

Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function

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According to one influential account, the anterior cingulate cortex (ACC) serves to monitor for conflicts in information processing. According to another influential account, the ACC monitors action outcomes and guides decision making. Both of these perspectives are supported by an abundance of data, making it untenable to reject one view in favor of the other. Instead, the apparent challenge is to discover how the two perspectives might fit together within a larger account. In the present article, we consider the prospects for such a reconciliation. Juxtaposing the conflict-monitoring and decision-making accounts suggests an extension of the conflict-monitoring theory, by which conflict would act as a teaching signal driving a form of avoidance learning. The effect of this mechanism would be to bias behavioral decision making toward cognitively efficient tasks and strategies. We discuss evidence favoring this proposal and present an initial computational model, which lays the foundation for further development.

The past decade has seen explosive growth in work addressing the cognitive function of the dorsal anterior cingulate cortex (ACC). As recently as 1990, only a few tentative proposals had been advanced to address the role of the ACC in behavior (MacLean, 1990; Mesulam, 1981; Papez, 1937). Since then, the situation has changed dramatically. The supply of empirical data has burgeoned, thanks to scores of new studies using human neuroimaging and psychophysiological techniques, human and monkey neurophysiology, and neuroanatomical and neuropsychological analysis. At the same time, an increasingly clear-cut set of theoretical proposals concerning ACC function has emerged. Most research on the ACC is now closely guided by specific predictions proceeding from explicit, although still evolving, theoretical perspectives.

In the present article, we will consider two such perspectives, which together have motivated a large portion of the research on the ACC over the past several years. The first of these perspectives maintains that the ACC serves in part to detect conflicts in information processing, a function that has been referred to as *conflict monitoring*. The second proposes that the ACC plays a central role in *outcome evaluation* and *decision making*. As we shall detail, these two perspectives appear often to have been understood as mutually exclusive competitors (see, e.g., Nachev, 2006). The central purpose of the present article is to propose an integrative account, indicating how the conflict-monitoring and decision-making perspectives might fit coherently into a larger whole.

Some headway toward this objective can be made by simply identifying potential points of alignment between the two theories as they currently stand. However, the case we will make here also involves a new proposal that significantly extends both the conflict-monitoring and the outcome-evaluation/decision-making accounts. Our proposal will be that, within the cost-benefit analyses that underlie behavioral decision making, the occurrence of conflict registers as a cost. More precisely, we will argue that conflict monitoring drives a form of avoidance learning, which biases behavior away from tasks and strategies that are prone to induce conflict and, thus, toward activities that afford relatively efficient information processing.

Before laying out this proposal, we will begin by briefly reviewing the two perspectives that, together, provide its motivation.

The ACC and Conflict Monitoring

A large body of experimental evidence has accrued to support the idea that the ACC is engaged by the occurrence of conflicts in information processing (for reviews, see Botvinick, Cohen, & Carter, 2004; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). The idea was first suggested by neuroimaging data, suggesting that common areas of the ACC are engaged by situations requiring the overriding of prepotent responses, by situations requiring selection among a set of equally permissible responses, and by situations involving errors, all contexts involving response conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001). Subsequent research has strongly con-

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firmed ACC engagement in all three of these contexts. The association of ACC activation with situations requiring response override, in particular, has become one of the best-established findings in cognitive neuroscience. The finding of greater ACC activation on incongruent than on congruent trials in the Stroop task, for example, has been replicated in well over 15 studies (for reviews, see Barch et al., 2001; MacLeod & MacDonald, 2000), and ACC activation has also been observed in various versions of the flanker task (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Casey et al., 2000; Durston et al., 2003; Hazeltine, Poldrack, & Gabrieli, 2000; van Veen, Cohen, Botvinick, Stenger, & Carter, 2001), in the Simon task (Kerns, 2006; Peterson et al., 2002), in the global-local paradigm (Lux et al., 2004; Weissman, Giesbrecht, Song, Mangun, & Woldorff, 2003), and in the go/no-go paradigm (Braver, Barch, Gray, Molfese, & Snyder, 2001; de Zubicaray, Andrew, Zelaya, Williams, & Dumanoir, 2000; Durston, Thomas, Worden, Yang, & Casey, 2002), as well as in other response override tasks (Badre & Wagner, 2004; Braver et al., 2001; Carter et al., 1998; Paus, Petrides, Evans, & Meyer, 1993). Selection among equally permissible responses (which we have sometimes referred to as *underdetermined responding*) has also now been extensively demonstrated to engage the ACC. Multiple studies have reported ACC activation during stem completion (Palmer et al., 2001) and verb generation (Barch, Braver, Sabb, & Noll, 2000; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997), as well as during simple motor tasks involving underdetermined responding (Frith, Friston, Liddle, & Frackowiak, 1991). Moreover, there is evidence that ACC activation increases with the number of responses associated with a stimulus (Barch et al., 2000; Thompson-Schill et al., 1997). ACC engagement with error commission is also now quite well established, having been observed with electroencephalography (see Falkenstein, Hoormann, Christ, & Hohnsbein, 2000), functional neuroimaging (e.g., Carter et al., 1998; Kiehl, Liddle, & Hopfinger, 2000), and single-unit recording (e.g., Amiez, Joseph, & Procyk, 2005; Ito, Stuphorn, Brown, & Schall, 2003). There has been some controversy as to whether this finding constitutes evidence for the conflict-monitoring theory, with some findings seeming to support this (e.g., van Veen, Holroyd, Cohen, Stenger, & Carter, 2004; Yeung, Botvinick, & Cohen, 2004) and others suggesting that it may not be the whole story (e.g., Frank, 2005b; Holroyd & Coles, 2002; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003). However, even the latter studies have often found it necessary to invoke conflict monitoring to account for some of their findings (see Frank, 2005b; Holroyd & Coles, 2002), suggesting that the debate bears more on the particular issue of error processing than on the viability of the conflict-monitoring theory as a whole.

There have been other, more direct challenges to the conflict-monitoring theory, but in each case, subsequent findings have raised doubts. For example, Nakamura, Roesch, and Olson (2005), in single-unit recordings in monkeys, failed to observe conflict-related activity in

the ACC (see also Ito et al., 2003; Stuphorn, Taylor, & Schall, 2000). However, recent single-unit recording work in human subjects has detected apparent conflict-related activity (Davis, Hutchison, Lozano, Tasker, & Dostrovsky, 2000; Davis et al., 2005), suggesting that there may be differences between species (as has been suggested by Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001). Brown and Braver (2005) reinterpreted much of the data that had previously been interpreted in terms of conflict monitoring as reflecting, instead, an error likelihood computation. This perspective purported to subsume, rather than contradict, the conflict-monitoring account. However, a subsequent multiexperiment study (Nieuwenhuis, Schweizer, Mars, Botvinick, & Hajcak, 2007) failed to replicate the findings of Brown and Braver (2005), leaving their implications uncertain (but see Brown & Braver, 2007).

Although there clearly remain issues to be resolved, it seems fair to say that there now exists strong support for the idea that the ACC is engaged by conflict. Once this point is accepted, however, it leads directly to a new question: What purpose might conflict monitoring fulfill? One proposal that has garnered considerable support is that conflict monitoring serves to modulate the functioning of cognitive control. A key insight underlying this proposal is that control serves, in large part, to prevent the occurrence of cross-talk between concurrent information processing activities and that, as a result, the occurrence of conflict can be interpreted as reflecting an unmet demand for control (Botvinick et al., 2001). In the Stroop task, for example, insufficient top-down support of color-naming pathways will permit interference from word reading (see Cohen, Dunbar, & McClelland, 1990; Miller & Cohen, 2001). Thus, in this context as in others, conflict can be seen as an index of the demand for control. This observation leads naturally to the idea that conflict monitoring might serve as a feedback signal to cognitive control mechanisms. According to this idea, the ACC response to conflict would trigger strategic adjustments in cognitive control, which serve to reduce conflict in subsequent performance.

Considerable evidence supports the idea that the ACC is involved in driving reactive adjustments in control. On the behavioral level, such adjustments have been observed in a wide range of task settings, including the flanker task (Gratton, Coles, & Donchin, 1992), the Stroop task (Kerns et al., 2004), the Simon task (Stürmer, Leuthold, Soetens, Schroeter, & Sommer, 2002), and elsewhere (Jones, Cho, Nystrom, Cohen, & Braver, 2002). Recent research has demonstrated (*pace* Mayr, Awh, & Laurey, 2003) that such sequence effects cannot be attributed entirely to perceptual or motor priming (Notebaert & Verguts, 2007; Ullsperger, Bylsma, & Botvinick, 2005) or to expectancy effects (Egner, 2007). Recent neuropsychological work also demonstrates (*pace* Fellows & Farah, 2005) that such reactive adjustment effects are attenuated following injury to the ACC (di Pellegrino, Ciaramelli, & Ladavas, 2007). Perhaps most conclusive, Kerns and colleagues observed a correlation between ACC activity on individual trials and the strength of top-down control on succeeding trials, both in the Stroop task (Kerns et al., 2004) and in the Simon

task (Kerns, 2006). Taken together, these findings provide compelling support for the idea that conflict-related activity in the ACC leads, at least under some circumstances, to compensatory adjustments in control.

The ACC, Outcome Evaluation, and Decision Making

Even as evidence has accrued in favor of the conflict-monitoring account, another stream of data has given rise to a different interpretation of ACC function. In particular, a series of studies has suggested that the ACC serves to evaluate action outcomes. Gehring and Willoughby (2002), for example, reported ACC engagement when subjects were informed of the outcomes of their decisions in a gambling task. This study, along with others (Bush et al., 2002; Holroyd & Coles, 2002; Luu et al., 2003; Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2004), suggests that the ACC responds particularly strongly to outcomes considered aversive or signaling reductions in reward. Indeed, a remarkably wide range of negative outcomes has been shown to engage the ACC, including monetary loss (Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003; Yeung & Sanfey, 2004), pain (see Rainville, 2002), negative feedback (Miltner, Braun, & Coles, 1997; Nieuwenhuis et al., 2004), and even social rejection (Eisenberger, Lieberman, & Williams, 2003) and the witnessing of pain in others (Botvinick et al., 2005; Singer et al., 2004).

It has been proposed that the overall function of the ACC might involve the use of outcome, and particularly reward-related, information to guide action selection (Bush et al., 2002; Hadland, Rushworth, Gaffan, & Passingham, 2003; Holroyd & Coles, 2002; Matsumoto, Suzuki, & Tanaka, 2003). Rushworth, Walton, Kennerley, and Bannerman (2004) suggested that the ACC guides action selection on the basis of a cost-benefit analysis, integrating information about past action outcomes. Consistent with this, Kennerley, Walton, Behrens, Buckley, and Rushworth (2006) found that ACC lesions produced dramatic departures from optimal behavior in a reward-based decision-making task, concluding that the "ACC has an essential role in both learning and using extended action-outcome histories to optimize voluntary choice behavior" (p. 940).

The ACC has been further linked to value-based decision making by data suggesting its involvement in avoidance learning. A series of studies in rabbits by Gabriel and colleagues (reviewed in Gabriel, 1993) provided early evidence for an ACC role in learning to avoid aversive events. Support for such a role in humans has been provided by subsequent fMRI data (e.g., Kim, Shimojo, & O'Doherty, 2006). Particularly strong evidence, again from animal research, has come from Johansen and Fields (2004), who found that glutamatergic activation of the ACC produced an aversive teaching signal, leading to subsequent avoidance behavior.

Further evidence suggests that the involvement of the ACC in avoidance learning may be based on the influence of the ACC on dopaminergic function. Dopamine has been extensively implicated in avoidance learning (Beninger,

1989). In particular, aversive stimuli have been shown to induce phasic inhibition of dopaminergic neurons in the ventral tegmental area (Ungless, Magill, & Bolam, 2004), which have been proposed to drive avoidance learning through their influence on synaptic plasticity in the basal ganglia (Frank, 2005a; Frank & Claus, 2006). Given such findings, it is of interest that manipulations of ACC activation induce changes in midbrain dopaminergic activity (Gariano & Groves, 1988; Murase, Grenhoff, Chouvet, Gonon, & Svensson, 1993; Svensson & Tung, 1989; Tong, Overton, & Clark, 1996). Of particular relevance is the finding that stimulation of the ACC can transiently inhibit dopamine release (Jackson, Frost, & Moghaddam, 2001). Pulling together such data, Frank (2005a) proposed that ACC activation might drive avoidance learning by inducing phasic dips in the activity of the mesolimbic dopaminergic system.

Are the Two Theories Competing or Compatible?

There is a natural temptation to view the conflict-monitoring and outcome-evaluation/decision-making perspectives as mutually exclusive alternatives, in direct competition. However, to take this stance would be a mistake, both for theoretical reasons and for empirical ones. On the theoretical level, it is important to recognize that the conflict-monitoring theory, at least in its original framing, was never advanced as an exhaustive account of ACC function. Rather, as was stated in Botvinick et al. (2001), "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" (p. 626). Thus, even in its original formulation, the conflict-monitoring theory envisioned a larger role for the ACC, which, it may fairly be said, featured outcome evaluation as a central component. On the empirical side, studies focusing on the role of the ACC in outcome evaluation and decision making have often noted that it is difficult to account for their findings in terms of conflict monitoring. However, it has been less often acknowledged that the converse is also true: The outcome-evaluation/decision-making account, in its present form, provides no explanation for much of the data addressed by conflict monitoring, such as the pervasive finding of ACC engagement in situations involving response override and underdetermined responding, and the relationship between ACC activation and subsequent performance, as reported by Kerns (2006; Kerns et al., 2004). Indeed, as was mentioned earlier, some of the very studies upon which the outcome-evaluation/decision-making view are based have found it necessary to invoke conflict monitoring to account for some of their findings (e.g., Frank, 2005b; Holroyd et al., 2004).

A satisfying account of existing observations thus seems to require provisional acceptance of *both* the conflict-monitoring view and the outcome-evaluation/decision-making view. However, although this allows a great deal of data to be explained, it also causes some legitimate discomfort, since it seems unparsimonious to accord two unrelated functions to a single parcel of cor-

tex. The challenge posed is thus not to decide between the conflict-monitoring and the outcome-evaluation/decision-making theories but, rather, to decide how, or whether, these can be integrated into a single, coherent account of ACC function. In the following section, we will propose a possible step toward this goal.

AN INTEGRATIVE ACCOUNT

As we have reviewed, a central tenet of the conflict-monitoring theory has been that the occurrence of conflict triggers, via the ACC, compensatory shifts in control that defend against conflict in later performance. In most of the work adopting this idea, such compensatory shifts have been understood to involve the intensification or focusing of top-down inputs from cognitive control to more basic information-processing pathways (see Botvinick et al., 2001; Egner, 2007; Kerns, 2006; Kerns et al., 2004). However, there is a second way in which conflict might be obviated, which would be to *avoid tasks or strategies that have given rise to it in the past*.

One way in which conflict monitoring could support this operating principle would be for conflict detection mechanisms to interact with learning mechanisms, so that the occurrence of conflict operated as a teaching signal. More precisely, under this arrangement, conflict would register as an aversive or negatively reinforcing event, penalizing the selection of associated tasks and strategies. The effect of this learning mechanism would manifest at the behavioral level as a bias toward the selection of tasks and strategies that minimize the risk of conflict or, by the logic introduced earlier, tasks and strategies that minimize the demand for control.

If this hypothesis is correct, it would establish a clear alignment between the conflict-monitoring and the outcome-evaluation/decision-making perspectives on ACC function. Conflict would be placed within the larger set of value-laden outcomes registered by the ACC. In particular, like monetary loss, negative feedback, social exclusion, and pain—other occurrences registered within the ACC—conflict would weigh as an aversive or costly event. Furthermore, this weighting would have a direct impact on decision making, influencing subsequent behavior through domain-general avoidance-learning mechanisms, which are already known to involve the ACC.

This ability to reconcile the conflict-monitoring and outcome-evaluation/decision-making perspectives makes the proposed hypothesis attractive. The question thus becomes whether there is any independent empirical evidence to motivate or support it. As it turns out, a range of evidence from diverse empirical domains lends plausibility to the idea that conflict influences decision making, as well as to the idea that this influence is mediated by the ACC. We turn now to a brief consideration of the relevant observations.

Avoidance of Cognitive Demand: The Law of Least Mental Effort

We focus first on the proposal that the occurrence of conflict triggers a form of avoidance learning, which re-

sults in a bias away from tasks and strategies that have given rise to conflict in past experience. Given the correlation between conflict and the demand for cognitive control, this proposal implies that behavioral decision making should display a bias away from tasks and strategies associated with high levels of cognitive demand.

Stating the proposal in this way calls to mind the time-honored *law of least work* (or effort), most famously pronounced by Hull (1943):

If two or more behavioral sequences, each involving a different amount of energy consumption or work, have been equally well reinforced an equal number of times, the organism will gradually learn to choose the less laborious behavior sequence leading to the attainment of the reinforcing state of affairs. (p. 294)

The law of least work has been a mainstay of animal behavior research since at least the 1930s and is supported by a wealth of empirical data (see Solomon, 1948). Of course, the vast majority of these data pertains to behavior involving physical demands. However, it has also been asserted that the law of least work applies to situations involving cognitive demands. The most direct statement along these lines may be that of Allport (1954) in his work on prejudice:

We like to solve problems easily. We can do so best if we can fit them rapidly into a satisfactory category and use this category as a means of prejudging the solution. . . . So long as we can get away with coarse overgeneralizations we tend to do so. Why? Well, it takes less effort, and effort, except in the area of our most intense interests, is disagreeable. (pp. 20–21)

McGuire (1969) reached a similar conclusion in work on the processing of political messages, asserting that human beings are “lazy organisms” who seek to spend as little mental energy as possible in processing complex information. Along the same lines, work on strategy selection in mathematical problem solving prompted Baroody and Ginsburg (1986) to posit a “drive for cognitive economy.” And a similar explanation has been applied to route selection in navigation tasks (Christenfeld, 1995).

In other work, the avoidance of cognitive demand has been seen as underlying broad and pervasive patterns in human behavior. For example, Rosch (1999) attributed the categorical structure of human semantic memory to a principle of “cognitive economy,” and Zipf (1949) applied a similar interpretation to regularities in the frequency distributions of words (see also Ferrer i Cancho & Sole, 2003). Indeed, Zipf portrayed the avoidance of cognitive effort as a universal principle governing all areas of human behavior, positing what has elsewhere been called the *law of least mental effort* (Balle, 2002).

Simpler and more direct evidence for a connection between cognitive demand and strategy selection has come from work by MacLeod, Hunt, and Mathews (1978; Mathews, Hunt, & MacLeod, 1980). Here, subjects performed a sentence–picture verification task in which either a visual or a verbal strategy could be adopted. Sub-

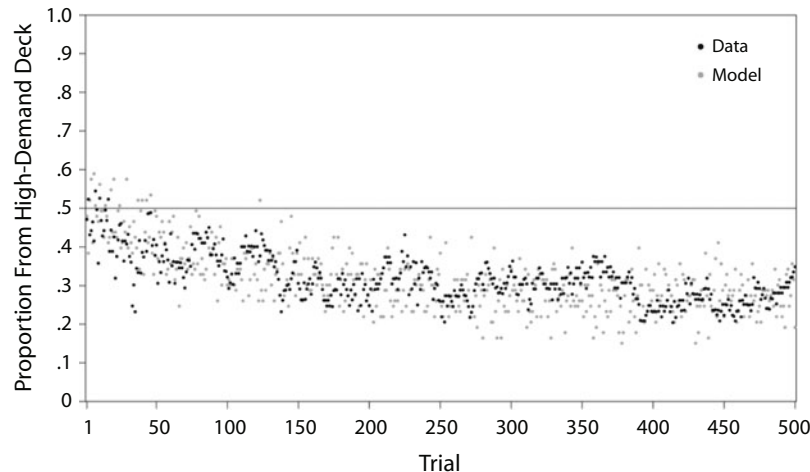


Figure 1. Black: Data from the demand selection task employed by Botvinick and Rosen (2007; Botvinick, Rosen, & Maguire, 2007). Points indicate the proportion of subjects ($N = 73$) who chose from the high-demand deck on each of 500 successive trials. Gray: Comparable values from 73 runs of the simulation model described in the present article (parameter settings: $c_{HD} = 1$, $c_{LD} = 0.25$, $\lambda = 0.007$).

jects with superior verbal working memory were found to prefer the verbal strategy, whereas subjects with superior visual working memory capacity were found to prefer the visual strategy. In an fMRI study based on this phenomenon, Reichle, Carpenter, and Just (2000) interpreted it as evidence for “one basis for strategy selection: minimization of cognitive workload.”

In recent work (Botvinick & Rosen, 2007; Botvinick, Rosen, & Maguire, 2007), we have developed an experimental paradigm that aims to test the law of least mental effort a bit more directly. This centers on what we refer to as the *demand selection task*. Here, the subject is faced with two decks of cards (displayed on a computer screen). On each trial, a card is chosen from one of the decks. When the face of the card is exposed, this reveals a single Arabic numeral. Depending on the color in which the numeral is displayed (purple or blue), the subject is expected to perform a magnitude judgment, saying “yes” if the number is smaller than 5 and “no” otherwise, or a parity judgment, saying “yes” if the number is even and “no” otherwise. The subjects are told that they may choose freely between the two decks, picking more frequently from one if they develop a preference. They are told that there may or may not be a difference between the two decks. In fact, in one deck, the color of each number matches the color from the previously chosen card 90% of the time. In the other deck, this is the case only 10% of the time. As a result, the latter deck requires the subjects to switch between the two categorization tasks more often than does the former, thus imposing a higher level of cognitive demand (see Monsell, 2003) and an increased tendency toward response conflict driven by cross-talk between the two tasks (see Gilbert & Shallice, 2002; Rushworth, Hadland, Paus, & Sipila, 2002; Waszak, Hommel, & Allport, 2003).

If such conflict or demand registers as a cost in decision making, one would expect to see a bias develop, over mul-

tiply card selections, away from the high-demand deck. As is shown in Figure 1, this was indeed observed. As has been reported by Botvinick and Rosen (2007; Botvinick et al., 2007), this pattern of performance cannot be explained in terms of error avoidance, since it was observed in a subset of subjects who made more errors on the low-demand deck than on the high-demand deck, as well as in a smaller subset who never made a single error on the high-demand deck. Nor can it be attributed in any straightforward way to a strategy aimed at reward maximization, since the subjects were not rewarded differentially on the basis of their performance. Remarkably, the bias toward the low-demand deck was also observed in a subset of subjects who failed to recognize (or, at least, were unable to report) the presence of any difference between the two decks.

If cognitive demand, as indexed by conflict, registers as a cost, one should expect the occurrence of conflict to be accompanied by markers associated with more conventional costs, such as monetary loss. Bechara and colleagues (Bechara, Damasio, Damasio, & Lee, 1999; Bechara, Tranel, Damasio, & Damasio, 1996) demonstrated the occurrence of a phasic elevation in skin conductance prior to actions associated with a high risk of monetary loss (selections from disadvantageous decks in the Iowa gambling task). Precisely the same phenomenon was observed in our demand selection task, where a phasic elevation in skin conductance was observed prior to selections from the high-demand deck (Botvinick & Rosen, 2007; Botvinick et al., 2007). This finding is open to more than one interpretation; for example, the skin conductance response could reflect increased arousal in anticipation of mental effort (see Botvinick et al., 2007). Nevertheless, when considered in the context of the findings of Bechara et al. (1999; Bechara et al., 1996), it appears at least consistent with the idea that anticipated cognitive demand, like an anticipated monetary loss, registers as a cost.

One interesting aspect of the performance data shown in Figure 1 is its indication that the bias toward the low-demand deck was not absolute. Even after the bias had developed, most subjects continued to select from the high-demand deck on a significant proportion of trials. Although this finding can be accounted for within the confines of a demand avoidance framework (as will be discussed further below), it also leaves open the possibility that any bias away from conflict or demand may coexist with other opposing influences on decision making, such as a tendency toward exploratory behavior (see Aston-Jones & Cohen, 2005) or toward the reward associated with feelings of competence or self-efficacy (see Cacioppo, Petty, Feinstein, & Jarvis, 1996). Teasing such influences apart from the putative underlying bias against cognitive demand is an important challenge for further work.

ACC As a Mediator in Demand-Based Decision Making

We have been making the case that cognitive demand, indexed on our account by conflict, registers as a cost in behavioral decision making. The other part of our proposal is that this cost is registered, at the neural level, within the ACC and that the ACC mediates its impact on decision making.

The idea that conflict registers as a cost within the ACC is consistent with the fact, already noted, that the ACC response to conflict occurs alongside responses to other negative outcomes, such as monetary loss, pain, negative feedback, and social rejection. A less circumstantial piece of evidence for the idea that the ACC response to conflict carries a negative value has come from a recent fMRI study conducted in our lab (Botvinick & Huffstetler, 2007a, 2007b). Here, subjects received monetary rewards for performing short blocks of a cognitive task. The blocks were of two types, carrying either high or low cognitive demand (and parallel levels of response conflict). Reward-related responses in the nucleus accumbens were found to vary with the level of demand involved in earning each reward, with stronger activation to easily earned rewards than to rewards that were hard-earned. More important, in the present context, was the finding that the strength of this effort-discounting effect in the nucleus accumbens was predicted by the degree of ACC activation during performance of the cognitive task preceding each reward. Stronger ACC activation during earning of the reward predicted a lower accumbens response to the reward itself.

Such data speak to a connection between conflict and negative value but do not yet engage the issue of decision making. However, ample motivation for a link between the ACC and decision making is, of course, ready to hand in the data that gave rise to the outcome-evaluation/decision-making theory of ACC function. Intriguingly, one version of that theory accords the ACC a special role in *effort-based* decision making (Walton, Bannerman, Alterescu, & Rushworth, 2003; Walton, Bannerman, & Rushworth, 2002; Walton, Kennerley, Bannerman, Phillips, & Rushworth, 2006). In considering this proposal, it is tempting

to draw the analogy made in least-effort theories between physical and cognitive effort. However, there is some ambiguity in the relationship between our present proposals and the specific findings underlying the effort-based decision-making account, which center on a bias against effort following ACC lesions in animals (Walton et al., 2003; Walton et al., 2002; Walton et al., 2006; although see Kennerley et al., 2006).

A clearer alignment holds between the account we are proposing and the evidence linking the ACC with avoidance learning. As was reviewed earlier, stimulation of the ACC induces avoidance learning, an effect that seems likely to depend on the influence of the ACC on dopaminergic activity. Our present proposal adds to this only the assumption that the same avoidance-learning mechanisms are engaged by the ACC response to conflict.

Relation to the Original Theory

The proposal that cognitive demand (as indexed by conflict) plays a role in decision making constitutes a significant extension to the conflict-monitoring theory. Figure 2 provides an illustration of how this proposal relates to the earlier proposal that conflict drives reactive online adjustments in control. The black portion of the diagram represents the account implemented in Botvinick et al. (2001). Here, conflict arising in the mapping from stimuli to responses triggers adjustments in the activation of task or strategy representations, which in turn serve to bias processing toward task-relevant stimulus-response pathways. The present extension to the theory is diagrammed in gray. Here, the occurrence of conflict during performance of a task, or during application of a particular strategy, weakens the tendency to adopt the same task or strategy in later behavior. Over time, this leads to a bias toward activities associated with relatively efficient information processing. These two effects of conflict could, in principle, operate in parallel, with conflict serving simultaneously as a recruitment signal for cognitive control and as a teaching signal influencing task and strategy selection.

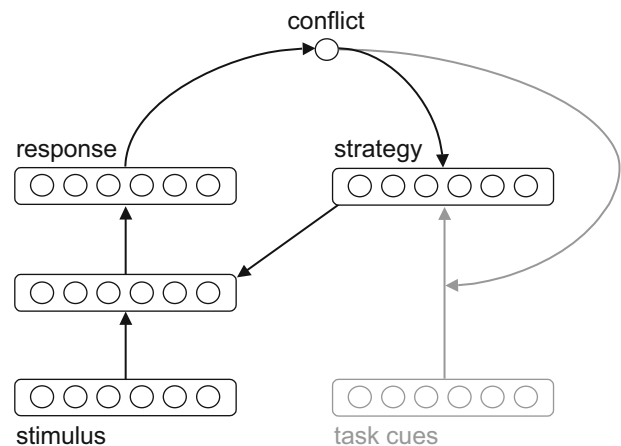


Figure 2. Schematic illustration of the dual roles proposed for conflict monitoring. See the text for explication.

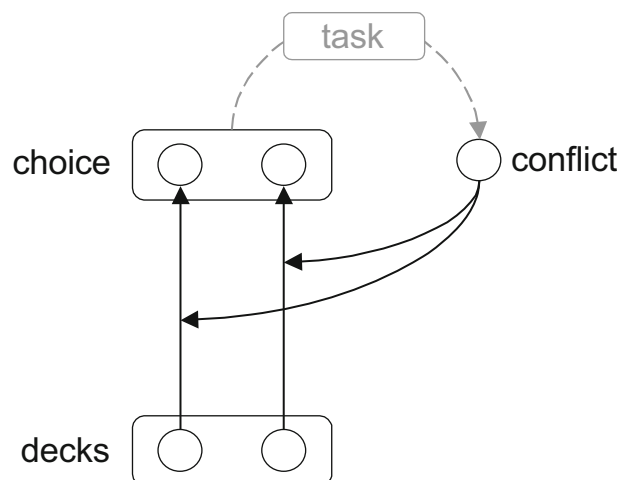


Figure 3. An initial implementation of the proposed account, as applied to the demand selection task.

AN INITIAL IMPLEMENTATION OF THE ACCOUNT

One reason that the conflict-monitoring account has been successful as a stimulus to empirical research is the fact that the theory was made explicit, early on, through computational modeling. Botvinick et al. (2001) articulated the conflict-monitoring account and investigated its implications through neural network models addressing empirically observed patterns of behavior in specific laboratory tasks. Although rather simple, these models have served as a useful point of reference for subsequent experimentation and debate and have provided the basis for more sophisticated modeling efforts (e.g., Jones et al., 2002; Yeung et al., 2004).

With this precedent in mind, we created a simple working model of the account of ACC function proposed in the preceding section, both to illustrate what is intended in the proposal and to provide a starting point for further development. The model addresses the demand selection task described earlier. Here, as will be recalled, subjects chose freely between two decks of cards, performing one of two digit categorization tasks on the basis of the color of the numeral revealed, and a preference gradually developed for the deck that required the subjects to switch tasks less often (see Figure 1). Under the general account we have put forth, the ACC would play a pivotal role in the emergence of this bias. Task performance following selection from the high-demand deck would lead to response conflict and, thus, to ACC engagement. This, in turn, would induce a form of avoidance learning, weakening the pathway that led the task display to trigger selection of the high-demand deck.

Our neural network implementation of this account is diagrammed in Figure 3. At the bottom of the figure are two input units, representing the two decks in the task display. Each of these units feeds forward to a corresponding response unit, coding for selection of one of the two decks. The connection weights are both initialized to a

value of 0.5. On each simulation trial, both input units are assigned an activation level of 1.0, and the activation of each response unit is set to a value equal to the product of its input unit's activation and the intervening weight. One response is chosen as the "winner," using each response unit's activation as its probability of selection.

The model assumes that selection of either deck results in the occurrence of some degree of conflict, induced by performance of the digit categorization task. For simplicity, only this outcome of the digit task, rather than the task itself, is modeled (although see below). Following each deck choice, the resulting conflict is quantified as a positive scalar value, assuming a higher value (c_{HD}) following selection from the high-demand deck and a lower value (c_{LD}) on all other trials. The chosen value then becomes the activation value for the one remaining unit in the model. This conflict-monitoring unit implements the role we have accorded to the ACC.

With the initial connection weights in place, the model, of course, shows no preference in selecting between the decks. However, the connection weights are altered by experience. Specifically, at the end of each trial, the connection weight leading to the response unit selected on that trial is updated as follows:

$$w \leftarrow w - \lambda c, \quad (1)$$

where w is the connection weight, c is the activity of the conflict-monitoring unit, and λ is a learning rate parameter. Negative weights are then set to zero, and the weights are subtractively normalized so as to sum to one.

In order to simulate performance in our experiment, the model was run for 500 trials (deck selections). Figure 1 shows its average performance over a set of runs matched in size to the number of subjects tested in our behavioral study (73). As in the empirical data, the model gradually develops a bias toward selection of the low-demand deck. This is driven by a progressive weakening of the pathway that drives selection of the high-demand deck. And this weakening is, in turn, induced by the occurrence of conflict.

A nuance of the model is that, like the subjects in the empirical study, its bias toward the low-demand deck is not absolute. This reflects the fact that some conflict does occur in the low-demand deck—in particular, in association with infrequent task switch trials. Because conflict occurring on recent trials has a greater impact on the model's weights than does conflict further back in time, the occurrence of conflict in the low-demand deck occasionally drives decision making back toward the high-demand deck.

For clarity of illustration, the implementation we have just described reduces the account to its barest essentials. However, each component of the model maps directly onto more elaborate and explicit models reported elsewhere. The mechanisms underlying performance of the two digit classification tasks, and the occurrence of conflict when switching between them, could be explicitly modeled on the basis of the task-switching model from Gilbert and Shallice (2002). More important, the portion of the model addressing the deck selection step, as well as the mechanism for adjusting weights within it, could be implemented in more detail, and in neuroscientifically explicit terms,

on the basis of the recent work of Frank and colleagues (Frank, 2005a; Frank & Claus, 2006). Under the resulting account, the influence of the ACC on response selection pathways would be indirect, mediated by the influence of the ACC on midbrain dopaminergic neurons.

Even in its present, minimalistic form, the model makes specific, testable predictions. One prediction is that damage to the ACC should be associated, in the demand selection task, with a reduced bias toward the low-demand deck. A second and related prediction is that the strength of individual subjects' bias in the demand selection task should correlate with the strength of ACC activation during task switching. The more strongly the ACC is engaged in a given subject, the stronger that subject's bias toward the low-demand deck should be. Further predictions would seem likely to emerge from the more elaborate implementation proposed above, including predictions about the impact on performance in the demand selection task of pharmacologic agents affecting dopaminergic function. However, to confidently frame specific predictions of this kind will necessarily require further development of the model.

RELATED ACCOUNTS

The present proposal is not the first to accord conflict monitoring a role in decision making, nor is it the first to accord the ACC a role in learning. It is therefore important to differentiate the proposal from some others that may appear to be closely related. For example, both Bogacz and Gurney (2007) and Frank (2006) have presented models of decision making in the basal ganglia, according to which the occurrence of conflict impacts the setting of response thresholds. Although not inconsistent with the present proposal, these models address a separate issue, since they are not centrally concerned with learning. Furthermore, in these models, the impact of conflict is focused on the same decision as that from which the conflict itself arises. In our proposal, there is an important distinction between the context that gives rise to conflict (task performance) and the locus of learning (task or strategy selection; see Figure 2).

Another proposal that must be differentiated from the present one has come from Holroyd and Coles (2002). In that work, the ACC is understood as housing a mechanism that decides among the outputs of competing motor controllers, and learning within the ACC is driven by inputs from midbrain dopaminergic nuclei. According to the theory we have advanced, the ACC instead serves to drive learning in decision-making mechanisms implemented elsewhere (most plausibly, in the basal ganglia), potentially through its influence on midbrain dopaminergic function. Although this proposal appears, on its face, to contradict the Holroyd and Coles account, it is not our intention to deny that dopaminergic inputs play an important role in ACC function, nor to deny that learning and decision-making processes occur in that brain area. Therefore, although the two theories are strongly contrasting, and although they do lead to different sorts of predictions, they are not necessarily incompatible.

CONCLUSION

The conflict-monitoring and outcome-evaluation/decision-making perspectives on ACC function appear to provide compelling accounts for rather different sets of empirical data. Neither account seems either eliminable or fully reducible to the other. Instead, the strength of the two theories leads to a different challenge, which is to understand how both might fit into an embracing account of ACC function. We have put forth a new proposal that, if correct, would begin to bridge the gap between the conflict-monitoring and the decision-making perspectives. Specifically, we have proposed not only that conflict, as an index of information-processing demands, drives reactive adjustments in cognitive control (as has been proposed, and supported, by previous research), but also that the ACC response to conflict also serves as a teaching signal, driving a form of avoidance learning. This mechanism, we have hypothesized, provides the neural basis for an empirically observed bias toward tasks and strategies that involve efficient information processing. As we have noted, this proposal can be implemented on the basis of existing ideas about the mechanisms underlying avoidance learning, including the respective roles of the ACC and of dopamine, and we have put forth a simple model taking a first step in this direction. In addition to drawing together a wide range of behavioral and neuroscientific data, the proposed account makes straightforward, testable predictions, which should make it possible to evaluate the theory's merit through further experimentation.

AUTHOR NOTE

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REFERENCES

- ALLMAN, J. M., HAKEEM, A., ERWIN, J. M., NIMCHINSKY, E., & HOF, P. (2001). The anterior cingulate cortex. The evolution of an interface between emotion and cognition. In A. R. Damasio, A. Harrington, J. Kagan, B. McEwen, H. Moss, & R. Shaikh (Eds.), *Unity of knowledge: The convergence of natural and human science* (Annals of the New York Academy of Sciences, Vol. 935, pp. 107-117). New York: New York Academy of Sciences.
- ALLPORT, G. W. (1954). *The nature of prejudice*. Reading, MA: Addison-Wesley.
- AMIEZ, C., JOSEPH, J.-P., & PROCYK, E. (2005). Anterior cingulate error-related activity is modulated by predicted reward. *European Journal of Neuroscience*, *21*, 3447-3452.
- ASTON-JONES, G., & COHEN, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*, *28*, 403-450.
- BADRE, D., & WAGNER, A. D. (2004). Selection, integration, and conflict monitoring: Assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron*, *41*, 473-487.
- BALLE, M. (2002). La loi du moindre effort mental: Les représentations mentales. *Sciences Humaines*, *128*, 36-39.
- BARCH, D. M., BRAVER, T. S., AKBUDAK, E., CONTURO, T., OLLINGER, J., & SNYDER, A. (2001). Anterior cingulate cortex and response conflict: Effects of response modality and processing domain. *Cerebral Cortex*, *11*, 837-848.

- BARCH, D. M., BRAVER, T. S., SABB, F. W., & NOLL, D. C. (2000). Anterior cingulate and the monitoring of response conflict: Evidence from an fMRI study of overt verb generation. *Journal of Cognitive Neuroscience*, **12**, 298-309.
- BAROODY, A. J., & GINSBURG, H. P. (1986). The relationship between initial meaningful and mechanical knowledge of arithmetic. In J. Hiebert (Ed.), *Conceptual and procedural knowledge: The case of mathematics* (pp. 75-112). Hillsdale, NJ: Erlbaum.
- BECHARA, A., DAMASIO, H., DAMASIO, A. R., & LEE, G. P. (1999). Different contributions of the human amygdala and ventromedial prefrontal cortex to decision-making. *Journal of Neuroscience*, **19**, 5473-5481.
- BECHARA, A., TRANEL, D., DAMASIO, H., & DAMASIO, A. R. (1996). Failure to respond automatically to anticipated future outcomes following damage to prefrontal cortex. *Cerebral Cortex*, **6**, 215-225.
- BENINGER, R. J. (1989). The role of serotonin and dopamine in learning to avoid aversive stimuli. In T. Archer & L.-G. Nilsson (Eds.), *Aversion, avoidance and anxiety* (pp. 265-284). Hillsdale, NJ: Erlbaum.
- BOGACZ, R., & GURNEY, K. (2007). The basal ganglia and cortex implement optimal decision making between alternative actions. *Neural Computation*, **19**, 442-477.
- BOTVINICK, M. M., BRAVER, T. S., BARCH, D. M., CARTER, C. S., & COHEN, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, **108**, 624-652.
- BOTVINICK, M. M., COHEN, J. D., & CARTER, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, **8**, 539-546.
- BOTVINICK, M. [M.], & HUFFSTETLER, S. (2007a, June). *Differential neural responses to hard- versus easily earned rewards*. Paper presented at the Thirteenth Annual Meeting of the Organization for Human Brain Mapping, Chicago.
- BOTVINICK, M. [M.], & HUFFSTETLER, S. (2007b). *Effort discounting in human nucleus accumbens*. Manuscript submitted for publication.
- BOTVINICK, M. [M.], JHA, A. P., BYLSMA, L. M., FABIAN, S. A., SOLOMON, P. E., & PRKACHIN, K. M. (2005). Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *NeuroImage*, **25**, 312-319.
- BOTVINICK, M. [M.], NYSTROM, L. E., FISSELL, K., CARTER, C. S., & COHEN, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, **402**, 179-181.
- BOTVINICK, M. [M.], & ROSEN, Z. (2007, May). *Is mental effort aversive? Some behavioral and psychophysiological evidence*. Paper presented at the Cognitive Neuroscience Society Annual Meeting, New York.
- BOTVINICK, M. M., ROSEN, Z., & MAGUIRE, J. T. (2007). *Action selection based on anticipated cognitive demand: A test of "the law of least mental effort"*. Manuscript submitted for publication.
- BRAVER, T. S., BARCH, D. M., GRAY, J. R., MOLFESE, D. L., & SNYDER, A. (2001). Anterior cingulate cortex and response conflict: Effects of frequency, inhibition and errors. *Cerebral Cortex*, **11**, 825-836.
- BROWN, J. W., & BRAVER, T. S. (2005). Learned predictions of error likelihood in the anterior cingulate cortex. *Science*, **307**, 1118-1121.
- BROWN, J. W., & BRAVER, T. S. (2007). Risk prediction and aversion by anterior cingulate cortex. *Cognitive, Affective, & Behavioral Neuroscience*, **7**, 266-277.
- BUNGE, S. A., HAZELTINE, E., SCANLON, M. D., ROSEN, A. C., & GABRIELI, J. D. E. (2002). Dissociable contributions of prefrontal and parietal cortices to response selection. *NeuroImage*, **17**, 1562-1571.
- BUSH, G., VOGT, B. A., HOLMES, J., DALE, A. M., GREVE, D., JENIKE, M. A., & ROSEN, B. R. (2002). Dorsal anterior cingulate cortex: A role in reward-based decision making. *Proceedings of the National Academy of Sciences*, **99**, 523-528.
- CACIOPPO, J. T., PETTY, R. E., FEINSTEIN, J. A., & JARVIS, W. B. G. (1996). Dispositional differences in cognitive motivation: The life and times of individuals varying in need for cognition. *Psychological Bulletin*, **119**, 197-253.
- 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 online monitoring of performance. *Science*, **280**, 747-749.
- CASEY, B. J., THOMAS, K. M., WELSH, T. F., BADGAIYAN, R. D., ECCARD, C. H., JENNINGS, J. R., & CRONE, E. A. (2000). Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences*, **97**, 8728-8733.
- CHRISTENFELD, N. (1995). Choices from identical options. *Psychological Science*, **6**, 50-55.
- 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.
- DAVIS, K. D., HUTCHISON, W. D., LOZANO, A. M., TASKER, R. R., & DOSTROVSKY, J. O. (2000). Human anterior cingulate cortex neurons modulated by attention-demanding tasks. *Journal of Neurophysiology*, **83**, 3575-3577.
- DAVIS, K. D., TAYLOR, K. S., HUTCHISON, W. D., DOSTROVSKY, J. O., MCANDREWS, M. P., RICHTER, E. O., & LOZANO, A. M. (2005). Human anterior cingulate cortex neurons encode cognitive and emotional demands. *Journal of Neuroscience*, **25**, 8402-8406.
- DE ZUBICARAY, G. I., ANDREW, C., ZELAYA, F. O., WILLIAMS, S. C., & DUMANOIR, C. (2000). Motor response suppression and the prepotent tendency to respond: A parametric fMRI study. *Neuropsychologia*, **38**, 1280-1291.
- DI PELLEGRINO, G., CIARAMELLI, E., & LADAVAS, E. (2007). The regulation of cognitive control following rostral anterior cingulate cortex lesion in humans. *Journal of Cognitive Neuroscience*, **19**, 275-286.
- DURSTON, S., DAVIDSON, M. C., THOMAS, K. M., WORDEN, M. S., TOTENHAM, N., MARTINEZ, A., ET AL. (2003). Parametric manipulation of conflict and response competition using rapid mixed-trial event-related fMRI. *NeuroImage*, **20**, 2135-2141.
- DURSTON, S., THOMAS, K. M., WORDEN, M. S., YANG, Y., & CASEY, B. J. (2002). The effect of preceding context on inhibition: An event-related fMRI study. *NeuroImage*, **16**, 449-453.
- EGNER, T. (2007). Congruency sequence effects and cognitive control. *Cognitive, Affective, & Behavioral Neuroscience*, **7**, 380-390.
- EISENBERGER, N. I., LIEBERMAN, M. D., & WILLIAMS, K. D. (2003). Does rejection hurt? An fMRI study of social exclusion. *Science*, **302**, 290-292.
- FALKENSTEIN, M., HOORMANN, J., CHRIST, S., & HOHNSBEIN, J. (2000). ERP components on reaction errors and their functional significance: A tutorial. *Biological Psychology*, **51**, 87-107.
- FELLOWS, L. K., & FARAH, M. J. (2005). Is anterior cingulate cortex necessary for cognitive control? *Brain*, **128**, 788-796.
- FERRER I CANCHO, R., & SOLE, R. V. (2003). Least effort and the origins of scaling in human language. *Proceedings of the National Academy of Sciences*, **100**, 788-791.
- FRANK, M. J. (2005a). Dynamic dopamine modulation in the basal ganglia: A neurocomputational account of cognitive deficits in medicated and nonmedicated Parkinsonism. *Journal of Cognitive Neuroscience*, **17**, 51-72.
- FRANK, M. J. (2005b). Error-related negativity predicts reinforcement learning and conflict biases. *Neuron*, **47**, 495-501.
- FRANK, M. J. (2006). Hold your horses: A dynamic computational role for the subthalamic nucleus in decision making. *Neural Networks*, **19**, 1120-1136.
- FRANK, M. J., & CLAUS, E. D. (2006). Anatomy of a decision: Striato-orbitofrontal interactions in reinforcement learning, decision making, and reversal. *Psychological Review*, **113**, 300-326.
- FRITH, C. D., FRISTON, K., LIDDLE, P. F., & FRACKOWIAK, R. S. (1991). Willed action and the prefrontal cortex in man: A study with PET. *Proceedings of the Royal Society B*, **244**, 241-246.
- GABRIEL, M. (1993). Discriminative avoidance learning: A model system. In B. A. Vogt & M. Gabriel (Eds.), *Neurobiology of cingulate cortex and limbic thalamus: A comprehensive handbook* (pp. 478-523). Boston: Birkhäuser.
- GARIANO, R. F., & GROVES, P. M. (1988). Burst firing in midbrain dopamine neurons by stimulation of the medial prefrontal and anterior cingulate cortices. *Brain Research*, **462**, 194-198.
- GEHRING, W. J., & WILLOUGHBY, A. R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Science*, **295**, 2279-2282.
- GILBERT, S. J., & SHALLICE, T. (2002). Task switching: A PDP model. *Cognitive Psychology*, **44**, 297-337.
- GRATTON, G., COLES, M. G. H., & DONCHIN, E. (1992). Optimizing the use of information: Strategic control of activation of responses. *Journal of Experimental Psychology: General*, **121**, 480-506.

- HADLAND, K. A., RUSHWORTH, M. F., GAFFAN, D., & PASSINGHAM, R. E. (2003). The anterior cingulate and reward-guided selection of actions. *Journal of Neurophysiology*, **89**, 1161-1164.
- HAZELTINE, E., POLDRACK, R., & GABRIELI, J. D. E. (2000). Neural activation during response competition. *Journal of Cognitive Neuroscience*, **12**(Suppl. 2), 118-129.
- HOLROYD, C. B., & COLES, M. G. H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, **109**, 679-709.
- HOLROYD, C. B., NIEUWENHUIS, S., YEUNG, N., & COHEN, J. D. (2003). Errors in reward prediction are reflected in the event-related brain potential. *NeuroReport*, **14**, 2481-2484.
- HOLROYD, C. B., NIEUWENHUIS, S., YEUNG, N., NYSTROM, L., MARS, R. B., COLES, M. G. H., & COHEN, J. D. (2004). Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. *Nature Neuroscience*, **7**, 497-498.
- HULL, C. L. (1943). *Principles of behavior*. New York: Appleton-Century.
- ITO, S., STUPHORN, V., BROWN, J. W., & SCHALL, J. D. (2003). Performance monitoring by the anterior cingulate cortex during saccade countermanding. *Science*, **302**, 120-122.
- JACKSON, M. E., FROST, A. S., & MOGHADDAM, B. (2001). Stimulation of prefrontal cortex at physiologically relevant frequencies inhibits dopamine release in the nucleus accumbens. *Journal of Neurochemistry*, **78**, 920-923.
- JOHANSEN, J. P., & FIELDS, H. L. (2004). Glutamatergic activation of anterior cingulate cortex produces an aversive teaching signal. *Nature Neuroscience*, **7**, 398-403.
- JONES, A. D., CHO, R. Y., NYSTROM, L. E., COHEN, J. D., & BRAVER, T. S. (2002). A computational model of anterior cingulate function in speeded response tasks: Effects of frequency, sequence, and conflict. *Cognitive, Affective, & Behavioral Neuroscience*, **2**, 300-317.
- KERNS, J. G. (2006). Anterior cingulate and prefrontal cortex activity in an fMRI study of trial-to-trial adjustments on the Simon task. *NeuroImage*, **15**, 399-405.
- KERNS, J. G., COHEN, J. D., MACDONALD, A. W., III, CHO, R. Y., STENGER, V. A., & CARTER, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, **303**, 1023-1026.
- KIEHL, K. A., LIDDLE, P. F., & HOPFINGER, J. B. (2000). Error processing and the rostral anterior cingulate: An event-related fMRI study. *Psychophysiology*, **37**, 216-223.
- KIM, H., SHIMOJO, S., & O'DOHERTY, J. (2006). Is avoiding an aversive outcome rewarding? Neural substrates of avoidance learning in the human brain. *PLOS Biology*, **4**, 1453-1461.
- LUU, P., TUCKER, D. M., DERRYBERRY, D., REED, M., & POULSEN, C. (2003). Electrophysiological responses to errors and feedback in the process of action regulation. *Psychological Science*, **14**, 47-53.
- LUX, S., MARSHALL, J. C., RITZL, A., WEISS, P. H., PIETRZYK, U., SHAH, N. J., ET AL. (2004). A functional magnetic resonance imaging study of local/global processing with stimulus presentation in the peripheral visual hemifields. *Neuroscience*, **124**, 113-120.
- MACLEAN, P. D. (1990). *The triune brain in evolution: Role in paleocerebral functions*. New York: Plenum.
- MACLEOD, C. M., HUNT, E. B., & MATHEWS, N. N. (1978). Individual differences in the verification of sentence-picture relationships. *Journal of Verbal Learning & Verbal Behavior*, **17**, 493-507.
- MACLEOD, C. M., & MACDONALD, P. A. (2000). Interdimensional interference in the Stroop effect: Uncovering the cognitive and neural anatomy of attention. *Trends in Cognitive Sciences*, **4**, 383-391.
- MATHEWS, N. N., HUNT, E. B., & MACLEOD, C. M. (1980). Strategy choice and strategy training in sentence-picture verification. *Journal of Verbal Learning & Verbal Behavior*, **19**, 531-548.
- MATSUMOTO, K., SUZUKI, W., & TANAKA, K. (2003). Neural correlates of goal-based motor selection in the prefrontal cortex. *Science*, **301**, 229-232.
- MAYR, U., AWH, E., & LAUREY, P. (2003). Conflict adaptation effects in the absence of executive control. *Nature Neuroscience*, **6**, 450-452.
- MCGUIRE, W. J. (1969). The nature of attitudes and attitude change. In G. Lindzey & E. Aronson (Eds.), *The handbook of social psychology* (Vol. 3, pp. 136-314). Reading, MA: Addison-Wesley.
- MESULAM, M. M. (1981). A cortical network for directed attention and unilateral neglect. *Annals of Neurology*, **10**, 309-325.
- MILLER, E. K., & COHEN, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, **24**, 167-202.
- 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.
- MONSELL, S. (2003). Task switching. *Trends in Cognitive Sciences*, **7**, 134-140.
- MURASE, S., GRENHOFF, J., CHOUVET, G., GONON, F. G., & SVENSSON, T. H. (1993). Prefrontal cortex regulates burst firing and transmitter release in rat mesolimbic dopamine neurons studied in vivo. *Neuroscience Letters*, **157**, 53-56.
- NACHEV, P. (2006). Cognition and medial frontal cortex in health and disease. *Current Opinion in Neurology*, **19**, 587-592.
- NAKAMURA, K., ROESCH, M. R., & OLSON, C. R. (2005). Neuronal activity in macaque SEF and ACC during performance of tasks involving conflict. *Journal of Neurophysiology*, **93**, 884-908.
- NIEUWENHUIS, S., SCHWEIZER, T. S., MARS, R. B., BOTVINICK, M. M., & HAJCAK, G. (2007). Error-likelihood prediction in the medial frontal cortex: A critical evaluation. *Cerebral Cortex*, **17**, 1570-1581.
- NIEUWENHUIS, S., YEUNG, N., HOLROYD, C. B., SCHURGER, A., & COHEN, J. D. (2004). Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. *Cerebral Cortex*, **14**, 741-747.
- NOTEBAERT, W., & VERGUTS, T. (2007). Dissociating conflict adaptation from feature integration: A multiple regression approach. *Journal of Experimental Psychology: Human Perception & Performance*, **33**, 1256-1260.
- PALMER, E. D., ROSEN, H. J., OJEMANN, J. G., BUCKNER, R. L., KELLEY, W. M., & PETERSEN, S. E. (2001). An event-related fMRI study of overt and covert word stem completion. *NeuroImage*, **14**, 182-193.
- PAPEZ, J. W. (1937). A proposed mechanism of emotion. *Archives of Neurology & Psychiatry*, **38**, 725-743.
- 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.
- PETERSON, B. S., KANE, M. J., ALEXANDER, G. M., LACADIE, C., SKUDLARSKI, P., LEUNG, H. C., ET AL. (2002). An event-related functional MRI study comparing interference effects in the Simon and Stroop tasks. *Cognitive Brain Research*, **13**, 427-440.
- RAINVILLE, P. (2002). Brain mechanisms of pain affect and pain modulation. *Current Opinion in Neurobiology*, **12**, 195-204.
- REICHLER, E. D., CARPENTER, P. A., & JUST, M. A. (2000). The neural bases of strategy and skill in sentence-picture verification. *Cognitive Psychology*, **40**, 261-295.
- RIDDERINKHOF, K. R., ULLSPERGER, M., CRONE, E. A., & NIEUWENHUIS, S. (2004). The role of the medial frontal cortex in cognitive control. *Science*, **306**, 443-447.
- ROSCHE, E. (1999). Principles of categorization. In E. Margolis & S. Laurence (Eds.), *Concepts: Core readings* (pp. 189-206). Cambridge, MA: MIT Press.
- RUSHWORTH, M. F. S., HADLAND, K. A., PAUS, T., & SIPILA, P. K. (2002). The role of the human medial frontal cortex in task switching: A combined fMRI and TMS study. *Journal of Neurophysiology*, **87**, 2577-2592.
- RUSHWORTH, M. F. S., WALTON, M. E., KENNERLEY, S. W., & BANNERMAN, D. M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in Cognitive Sciences*, **8**, 410-417.
- SINGER, T., SEYMOUR, B., O'DOHERTY, J., KAUBE, H., DOLAN, R. J., & FRITH, C. D. (2004). Empathy for pain involves affective but not sensory components of pain. *Science*, **303**, 1157-1162.
- SOLOMON, R. L. (1948). The influence of work on behavior. *Psychological Bulletin*, **45**, 1-40.
- STUPHORN, V., TAYLOR, T. L., & SCHALL, J. D. (2000). Performance monitoring by the supplementary eye field. *Nature*, **408**, 857-860.
- STÜRMER, B., LEUTHOLD, H., SOETENS, E., SCHROETER, H., & SOMMER, W. (2002). Control over location-based response activation in the Simon task: Behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception & Performance*, **28**, 1345-1363.
- SVENSSON, T. H., & TUNG, C. S. (1989). Local cooling of pre-frontal

- cortex induces pacemaker-like firing of dopamine neurons in rat tegmental area in vivo. *Acta Psychologica Scandinavica*, **136**, 135-136.
- 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*, **94**, 14792-14797.
- TONG, Z. Y., OVERTON, P. G., & CLARK, D. (1996). Stimulation of the prefrontal cortex in the rat induces patterns of activity in midbrain dopaminergic neurons which resemble natural burst events. *Synapse*, **22**, 195-208.
- ULLSPERGER, M., BYLSMA, L. M., & BOTVINICK, M. M. (2005). The conflict adaptation effect: It's not just priming. *Cognitive, Affective, & Behavioral Neuroscience*, **5**, 467-472.
- UNGLESS, M. A., MAGILL, P. J., & BOLAM, J. P. (2004). Uniform inhibition of dopamine neurons in the ventral tegmental area by aversive stimuli. *Science*, **303**, 2040-2042.
- VAN VEEN, V., COHEN, J. D., BOTVINICK, M. M., STENGER, V. A., & CARTER, C. S. (2001). Anterior cingulate cortex, conflict monitoring, and levels of processing. *NeuroImage*, **14**, 1302-1308.
- VAN VEEN, V., HOLROYD, C. B., COHEN, J. D., STENGER, V. A., & CARTER, C. S. (2004). Errors without conflict: Implications for performance monitoring theories of anterior cingulate cortex. *Brain & Cognition*, **56**, 267-276.
- WALTON, M. E., BANNERMAN, D. M., ALTERESCU, K., & RUSHWORTH, M. F. (2003). Functional specialization within medial frontal cortex of the anterior cingulate for evaluating effort-related decisions. *Journal of Neuroscience*, **23**, 6475-6479.
- WALTON, M. E., BANNERMAN, D. M., & RUSHWORTH, M. F. (2002). The role of rat medial frontal cortex in effort-based decision making. *Journal of Neuroscience*, **22**, 10996-11003.
- WALTON, M. E., KENNERLEY, S. W., BANNERMAN, D. M., PHILLIPS, P. E. M., & RUSHWORTH, M. F. (2006). Weighing up the benefits of work: Behavioral and neural analyses of effort-related decision making. *Neural Networks*, **19**, 1302-1314.
- WASZAK, F., HOMMEL, B., & ALLPORT, A. (2003). Task-switching and long-term priming: Role of episodic stimulus-task bindings in task-shift costs. *Cognitive Psychology*, **46**, 361-413.
- WEISSMAN, D. H., GIESBRECHT, B., SONG, A. W., MANGUN, G. R., & WOLDORFF, M. G. (2003). Conflict monitoring in the human anterior cingulate cortex during selective attention to global and local object features. *NeuroImage*, **19**, 1361-1368.
- YEUNG, N., BOTVINICK, M. M., & COHEN, J. D. (2004). The neural basis of error-detection: Conflict monitoring and the error-related negativity. *Psychological Review*, **111**, 931-959.
- YEUNG, N., & SANFEY, A. G. (2004). Independent coding of reward magnitude and valence in the human brain. *Journal of Neuroscience*, **24**, 6258-6264.
- ZIPF, G. K. (1949). *Human behavior and the principle of least effort: An introduction to human ecology*. Cambridge, MA: Addison-Wesley.

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