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Beyond Conflict Monitoring: Cognitive Control and the Neural Basis of Thinking Before You Act

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Abstract

Cognitive control refers to the processes by which individual cognitive functions are coordinated in the service of higher-level goals. The anterior cingulate cortex (ACC) in the middle front of the brain monitors performance, and it is activated when the need for control increases—for instance, in difficult situations or when errors occur. Since the late 1990s, the ACC has been thought to signal when there is conflict between competing action plans so that the conflict can be resolved. More recently, an alternative model has reconceptualized the role of ACC as that of a predictor and evaluator of the likely outcomes of planned actions before the actions are performed. This new Predicted Response Outcome model accounts for a broader range of findings than the earlier framework and suggests that the ACC might support the cognitive operations by which individuals can "think before they act" in order to avoid risky or otherwise poor choices.

Keywords
cognitive control, performance monitoring, anterior cingulate cortex, risk, conflict monitoring

Introduction

Cognitive control (i.e., directing behavior toward goals) is heavily intertwined with performance monitoring, or detecting when control must be exerted in the first place. Greater cognitive control is generally required in more difficult situations in which automatic responses might lead to an error (Norman & Shallice, 1986). Still, excessive cognitive control might waste limited cognitive resources. How, then, does an individual know when to exert greater control? The idea that the anterior cingulate cortex (ACC) serves as a potential basis for performance monitoring first emerged with the observation of error signals (Gehring, Coles, Meyer, & Donchin, 1990). Interest in the ACC exploded with a series of papers proposing that the ACC served to detect conflict between incompatible response processes (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter et al., 1998). For the past 15 years, conflict monitoring has become nearly synonymous with the ACC region, and the conflict-monitoring model has inspired many studies of the ACC, including those of my research group.

More recently, though, a number of papers have either challenged the conflict-monitoring hypothesis (Brown & Braver, 2005; Holroyd & Coles, 2002) or simply shown other effects in the ACC that are not clearly accounted for by the conflict-monitoring framework. These effects include positive correlations between ACC activity and reaction times (Grinband et al., 2011; but see Yeung, Cohen, & Botvinick, 2011) and effects associated with error likelihood (Brown & Braver, 2005, 2007), reward and unexpected reward (Ito, Stuphorn, Brown, & Schall, 2003), nonstationarity in the environment (Behrens, Woolrich, Walton, & Rushworth, 2007), and foraging behavior (Kolling, Behrens, Mars, & Rushworth, 2012). The number of reported effects in the ACC has proliferated to the point where more than 20% of a sample of thousands of published fMRI studies reported some effects in the ACC (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011).

A New Model

In Samuel Beckett's *Waiting for Godot*, two hapless characters wait endlessly for a character named Godot, who

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never arrives. It is easy enough to recognize an explicit signal that an event has occurred, but it is harder to build an expectation of an event and then to infer at a certain time that it is not going to occur, because if it were to occur, it would already have happened. Put simply, how and when do Beckett's characters determine that Godot is not coming—or, more generally, how and when does one determine that a reward is not to be found (Kolling et al., 2012)? Such an inference requires two pieces of information: First, the characters must form predictions about what will happen as a consequence of their waiting, and when it will happen. There is some probability that Godot will arrive by a certain time, and there is some probability that Godot will be a no-show or, perhaps, that something else will interrupt the waiting period. Second, the characters must be able to compare their expectations about what will *probably* happen against what *actually* happens.

Here, I argue that it is possible to account for the variety of ACC effects with a unified theoretical framework, which my research group and I call the Predicted Response Outcome (PRO) model (Alexander & Brown, 2011). Like the characters in *Waiting for Godot*, the PRO model represents predictions about likely outcomes (Fig. 1a, Fig. 1b), as well as separate evaluations of how well the predictions match the outcomes (Fig. 1c, Fig. 1d). In this way, the new theory clarifies the psychological processes of how people predict the potential consequence of an action before acting and how they evaluate the outcomes of their actions. (A highly similar computational framework has also been proposed independently by another group; Silvetti, Seurinck, & Verguts, 2011).

The PRO model begins with an earlier proposal that the ACC learns to predict the likelihood of various possible consequences of actions, particularly errors (Brown & Braver, 2005, 2007). When response conflict is present, errors are more likely, so conflict and error likelihood are often confounded (Brown & Braver, 2005). These were deconfounded by isolating trials in which the cue color indicated an increased error likelihood but the conflicting

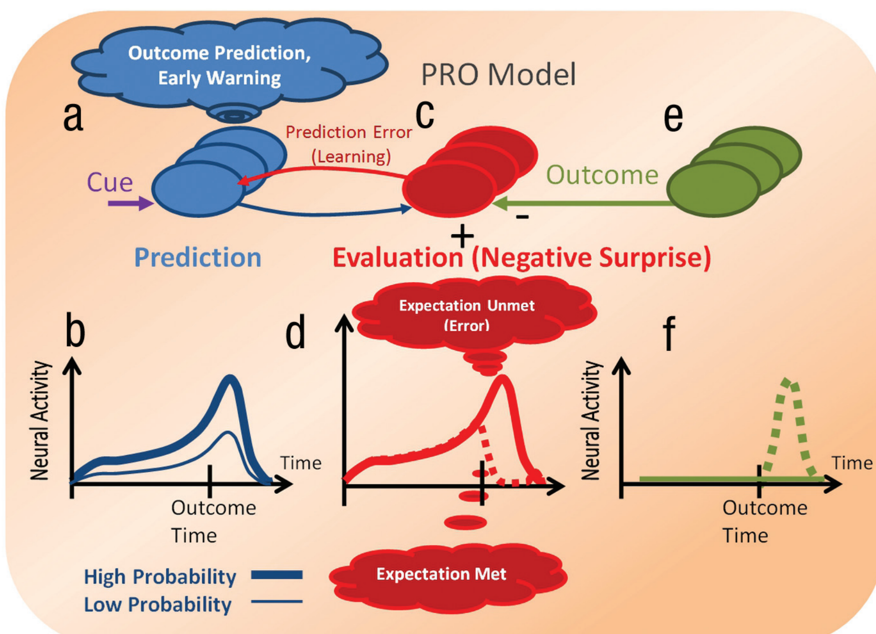

Fig. 1. The Predicted Response Outcome (PRO) model of the anterior cingulate cortex (ACC). The prediction units (a) generate a timed prediction of what outcomes are expected, with what probability, and when. As shown in the graph in (b), greater probabilities are associated with greater prediction activity, and the activity peaks at the time the outcome is expected to occur. Prediction signals of aversive outcomes may influence decisions away from risk. The evaluation units compute *negative surprise*—that is, they detect when an expected outcome fails to occur (c). Negative surprise is computed simply by subtracting the actual outcome signal from the prediction-unit signal at each point in time. As shown in the graph in (d), events that are predicted with a high probability yield greater surprise signals when they fail to occur (solid line) than when they do occur as expected (dashed line). This mechanism accounts for error signals within the ACC and might drive corrective actions when errors occur. Outcome units signal when an actual outcome occurs (e). As shown by the graph in (f), an outcome unit is transiently activated at the moment a corresponding outcome actually occurs (dashed line); if no outcome occurs, the outcome unit remains inactive (solid line).

stimulus nevertheless did not subsequently appear. The result was that ACC activity remained elevated when error likelihood increased, even without response conflict (Brown & Braver, 2005). Thus, apparent response-conflict effects might in part reflect increased error likelihood rather than conflict. Further studies showed that individuals who were more loss averse had stronger ACC activity related to error likelihood, which suggested that ACC might not only predict potential errors but also control behavior to avoid errors (Brown & Braver, 2007, 2008).

Despite its successes, the error-likelihood model was still incomplete. In the neuroimaging study that showed error-likelihood effects, we also found that ACC activity following an actual error (not just a predicted error) was *higher* when the error likelihood was lower (Brown & Braver, 2005). The error-likelihood model could not account for this effect of surprise. To address this, we returned to the idea that the ACC compares actual outcomes with intended outcomes (Holroyd & Coles, 2002; Ito et al., 2003; Scheffers & Coles, 2000), which had been a dominant account of ACC prior to the development of the conflict model. The concept of the ACC as an outcome predictor, as postulated in the error-likelihood model, and the concept of it as a comparator fit together remarkably well: The predictor (Fig. 1a, Fig. 1b) simply provides the basis against which to compare the actual outcome (Fig. 1e, Fig. 1f). This comparison is simply between the expected and actual outcome (Ito et al., 2003), as illustrated in Figure 1c and Figure 1d. This structure, collectively, is the essence of the PRO model (Fig. 1) (Alexander & Brown, 2010, 2011; Silvetti et al., 2011).

A key function of the PRO model is detecting the absence of an expected outcome—for example, that Godot did not come by the expected time. The model suggests that the ACC predicts not only error likelihood but, more generally, the respective likelihoods of all reasonably possible outcomes. Furthermore, the PRO model introduces a timing element: Prediction-related activity increases over time and peaks when the outcome is expected to occur. Finally, the PRO model introduces the concept of *negative surprise* (Fig. 1c, Fig. 1d). If the outcome does occur when predicted, then the outcome inhibits the prediction signal (Fig. 1c, Fig. 1d). Conversely, if the outcome fails to occur at the expected time, then the prediction signal grows unabated. This unmet prediction signal, when it exceeds a certain threshold, indicates that a prediction error has occurred (Fig. 1d). This is the essence of negative surprise, or surprise that an expected outcome has failed to occur. Note that "negative" here does not necessarily mean aversive; an unexpected omission can be aversive (e.g. you expected a reward but did not get it) or appetitive (e.g., a police officer pulled you over and you expected a fine, but then you were not given one).

Incidentally, the PRO model also computes *positive surprise*, in which predicted and actual outcomes are compared, but with the signs reversed—in this case, the evaluation signal is the actual outcome minus the predicted outcome. The net result is a signal that detects events that occur unexpectedly, as distinct from negative surprise, the detection that expected events have failed to occur.

Are all of the prediction and negative-surprise signals generated within the ACC, or do they originate from elsewhere in the brain? The ACC is a large and varied structure (Nee, Kastner, & Brown, 2011), and conflict and error effects ascribed to it often extend into the presupplementary motor area (Rushworth, Hadland, Paus, & Sipila, 2002). There is evidence that predictions of outcomes, regardless of whether they are good or bad, are represented in the hippocampus (Van der Meer & Redish, 2010) but integrated with desirability information in the ACC (Jahn, Nee, & Brown, 2011).

Model Accounts of Existing Data

From conflict to foresight

The dominant conflict model of ACC function achieved its status because it provided a simple and elegant account of the ACC. If the PRO model does not compute conflict, one might ask, how can it simulate conflict effects? The PRO model has been simulated as a computational neural model, and the basic computational properties of the model have been reported (Alexander & Brown, 2010, 2011). Consider the case of an incongruent stimulus versus a congruent stimulus, as in the Flanker task, in which incongruent stimuli lead to ACC activation (Botvinick, Nystrom, Fissel, Carter, & Cohen, 1999; see Fig. 2). The congruent stimulus may lead to a predicted correct outcome, but the incongruent stimulus leads to a prediction of both a correct outcome and, with some probability, an incorrect outcome. The point is that incongruent stimuli predict two possible outcomes, but congruent stimuli predict a single outcome. When these activities are summed across a prediction layer (much as neural activity is aggregated in fMRI measures), the result is greater ACC activation for incongruent trials.

The PRO model makes the striking prediction that apparent conflict effects will not depend on actual conflict. In other words, if two possible outcomes are not mutually exclusive (i.e., they do not conflict), then apparent conflict effects should still be found. To test this, we asked subjects to perform a flanker task in which they pressed buttons with their left or right index finger according to a central stimulus (Fig. 2), with congruent or incongruent flankers. We then included an *all* condition in which the conflict was removed: For incongruent stimuli, subjects were instructed to press both the left and right buttons simultaneously. The results showed that the

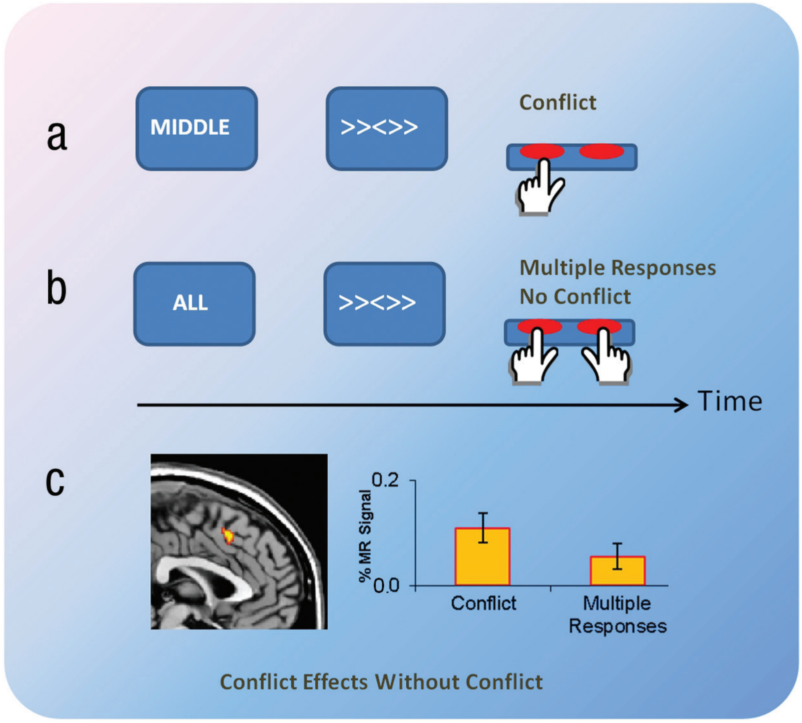

Fig. 2. Conflict effects without conflict computation, as predicted by the Predicted Response Outcome (PRO) model. In the standard flanker task (a), a subject presented with a "MIDDLE" cue must press a button corresponding to the direction of the arrow in the middle of the array and ignore the flankers. The flankers sometimes point in the same direction as the central arrow (congruent flankers) and sometimes point in the opposite direction (incongruent flankers). Here, the middle arrow points to the left, so the subject presses only the left button. In the modified flanker task (b), a subject presented with an "ALL" cue must press one or both buttons, as cued by both the middle arrow and the flanker arrows. Here, the middle and flanker arrows point in both directions, but the subject need not suppress the response to the incongruent flankers, so the subject presses both buttons simultaneously. The dorsal anterior cingulate cortex (ACC; c) shows greater activity (percent magnetic resonance, or MR, signal) for the incongruent condition than the congruent conditions, in both the *middle* and *all* conditions, which suggests that apparent response-conflict effects in ACC may not depend on conflict. Adapted from "Conflict Effects Without Conflict in Anterior Cingulate Cortex: Multiple Response Effects and Context Specific Representations," by J. W. Brown, 2009, *NeuroImage, 47*, p. 339. Copyright 2009 by Elsevier. Adapted with permission.

same ACC regions signaling apparent conflict were also more active in the incongruent *all* condition, thus suggesting that apparent conflict effects do not depend on the presence of response conflict. The same results were found in a change-signal task that also included a response-conflict manipulation; we called this the *multiple-response effect* (Brown, 2009).

From foresight to better decisions

It would be useful enough to have signals that predict the impending consequences of your actions, but it would be even more useful to predict the consequences of your action *before* you execute it. That way, you could avoid making poor choices in the first place. Could the ACC provide such a signal that aversive consequences might follow from an action? To test this, we asked subjects to choose between two buttons; pressing one of the buttons usually resulted in a reward, but pressing the other seldom led to a reward. We then asked subjects to simply imagine the consequences of each of the two possible actions in turn before making their selection. We found that when subjects contemplated the action that was less likely to pay off, their ACC activity increased, and this effect was independent of anticipated response conflict and the subjects' subsequent choice (Jahn et al., 2011). This activity related to imagining an error would correspond to the prediction component of the PRO model (i.e., predicting a probable error) rather than the evaluation component of the model (i.e., negative surprise). This finding also suggests that the ACC serves as a kind of early warning system, anticipating potential dangers so that they can be avoided. If this is the case, then we might ask whether those who tend to avoid risky behavior show more ACC activity. The answer to this question is yes: Subjects with higher trait risk aversion show more sensitivity to error likelihood (Brown & Braver, 2007). Furthermore, subjects who make more risk-averse decisions in the Iowa Gambling Task and the Balloon Analogue Risk Task also show greater ACC activity during decision making (Fukunaga, Brown, & Bogg, 2012; Krawitz, Fukunaga, & Brown, 2010).

From error effects to surprise

The first studies of the ACC described its sensitivity to errors (Gehring et al., 1990; Gemba, Sasaki, & Brooks, 1986; Niki & Watanabe, 1979), and error effects have been foundational to subsequent theories of ACC, such as the conflict-monitoring model. The PRO model makes a strong claim regarding error effects, namely that they do not reflect aversive outcomes per se. Instead, error effects are specific cases of the negative surprise discussed above. In many tasks that probe ACC error signals, error and unexpectedness are confounded because error rates are typically under 10%. What if error rates were high (e.g., 90% or higher)? In that case, an error would no longer be surprising. Would error effects persist, or, as the PRO model predicts, would they go away or even invert themselves so that (surprising) correct trials led to greater ACC activity than (unsurprising) error trials did? We tested this and found the latter to be the case: Our results showed that the ACC responded to surprise (Jessup, Busemeyer, & Brown, 2010; Nee et al., 2011), consistent with reports from others (Hayden, Heilbronner, Pearson, & Platt, 2011; Oliveira, McDonald, & Goodman, 2007; Wessel, Danielmeier, Morton, & Ullsperger, 2012). Similarly, an expected event that occurs but does so at a surprising time also leads to surprise signals in the PRO model, a prediction that was supported by a subsequent fMRI study (Forster & Brown, 2011).

Current Directions

The nature of ACC computations continues to be a topic of lively debate with significant implications, given that the ACC plays a key role in a number of clinical disorders, including schizophrenia (Carter, MacDonald, Ross, & Stenger, 2001), drug abuse (Fishbein et al., 2005), and obsessive compulsive disorder (Fitzgerald et al., 2005). The PRO model suggests how these might be manifested through impairments of ACC prediction mechanisms. For example, schizophrenia may be understood in part as involving a failure to accurately predict the likely outcomes of one's actions (Krawitz, Braver, Barch, & Brown, 2011), and drug abuse may reflect an impaired ability to represent the risks associated with drug taking (Brown & Braver, 2007, 2008). Conversely, the compulsions of obsessive compulsive disorder may reflect an exaggerated prediction of the risks associated with ongoing behavior (Fitzgerald et al., 2005).

Going forward, a number of questions remain open. The first is how (and how strongly) the predictive and evaluative ACC signals posited by the PRO model influence decision making (Fukunaga et al., 2012). Relatedly, how do they influence current goals and working memory contents? A better understanding of these issues will be the key to a deeper theoretical understanding of the role of ACC dysfunction in clinical disorders. A second question is how ACC avoidance signals relate to various definitions of risk—does the ACC represent the probability of aversive outcomes, or does it represent the variance of all possible outcomes (Schonberg, Fox, & Poldrack, 2011)? A third question concerns how information flows in the cognitive-control networks involving the ACC and where the outcome predictions originate.

Recommended Reading

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Alexander, W. H., & Brown, J. W. (2011). (See References). A definitive computational description of the PRO model showing its ability to simulate the broad range of effects from the ACC in humans and macaques.
Silvetti, M., Seurinck, R., & Verguts, T. (2011). (See References). An independently developed computational model of the anterior cingulate that is similar to the PRO model.

Declaration of Conflicting Interests

The author declared no conflicts of interest with respect to his authorship or the publication of this article.

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