

Dorsal anterior cingulate: a Rorschach test for cognitive neuroscience

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The dorsal anterior cingulate cortex is one of the most beguiling regions of the brain. Understanding its essential function has become a holy grail for many cognitive neuroscientists. With this scrutiny has come contention. In this issue, two teams of neuroscientists with different views argue for their favored interpretation of neural activity in this region. Here, we provide some background and context for this debate.

It sometimes seems like the dorsal anterior cingulate cortex (dACC) is a Rorschach test for cognitive neuroscience. We all see something different in it, and what we see may tell us more about ourselves—and our research priorities—than about the function of the region.

Why does discerning the function of dACC feel so much like a projective test? First, its responses are tantalizingly correlated with many interesting psychological variables. These include rewards, errors, unexperienced outcomes, surprise, conflict, decision costs, uncertainty, learning and arousal, among many other variables¹. Lesions of dACC lead to fascinating effects, including both apathy and impulsive decision-making. At the same time, electrical stimulation of the dACC promotes the subjective sense of a 'will to persevere', the preparation to overcome a challenge². Given the morass of empirical evidence, it should come as no surprise that the list of cognitive functions ascribed to dACC resembles a list of chapters in a cognitive neuroscience textbook: executive control, attention, reward, learning and memory, basic sensorimotor transformations, self-control, social decision-making and strategic decisions¹. For these reasons, the dACC has become a place of intersection for researchers with varied interests and theoretical dispositions. This confluence has produced a heterogeneous literature beset with conflicting terminology and divergent syntheses.

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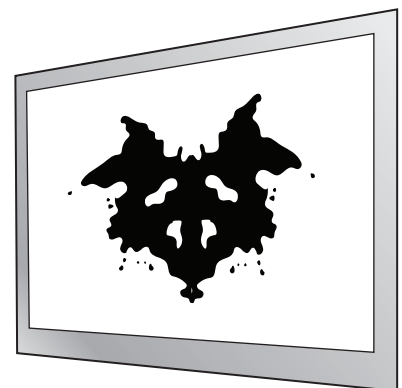
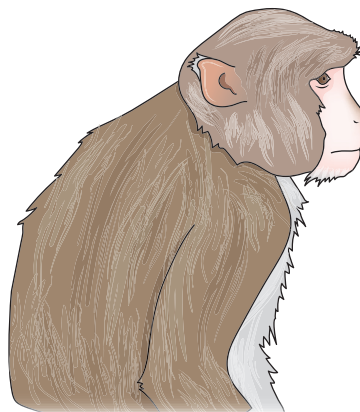
In the present issue, two groups, one centered in Oxford and one in Princeton, both of whom have made prominent contributions to understanding dACC, advocate for their favored theories^{3,4}. Both groups have a long history of studying the problem of dACC function and bring very different perspectives. To allow the groups to address their disagreements directly, the editors of *Nature Neuroscience* have decided to create a forum for debate. Both groups started with a set of questions prepared by the moderator, Benjamin Hayden (**Supplementary Note**), and each wrote a piece making their point, including answers to these questions. Both pieces were peer reviewed, and both groups had an opportunity to read and respond to the other's work before finalizing the papers presented here. Below, we briefly discuss only some of the functional accounts attributed

to this elusive brain region, including those described in the two perspectives.

Evolving theories on dACC function

Conflict. Of the major theories about dACC function, the conflict theory is arguably the best known⁵. This is not to say it is universally accepted; some of its popularity may be as a good target for critics. Still, many discussions of dACC function begin with a conflict account and then move to support, reject or complicate it.

Conflict refers to a competition between mutually incompatible sensorimotor mappings. One well-known example of conflict comes from the Stroop task: when asked to say the color of the ink in which a word is printed (rather than the word itself), we experience a form of interference from the meaning of the text⁶. Reading is so routine that a word-reading



action plan is activated, which competes with the ink-naming action plan for expression. This competition is the conflict.

Behavioral adaptation and persistence: the Oxford view

Many of the alternative interpretations of dACC activations begin with its role in decision-making, rather than cognitive control. Activity in dACC strongly encodes the values of offers and outcomes and may play a role in implementing value comparisons^{1,3,6,7}. In contrast to other regions, it often signals the value of rejecting an offer, of a default option or of switching⁶. In sequential decision-making tasks, dACC activity is highest when subjects decide to reject the default option and select the alternative; this view thus has links with foraging theory. In contrast to economic views of decision making (in which it is assumed that multiple choice options are processed and compared in parallel), in foraging models, decision-makers often choose between maintaining the status quo and switching away from it.

These findings and others have led this group to the notion that the function of dACC is to adjust the current state of the organism: moving it between behavioral stasis and adaptation. The dACC signals the value and costs of behavioral shifts but only insofar as these factors regulate behavioral adaptation³. The consequence of dACC's involvement is proposed to have broad effects on subsequent behavior, changing one's estimate of the environment, adjusting learning rates or altering high-level strategies. From this perspective, the primary role of the dACC is in dynamically updating behavioral policies in changing environments.

Expected value of control: the Princeton view

The neuroeconomic challenges and others exposed weaknesses in the original conflict theory. Its proponents have accepted several of the criticisms and have redeveloped the theory to account for newer results^{4,8}. Modern expected value of control (EVC) theory is quite different from the original formulation, but, at its heart, it still proposes that the dACC still detects the need for top-down control and summons additional control. However, in the updated theory, not only does dACC also calculate the value of that control, its signal strength depends, in a graded fashion, on how beneficial and/or effortful the control will be. Their theory accomplishes two things.[^] First, it provides a framework for explaining many recent results that do not fit a simple conflict account of dACC function. Second, it provides

an alternative to the behavioral adaptation and persistence hypothesis while still placing the role of dACC within in the domain of cognitive control.

The bigger picture

A reader new to the debate may be forgiven for asking why dACC needs to have one singular function. Indeed, both groups suggest that cingulate cortex almost certainly has multiple overlapping functions^{3,4}. Isn't it possible that both groups are right but just examining distinct domains of dACC function like the proverbial blind men and the elephant?

We think this is unlikely. The core of this debate is the interpretation of specific signals in specific tasks. All parties largely agree that they are looking at the same signals and then debating the interpretation of those signals[^]. For example, the EVC model offers a specific reinterpretation of the foraging signal of reported in dACC⁴. Likewise, the Oxford group has specific reinterpretations of conflict correlates³. It is also important to note that the signals in question are quite robust. They are seen in a variety of circumstances, and measures with multiple methods seem to converge on similar types of signals.

There are a lot of points of agreement here, which highlight the substantial progress these groups and others have made in understanding these aspects of dACC function. In each theory, dACC is more active when one response is not performed (suppressed or rejected) in favor of another, particularly when one of the potential responses represents a default choice (though the different theories differently emphasize reflexive and habitual default behaviors[^]). In each theory, dACC signals the value and costs of such behavioral policies and the ultimate function of dACC is to set behavioral policies one or more trials into the future.

These points may provide insight into the well-known disjunction between the conflict signals observed in functional MRI and (inconsistently observed) in single neurons^{1,9,10}. In the single-unit studies that do find dACC conflict signals, conflict signals were linked to long-timescale adjustments in behavioral state¹. Behavioral adaptations often follow high-conflict trials in typical human paradigms but tend to be much weaker in primate studies, which are necessarily overtrained.

Our discussion of the similarities between these papers should not be misunderstood as suggesting that these papers agree on all points[^]. It may sometimes seem that the papers differ largely in their choice of terms, but such a cynical reading risks missing the point of this debate. The differing views of

dACC function presented here highlight major open questions about the role of dACC in executive functions.

First, the theories have very different implications for where dACC should be placed in our broader understanding of its function¹. One approach describes dACC as fundamentally auxiliary: a controller that sits on top of sensorimotor transformations⁴. The other describes it as a central part of the system that converts inputs to outputs³. Should we think of the dACC as a regulator of cognition or as an integral part of cognition itself, subject to regulation by other factors?

These two views relate to the question of the best way to look at the cingulate cortex as a whole. The cingulum is sometimes called the fifth lobe of the brain, suggesting that the dACC may have a distinct role from surrounding frontal cortex regions, one that is shared with subgenual and pregenual cingulum and with posterior cingulate cortex. Such a role may be as an auxiliary to ongoing cognitive processes. On the other hand, the fifth lobe idea may be a superficial one, and dACC may be functionally contiguous with neighboring tissue; we don't really know. If dACC has a distinct role, then its special anatomy, with its diverse inputs and outputs, may be a special feature of that role.

Second, resolutions to thorny problems often have beneficial and unexpected side effects. It is sobering (and revealing about the confusion surrounding dACC) to note that these two documents represent but one of several ongoing major debates about the function of dACC. These include the Cingulategate controversy (the question of whether dACC activity is selective for pain), questions about dACC's contributions to value comparison and debates about the putative social roles of the anterior cingulum^{1,11,12}. There are also contentious questions about homology, such as whether rodents have a true cingulate and where it is if they do, and what the monkey-human homologies are¹. On one hand, it may seem overwhelming to consider that resolution of this debate will not even solve the majority of problems in even dACC. On the other hand, progress on this one small piece of the puzzle will surely lead to further progress on other puzzles.

Conclusion

What are the hopes for such progress? We remain sanguine. First, by taking the time to work through their arguments in detail in a public forum, both groups have the chance to make their case to the broader scholarly community, highlighting the points of contention and agreement between the two views.

We hope this work will spur independent assessment of these ideas and motivate development of both viewpoints, as well as the synthesis of new ones. Second, neuroimaging methods continue to improve, meaning their sensitivity will continue to develop as well. These and other methodological improvements will lead to more rigorous tests of specific hypotheses. Third, animal methods of investigating dACC, especially primate and rodent physiology, are continuing to grow and, with new molecular tools, are joining the conversation. Anatomy still has a great deal to add; it would be a mistake to think we have anything close to a full picture of the connections of the dACC¹.

Fourth, our understanding of adjacent tissue will enrich and constrain our understanding of the dACC. Recent recordings in supplementary eye fields¹³, posterior cingulate cortex¹⁴ and subgenual cingulum¹⁵, for example, have led to greater understanding of these areas that reframes our understanding of dACC.[^]

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