

Dorsal anterior cingulate cortex and the value of control

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Debates over the function(s) of dorsal anterior cingulate cortex (dACC) have persisted for decades. So too have demonstrations of the region's association with cognitive control. Researchers have struggled to account for this association and, simultaneously, dACC's involvement in phenomena related to evaluation and motivation. We describe a recent integrative theory that achieves this goal. It proposes that dACC serves to specify the currently optimal allocation of control by determining the overall expected value of control (EVC), thereby licensing the associated cognitive effort. The EVC theory accounts for dACC's sensitivity to a wide array of experimental variables, and their relationship to subsequent control adjustments. Finally, we contrast our theory with a recent theory proposing a primary role for dACC in foraging-like decisions. We describe why the EVC theory offers a more comprehensive and coherent account of dACC function, including dACC's particular involvement in decisions regarding foraging or otherwise altering one's behavior.

The computational function of the dACC has remained perennially controversial¹⁻⁵. Many points of disagreement stem from differential weightings across a body of empirical findings that can be complex and contradictory. However, there are at least two broad findings upon which most researchers agree and which therefore offer a potential foundation for building a successful, unifying theory. First, the dACC—encompassing regions referred to as the anterior midcingulate cortex and the rostral cingulate zone⁵⁻⁹—is a key hub in a network of brain regions implicated in domain-general executive functions in humans^{4,10}. The dACC thus appears to be important to cognitive control; that is, our ability to flexibly adjust behavior in accord with internally maintained goals and away from behaviors that are more automatic but distract from those goals¹¹. Second, and closely related to the first point, is the consistent association of dACC function with motivation and reward-based decision-making^{3,12,13}. In recent work, we have advanced a theory of dACC function that seeks to integrate these two sets of observations, attributing to the dACC a specific role in linking executive function with reward-based decision making⁴ (for related accounts, see refs. 2,6,14,15). Specifically, we suggest that

dACC plays a central role in decisions about the allocation of cognitive control based on a cost/benefit analysis that identifies the highest expected value of control (EVC).

The EVC theory builds on one of the most basic theoretical premises in cognitive psychology: that the processes governing human behavior lie along a continuum from automatic to controlled, a continuum that is as foundational as it is easily observed^{11,16}. Some behaviors are carried out quickly, effortlessly and with little risk of intrusion from distraction. The processes underlying such behaviors typically involve stereotyped and ballistic responses, making them efficient but inflexible; they are therefore characterized as 'automatic'. In contrast, other behaviors have the opposite properties: they exhibit greater flexibility but require more time, are experienced as effortful and are more subject to interference. It is generally assumed that such processes rely on cognitive control signals, the functions of which are to parameterize processing in a way that maximizes desired outcomes when those outcomes would not otherwise be achieved by 'default' settings (i.e., those that give rise to automatic behavior)¹¹. The EVC theory focuses on the evaluation and selection of control signals required to carry out control-demanding behavior, identifying the computational problem that this selection process seeks to solve and proposing a candidate set of algorithms used to accomplish this.

Control signals can vary along two dimensions: identity, determining which process(es) should be engaged (for example, which stimulus or rule should be attended); and intensity, determining how much control should be allocated (for example, how much to augment attention to the stimulus or rule above the default level). These signals can be understood by analogy with motor control signals, which similarly vary in their identity (for example, which muscles to contract) and their intensity (the level of force required) according to task demands. And as in the case of motor control, the allocations across available control signals have a direct consequence for behavior and reward.

Choosing how to allocate control requires taking into account the benefits of control allocation (for example, improved performance and accrual of otherwise foregone rewards), but also its inherent costs; the EVC theory assumes that such costs register as 'effortful'. By taking these costs into account the theory can explain not only why individuals exert more cognitive effort for more difficult tasks or when incentives and/or task demands increase¹⁷, but also why, all other things being equal, they avoid exerting too much effort and instead prefer less difficult tasks¹⁸.

At the neural level, the EVC theory provides a computational account of the role that dACC plays in making decisions about how to allocate control, based on the weighted sums of estimated reward outcome and effort cost. In so doing, it integrates and formalizes previous accounts that have identified dACC at the interfaces between monitoring and control^{1,6,15}, between evaluation and action^{3,19}, between evaluation and motivation^{2,12,20} and between the allocation and

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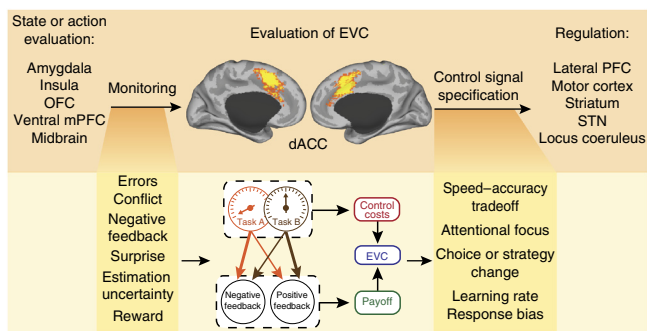


Figure 1 dACC's proposed role in control allocation based on EVC. Top: the EVC theory proposes that dACC monitors for information relevant to evaluating EVC and specifies the optimal control allocation to downstream regions. dACC is shown in the central panel, based on a Neurosynth meta-analysis of 428 human neuroimaging studies associated with cognitive control (<http://neurosynth.org/analyses/terms/cognitive%20control/>). Example input and output structures are shown at the left and right sides of the panel. Bottom: Previous findings suggest a role for dACC in using each of the monitoring signals listed (for example, errors, conflict) as the basis for one or more subsequent adjustments in control (for example, adjustment in one's speed-accuracy tradeoff or attentional focus). As indicated in the central panel, the EVC theory proposes that dACC evaluates the expected future benefits of applying varying intensities of control (arrow in each gauge) for each candidate control signal (different gauges; for example, different rules and the degree to which they could be attended) and subtracts from this the intrinsic cost of applying a given control intensity. This results in an estimate of the EVC. dACC then selects for execution the control signal settings that maximize EVC, projecting information about these signals to relevant downstream regions responsible for implementing the corresponding signals. Elsewhere we have provided a formal description of this process that aligns EVC and its components with ideas from artificial intelligence and control theory^{4,74} and shown how a computational implementation of the theory can account for observed influences of incentives on control adjustments (and associated behavior)⁷⁴. OFC: orbitofrontal cortex; STN: subthalamic nucleus; mPFC: medial prefrontal cortex; PFC: prefrontal cortex. Center panel adapted with permission from ref. 4, Elsevier.

implementation of control¹⁰. The EVC theory identifies and makes computationally explicit an interface that is common across most of these theoretical perspectives, between the monitoring for control-relevant information and the allocation of control. In this respect, it can be viewed as an extension of its historical predecessor, the conflict monitoring theory¹. This theory proposed that dACC monitors ongoing processing, including the amount of conflict between potential responses, for signals indicative of the need for control. However, it made highly simplified assumptions about how those signals are evaluated and used to allocate control.

The EVC theory extends this monitoring framework to address how this process occurs in greater detail (Fig. 1). In doing so, it provides a more comprehensive account of dACC function, accommodating previously unaddressed empirical data (for example, dACC's associations with reward and motivation) and filling explanatory gaps regarding control allocation (for example, how the demanded control is deemed worth allocating). Because much of the force of the theory lies in its ability to integrate a wide range of findings that have previously been considered to reflect disparate functions, we provide a brief review of these findings below (see Fig. 1 and ref. 4 for a fuller discussion). While necessarily selective, this review of the literature attempts to highlight convergent findings across species and measurement techniques within regions potentially homologous to those highlighted in Figure 1, in particular anterior midcingulate cortex.

We focus primarily on potential functional homologies within and adjacent to this circumscribed region of cortex, an approach that, in spite of its benefits, risks blurring potential distinctions between species, methods and cytoarchitectonic boundaries. We will return to these considerations later.

dACC's role in monitoring for EVC-relevant signals

The EVC theory explains why dACC is more active in control-demanding situations^{10,21}; for instance, those that require processes that are complex, deliberate, novel, and/or exploratory versus habitual and/or externally driven. Overwhelming evidence links dACC activity to signals indicating a demand for control^{6,14,15,21}—including errors^{22–26}, explicit negative feedback^{27–29}, conflict^{1,30–34} and surprise^{35,36}—as well as its payoff^{3,37,38}. Furthermore, dACC responses to these signals can carry information about the particular type of control that is required^{22,26,38} and are weaker in situations that pose less of a demand for control (for example, when correct feedback is predicted^{28,29} or when a surprising event does not bear on future task performance³⁶).

dACC's role in specifying control based on EVC

The EVC theory extends performance-monitoring accounts of dACC to explain how signals indicating the need for and/or value of control are translated into the adaptive execution of control (Fig. 1). In particular, the theory proposes that dACC uses estimates of EVC to select appropriate control signals, which are then implemented by other neural structures to influence processing. This explains a number of findings tying performance-monitoring-related responses in dACC or nearby regions to subsequent control adjustments^{4,14,15}, including slower and/or more accurate responding^{25,39}; increased allocation of attention toward task-relevant stimulus properties and away from irrelevant ones^{14,31,33,34}; and adaptive changes in switching behavior³⁹, response bias⁴⁰ and the pace of learning^{35,41} (Fig. 1).

The proposition that dACC is responsible for specifying control signals required to execute control-demanding tasks also explains correlations observed between task performance and dACC's encoding of the task environment^{5,42}. For instance, the strength of rule encoding in monkey dACC predicts whether that rule will be executed properly on a forthcoming trial⁴³, appears earlier on trials following an error⁴³ and weakens with more repetitions following a rule switch (as lateral prefrontal cortex rule selectivity increases)⁴⁴. Similarly, in humans, stronger white matter tracts between dACC and other regions are associated with improved cognitive control^{45,46}.

This proposition also explains why causal manipulations involving dACC can influence one's ability to adjust control. Inactivating or lesioning dACC can impair within-trial error correction⁴⁷ and post-error slowing²⁵, decrease conflict-related adaptation^{31,48} and impair adaptive reversal between responses^{49,50} and task sets⁵¹. Moreover, dACC inactivation impairs antisaccade performance⁵² whereas microstimulation facilitates it⁵³. Similar effects are found when transcranial direct current stimulation (tDCS) is used to modulate activity within dACC and surrounding cortex^{54,55}. Inhibitory tDCS produces weaker error- and feedback-related dACC responses and concomitant impairments in performance (accuracy, learning rate and post-error slowing); excitatory tDCS produces the opposite patterns⁵⁴. While the tDCS configuration in these studies likely resulted in spillover modulation of other regions (including parts of lateral prefrontal cortex), preventing strong inference about the locus of influence, these findings point to a potentially valuable avenue for noninvasively studying causal relationships between human dACC and control allocation. This would supplement studies of lesion patients, which can produce variable findings (for example, ref. 56) partly due to factors out of the

experimenter’s control (for example, compensatory mechanisms and lesion location; but see also ref. 57).

dACC’s role in motivating effortful behavior

The findings reviewed above all concern the role of the dACC in promoting control-demanding processes in the service of maximizing subjective estimates of reward. However, another critical component of the EVC theory is that there is an intrinsic cost to the allocation of these costs alongside environmental signals indicating the demands and incentives for control. The EVC theory thus serves to integrate the aforementioned literature on dACC’s role in performance monitoring and decision-making with the literature linking this region to motivation and effort and their relationship to control. Consistent with the EVC theory, dACC signals associated with control-demanding tasks correlate with avoidant preferences^{58,59} and negative affective reactions⁶⁰ associated with such tasks, as well as with decreased reward-related responses in the ventral striatum following completion of the demanding task⁶¹. Similarly, dACC reactions to response conflict predict subsequent discounting of the reward associated with the conflict-related stimulus⁶². These findings can be explained by a role for dACC in signaling not only the benefits of exerting control (as discussed above) but also the costs of doing so, discounting the former by the latter. Similar observations have been made for dACC responses to demands for physical effort²⁰.

The idea that dACC is responsible for a cost/benefit analysis of control-demanding behavior helps explain the longstanding link between dACC and motivation. The estimation of EVC is, simply put, an assessment of the motivational value of control-demanding behavior (cf. ref. 2), cast in formally explicit terms. This, in turn, helps explain the types of global motivational deficits that have led researchers to tie dACC to the “energization” of behavior^{2,12}. Lesions to dACC have been associated with general slowing of performance¹² and a higher threshold for overcoming effortful obstacles, both physical² and cognitive⁶³. Extreme lesion cases result in severe impairments in motivating action, such as akinetic mutism. Conversely, dACC stimulation produces experiences of a “willingness to persevere” through impending challenges⁶⁴. These observations can be readily explained by alterations in the adaptive allocation of cognitive control.

dACC’s role in foraging and behavioral flexibility

Among the many functions that have been ascribed to dACC is a role in promoting behavioral flexibility. This view has been articulated explicitly by Kolling and colleagues^{3,65}, who have referred to this function in various forms, including a role in the “valuation and promotion of behavioural change and search”³ and encoding “the value of switching to a course of action alternative to that which is taken or is the default.”⁶⁵ They have operationalized this in terms of foraging decisions and proposed that dACC represents, among other things, the value of the foraging option—that is, the value of abandoning a previously chosen option or one typically chosen in a given context (the ‘default’) in favor of an alternative. For convenience, we refer to this as the foraging value theory (FVT). Like the conflict-monitoring theory and many other previous theories, we believe that this characterization accurately reflects a frequently observed characteristic of dACC responses but misidentifies the fundamental computational function responsible and thus fails to capture the fuller picture.

Specifically, FVT ties dACC responses to the value of a particular option or behavioral choice, one that is different from the default—for example, traveling to a new patch versus continuing to exploit resources within the current one. In contrast, EVC proposes that

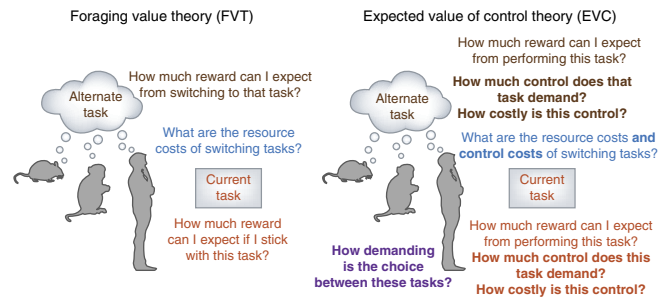


Figure 2 Decisions about engaging in a current task versus an alternate task from the perspective of FVT and EVC. Left: FVT focuses on the expected reward for remaining on the current task (the default) and for switching to the alternate, nondefault task (including the time and resources consumed during the switch). (Note that these are not argued to be the only signals in dACC but to comprise the key foraging decision-related components of the dACC signal.) Right: by contrast, EVC considers the degree to which allocating different amounts of control to each task (separately or jointly) will accrue reward and effort-like costs. EVC also considers the switch costs in terms of both time and the demands of adjusting control signals, as well as the cognitive demands associated with decision conflict (as when the two tasks are mutually exclusive and close in value). Differences are highlighted in bold.

dACC responses are not tied to the intrinsic status of any particular behavior as default versus nondefault or stay versus leave but rather the extent to which, in the current context, those behaviors, and/or the choice between them, demands control (Fig. 2). In general, switching tasks or overriding a default carries costs associated with the demands for control^{4,18,21,58}. The distinction between automatic and default is a subtle but crucial one. Often these factors may be aligned (i.e., the default behavior may be the strongest or most compelling behavior) but not always. This alignment is particularly likely to occur in naturalistic foraging settings, where decisions are made in the context of a progressively depleting resource. Early in the process of exploiting a patch, the stay option may be most compelling but, as the resource depletes, continuing the same behavior (i.e., the default) becomes less compelling. Foraging theory⁶⁶ indicates that the optimal point at which to choose the foraging option is when its relative value matches the value of that stay or default option (Fig. 3a). This circumstance highlights the distinction between the status of a behavior as default and its demands for control, as well as how they can be confounded. When the values of the default and the alternative are roughly comparable—confounding decision difficulty (and corresponding demands for control^{15,21}) with the relative value of the foraging option (which has been steadily increasing)—both theories would predict dACC engagement. Critically, however, decision difficulty and relative value are de-confounded when the value of the foraging option greatly exceeds the current option. FVT predicts that dACC should be even more engaged in such conditions, whereas EVC predicts the opposite (since the decision is now easy: pick the foraging option). In two studies^{67,68}, we exploited this observation and found that when decision difficulty was experimentally dissociated from the relative value of foraging, dACC activity varied with the former and not the latter (Fig. 3b,c; see also ref. 69).

Kolling and colleagues have allowed that, in addition to foraging value, dACC may also encode the difficulty of the decision itself, possibly as a consequence of the foraging value comparison process⁷⁰ (but note that this predicts that difficulty signals should be accompanied by foraging value signals, which we have failed to find^{67,68}). They argue that dACC may in fact encode many decision-related variables,

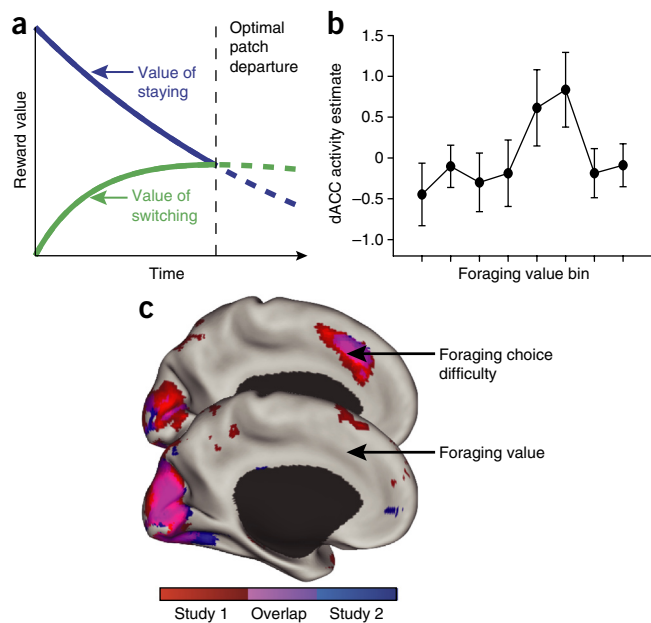


Figure 3 Disentangling potential explanations for dACC involvement in foraging settings. **(a)** For foraging situations in which the value of the current or default behavior diminishes in a progressive manner (for example, through patch depletion, satiety, etc.), the marginal value theorem (MVT)⁶⁶ predicts that it is optimal to switch when the value of the current behavior eventually reaches the value of switching (as estimated by the average expected value of the environment); this corresponds to the point of maximum decision difficulty (when the stay/switch options are closest in value), which is likely to increase the demands for control^{1,15,21} (for example, to support higher-fidelity judgments⁷⁵ or adjustments in other default decision parameters such as response threshold¹⁵). Real-world foraging decisions therefore populate the area to the left of this indifference point. Foraging value signals can be examined past this indifference point, but care must be taken to estimate difficulty ideographically and to include sufficient choices on either side of the indifference point so that trials with high foraging values are neither especially difficult nor especially rare (i.e., potentially surprising)⁶⁷. **(b)** We found that human dACC activity was best explained by an inverse U, with activity maximal around indifference and decreasing with less difficult choices. **(c)** Across two studies^{67,68} we found that dACC was reliably engaged by the difficulty of foraging choices but saw no evidence of overlapping or adjacent regions signaling the value of foraging *per se*, even when excluding the easiest choices. Activations reflect liberally thresholded *t*-statistics ($t \geq 2.0$) but dACC's choice-difficulty responses are robust to standard statistical thresholds. Panels adapted from ref. 67, Nature Publishing Group, and ref. 68, Psychonomic Society, Inc. Error bars reflect s.e.m.

among which difficulty is one. As we have argued above, EVC concurs with this latter prediction. However, what it adds is a computationally explicit account of the relationship among the functions associated with dACC (for example, the role of task difficulty in signaling the need for control), and therefore it offers an account of dACC activity that is simultaneously more coherent and more tightly constrained (Fig. 1). What remains in question is whether dACC encodes foraging value as such, specifically and over and above its role in determining decision difficulty and other demands or incentives for control (for example, surprise⁶⁷).

Current challenges

This review of the EVC theory and its relation to FVT helps bring into focus challenges and promising directions for future research.

Historically, progress in research on the dACC has been marked by the discovery of an increasing variety of signals in this region, across species and methodologies, that have often appeared to present contradictions in the interpretation of its function^{23,24,56}. Such apparent contradictions have at points led to the hypothesis that certain dACC signals (for example, those associated with conflict) are unique to humans and/or to particular measures of neural activity⁷. However, recent data call this hypothesis into question^{9,30–32,34,48} and instead suggest that the diversity of experimental observations may reflect strong context-dependence in dACC function⁵, rather than species or measurement specificity *per se* (see also ref. 71).

The EVC theory seeks to accommodate this diversity by suggesting that it reflects differential engagement of component computations that contribute to an overarching function: the evaluation and specification of control signals. These component computations include estimating the reward anticipated from implementing a candidate control signal, the costs associated with implementing that signal (including opportunity costs and difficulty) and the consequence(s) of not doing so. Insofar as different circumstances may engage these functions in different degrees, and insofar as these functions are likely to be distributed differentially over different subpopulations of units within dACC (and that these, in turn, may interact differently with other brain structures), it is not hard to imagine how different experiments will yield different results. Accordingly, a primary aim of theory development should be to formalize such component computations, determine how they are engaged by experimental manipulations and, based on such determination, generate testable, quantitative predictions about how dACC activity should change according to the relevant variables (i.e., when increases or decreases are expected at the single-unit or population level). This would not only allow theories to better capture the nuances of the brain as a dynamical system, it would also help disambiguate terminological overlap (for example, different types of conflict^{21,30}, estimates of task difficulty¹⁸ and senses in which an option is a default^{4,65}) that often impedes direct contrasts between theories. Of course, greater precision at the level of theorizing must be accompanied by more detailed neural data. In particular, this should include a deeper consideration of cross-species differences in the extent and topographic heterogeneity of the region subsumed by dACC⁵, which includes a prominent extension in humans (area 32') that lacks a clear anatomical homolog in nonhuman primates⁸ but does have a potential functional homolog⁹.

While these are challenging goals, we believe they are essential for progress to be made in this area of research. An important related aim will be to gain a better understanding of the relationship between motor and cognitive control specification by dACC and surrounding regions and to determine whether these together constitute a hierarchical^{2,72} or otherwise topographically organized^{9,21} map of potential control outputs. Future work should also examine the relationship between the computations and circuitry underlying the learning of rewards and control costs in these two domains, given previous work tying striatal learning signals to both motor and cognitive actions⁷³. We hope that the EVC theory provides a helpful framework for pursuing these goals and thus contributes to progress in deepening and expanding our understanding of dACC function.

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COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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