Conflict monitoring and anterior cingulate cortex: an update

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One hypothesis concerning the human dorsal anterior cingulate cortex (ACC) is that it functions, in part, to signal the occurrence of conflicts in information processing, thereby triggering compensatory adjustments in cognitive control. Since this idea was first proposed, a great deal of relevant empirical evidence has accrued. This evidence has largely corroborated the conflict-monitoring hypothesis, and some very recent work has provided striking new support for the theory. At the same time, other findings have posed specific challenges, especially concerning the way the theory addresses the processing of errors. Recent research has also begun to shed light on the larger function of the ACC, suggesting some new possibilities concerning how conflict monitoring might fit into the cingulate's overall role in cognition and action.

The term cognitive control refers to a set of functions serving to configure the cognitive system for the performance of specific tasks, especially in challenging and non-routine situations. A crucial question concerning these functions is: How are they recruited? One possibility is that control is recruited based, in part, on a function that detects *conflicts* in information processing. In a series of papers, beginning in 1998 [1–4], we and several colleagues suggested that direct evidence for a conflict-monitoring function could be discerned in data from cognitive neuroscience, and in particular work pertaining to the anterior cingulate cortex (ACC). To be more precise, we advanced two interrelated hypotheses: (1) Specific brain regions, most notably the dorsal ACC, respond to the occurrence of conflicts in information processing, for example response competition; (2) This conflict signal triggers strategic adjustments in cognitive control, which serve to prevent conflict in subsequent performance. A third proposal, also included from the outset, was that conflict monitoring might represent one aspect of a more general monitoring function, which detects internal states signaling a need to intensify or redirect attention or control.

Since the conflict-monitoring hypothesis was first proposed, a wealth of new data has appeared, bearing on all three of the foregoing proposals. In many cases, such data has bolstered the account. In others, it has posed challenges. Meanwhile, new proposals have emerged

concerning ACC function, modifying the context of the debate. In the present article, we summarize these recent developments, and consider their implications for the conflict-monitoring theory.

A cortical response to conflict

The first claim of the conflict-monitoring theory is that specific brain structures, and in particular the ACC, respond to the occurrence of conflict. This idea was originally motivated by a review of studies in which ACC activation had been observed during the performance of cognitive tasks [4,5]. In the majority of such studies, ACC engagement was associated with one of three behavioral contexts: (1) tasks that required the overriding of prepotent responses, (2) tasks that required selection among a set of equally permissible responses (underdetermined responding), or (3) tasks that involved the commission of errors (Figure 1). Through a series of computational models [4,6] (see Boxes 1 and 2), we demonstrated how ACC activation in each of these contexts could be explained based on a single function – the detection of conflict.

Subsequent studies have provided additional evidence concerning the involvement of the ACC in the settings of response override, underdetermined responding, and error commission. In the following, we revisit these three domains, focusing on work published within the past five years.

Response override

Tasks requiring the overriding of prepotent responses often involve conflict, in the form of competition between the correct response and the one being overridden. The finding of ACC engagement under such circumstances is, at this point, one of the most firmly established findings in all of cognitive neuroscience. The most frequent observation pertains to the Stroop task, where relative ACC activation has been observed in association with incongruent trials (Box 1), a finding that has been replicated in well over 15 studies (see [5,7] for reviews).

ACC activation has also been observed in various versions of the flanker task [3,8–12] (Box 2), in the Simon task [13], in the global–local paradigm [14,15], and in the go/no-go paradigm [16–18], as well as in other response override tasks [1,18–20].

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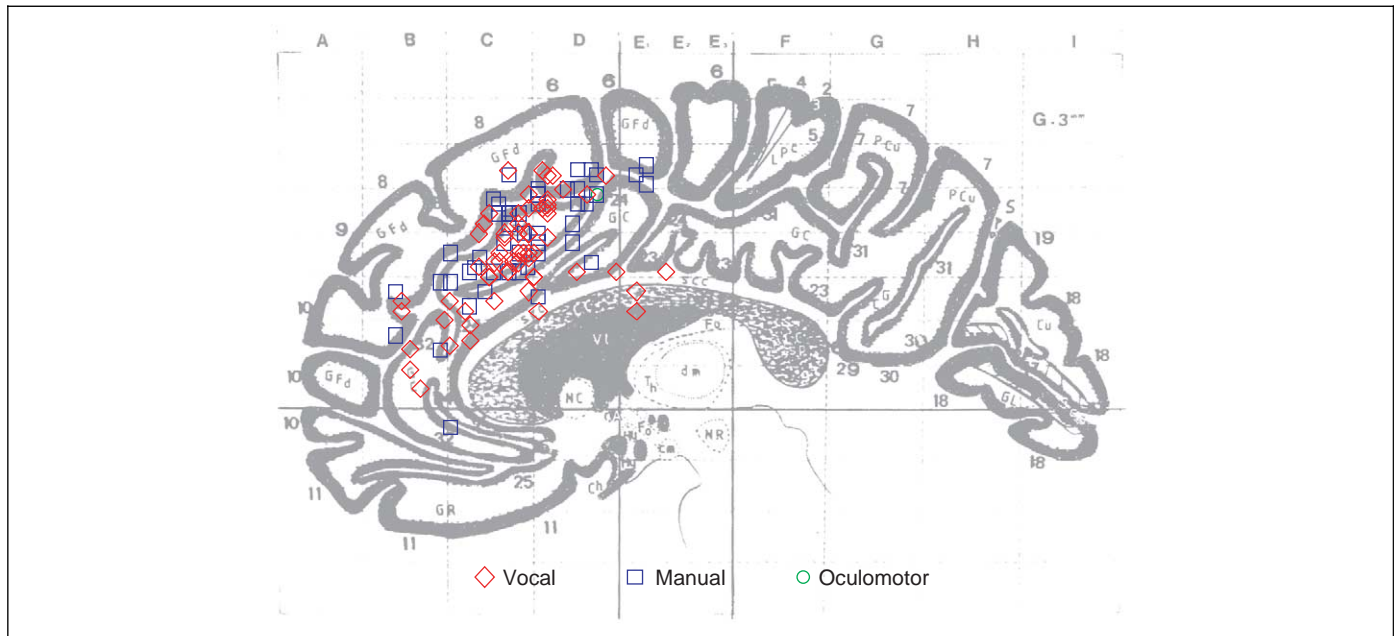Available online 2 November 2004

Figure 1. Activation maxima from imaging studies involving conflict (i.e. tasks involving response override, underdetermined responding or error commission), as reviewed by Barch and colleagues [5]. Color coding refers to response modality (red, vocal; blue, manual; green, oculomotor). Modified with permission from [5].

Underdetermined responding

Underdetermined responding constitutes a second context in which conflict is likely to arise, here in the form of competition among permissible responses [4]. Consistent with the conflict-monitoring hypothesis, underdetermined responding is also a context in which ACC activation is reliably observed. Multiple studies have reported ACC engagement during performance of the stem-completion task [21], and the verb generation task [22,23], as well as during simple motor tasks involving underdetermined responding [24]. Moreover, there is evidence that ACC activation varies with the number of responses associated with a stimulus, such that greater ACC activation occurs during more underdetermined responding [22,23].

Errors

Another well-established finding is that the ACC transiently activates in association with the commission of errors. This activation has been studied most extensively using electroencephalography (EEG), where it takes the form of a transient potential referred to as the error-related negativity (ERN) [25,26], but error-related ACC engagement has also been observed using fMRI [1,18,27,28].

Behavioral and electromyographic observations indicate that errors in speeded response tasks are frequently associated with response conflict [6]. This is because, even as an error response is being executed, ongoing processing of the stimulus often leads to a belated activation of the correct response, giving rise to a transient period during which both correct and incorrect responses are activated. The resulting association of errors with post-response conflict suggests that ACC activation during errors, like its activation during response override and underdetermined responding, might reflect another instance of conflict detection.

Recent computational modeling work by Yeung *et al.* [6] shows that the conflict-monitoring theory can account for numerous detailed aspects of the ERN, including several features that were previously unexplained. One important prediction of this work was that an EEG potential resembling the ERN should be discernable in association with *correct* responses, if these are associated with response conflict. Just such a potential, referred to as the N2, has now been reported in multiple studies [6,29,30] (Box 2).

It follows from the conflict-monitoring theory that error-related activity should be observed in the same area within the ACC that responds during high-conflict correct responses. This prediction has been confirmed with fMRI [1,31]. However, other studies have added a twist. In three experiments [18,27,28], errors have been found to engage two distinct regions within the ACC: a posterior region that responds during both errors and high-conflict correct responses, but also a more anterior region, which responds preferentially to errors. The dissociation is not clear-cut: Braver *et al.* [18] have provided evidence that the anterior region does respond during high-conflict correct trials, although less strongly than to errors. Furthermore, evidence suggests that the ERN, a focus of work on error processing, is linked to the more posterior area [30]. Nevertheless, this possible fractionation of function within the ACC is an important area for further research.

Another finding with apparent implications for the conflict-monitoring theory is that an evoked potential, resembling the ERN, occurs in response to feedback indicating the commission of an error [32,33]. It is not known, at present, whether this 'feedback-related negativity' (FRN) derives from the same portion of the cingulate that generates the ERN; fMRI experiments, aimed at answering this question, have yielded conflicting results [34,35]. Furthermore, some evidence suggests that the FRN might be linked to conflict between actual and expected events [36]. Even if the FRN did turn out to

Box 1. Conflict monitoring in the Stroop task

The Stroop task has provided a useful setting in which to evaluate the conflict-monitoring hypothesis. Here, subjects name the color in which words are displayed, and respond faster when the words themselves name that same color (congruent trials) than when they name a different color (incongruent). Computational models have accounted for this reaction time difference in terms of crosstalk between processing pathways underlying color-naming and word-reading, culminating in conflict – the simultaneous activation of incompatible, and competing, representations.

We used one such model (Figure Ia) to show how conflict monitoring might explain the frequent finding of ACC activation during incongruent trials in the Stroop task [4]. The approach was to add a new element to the Stroop model, a 'conflict-monitoring' unit that took input from the response layer of the base model, and became active during response competition (blue elements in Figure Ia).

This model also implemented the claim that conflict monitoring influences control: the activity level of the conflict-monitoring unit influenced the state of units responsible for representing the current task, such that periods of high conflict caused the model to become more focused on the color-naming task, displaying less interference from the task-irrelevant word-reading pathway. This led the model to show less Stroop interference when incongruent trials were frequent than when they were rare, a pattern that has been observed in human performance (Figure Ib).

Note that, if the conflict-monitoring theory is correct, variations in trial-type frequency should affect not only behavior, but ACC activation as well. Just as the behavioral data indicate that incongruent trials induce more conflict when such trials are rare, ACC activation during incongruent trials should also be greater under these conditions. fMRI data have confirmed this prediction [38] (Figure Ic).

Another prediction of the conflict-monitoring theory is that the state of cognitive control should vary depending on the level of ACC activation on *preceding* trials. In the setting of the Stroop task, the theory predicts that high ACC activation should trigger an increased focus on the color-naming task, leading to less Stroop interference on the next trial. This prediction was confirmed in a recent neuroimaging study [63] (Figure Id).
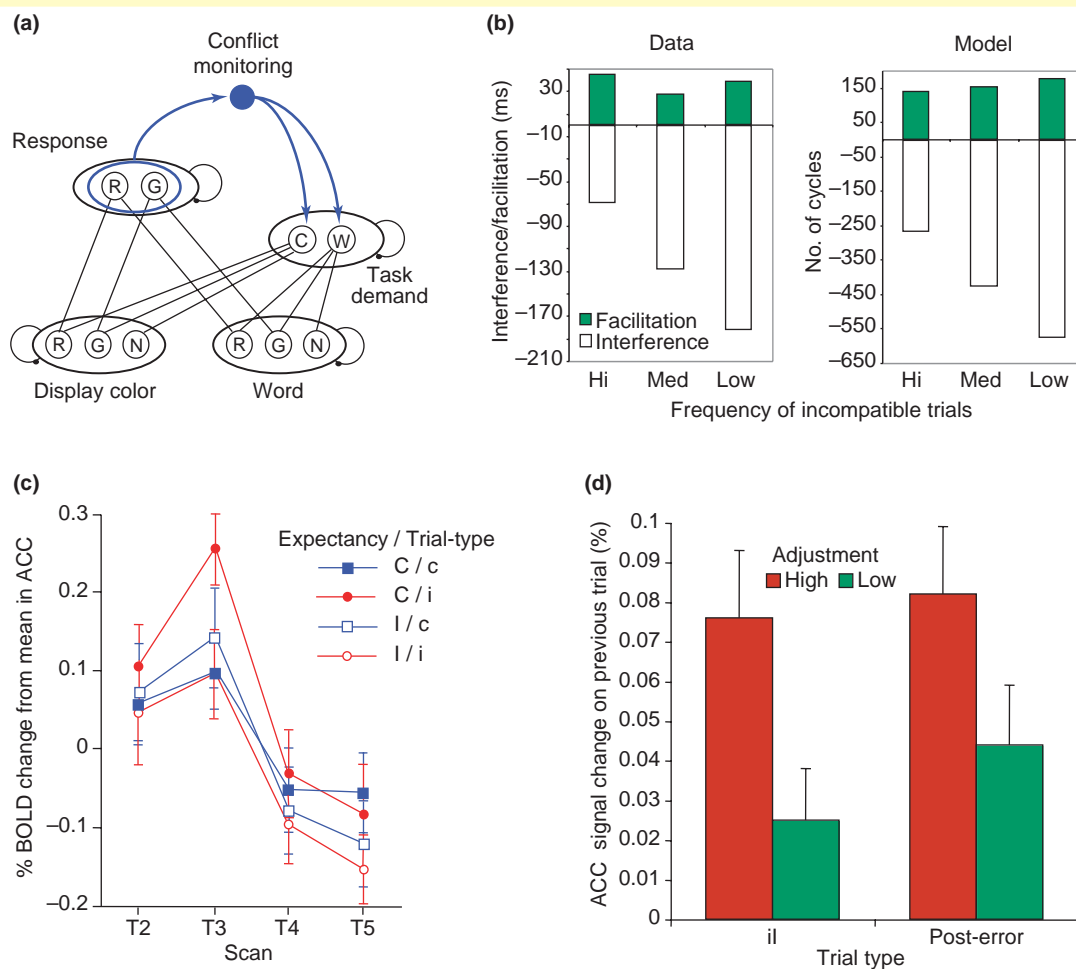

Figure I. (a) A neural network implementation of conflict monitoring in the Stroop task [4]. In the base model (shown in black), word-reading and color-naming pathways converge on a response layer, and task units bias processing towards one pathway or the other. Conflict in the response layer leads to activation of a conflict-monitoring element (blue), which, in turn, modulates activity of the task units. Base model (black) redrawn with permission from [79]. **(b)** Stroop interference (neutral trial RT – incongruent trial RT) increases as incongruent trials become more infrequent, both in human performance (left; data redrawn with permission from [80]) and in the conflict-monitoring model (right; redrawn with permission from [4]). **(c)** ACC activation on incongruent Stroop trials is higher when such trials are infrequent (C/i) than when they are frequent (I/i), as predicted by the conflict-monitoring theory. T2 to T5 are different scans within a 12.5 s trial. The peak at T3 is due to the lag in hemodynamic response. Data redrawn with permission from [38]. **(d)** As predicted by the conflict-monitoring account, trials with high ACC activation are followed by shifts towards more focused behavior (i.e. less Stroop interference). Among iI trials (left; incompatible trials that were preceded by another incompatibe trial) those with relatively short RTs ('high adjustment') occurred only following high ACC activation. Among trials following errors (right) relatively long RTs ('high adjustment' in this case) occurred when the error itself induced high ACC activation. Data redrawn with permission from [63].

Box 2. Conflict monitoring in the flanker task

In the flanker task, subjects are asked to identify a central letter (or other simple target) but to ignore flanking items. Subjects respond more slowly when the flankers are associated with a different response from the one associated with the target (incompatible, as opposed to compatible, trials). Like incongruent trials in the Stroop task (see Box 1), incompatible flanker trials involve crosstalk between task-relevant and task-irrelevant processing pathways, leading to the activation of incompatible and competing representations – that is, conflict. A specific account of this crosstalk has been provided by computational models such as the one shown in Figure Ia (black portion) [78].

In neuroimaging studies of the flanker task, greater ACC activation has been observed on incompatible than compatible trials [3,8–10,12], a finding interpreted by the conflict-monitoring theory as a signal of conflict. Botvinick *et al.* [4] simulated this imaging result by adding a conflict-monitoring unit to the basic flanker task model (blue elements in Figure Ia). This unit became active when units in the response layer of the underlying model were simultaneously active; that is, during response conflict. In keeping with the conflict-monitoring theory, this unit also fed forward to influence the control state of the underlying model; high activation of the conflict-monitoring unit triggered an intensification of top-down support for the processing of the central target item in the input. This link from conflict monitoring to control led the model to show more target-focused behavior following

incompatible trials than following compatible trials, a pattern also observed in human performance (Figure Ib).

In addition to this behavioral sequence effect, the conflict-monitoring theory predicts a sequence effect at the level of ACC activation. The fact that behavior becomes more focused following incompatible trials means that less conflict should occur *during* incompatible trials when these follow other incompatible trials. Based on this, the theory predicts that ACC activation on incompatible trials should be greater following compatible trials than following incompatible ones. This prediction was confirmed in an fMRI study of the flanker task [3] (Figure Ic), the results of which have recently been replicated and extended [8].

The flanker task has also been frequently used in studies of the neural response to error-commission, and in particular in studies of the ERN. Yeung *et al.* [6] used the model in Figure Ia to show how ACC activation associated with errors could reflect a reaction to conflict, specifically conflict between the error response and the (belatedly activated) correct response. A key aspect of the model is that it explains why ACC activation should be linked both to errors and to high-conflict correct responses. Importantly, however, the model also suggests that the timing of conflict – and thus of ACC activation – should be qualitatively different in the two cases, tending to *precede* the overt response on correct trials and to *follow* it on errors. This predicted difference in the timing of ACC activation has been confirmed in two separate EEG experiments [6,30] (Figure Id).

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represent a genuine response to feedback, this would still leave the question of how errors are detected *as they occur* (that is, before or in the absence of feedback), because this is when the ERN occurs. At present, the only available explanations for this on-line form of error detection rest upon some version of conflict monitoring [6,25,36].

An evaluative rather than regulative role

According to a competing account, ACC activation reflects not a signal of conflict, but instead the application of top-down control [37]. At least five studies have tested between these two views, and in each case the evaluative account provided by the conflict-monitoring theory has been supported over the competing, regulative view. In each study, two conditions of ACC activation were compared: one involving high response conflict and weak top-down control, and one involving low conflict and a high level of top-down control. In two studies involving the Stroop task [38,39] (Box 1) and three using the flanker task [3,8,9] (Box 2), ACC activation was found to be greater in high-conflict/low-control trials, suggesting that it is more closely tied to conflict detection than to top-down control.

The special status of response conflict

Conflict can occur at numerous levels of information processing, ranging from perceptual representation, to stimulus categorization, to response selection and task representation. Several studies have examined whether the ACC responds to conflict at all of these levels, or whether it is sensitive only to certain forms of conflict. In general, such studies have supported the conclusion that the ACC is engaged most strongly during conflicts at the level of response selection [10,11,15,40–42], a finding that accords with the strong connectivity between the ACC and motor structures including premotor, supplementary motor, and primary motor areas [43,44].

If response conflict were the only type of conflict to engage the ACC, the data might be consistent with the view that the ACC is itself essentially a motor structure, but perhaps one concerned with selecting among competing responses [19,45]. Although this possibility cannot be ruled out, it is important to note that several studies have provided evidence for ACC activation in the setting of conflict at other levels of processing, including stimulus evaluation [15,41,46] and task representation [20], pointing to a broader monitoring function.

Localization of the conflict response

In the majority of studies addressing the issue, the ACC response associated with conflict has been localized to a region overlying the cingulate sulcus, approximately two centimeters rostral to the anterior commissure plane [44,47,48] (Figure 1). This lies within Brodmann's areas 24 and 32, in a region also referred to as the anterior rostral cingulate zone [47]. In some recent work [12,49–52], it has been suggested that the relevant activations might instead lie more dorsally, within the pre-supplementary motor area. One limitation shared by the relevant studies is that, given their design, comparisons between conditions could reflect differences in strategy or control state rather than differences in conflict, either because stimulus presentation was blocked, or because (as in [50]) different portions of the reaction-time distribution were considered for different trial types. This, combined with the large number of studies where conflict-related responses have been localized to the ACC, creates some difficulty in accepting the idea that such responses in fact reside more dorsally. However, this is clearly an issue that deserves further research.

Further questions about localization arise from work with non-human primates. Schall and colleagues [53,54] observed conflict-related neural activity in supplementary
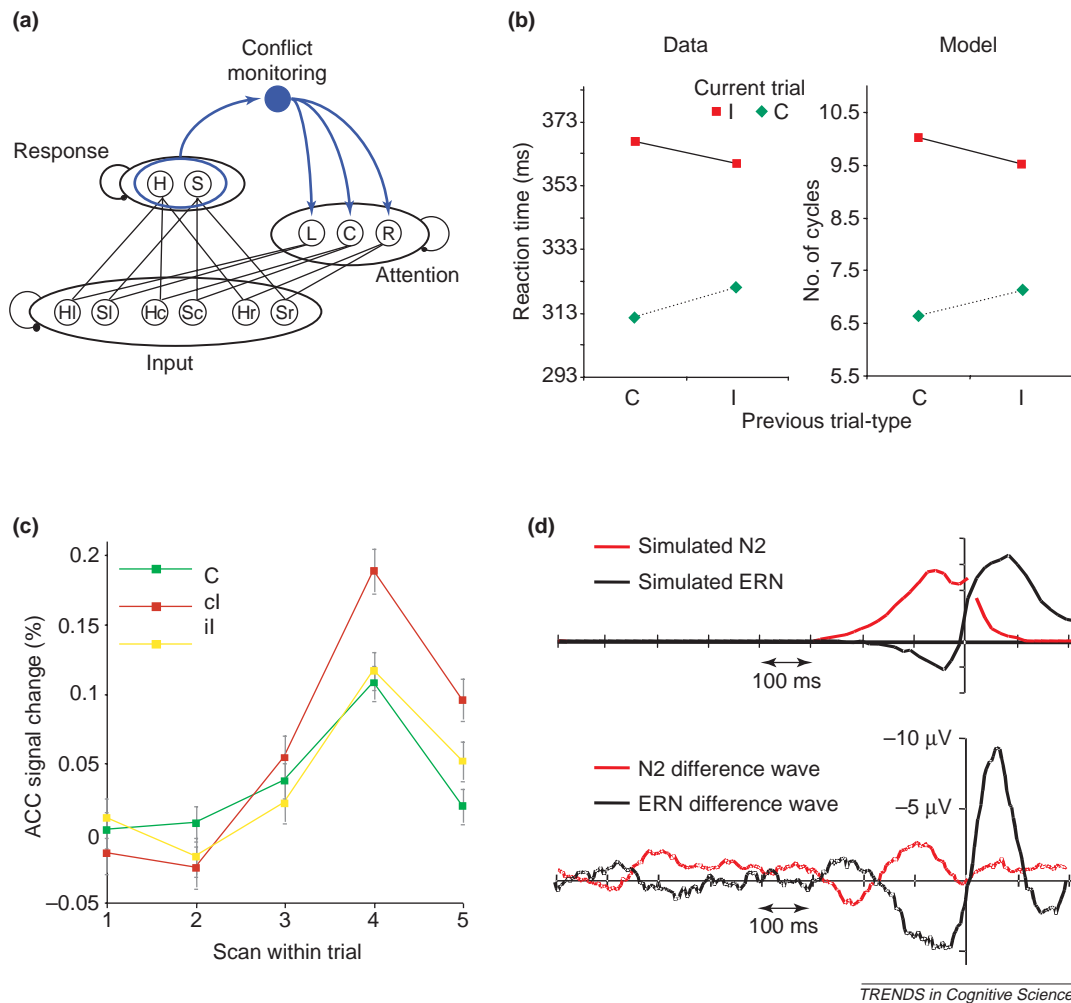
Figure I (Box 2). **(a)** A neural network implementation of conflict monitoring in the flanker task [4]. In the base model (shown in black), target and flanker inputs send activation to a response layer, and attention units bias processing towards the target input. Conflict in the response layer leads to activation of a conflict-monitoring element (blue), which, in turn, modulates activity of the attention units. Redrawn with permission from [78]. **(b)** Performance is more focused on the target item (less influenced by the flankers, so response is faster) on trials following incompatible trials, both in human performance (left; data redrawn with permission from [58]) and in the conflict-monitoring model (right; data redrawn with permission from [4]). **(c)** As predicted by the conflict-monitoring theory, ACC activation is greater on incompatible trials following compatible trials (cI) than on incompatible trials following incompatible trials (iI) (C = compatible trials). Data redrawn with permission from [3]. **(d)** In the model shown in (a), errors are associated with post-response conflict, providing an account for how the error-related negativity (ERN) measured in the ACC might arise from conflict monitoring. The same model predicted that an ERN-like potential should occur on high-conflict correct trials, but that this potential should peak *before* the overt response, a prediction that was confirmed by EEG. Model and EEG data redrawn with permission from [6].

Box 3. Questions for future research

• How is conflict detection translated into compensatory adjustments in cognitive control? How detailed is the information that the conflict-monitoring function conveys to centers responsible for cognitive control, and how is this information used to generate a strategic response?

• What are the neuronal events underlying conflict-associated ACC activation, as observed with neuroimaging? What factors explain the fact that conflict-related ACC activity is ubiquitous in human neuroimaging studies, but has not yet been clearly observed in monkeys?

• What is the relationship between conflict monitoring and error monitoring in the brain? Are errors detected based on the conflict they involve, or does error monitoring rely upon fundamentally different mechanisms (or are both of these statements true)?

• Data support the view that the ACC is involved in conflict monitoring, but also the view that it is involved in action-outcome monitoring and/or reward-based decision-making. Are these perspectives mutually exclusive, or can they be reconciled?

eye field, but not in ACC (but see [45]). Although these studies encourage the idea that conflict-related activation lies outside the ACC, it should be noted that they used a version of the go/no-go task, a task which has been clearly shown to engage the ACC in humans [16,18]. The reasons for this and other contradictions between human and monkey data are not fully understood. It could be that the cingulate response reflects neural synchronization [55] or synaptic events, detectable through EEG or fMRI (the techniques usually applied in humans), but not evident at the level of single-unit spike trains (as collected from monkeys). Furthermore, there are cytoarchitectonic differences between human and monkey ACC [56], which make it plausible that functional differences also exist.

In view of such considerations, it would be very useful if single-unit recording experiments like those that have been undertaken with monkeys could be conducted with

humans. The feasibility of such work has been demonstrated by Davis and colleagues [57], who reported activation of single neurons within human ACC during performance of cognitively demanding tasks. It would also undoubtedly prove illuminating to apply fMRI or intracranial EEG to non-human primates, in behavioral contexts similar to those that have produced ACC activation in humans.

Conflict monitoring and the modulation of control

According to the conflict-monitoring hypothesis, the ACC response to conflict triggers strategic adjustments in cognitive control, which serve to reduce conflict in subsequent performance. Initial evidence for this proposal was drawn from cognitive psychology, where several observations suggested the occurrence of adjustments in strategy following the occurrence of conflict. For example, Gratton *et al.* [58] showed, in the flanker task, that interference is reduced following incompatible trials (Box 2), and analogous effects have been observed in the Stroop task (Box 1), the Simon task [59], and elsewhere [60]. Recent research has demonstrated (*pace* [61]) that such sequence effects cannot be attributed entirely to perceptual or motor priming [62]. By contrast, as has been shown through computational modeling [4], such effects can be explained in quantitative detail by the conflict-monitoring hypothesis (Boxes 1 and 2). According to this explanation, the observed fluctuations in behavior reflect reactive adjustments in cognitive control, triggered on a trial-by-trial basis by conflict signals from the ACC.

This account gives rise to a crucial prediction concerning the relationship between ACC activation and subsequent performance. Specifically, strong ACC engagement should be followed by behavior reflecting relatively focused attention (strong top-down control), and weak ACC engagement by less focused behavior. A striking confirmation of this prediction was reported by Kerns and colleagues [63], in the context of the Stroop task (Box 1). They found that, when incongruent trials were associated with high ACC activity, relatively low interference was observed on the *subsequent* trial. This fits well with the idea that strong ACC engagement leads to a reinforcement of top-down control. Consistent with this, Kerns and colleagues observed that, following trials with strong ACC engagement, there was relatively strong activation in dorsolateral prefrontal cortex, a brain region closely associated with cognitive control.

Consistent with previous studies, Kerns also observed ACC engagement in association with errors [63]. Interestingly, the magnitude of this error response was related to post-error performance, with higher activation associated with a relatively large slow-down in reaction times. This finding is consistent with the proposal, put forth by Botvinick *et al.* [4], that post-error slowing might be a consequence of conflict monitoring. Although the same relationship between ACC activation and post-error slowing has been observed elsewhere [26,31], this must be reconciled with other studies, where apparent dissociations between the ERN and post-error behavior have been reported [64,65].

The data presented by Kerns and colleagues [63] provide strong support for the proposal that ACC activity is linked to subsequent shifts in cognitive control. Also consistent with this claim are the results of several neuropsychological studies, where abnormalities in cognitive control have been observed following ACC lesions [66,67]. Having said this, it should be acknowledged that neuropsychological findings have been quite variable. Some studies have found no clear-cut deficits in cognitive control, noting instead problems with response selection [68] or autonomic function [69]. Further work clarifying the effects of ACC damage is warranted.

Conflict monitoring in the larger context of ACC function

As noted earlier, an important assertion of the conflict-monitoring hypothesis is that conflict monitoring constitutes one instance of a more general evaluative function. In earlier work, we suggested that the ACC might serve to detect events or internal states indicating a need to shift the focus of attention or strengthen top-down control ([4], see also [20]), an idea consistent, for example, with the fact that the ACC responds to pain [48]. Although this idea remains plausible, recent research also provides a larger context in which to consider the relation between conflict monitoring and the overall function of the ACC.

Action-outcome evaluation and reward-based action selection

Several recent studies have suggested that the ACC serves to evaluate action outcomes. Gehring and Willoughby [70], for example, reported ACC engagement when subjects were informed of the outcomes of their decisions in a gambling task. This study, and others [33,71–73], suggest that the ACC responds disproportionately to outcomes considered aversive or signaling reductions in reward. It has been proposed, further, that the overall function of the ACC might involve the use of outcome, and particularly reward-related, information to guide action selection [45,72–74]. Rushworth and colleagues [49] suggest that the ACC guides action selection based on a cost–benefit analysis, integrating information about past action outcomes. A particularly interesting suggestion is that this cost–benefit analysis might take into account the effort associated with candidate actions [75].

It might turn out that some findings underlying the action-outcome account can be better explained in terms of conflict detection (see [35]). However, on the whole, the evidence for this view of ACC function appears reasonably compelling. What are the implications of this new perspective for the conflict-monitoring theory?

It is tempting to view the outcome evaluation account as an exclusionary alternative to the conflict-monitoring view. After all, the outcome account addresses phenomena that seem difficult to explain in terms of conflict monitoring (for example, ACC activation relating to reward expectation [72]). However, it should be noted that the converse is also true: the outcome evaluation account, in its present form, provides no explanation for much of the data addressed by conflict monitoring (e.g. the pervasive finding of ACC engagement in situations involving response override and underdetermined

responding). Indeed, some of the very studies upon which the outcome evaluation view are based have found it necessary to invoke conflict monitoring to account for all of their findings (e.g. [34]). In view of this, it seems misguided to reject one of these two views of ACC function in favor of the other. Instead, the data invite a consideration of how action–outcome evaluation and conflict monitoring might fit together within a larger account of ACC function.

Towards an integrative account

One promising way of reconciling the two accounts is to consider that conflict monitoring might simply constitute one instance of a more general outcome monitoring function. That is, if the ACC is involved in monitoring and evaluating the outcomes of actions, it may be that conflict is among the outcomes to which the ACC is sensitive. This proposal fits with the suggestion that the ACC responds to events indicating a reduction in reward [73], given that responses associated with conflict tend to be slower and less accurate than low-conflict responses, and thus less likely to fulfill task objectives (indeed, post-response conflict can be a very sensitive and specific indicator of error; see Box 2). At the same time, the proposal provides a way of linking the putative role of the ACC in action–outcome evaluation with ACC engagement during response override and underdetermined responding.

A possible extension of this proposal is suggested by the claim that the ACC encodes information about effort [49,75]. With this in mind, it is interesting to consider the hypothesis that conflict might serve as an index of the demand for mental effort. Consistent with this, it has been noted that the ACC becomes active in just those task settings that are experienced as cognitively difficult [37,76]. Indeed, as we have argued elsewhere [4], the induction of conflict can plausibly be considered to be a defining feature of difficult tasks. The ACC has also been shown to be the generator of the midline theta rhythm, an EEG oscillation that is characteristically observed during intense concentration [77]. In addition, there is evidence suggesting that the ACC is importantly involved in linking mental effort to the autonomic changes that typically accompany it [69].

Together, these existing findings make it seem plausible that the ACC might monitor conflict as an index of task difficulty (and/or the mental effort it demands), entering this into cost–benefit analyses underlying action or strategy selection. This proposal is, of course, speculative, and further research will be needed to evaluate its merit (see also Box 3 for other future research issues). However, it does serve to indicate how recent findings concerning the ACC might be integrated with the increasingly abundant evidence for engagement of the ACC by conflict.

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