish that conflict monitoring indeed occurs, and if so to characterize what mechanisms it involves and the specific ways in which it impacts cognition.

References

Allport, A. (1980). Patterns and actions. In G. Claxton (Ed.), Cognitive psychology: New directions (pp. 26-64). London: Routledge & Kegan Paul.

Allport, A. (1987). Selection for action: Some behavioral and neurophysiological considerations of attention and action. In H. Heuer & A. F. Sanders (Eds.), *Perspectives on perception and action* (pp. 395–419). Hillsdale, NJ: Erlbaum.

Anderson, J. R. (1982). Acquisition of cognitive skill. *Psychological Review*, 89, 369-406.

Andreason, N. C., O'Leary, D. S., Cizadlo, T., Arndt, S., Rezai, K., Watkins, L., Boles Ponto, L. L., & Hichwa, R. D. (1995). Remembering the past: Two facets of episodic memory explored with positron emission tomography. *American Journal of Psychiatry*, 152, 1576-1585.

Baddeley, A. (1966). Short-term memory for word sequences as a function of acoustic, semantic, and formal similarity. *Journal of Experimental Psychology*, 18, 334–336.

Baddeley, A. (1986). Working memory. Oxford, England: Clarendon Press.
Baddeley, A., & Della Sala, D. (1996). Working memory and executive control. Philosophical Transactions of the Royal Society of London, Series B, 351, 1397-1404.

Baker, S. C., Rogers, R. D., Owen, A. M., Frith, C. D., Dolan, R. J.,

¹⁴ Of course, the possibility must be considered that ACC activity seen in response to such sensory events as pain and itch may be due to response competition induced by the usual requirement to remain still in experimental settings.

- Frackowiak, R. S. J., & Robbins, T. W. (1996). Neural systems engaged by planning: A PET study of the Tower of London task. *Neuropsychologia*, 34, 515–526.
- Barch, C. M., Sabb, F. W., Braver, T. S., & Noll, D. C. (2000). Anterior cingulate and the monitoring of response conflict: Evidence from an fMRI study of verb generation. *Journal of Cognitive Neuroscience*, 12, 298-305.
- Bench, C. T., Frith, C. D., Grasby, P. M., Friston, K. J., Paulesu, E., Frackowiak, R. S. J., & Dolan, R. J. (1993). Neuropsychologia, 31, 907–922.
- Berlyne, D. E. (1957). Uncertainty and conflict: A point of contact between information-theory and behavior-theory concepts. *Psychological Review*, 64, 329–339.
- Berlyne, D. E. (1960). Conflict, arousal and curiosity. New York: McGraw-Hill.
- Bernstein, P. S., Scheffers, M. K., & Coles, G. H. (1995). "Where did I go wrong?": A psychophysiological analysis of error detection. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 1312–1322.
- Bishop, C. M. (1995). Neural networks for pattern recognition. Oxford, England: Oxford University Press.
- Borowsky, R., & Masson, M. E. J. (1996). Semantic ambiguity effects in word identification. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 22, 63–85.
- Botvinick, M., Nystrom, L., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, 402, 179-181.
- Braver, T. S. (1997). Mechanisms of cognitive control: A neurocomputational control. Unpublished doctoral dissertation, Carnegie Mellon University.
- Braver, T. S., Cohen, J. D., Nystrom, L., Jonides, J., Smith, E., & Noll, D. C. (1997). A parametric study of prefrontal cortex involvement in human working memory. *NeuroImage*, 5, 49-62.
- Buckner, R. L., Petersen, S. E., Ojemann, J. G., Miezin, F. M., Squire, L. R., & Raichle, M. E. (1995). Functional anatomical studies of explicit and implicit memory retrieval tasks. *Journal of Neuroscience*, 15, 12-29.
- Bush, G., Whalen, P. J., Rosen, B. R., Jenike, M. A., McInerney, S. C., & Rauch, S. L. (1998). The counting Stroop: An interference task specialized for functional neuroimaging: Validation study with functional MRI. Human Brain Mapping, 6, 270–282.
- Cabeza, R., & Nyberg, L. (1997). Imaging cognition: An empirical review of PET studies with normal subjects. *Journal of Cognitive Neuro*science, 9, 1-26.
- Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the on-line monitoring of performance. *Science*, 280, 747-749.
- Carter, C. S., MacDonald, A. M., Botvinick, M., Ross, L. L., Stenger, A., Noll, D., & Cohen, J. D. (2000). Parsing executive processes: Strategic versus evaluative functions of the anterior cingulate cortex. *Proceedings* of the National Academy of Sciences, 97, 1944–1948.
- Carter, C. S., Mintun, M., & Cohen, J. D. (1995). Interference and facilitation effects during selective attention: An H₂¹⁵O PET study of Stroop task performance. *NeuroImage*, 2, 264–272.
- Casey, B. J., Trainor, R. J., Orendi, J. L., Schubert, A. B., Nystrom, L. E., Giedd, J. N., Castellanos, F. X., Haxby, J. V., Noll, D. C., Cohen, J. D., Forman, S. D., Dahl, R. E., & Rapoport, J. L. (1997). A developmental functional MRI study of prefrontal activation during performance of a go-no-go task. *Journal of Cognitive Neuroscience*, 9, 835-847.
- Cheesman, J., & Merikle, P. M. (1986). Distinguishing conscious from unconscious perceptual processes. *Canadian Journal of Psychology*, 40, 343–367.
- Cohen, J. D., Braver, T. S., & O'Reilly, R. C. (1996). A computational approach to prefrontal cortex, cognitive control and schizophrenia: Re-

- cent developments and current challenges. *Philosophical Transactions of the Royal Society, Series B, 351,* 1515–1527.
- Cohen, J. D., Dunbar, K., & McClelland, J. L. (1990). On the control of automatic processes: A parallel distributed processing account of the Stroop effect. *Psychological Review*, 97, 332–361.
- Cohen, J. D., & Huston, T. A. (1994). Progress in the use of interactive models for understanding attention and performance. In C. Umilta & M. Moscovitch (Eds.), Attention and performance XV (pp. 453–456). Cambridge, MA: MIT Press.
- Cohen, J. D., & Servan-Schreiber, D. (1992). Context, cortex, and dopamine: A connectionist approach to behaviour and biology in schizophrenia. *Psychological Review*, 99, 45–77.
- Cohen, J. D., Servan-Schreiber, D., & McClelland, J. L. (1992). A parallel distributed processing approach to automaticity. *American Journal of Psychology*, 105, 239-269.
- Coles, M. G. H., Sheffers, M. K., & Fournier, L. (1995). "Where did you go wrong?": Errors, partial errors, and the nature of human information processing. Acta Psychologica, 90, 129-144.
- Cooke, J. D., & Diggles, V. A. (1984). Rapid error correction during human arm movements: Evidence for central monitoring. *Journal of Motor Behavior*, 4, 348-363.
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed: Functional anatomy by positron emission tomography. *Journal of Neuroscience*, 11, 2383–2402.
- Dahaene, S., Posner, M. I., & Tucker, D. M. (1994). Localization of a neural system for error detection and compensation. *Psychological Sci*ence, 5, 303–305.
- Deiber, M. P., Passingham, R. E., Colebatch, J. G., Friston, K. J., Nixon, P. D., & Frackowiak, R. S. J. (1991). Cortical areas and the selection of movement: A study with positron emission tomography. *Experimental Brain Research*, 84, 393–402.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.
- D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., & Grossman, M. (1995). The neural basis of the central executive of working memory. *Nature*, 378, 279-281.
- Duncan, J. (1986). Disorganization of behavior after frontal lobe damage. Cognitive Neuropsychology, 3, 271–290.
- Duncan, J. (1996). Cooperating brain systems in selective perception and action. In T. Inui & J. L. McClelland (Eds.), Attention and performance 16: Information integration in perception and communication (pp. 549– 578). Cambridge, MA: MIT Press.
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception and Psychophysics*, 16, 143–149.
- Eriksen, C. W., & Schultz, D. W. (1979). Information processing in visual search: A continuous flow conception and experimental results. *Perception and Psychophysics*, 25, 248–263.
- Falkenstein, M., Hohnsbein, J., & Hoorman, J. (1995). Event related potential correlates of errors in reaction tasks. In G. Karmos, M. Molnar, V. Csepe, I. Czigler, & J. E. Desmedt (Eds.), Perspectives of eventrelated potentials research (pp. 287–296). Amsterdam: Elsevier Science B.V.
- Falkenstein, M., Hohnsbein, J., Hoorman, J., & Blanke, L. (1991). Effects of crossmodal divided attention on late ERP components: II. Error processing in choice reaction tasks. Electroencephalography and Clinical Neurophysiology, 78, 447-455.
- Friston, K. J., Frith, C. D., Liddle, P. F., & Frackowiak, R. S. J. (1993). Functional connectivity: The principal-component analysis of large (PET) data sets. *Journal of Cerebral Blood Flow and Metabolism*, 13, 5-14.
- Frith, C. D., Friston, K. J., Liddle, P. F., & Frackowiak, R. S. J. (1991a). A PET study of word-finding. *Neuropsychologia*, 29, 1137–1148.
- Frith, C. D., Friston, K. J., Liddle, P. F., & Frackowiak, R. S. J. (1991b).

- Willed action and the prefrontal cortex in man: A study with PET. Proceedings of the Royal Society of London, Series B, 244, 241-246.
- Fuster, J. M. (1980). The prefrontal cortex: Anatomy, physiology, and neuropsychology of the frontal lobe. New York: Raven.
- Gabriel, M. (1993). Discriminative avoidance learning: A model system. In
 M. Gabriel & B. Vogt (Eds.), Neurobiology of cingulate cortex and limbic thalamus (pp. 478-523). Toronto, Ontario, Canada: Birkhauser.
- Gariano, R. F., & Groves, P. M. (1988). Burst firing induced in midbrain dopamine neurons by stimulation of the medial prefrontal and anterior cingulate cortices. *Brain Research*, 462, 194-198.
- Gathercole, S. E. (1994). Neuropsychology and working memory: A review. Neuropsychology, 8, 494-505.
- Gehring, W. J., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1990). The error-related negativity: An event-related potential accompanying errors. *Psychophysiology*, 27, S34.
- Gehring, W. J., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1995). A brain potential manifestation of error-related processing. In G. Karmos, M. Molnar, V. Csepe, I. Czigler, & J. E. Desmedt (Eds.), Perspectives of event-related potentials research (pp. 261-272). Amsterdam: Elsevier Science B.V.
- Gehring, W. J., & Fencsik, D. (1999, April). Slamming on the brakes: An electrophysiological study of error response inhibition. Poster presented at the annual meeting of the Cognitive Neuroscience Society, Washington, DC.
- Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science*, 4, 385–390.
- George, M. S., Ketter, T. A., Parekh, P. I., Rosinsky, N., Ring, H., Casey, B. J., Trimble, M. R., Horowitz, B., Herscovitch, P., & Post, R. M. (1994). Regional brain activity when selecting a response despite interference: An H₂¹⁵O PET study of the Stroop and emotional Stroop. Human Brain Mapping, 1, 194-209.
- Goldman-Rakic, P. S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In F. Plum (Ed.), Handbook of physiology: Vol. V. Higher functions of the brain. Section I. The nervous system (pp. 373-417). Bethesda, MD: American Psychological Society.
- Goldman-Rakic, P. S. (1996). The prefrontal landscape: Implications of functional architecture for understanding human mentation and the central executive. *Philosophical Transactions of the Royal Society of Lon*don, Series B, 351, 1445–1453.
- Goldman-Rakic, P. S. (1998). The cortical dopamine system: Role in memory and cognition. Advances in Psychopharmacology, 42, 707-711.
- Grasby, P. M. Frith, C. D., Friston, K. J., Bench, C., Frackowiak, R. S. J., & Dolan, R. J. (1993). Functional mapping of brain areas implicated in auditory-verbal memory function. *Brain*, 116, 1-20.
- Gratton, G., Coles, M. G. H., & Donchin, E. (1992). Optimizing the use of information: Strategic control of activation and responses. *Journal of Experimental Psychology: General*, 4, 480-506.
- Gratton, G., Coles, M. G. H., Sirevaag, E. J., Eriksen, C. W., & Donchin, E. (1988). Pre- and post-stimulus activation of response channels: A psychophysiological analysis. *Journal of Experimental Psychology: Human Perception and Performance*, 14, 331-344.
- Groh, J. M., Born, R. T., & Newsome, W. T. (1997). How is a sensory map read out? Effects of microstimulation in visual area MT on saccades and smooth pursuit eye movements. *Journal of Neuroscience*, 17, 4312– 4330.
- Grossman, M., Crino, P., Reinich, M., Stern, M. B., & Hurtig, H. I. (1992).
 Attention and sentence processing deficits in Parkinson's disease. Cerebral Cortex, 2, 513-525.
- Henik, A., Bibi, U., Yanai, M., & Tzelgov, J. (1997). The Stroop effect is largest during first trials. Abstracts of the Psychonomic Society, 2, 57.
- Hohnsbein, J., Falkenstein, M., & Hoorman, J. (1989). Error processing in visual and auditory choice reaction tasks. *Journal of Psychophysiol*ogy, 3, 32.

- Hopfield, J. J. (1982). Neural networks and physical systems with emergent collective computational abilities. Proceedings of the National Academy of Sciences, USA, 79, 2554-2558.
- Hsieh, J-C., Hagerman, O., Stahle-Backdahl, M., Ericson, K., Eriksson, L., Stone-Elander, S., & Ingvar, M. (1994). Urge to scratch represented in the human cerebral cortex during itch. *Journal of Neurophysiology*, 72, 3004-3008.
- Janer, K. W., & Pardo, J. V. (1991). Deficits in selective attending following bilateral anterior cingulotomy. *Journal of Cognitive Neuro*science, 3, 231-241.
- Jeuptner, M., Frith, C. D., Brooks, D. J., Frackowiak, R. S. J., & Passingham, R. E. (1997). Anatomy of motor learning: II. Subcortical structures and learning by trial and error. *Journal of Neurophysiology*, 77, 1325–1337.
- Jodo, E., Chiang, C., & Aston-Jones, G. (1998). Potent excitatory influence of prefrontal cortex activity on noradrenergic locus coeruleus neurons. *Neuroscience*, 83, 63–80.
- Jones, A. K. P., Brown, W. D., Friston, K. J., Qi, L. Y., & Frackowiak, R. S. J. (1991). Cortical and subcortical localization of response to pain in man using positron emission tomography. *Proceedings of the Royal Society of London: Biology*, 244, 39-44.
- Joordens, S., & Becker, S. (1997). The long and short of semantic priming effects in lexical decision. *Journal of Experimental Psychology: Learn*ing, Memory, and Cognition, 5, 1083-1105.
- Kahneman, D. (1973). Attention and effort. Englewood Cliffs, NJ: Prentice-Hall.
- Kawashima, R., Satoh, K., Itoh, H., Ono, S., Furumoto, S., Gotoh, R., Koyoma, M., Yoshioka, S., Takahashi, T., Takahashi, K., Yanagisawa, T., & Fukuda, H. (1996). Functional anatomy of GO/NO-GO discrimination and response selection: A PET study in man. *Brain Research*, 728, 79-89.
- Kleinschmidt, A., Buchel, C., Zeki, S., & Frackowiak, R. S. (1998). Human brain activity during spontaneously reversing perception of ambiguous figures. Proceedings of the Royal Society of London-Series B: Biological Sciences, 265, 2427-2433.
- Kopp, B., Rist, F., & Mattler, U. (1996). N200 in the flanker task as a neurobehavioral tool for investigating executive control. *Psychophysiology*, 33, 282–294.
- LaBerge, D. (1990). Thalamic and cortical mechanisms of attention suggested by recent positron emission tomography experiments. *Journal of Cognitive Neuroscience*, 2, 358–371.
- Laird, J. E., Newell, A., & Rosenbloom, P. S. (1987). SOAR: An architecture for general intelligence. *Artificial Intelligence*, 33, 1-64.
- Laming, D. R. J. (1968). Information theory of choice-reaction times. London: Academic Press.
- Laming, D. R. J. (1979a). Autocorrelation of choice-reaction times. Acta Psychologica, 43, 381–412.
- Laming, D. R. J. (1979b). Choice reaction performance following an error. *Acta Psychologica*. 43. 199-224.
- Lindsay, D. S., & Jacoby, L. L. (1994). Stroop process dissociations: The relationship between facilitation and interference. *Journal of Experimen*tal Psychology: Human Perception and Performance, 20, 219-234.
- Logan, G. D. (1980). Attention and automaticity in Stroop and priming tasks: Theory and data. Cognitive Psychology, 12, 523-553.
- Logan, G. D., & Zbrodoff, N. J. (1979). When it helps to be misled: Facilitative effects of increasing the frequency of conflicting stimuli in a Stroop-like task. *Memory and Cognition*, 7, 166-174.
- Luce, R. D. (1986). Response times: Their role in inferring elementary mental organization. New York: Oxford University Press.
- Lumer, E. D., Friston, K. J., & Rees, G. (1998, June 19). Neural correlates of perceptual rivalry in the human brain. Science, 280, 1930-1934.
- Luria, A. R. (1973). The working brain. London: Penguin Books.
- MacCleod, C. M. (1991). Half a century of research on the Stroop effect: An integrative review. *Psychological Bulletin*, 109, 163–203.
- MacDonald, A. W., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000).

- Dissociating the role of dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*, 288, 1835–1838.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, 270, 102–105.
- McClelland, J. L. (1992). Toward a theory of information processing in graded, random, interactive networks. In D. Meyer & S. Kornblum (Eds.), Attention and performance (Vol. 14, pp. 655–688). Cambridge, MA: MIT Press.
- McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: Part 1. An account of basic findings. *Psychological Review*, 88, 375–407.
- Mesulam, M. M. (1981). A cortical network for directed attention and unilateral neglect. *Annals of Neurology*, 10, 309-325.
- Miltner, W. H. R., Braun, C. H., & Coles, M. G. H. (1997). Event-related brain potentials following incorrect feedback in a time-estimation task: Evidence for a "generic" neural system for error detection. *Journal of Cognitive Neuroscience*, 9, 788-798.
- Mozer, M. C. (1991). The perception of multiple objects: A connectionist approach. Cambridge, MA: MIT Press.
- Mozer, M. C., & Sitton, M. (1998). Computational modeling of spatial attention. In H. Pashler (Ed.), *Attention* (pp. 341–393). London: UCL Press.
- Navon, D. (1985). Attention division or attention sharing? In M. I. Posner & O. S. M. Marin (Eds.), Attention and performance XI (pp. 133-146). London: Erlbaum.
- Navon, D., & Miller, J. (1987). Role of outcome conflict in dual-task interference. *Journal of Experimental Psychology: Human Perception* and Performance, 13, 435-448.
- Niki, H., & Watanabe, M. (1979). Prefrontal and cingulate unit activity during timing behavior in the monkey. Brain Research, 171, 213-224.
- Noelle, D. C., & Cottrell, G. W. (1995). A connectionist model of instruction following. In *Proceedings of the 17th annual conference of the Cognitive Science Society* (pp. 369-374). Hillsdale, NJ: Erlbaum.
- Norman, D. A., & Shallice, T. (1986). Attention to action: Willed and automatic control of behavior. In R. J. Davidson, G. E. Schwartz, & D. Shapiro (Eds.), Consciousness and self-regulation: Vol. 4. Advances in research and theory (pp. 1-18). New York: Plenum Press.
- Oades, R. D. (1985). The role of noradrenaline in tuning and dopamine in switching between signals in the central nervous system. *Neuroscience* and Biobehavioral Reviews, 9, 261–282.
- Pardo, J. V., Pardo, P., Janer, K. W., & Raichle, M. E. (1990). The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proceedings of the National Academy of Science*, USA, 87, 256-259.
- Paus, T., Koski, L., Caramanos, Z., & Westbury, C. (1998). Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex: A review of 107 PET activation studies. *Neuroreport*, 9, R37-47.
- Paus, T., Petrides, M., Evans, A. C., & Meyer, E. (1993). Role of the human anterior cingulate cortex in the control of oculomotor, manual and speech responses: A positron emission tomography study. *Journal of Neurophysiology*, 70, 453–469.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature*, 331, 985–989.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1989). Positron emission tomography studies of the processing of single words. *Journal of Cognitive Neuroscience*, 1, 153-170.
- Playford, E. D., Jenkins, I. H., Passingham, R. E., Nutt, J., Frackowiak, R. S. J., & Brooks, D. J. (1992). Impaired mesial frontal and putamen activation in Parkinson's disease: A positron emission tomography study. Annals of Neurology, 32, 151-161.
- Pomerleau, D. A. (1992). Neural network perception for mobile robot

- guidance. Unpublished doctoral dissertation, Carnegie Mellon University.
- Posner, M. I., & Dehaene, S. (1994). Attentional networks. Trends in Neurosciences. 17, 75-79.
- Posner, M. I., & DiGirolamo, G. J. (1998). Executive attention: Conflict, target detection and cognitive control. In R. Parasuraman (Ed.), *The attentive brain* (pp. 401–423). Cambridge, MA: MIT Press.
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Reviews in Neuroscience*, 13, 25-42.
- Posner, M. I., Petersen, S. E., Fox, P. T., & Raichle, M. E. (1988). Localization of operations in the human brain. Science, 240, 1627-1631.
- Rabbitt, P. M. A. (1966). Errors and error-correction in choice-response tasks. *Journal of Experimental Psychology*, 71, 264-272.
- Rabbitt, P. (1979). How old and young subjects monitor and control responses for accuracy and speed. *British Journal of Psychology*, 70, 305–311.
- Rabbitt, P., & Rodgers, B. (1977). What does a man do after he makes an error?: An analysis of response programming. *Quarterly Journal of Experimental Psychology*, 29, 727–743.
- Rabbitt, P., & Vyas, S. (1981). Processing a display even after you make a response to it: How perceptual errors can be corrected. Quarterly Journal of Experimental Psychology, 33, 223–239.
- Raichle, M. E., Fiez, J. A., Videen, T. O., MacCleod, A. K., Pardo, J. V., Fox, P. T., & Petersen, S. E. (1994). Practice-related changes in human brain functional anatomy during nonmotor learning. *Cerebral Cortex*, 4, 8–26
- Rogers, R. D., & Monsell, S. (1995). Costs of a predictable switch between simple cognitive tasks. *Journal of Experimental Psychology: General*, 124, 207–231.
- Rosvold, H. E., Mirsky, A. F., Sarason, I., Bransome, E. D., & Beck, L. H. (1956). A continuous performance test of brain damage. *Journal of Consulting Psychology*, 20, 343–350.
- Rugg, M. D., & Coles, M. G. H. (Eds.). (1995). Electrophysiology of mind. Oxford, England: Oxford University Press.
- Rumelhart, D. E., & McClelland, J. L. (1982). An interactive activation model of context effects in letter perception: Part 2. The contextual enhancement effect and some tests and extensions of the model. *Psy*chological Review, 89, 69-94.
- Rumelhart, D. E., & McClelland, J. L. (Eds.). (1986). Parallel distributed processing: Explorations in the microstructure of cognition. Cambridge, MA: MIT Press.
- Rumelhart, D. E., Smolensky, P., McClelland, J. L., & Hinton, G. E. (1986). Schemata and sequential thought processes in PDP models. In J. L. McClelland & D. E. Rumelhart (Eds.), Parallel distributed processing: Explorations in the microstructure of cognition (Vol. II, pp. 7-57). Cambridge, MA: MIT Press.
- Scheffers, M. K., Coles, M. G. H., Bernstein, P., Gehring, W. J., & Donchin, E. (1996). Event-related potentials and error-related processing: An analysis of incorrect responses to go and no-go stimuli. *Psychophysiology*, 33, 42–53.
- Schneider, W., & Detwiler, M. (1987). A connectionist/control architecture for working memory. *The Psychology of Learning and Motivation*, 21, 53–119.
- Schneider, W., & Detwiler, M. (1988). The role of practice in dual-task performance: Toward workload modeling in a connectionist/control architecture. *Human Factors*, 30, 539-566.
- Servan-Schreiber, D. (1990). From physiology to behavior: Computational models of catecholamine modulation of information processing. Unpublished doctoral dissertation, Carnegie Mellon University.
- Shaffer, L. H. (1975). Multiple attention in continuous verbal tasks. In P. M. A. Rabbitt & S. Dornic (Eds.), Attention and performance V (pp. 157–167). London: Academic Press.
- Shallice, T., & Burgess, P. (1993). Supervisory control of action and thought selection. In A. Baddeley & L. Weiskrantz (Eds.), *Attention:*

- Selection, awareness, and control (pp. 171-187). Oxford, England: Clarendon Press.
- Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychological Review*, 84, 127–190.
- Smolensky, P. (1986). Information processing in dynamical systems: Foundations of harmony theory. In D. E. Rumelhart & J. L. McClelland (Eds.), Parallel distributed processing: Explorations in the microstructure of cognition (Vol. I, pp. 194-281). Cambridge, MA: MIT Press.
- Spreen, O., & Benton, A. L. (1969). Neurosensory Center Comprehensive Examination for Aphasia. Victoria, British Columbia, Canada: University of Victoria, Department of Psychology, Neuropsychological Laboratory.
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. Journal of Experimental Psychology, 18, 643-662.
- Stuss, D. T., & Benson, D. F. (1984). Neuropsychological studies of the frontal lobes. *Psychological Bulletin*, 95, 3-28.
- Taylor, S. F., Kornblum, S., Minoshima, S., Oliver, L. M., & Koeppe, R. A. (1994). Changes in medial cortical blood flow with a stimulus–response compatibility task. *Neuropsychologia*, 32, 249–255.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences*, USA, 94, 14792-14797.
- Treisman, A. (1988). Features and objects: The Fourteenth Bartlett Memorial Lecture. Quarterly Journal of Experimental Psychology, 40, 201–237
- Turken, A. U., & Swick, D. (1999). Response selection in the human anterior cingulate cortex. *Nature Neuroscience*, 2, 920-924.
- Tzelgov, J., Henik, A., & Berger, J. (1992). Controlling Stroop effects by manipulating expectations for color words. *Memory and Cognition*, 20, 727-735.
- Usher, M., & Cohen, J. D. (2000). A connectionist model of the Stroop task revisited: Reaction time distributions and differential effects on facilitation and interference captured by a single set of mechanisms. Manuscript in preparation.
- Usher, M., Cohen, J. D., Servan-Schreiber, D., Rajkowski, J., & Aston-Jones, G. (1999). The role of locus coeruleus in the regulation of cognitive performance. *Science*, 283, 549-554.
- Usher, M., & McClelland, J. L. (1995). On the time course of perceptual

- choice: A model based on principles of neural computation (Tech. Rep. PDP.CNS.95.5). Carnegie Mellon University, Department of Psychology.
- Usher, M., & McClelland, J. L. (2001). The time course of perceptual choice: The leaky, competing accumulator model. *Psychological Review*, 108, 550-592.
- Usher, M., & Niebur, E. (1996). A neural model for parallel, expectationdriven attention for objects. *Journal of Cognitive Neuroscience*, 8, 305-321
- Van Hoesen, G. W., Morecraft, R. J., & Vogt, B. A. (1993). Connections of the monkey cingulate cortex. In B. A. Vogt & M. Gabriel (Eds.), Neurobiology of cingulate cortex and limbic thalamus: A comprehensive handbook (pp. 249-284). Boston: Birkhauser.
- van Veen, V., Cohen, J. D., Botvinick, M., Stenger, V. A., & Carter, C. S. (2000). Conflict related activity and the anterior cingulate: An event-related fMRI analysis of stimulus versus response-based conflict [Abstract]. Cognitive Neuroscience Society Annual Meeting Program, 2000, 114
- Vogt, B. A., Finch, D. M., & Olson, C. R. (1992). Functional heterogeneity in cingulate cortex: The anterior executive and posterior evaluative regions. *Cerebral Cortex*, 2, 435–443.
- Warburton, E., Wise, R., Price, C. J., Weiller, C., Hadar, U., Ramsay, S., & Frackowiak, R. S. J. (1996). Noun and verb retrieval by normal subjects: Studies with PET. Brain, 119, 159-179.
- Wickelgren, W. A. (1977). Speed-accuracy tradeoff and information processing dynamics. Acta Psychologica, 41, 67-85.
- Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E., & Frackowiak, R. S. J. (1991). *Brain*, 114, 1803–1817.
- Yetkin, F. Z., Hammeke, T. A., Swanson, S. J., Morris, G. L., Mueller, W. M., & McAuliffe, T. L. (1995). A comparison of functional MR activation patterns during silent and audible language tasks. American Journal of Neuroradiology, 16, 1087-1092.
- Yeung, N., Botvinick, M. M., & Cohen, J. D. (2000). The neural basis of error-detection: Conflict monitoring and the error-related negativity. Manuscript submitted for publication.

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Correction to Huber et al. (2001)

The article "Perception and Preference in Short-Term Word Priming," by David E. Huber, Richard M. Shiffrin, Keith B. Lyle, and Kirsten I. Ruys (*Psychological Review*, 2001, Vol. 108, No. 1, pp. 149–182), contained two errors.

Equation 3 (p. 162) should read

$$L_{C} = [o_{i} \log(p_{i})] + [(1 - o_{i}) \log(1 - p_{i})].$$

Equation 4 (p. 162) should read

$$L_{U} = [o_{i} \log(o_{i})] + [(1 - o_{i}) \log(1 - o_{i})]$$