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Strategic Control in Decision Making under Uncertainty

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Abstract

Complex economic decisions – whether investing money for retirement or purchasing some new electronic gadget – often involve uncertainty about the likely consequences of our choices. Critical for resolving that uncertainty are strategic meta-decision processes, which allow people to simplify complex decision problems, to evaluate outcomes against a variety of contexts, and to flexibly match behavior to changes in the environment. In recent years, substantial research implicates the dorsomedial prefrontal cortex (dmPFC) in the flexible control of behavior. However, nearly all such evidence comes from paradigms involving executive function or response selection, not complex decision making. Here, we review evidence that demonstrates that the dmPFC contributes to *strategic* control in complex decision making. This region contains a functional topography such that the posterior dmPFC supports response-related control while the anterior dmPFC supports strategic control. Activation in the anterior dmPFC signals changes in how a decision problem is represented, which in turn can shape computational processes elsewhere in the brain. Based on these findings, we argue both for generalized contributions of the dmPFC to cognitive control, and for specific computational roles for its subregions depending upon the task demands and context. We also contend that these strategic considerations are also likely to be critical for decision making in other domains, including interpersonal interactions in social settings.

Introduction

The term *cognitive control* broadly describes the ability to shape behavior in an adaptive manner, as a function of current goals and constraints. Different theoretical models and definitions have emphasized different aspects of control in the past. These include (i) the ability of the human cognitive system to configure itself for the performance of specific tasks (Botvinick et al., 2001); (ii) the ability to coordinate thoughts or actions in relation with internal goals (Koechlin et al., 2003); (iii) the acquisition and implementation of the behavioral rules needed to achieve a given goal in a given situation (Miller and Cohen, 2001) or (iv) the support of flexible behavior by selecting actions that are consistent with our goals and appropriate for our environment (Badre, 2008). The diversity in conceptual models follows from the remarkable progress made in understanding cognitive control and flexible selection of behavior over the past couple of decades.

In parallel, there has been intense research interest in the ability of humans to make decisions adaptively (Payne et al., 1993; Gigerenzer and Goldstein, 1996). Humans are often faced with complex decisions that involve acquiring and integrating information across different input variables. Importantly, they often employ a variety of strategies to simplify the representation of these problems (Tversky and Kahneman, 1974; Payne et al., 1988;

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Payne et al., 1992; Gigerenzer and Goldstein, 1996). The ability to adapt to subtle changes in decision context involves the dynamic selection of decision strategies based on goals and available cognitive resources (Simonson and Tversky, 1992; Tversky and Simonson, 1993). More importantly, this requires the ability to exert strategic control and switch between these strategies according to demands of the current decision environment. Despite the striking overlap conceptually between strategic control in decision making and cognitive control in executive function, there has been relatively little integration between these two research domains.

In this review, we address this gap by developing a framework for control that considers the adaptive use of strategies in complex decision environments. Specifically, we contend that three properties are fundamental to strategic control: *selection*, *optimization*, and *hierarchy*.

- *Selection*: Cognitive control involves selection of actions that are consistent with present goals and context (Badre, 2008). This selection can occur at several levels ranging from simple response selection to complex strategy selection and task switching. An effective control system is therefore one that facilitates processing in uncertain environments, as well as supports multitasking in the pursuit of multiple goals simultaneously.
- *Optimization*: A cognitive control system should have the ability to monitor and compare actual performance with internal goals and standards and use this information to optimally and adaptively organize behavior. Therefore, such a system should detect errors and unfavorable outcomes and use this error-related feedback to guide subsequent performance adjustments.
- *Hierarchy*: Similar to an organization hierarchy that consists of superiors, subordinates and well-defined lines of communication, efficient control systems operate at multiple levels. Each level is influenced by a higher level and in turn influences representations in lower levels. For example, the lowest level of control could be associated with sensory processing and selection of motor actions, while the highest level of control might involve multi-tasking and selecting between several concurrent actions. Control signals within a hierarchy flow primarily, but not exclusively, in a top-down manner.

Historically, the flexible control of behavior has been associated with dorsolateral prefrontal cortex (dlPFC) function (Miller, 2000; Koechlin et al., 2003; Ridderinkhof et al., 2004; Badre, 2008; Egner, 2009). Therefore, we begin our discussion with a review of the role of dlPFC in cognitive control. We then discuss the role of dmPFC, a region that has also been associated with control functions like error monitoring, learning and reward processing in complex decision making. A number of past studies refer to this region also as the anterior cingulate cortex (ACC), though the latter can also include a swath of the medial prefrontal cortex that is often broader and more ventral to the dmPFC. Here, we present evidence that the dmPFC plays a key role in the ability to exert strategic control. We then develop a framework for cognitive control that involves hierarchical connectivity between the lateral and medial aspects of prefrontal cortex with increasing level of abstraction. Specifically, we propose a model for cognitive control that is based on hierarchical interactions between the medial and lateral prefrontal cortex as a function of environmental uncertainty.

Role of DLPFC in Cognitive Control

Dorsolateral PFC neurons assimilate and process contextual information, and bias subsequent selection of appropriate action pathways in other brain regions (Miller and Cohen, 2001). These functions become particularly important when inputs are ambiguous; involve uncertainty or when one has to choose flexibly between multiple responses depending on task context. The prefrontal cortex can facilitate these functions due to its strong connections to other sensory regions in the brain (Petrides, 1985; Barbas and Pandya, 1989), its capacity for actively maintaining task and goal-related representations (Passingham, 1998; Miller, 1999), and its ability to learn and update these representations over time (Miller and Cohen, 2001).

Several recent lines of research also suggest a strong hierarchical organization within dlPFC, with the more rostral regions involved in contextual control and more caudal regions associated with sensory control (Koechlin et al., 2003; Badre, 2008). For example, the cascade model proposed by Koechlin and colleagues argues for a hierarchy of executive processes from premotor to more anterior prefrontal regions; these control behavior according to the stimuli (sensory control), current environmental constraints (contextual control), and the temporal episode (branching control) in which the stimulus occurs (Koechlin et al., 2003). Along similar lines, Badre and colleagues posit that the rostral-caudal hierarchy can be better understood in terms of levels of abstractions in representations of rules for action selection (Badre and D’Esposito, 2007). Yet another proposal argues for a rostral-caudal hierarchy in the prefrontal cortex based on relational complexity (Christoff and Gabrieli, 2000; Christoff et al., 2001). Although these models differ in the details of their hypotheses about specific regions, what is common to all of them is a posterior-to-anterior gradient characterized by increasing level of abstractness.

In summary, most of the postulated functions for the dlPFC involve the implementation of cognitive control. However, when there is a need to monitor and detect changes in the environment, the dlPFC still relies on feedback inputs from other brain systems, most notably the dmPFC. For this reason, the dmPFC has also been consistently associated with an active role in cognitive control, particularly in terms of performance monitoring as well as in shaping behavior in a flexible manner based on context, goals and motivation.

Role of Dorsomedial PFC in Cognitive Control

The interest in dmPFC arises from several lines of research that implicate this region in functions integral to cognitive control, including error monitoring (Carter et al., 1998; Brown and Braver, 2005b), conflict monitoring (Botvinick et al., 1999; Barch et al., 2000; Kerns et al., 2004), reward processing and outcome evaluation (Hadland et al., 2003; Rogers et al., 2004), reinforcement learning (Kim et al., 2006), and decision making under risk and uncertainty (Hadland et al., 2003; Rushworth et al., 2004; Kennerley et al., 2006). More importantly, the dmPFC satisfies all three characteristics of a control system: selection, optimization, and hierarchy.

Selection: DmPFC exerts control preferentially in uncertain environments

Activation in the dorsomedial prefrontal cortex has been consistently associated with detection of conflict, overriding of prepotent responses as well as selection among a set of mutually incompatible response processes (Carter et al., 1998; Botvinick et al., 1999). The detected conflict signal then triggers strategic adjustments in cognitive control, which then serve to prevent conflict in subsequent performance. Many such studies have used variants of the Stroop paradigm (MacLeod, 1992), which requires individuals to inhibit a fast, prepotent response (e.g., color word reading) and instead engage in a slower, less common process (e.g., naming an ink color). There is consistent activation in the dmPFC under such task conditions in a number of studies (Bush et al., 1998; Derrfuss et al., 2005), as articulated in influential reviews (Bush et al., 2000). Similar findings have also been observed with other tasks that involve response incompatibilities like the flanker task (Bugg, 2008), Simon task (Kerns, 2006) and go/no-go paradigms (Kawashima et al., 1996; Tsujimoto et al., 1997).

Given that conflict can occur at various levels, a key question that arises then is whether the involvement of dmPFC is specific to conflicts at the level of response selection or whether it extends to other types of conflict. While vast majority of initial studies suggest a specificity for response-related conflict especially given the strong connectivity of this region to motor structures including premotor cortex, many recent studies posit a more broader functional role for dmPFC in detecting conflict at other levels including stimulus evaluations and task representation (Botvinick et al., 2004). Several other studies have also found increased activation in the dmPFC for complex decisions, though these could have been confounded with activation related to response preparation (Paulus et al., 2002; Walton et al., 2003; Rushworth et al., 2004; Zysset et al., 2006; Botvinick and Rosen, 2008; Pochon et al., 2008).

In one such study, Pochon and colleagues explicitly investigated whether the conflict monitoring role extended to complex decisions that involve the integration of higher-order beliefs and preferences (Pochon et al., 2008). Here, male subjects were asked to choose between two attractive female faces. The similarity of the two faces was modulated such that some trials invoked higher decision conflict (choosing between two highly attractive faces, as determined from a pretest) while others evoked lower levels of decision conflict (choosing between one attractive and one unattractive face). Activity in the dmPFC was greater for trials involving higher decision conflict. Importantly, this increased activation was found even in trials where the subjects did not have to respond, suggesting that it was specific to decision conflict and not due to selecting between multiple motor responses (Pochon et al., 2008).

Activation in the dmPFC has also been associated with conflict arising from subjective decision preferences, particularly when choices run counter to general behavioral tendencies or strategies. We define the conflict arising in these instances as strategy-related control demands. For instance, in a study involving the framing task, all subjects exhibited a strong tendency towards the framing heuristic, driven by increased activation in the emotional amygdala system (De Martino et al., 2006). Subjects also showed increased activation in the dmPFC for choices that were inconsistent with framing effects. The authors argued that increased activation in dmPFC represents a conflict between the generally preferred emotional heuristic response and a more rational analytical choice (De Martino et al., 2006). In other words, increased activation in this region helps control the automatic activation of the emotional system, leading to more rational choices.

In a recent study, we sought to explore whether the dmPFC also plays a critical role in exerting the strategic-control necessary to make decisions in an adaptive manner, using a complex multi-outcome decision-making task (Venkatraman et al., 2009b). Subjects could use two different strategies for these problems: choose a simplifying strategy that focuses on the overall probability of winning while discounting several aspects of the complex gambles, or a more compensatory strategy where subjects utilize all available information in making their choice (Fig. 1A). We found that subjects showed variability in their strategic preference consistent with adaptive decision making. This strategic variability was related to a trait measure of satisficing, such that the satisficers where more likely to choose a simplifying strategy. More importantly, we found that activation in dmPFC predicted whether an individual adaptively made a choice that was inconsistent with their overall preferred strategy (Fig. 2). In other words, activation in this region was greater when people who normally prefer the simplifying choice made a compensatory choice and vice versa (Venkatraman et al., 2009b). Since our experimental design explicitly separated the decision and response components, the alternative explanation of activation being related to response selection can be ruled out. Therefore, we argued that a more parsimonious explanation for dmPFC function in complex decision making could be that it supports aspects of decisions that are coded in relation to an underlying strategic tendency.

We replicated these findings in an independent study where subjects chose between multiple stock options instead of gambles (Venkatraman et al., 2009a). Here, subjects were asked to choose between two stocks that were rated on two independent attributes. Similar to the study by Pochon and colleagues involving faces, the difficulty of the decision was manipulated by increasing or decreasing the values of the attributes for the two stocks. Subjects could again choose adaptively between two different strategies: choose to invest in the stock with highest expected value (as calculated by the sum of ratings on the two attributes) or choose the stock that is more balanced on the two attributes. The later choice is consistent with an attribute-balancing heuristic, where subjects prefer the more balanced option and avoid options that are extreme on the two attributes. Consistent with the first study, we show that a region in the anterior dmPFC predicted strategic variability across subjects. In other words, activation in this region was again greatest when subjects made choices that ran counter to their preferred strategy, validating the hypothesis that the dmPFC codes for preferences at a strategic level (Venkatraman et al., 2009a).

Optimization: DmPFC regulates other brain regions

A key aspect of any control system is the ability to optimize: to monitor and evaluate the performance of various other systems, and to make appropriate adjustments as necessary. We contend that the dmPFC performs such a function in cognitive control, based on evidence from neuropsychological and imaging studies. For example, lesions to the anterior cingulate cortex have been shown to lead to deficiencies in the ability to exert cognitive control (Ochsner et al., 2001; Swick and Jovanovic, 2002). The dmPFC has been shown to play an important role in the continuous assessment of ongoing actions and their corresponding outcomes. Of particular interest is the postulated role of the dmPFC in commission of errors, demonstrated both using the transient potential known as the error-related negativity (ERN) in EEG (Gehring et al., 1995) as well as fMRI (Kiehl et al., 2000; Menon et al., 2001). Subsequent studies also demonstrate an increase in dmPFC activity when actions specifically lead to errors (Ullsperger and von Cramon, 2003).

A slightly different perspective argues for a more general error-likelihood estimation function within the dmPFC, of which conflict monitoring and error detection are special cases (Brown and Braver, 2005a). Brown and Braver demonstrate, using integrated computational neural modeling and neuroimaging experiments, that activation in dmPFC might predict error likelihood in a given context, even when these trials have no error or response conflict. According to this model, activation in dmPFC to a given task condition will be proportional to the perceived likelihood of an error in that condition, even before any external feedback is provided. The authors further speculate that this signal may be dopaminergic in nature and hence could play an important role in reinforcement learning and recruitment of cognitive control (Brown and Braver, 2005a).

Other research indicates that dmPFC contributes to representing and updating action values (Behrens et al., 2007). For instance, non-human primates could no longer use the most recent outcome to guide choice following lesions to the anterior cingulate sulcus (Kennerley et al., 2006). As shown by Behrens and colleagues (2007), volatility in the information content of an environment is reflected by fMRI activation in the dmPFC when each trial outcome is observed. When a new piece of information becomes available, activity in this region increases proportional to its salience for predicting future events (Behrens et al., 2007). Since prediction error signals are often associated with dopaminergic regions and ventral striatum, the authors speculate that the projection from dmPFC to ventral striatum might allow the volatility-based learning rate to modulate the influence of current prediction error on the next value estimate. This model could also explain the increased activation in this region during task switching, as the environment is highly volatile in these situations and hence outcomes are especially informative.

Any region that plays an optimizing role for cognitive control should also detect the need for greater control and subsequently signal this need for reactive adjustments to other regions of the brain. As discussed earlier, the lateral PFC has been postulated to play an important role in implementing cognitive control. Consistent with this notion, Kerns and colleagues hypothesized that increased activation in dmPFC should lead to greater implementation of cognitive control in the subsequent trial, as manifest in increased lateral PFC activation (Kerns et al., 2004). They found that when incongruent trials were associated with strong activity in the dmPFC, relatively low interference was observed in the next trial. More importantly, they demonstrated that the magnitude of activation change in the dmPFC for the current trial predicted subsequent change in dorsolateral PFC activation on the next trial, suggesting that dmPFC may engage executive control regions based on task demands (Kerns et al., 2004).

In our own study involving complex risky choice gambles introduced earlier, we showed that the dmPFC demonstrates differential task-specific functional connectivity with the choice-related brain regions (Fig. 2). Specifically, we found increased functional connectivity between dmPFC and dorsolateral PFC only for simplifying choices and increased functional connectivity between dmPFC and anterior insula for compensatory choices (Venkatraman et al., 2009b). (Note that in this study, activation in dlPFC and posterior parietal cortex predicted simplifying choices while activation in the anterior insula and vmPFC predicted compensatory choices). Though these effects are correlative and cannot be used to attribute causality, we hypothesize that dmPFC shapes decision-making at a strategic level by switching between appropriate brain systems as a function of decision context and individual traits. Such strategic considerations are unlikely to be limited to economic contexts; they are likely to extend to emotional and social contexts. For instance, evidence across primate lesion and neuroimaging studies suggest a spatial topography within dmPFC such that distinct subregions support volatility associated with social and non-social contexts, and that those subregions have distinct functional connectivity to regions in ventral PFC (Rushworth et al., 2007; Behrens et al., 2008).

In another recent study, Kouheiner and colleagues argue that the activation in the medial prefrontal cortex shown across several studies for errors, conflict situations, rewards and penalties represents its underlying role in monitoring motivationally salient events (Kouneiher et al., 2009). Further, they argue that the motivational processes in the medial prefrontal cortex energize a cascade of top-down control processes in the lateral prefrontal cortex, along the lines demonstrated by Kerns and colleagues. Importantly, they also argue that motivational processes in the dmPFC operate according to the rewarding values of the actions rather than demands of cognitive control (Kouneiher et al., 2009).

Hierarchy: DmPFC exerts control in a topographic manner

For a control system to effectively monitor and evaluate the performance of other systems requires some sort of a functional hierarchical organization. Within the dmPFC, an early form of such organization involved diving this region into a dorsal aspect involved in cognitive control and an anterior aspect associated with emotional processing (Bush et al., 2000; Bush et al., 2002). More recently, Kouheiner and colleagues found an anterior-posterior organization of motivational processes in the dmPFC (Kouneiher et al., 2009). The posterior regions, specifically the pre-SMA, showed transient responses to immediate contextual incentives signaling the rewards and penalties at stake in immediate action. Similarly, more anterior regions, particularly the dorsal anterior cingulate cortex, showed sustained activations that were associated with the rewards and penalties at stake in the ongoing behavioral episode, regardless of immediate contextual incentives (Kouneiher et al., 2009). Overall, these findings indicate that the dmPFC implements multiple levels of control processes that may reflect distinct sorts of motivational demands.

Beckmann and colleagues used magnetic resonance diffusion tractography to delineate probabilistically the anatomical connectivity of the cingulate cortex to other brain regions (Beckmann et al., 2009). The authors first identified nine distinct subregions within the cingulate cortex based on its probabilistic connectivity profiles with the rest of the brain. Specifically, the authors found three distinct subregions within the dmPFC based on differential probabilistic connectivity to lateral PFC, premotor and precentral cortices respectively, strongly suggesting functional specialization within the region. Based on the anatomical connectivity profiles (Beckmann et al., 2009), one hypothesis is that the posterior regions would be more involved in response-related control while the anterior regions would be associated with more decision-related control.

To explicitly test this hypothesis, we used two different tasks in the same subjects to evoke three different forms of control demands – response, decision and strategy (Venkatraman et al., 2009a). To identify regions associated with simple response-related control, we measured activation during incongruent trials in a counting Stroop task, covaried with a response-time based incongruency measure obtained for each subject. For decision- and strategy-related control, we used an attribute-balancing task where individuals had to choose between different stocks (Fig. 1B). Decision-related control demands were characterized by manipulating the relative desirability of the various options across trials. The magnitude of strategy-control was defined based on the degree of bias towards one of the two available decision strategies across subjects. We took care to address several potential confounds when designing the experiment. For instance, the decision and response phases were explicitly separated to prevent activations for decision-related control being confounded by motor preparation and response selection. Similarly, no feedback was provided in these trials to prevent learning as well as to preclude alternative explanations for activation in brain regions based on error detection, reinforcement learning and the like. Finally, though we used two different tasks, data for all types of control were acquired in the same subjects within the same session and were associated with unique and independent behavioral covariates.

As hypothesized, we found strong evidence for an anterior-to-posterior topography within the dmPFC, based on varying control demands (Fig. 3). The more posterior regions were associated with response-related control while the middle regions within the dmPFC were associated with decision-related control. Finally, the more anterior regions were associated with more abstract strategy-related control demands. We performed an activation-likelihood estimation based meta-analysis of over 40 studies involving decision making and response inhibition and found that the peak activations for decision- and response-related control obtained using fMRI in this study overlapped with centroids obtained using the meta-analysis. We contend that these results provide strong evidence in favor of a functional organization within the dmPFC that parallels the anterior-to-posterior organization demonstrated in the lateral PFC.

A Hierarchical Model for Cognitive Control in PFC

The different functional divisions within dmPFC may exert hierarchical control through their different connections to other regions in the brain, as suggested by evidence from magnetic resonance tractography (Beckmann et al., 2009) and from functional connectivity data in active tasks (Venkatraman et al., 2009b). A natural target is lateral prefrontal cortex, which exhibits similar variation along its posterior to anterior axis (Koechlin et al., 2000;

Koechlin et al., 2003). Specifically, the more posterior regions that are immediately adjacent to premotor cortex, are associated with setting up general rules for behavior and the more anterior regions support the instantiation of these rules based on the current context. Findings from functional neuroimaging studies argue for further divisions within anterior prefrontal cortex, such that regions around the frontal pole support relational integration, or the combination of disparate information into a single judgment (Christoff et al., 2001). A natural conjecture, accordingly, is that different regions of dmPFC differ in their lateral prefrontal targets.

To test this hypothesis, we used spontaneous fluctuations in BOLD activity to characterize further the functional connectivity between the medial and lateral prefrontal regions in the absence of task-associated cognitive processes (Taren et al., 2011). This task-free approach using resting-state data relies on correlations among low-frequency BOLD changes to identify regions that function in tandem. Using such an approach, we demonstrated a posterior-to-anterior gradient in connectivity between the medial and lateral prefrontal regions (Fig. 4). Specifically, the posterior cluster within dlPFC was maximal connected to posterior dmPFC seed and the anterior cluster within dlPFC to anterior dmPFC seed. This pattern replicated in three independent datasets collected using three different MR scanners and was evident even in individual subjects (Taren et al., 2011).

These findings are consistent with earlier divisions found using diffusion-based tractography, where the lateral prefrontal cortex exhibited the highest probability of anatomical connectivity with a cluster that corresponds spatially to the dmPFC cluster associated with decision-related control in our study. Similarly, the premotor and precentral cortices showed highest probability of connection with a cluster in dmPFC that was associated with response-related control. Therefore, one perspective points to a generalized role for the dmPFC in cognitive control, but specific computational roles for its subregions depending upon the task demands and current context. The studies presented above provide independent evidence across different modalities about the robustness of the functional connections between these regions. Though these methods are largely agnostic about the directionality of these interactions, the findings of Kouneiher and colleagues suggests that the medial frontal regions may regulate the cognitive control resources in the lateral regions according to motivational incentives (Kouneiher et al., 2009). Therefore, we speculate that dmPFC exerts a regulatory or modulatory influence on dlPFC (Wood and Grafman, 2003; Egner, 2009; Kouneiher et al., 2009).

In summary, different regions of dmPFC and dlPFC interact to guide the adaptive control of behavior according to the computational demands of the task. This leads us to propose a conceptual model for cognitive control that extends the previously postulated hierarchical organization within dlPFC to include a parallel organization in dmPFC, whose subregions shape processing in their lateral counterparts (Fig. 5). That is, the anterior dmPFC regulates activity in the anterior dlPFC when the control demands are associated with high levels of abstraction (e.g., implementing strategic planning in a decision-making task), while the posterior dmPFC works in concert with posterior dlPFC and premotor cortices when the control demands are limited to choosing between two competing responses. Such a functional gradient in connectivity could reflect a dynamic mechanism for identifying and responding adaptively to contextual changes in behavior.

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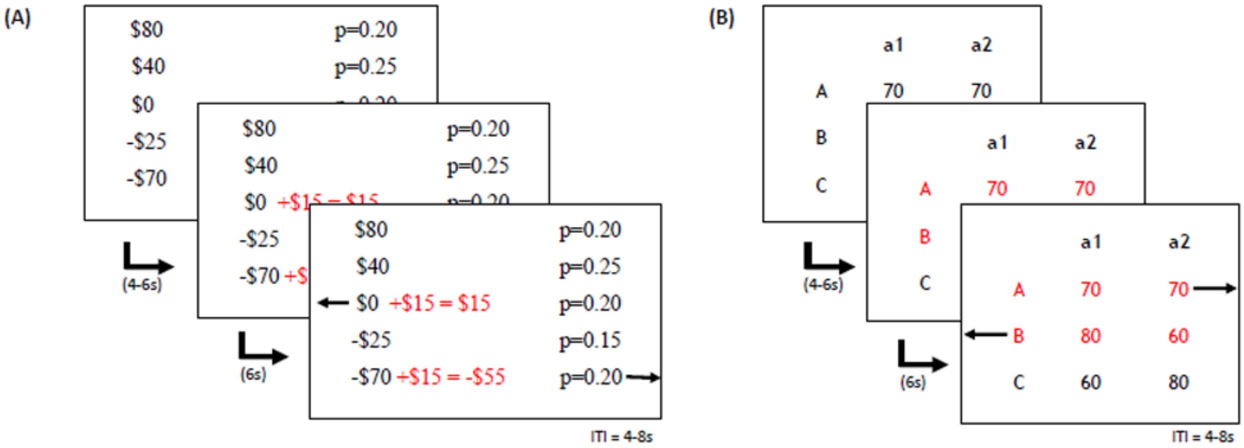

Figure 1. Schematic of decision-making tasks

(A) Multi-outcome risky choice task. Subjects were presented with a series of five-outcome complex mixed gambles, each containing both gain and loss outcomes. They then improved each gamble by adding money in one of three ways: increasing the magnitude of the highest gain (Gmax), decreasing the magnitude of the worst loss (Lmin), or by improving the overall probability of winning by adding money to a central reference outcome (Pmax). While Gmax and Lmin choices represent a compensatory strategy consistent with most economic models of risky choice, Pmax represents a simplifying heuristic strategy. **(B) Attribute-balancing task.** Subjects were first shown, for 4–6s, three anonymized stocks (A, B and C) with percentile ratings on two attributes. Then, two stocks were highlighted in red, whereupon subjects had 6s to decide which they preferred. Finally, after two arrows identified the buttons corresponding to the choices, subjects indicated their choice by pressing the corresponding button as soon as possible. Here, stock A represents a balanced option (with equal ratings on both attributes) while stock B represents an extreme option (with a good rating on one attribute but a poor rating on the other). In this example, both highlighted stocks have similar relative ratings; however, on other trials the stocks differed in their relative ratings.

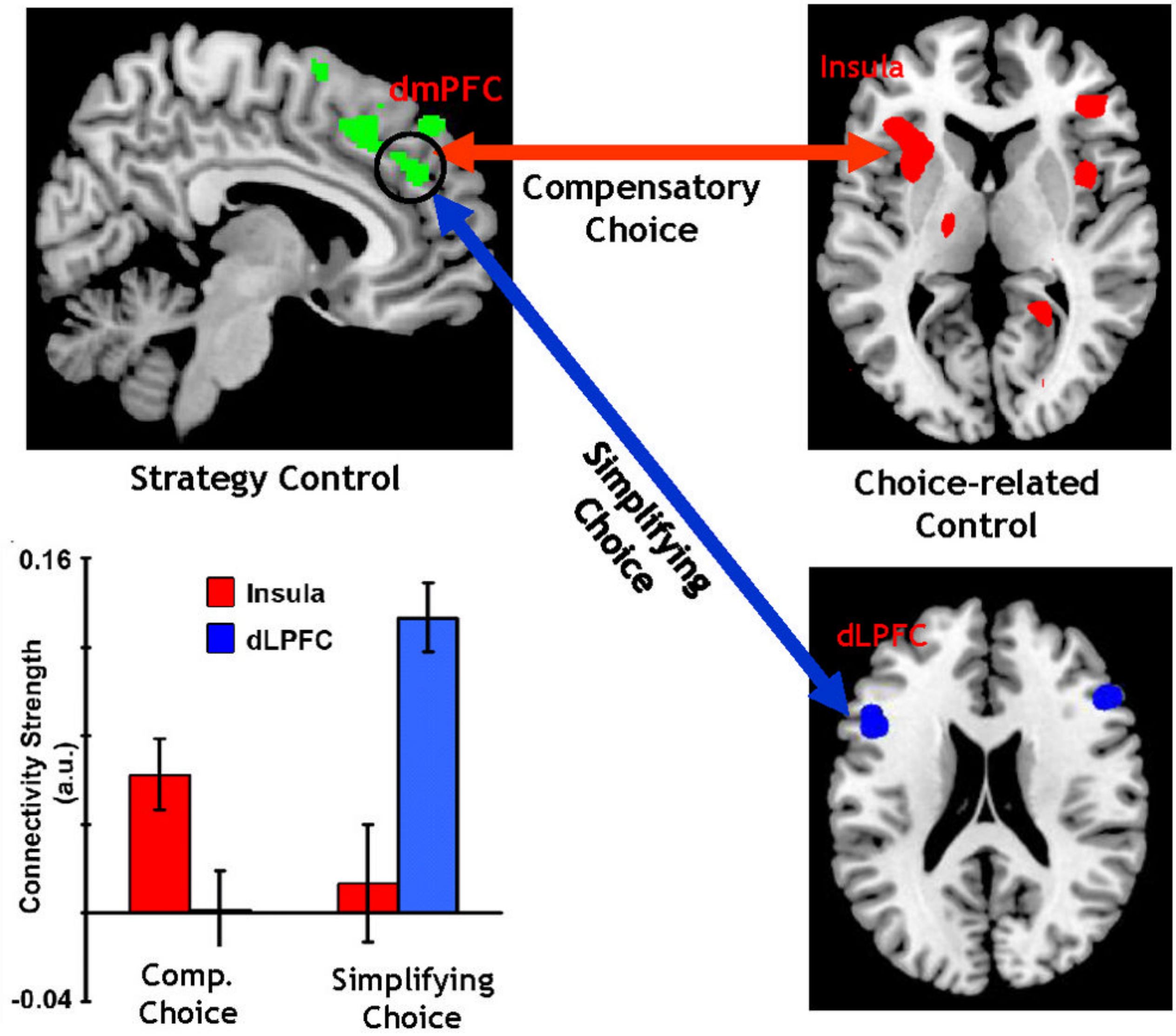

Figure 2. Dorsomedial prefrontal cortex plays a role in strategic control during decision making

Work by Venkatraman and colleagues (2009b) indicated that activation in dmPFC was greater when individuals made a decision opposite their typical strategic bias (upper left panel). Moreover, psychophysiological interaction analyses revealed a double dissociation in the connectivity of dmPFC with different choice-related regions (lower left panel). When people made compensatory choices, changes in dmPFC signal over time were positively correlated with regions like the insular cortex that showed greater overall activation to those choices (upper right panel). Conversely, when people made choices consistent with a simplifying strategy, the dmPFC signal was positively correlated with regions like the dlPFC that exhibited increased overall activation on those trials (lower right panel).

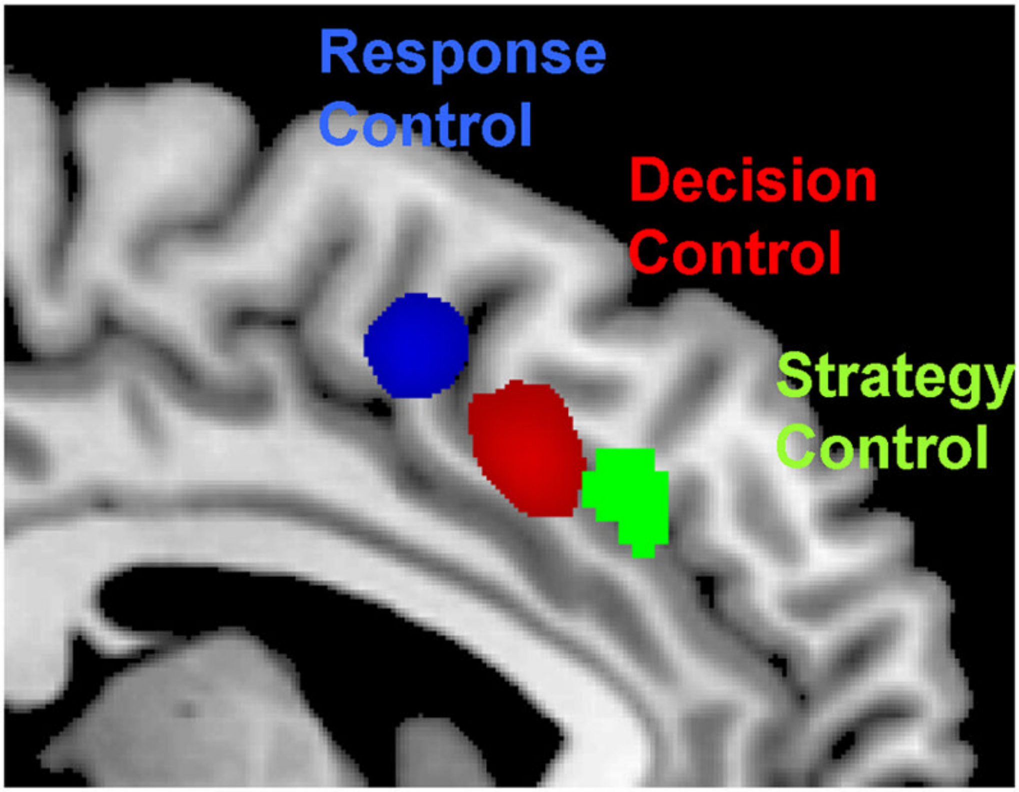

Figure 3. Evidence for functional topography in dmPFC

Using tasks that evoke different kinds of control demands, we found an anterior-to-posterior functional topography within the dmPFC with three separate regions predicting strategy, decision, and response-related control (Venkatraman et al., 2009a).

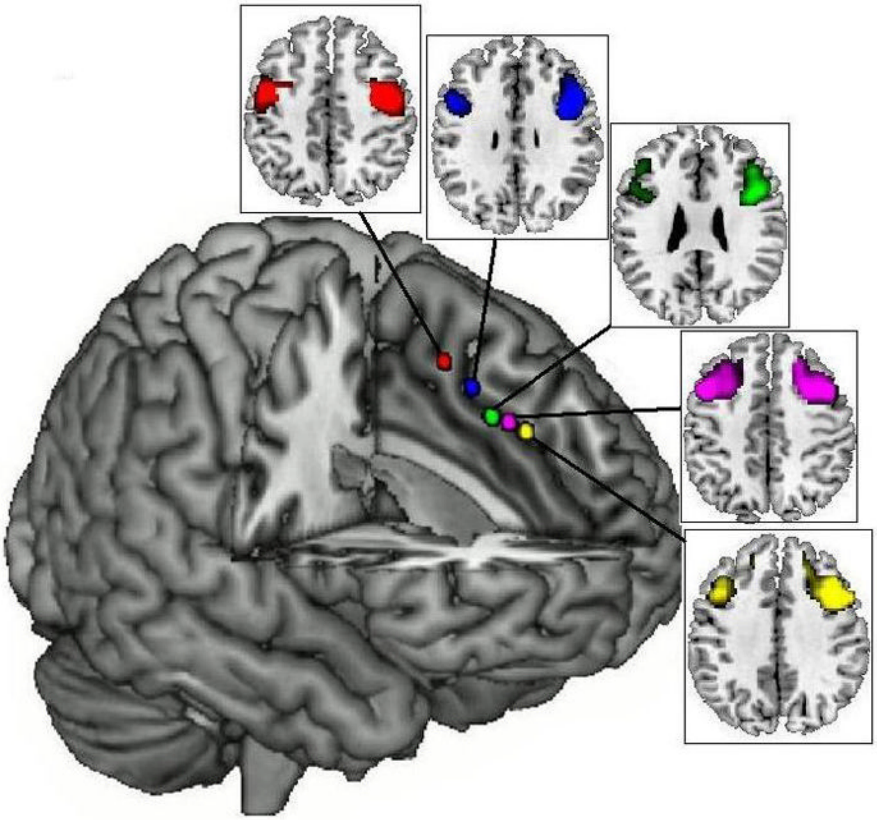

Figure 4. There is topographically organized connectivity between dmPFC and dlPFC

Voxel-by-voxel correlation between five seed regions in the dmPFC and every voxel in the dlPFC demonstrated an anterior-to-posterior topography in the connectivity between these regions (Taren et al., 2011). For each dmPFC seed region, the correlated dlPFC voxels (threshold: $r > 0.15$) are shown in the connecting inset. The anterior dmPFC seed was maximally connected to the anterior regions in the dlPFC while the posterior dmPFC seed was maximally connected to the posterior regions in the dlPFC.

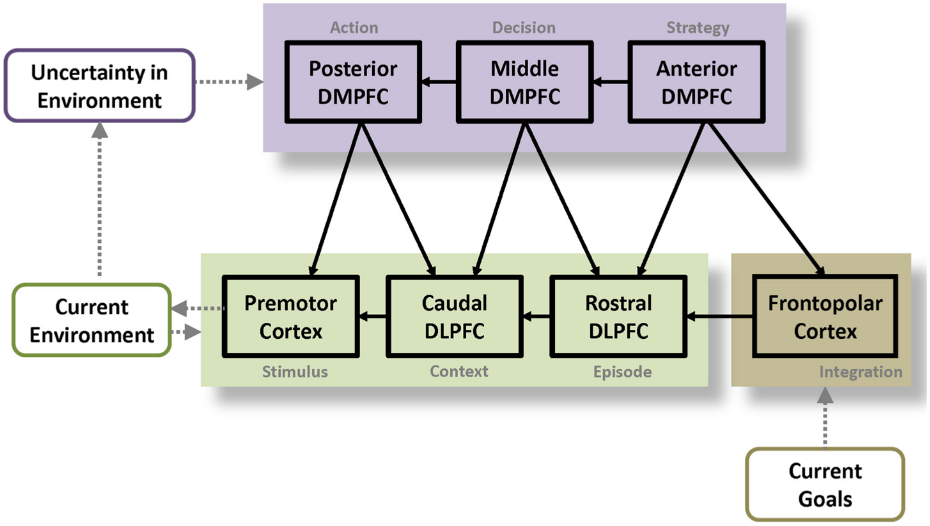

Figure 5. A hierarchical model for cognitive control

We contend that the prefrontal cortex contains parallel topographies for the adaptive control of behavior. The dlPFC maintains and updates rules for behavior in a topographical manner, with more anterior regions processing increasingly complex rules. The dmPFC shapes the engagement of the lateral prefrontal regions in a topographical manner, based on the type of environmental uncertainty.