Chapter 9

Hierarchical cognitive control and the frontal lobes

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Abstract

Cognitive control refers to our ability to choose courses of thought and action that achieve our goals over habitual but contextually inappropriate ones. Hierarchical control problems are those in which multiple goals or contextual contingency must be managed at once and related to one another. In the open-ended complexity of the real world, hierarchical control arguably characterizes most of the problems faced by our control systems. And, it is these cases of hierarchical control where patients with damage to executive systems are most apt to fail, even those that perform well on simplified laboratory tasks. In this chapter, we consider the functional organization of frontal brain systems that support hierarchical cognitive control. We focus on two particular cases of hierarchical control. First, we discuss a line of work testing how managing multiple contingencies en route to a response relates to processing along the rostrocaudal axis of frontal cortex. Second, we consider cases of sequential tasks that require monitoring and behaving according to a series of tasks performed in time. In this latter case, we focus on the particular role of rostrolateral prefrontal cortex. We conclude with considerations of future directions of basic and clinically relevant research in this domain.

INTRODUCTION

Humans routinely use complex contextual information to choose appropriate actions over habitual and routine ones. For example, though we routinely check our cell phones, we should refrain from doing so while driving, given the known hazards of distracted driving. In this case, we must rely on our context, driving a car, to overcome a strong habitual tendency to check our phones, even if they signal that we have a new message. Our general capacity to use an internal contextual representation to choose appropriate courses of action is referred to as *cognitive control* (Miller and Cohen, 2001; Badre and Nee, 2018), and it lies at the heart of intelligent, purposeful, and goal-directed behavior. Cognitive control function, sometimes termed executive function, has an established association with the frontal lobes in general and the prefrontal cortex (PFC) in particular (Stuss and

Benson, 1987; Duncan et al., 1996; Miller and Cohen, 2001; Badre, 2008). Deficits in cognitive control are prevalent across a wide range of neurologic and psychiatric conditions (Ceravolo et al., 2012; Cholerton et al., 2013; Middleton et al., 2014; Rostamian et al., 2014; Insel et al., 2015; Soros et al., 2015). Patients experiencing problems in cognitive control face significant problems performing activities of independent living or maintaining successful work or academic performance (Eslinger and Damasio, 1985; Shallice and Burgess, 1991; Goel et al., 1997; Schwartz et al., 2002).

Whereas the term cognitive control refers to our general ability to guide our actions based on an internal representation of a goal, *hierarchical cognitive control* refers to the more complex problem of controlling immediate actions, while also holding more abstract goals in mind (Badre, 2008; Botvinick, 2008; Badre and Nee, 2018). Consider an everyday task like making coffee.

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To perform such tasks, it has long been known that we hold an abstract, overarching task goal in mind (e.g., "make some coffee") which runs in the background while subgoals, such as grinding beans, pouring water, etc., are set and executed along the way (Lashley, 1951; Cooper and Shallice, 2006). Relating all these goals to one another and choosing the right actions to perform at the right time requires control at multiple levels of a hierarchy. So, hierarchical control is needed to carry out most routine tasks that require juggling multiple goals, subgoals, and motor actions. Hierarchical control also allows us to follow abstract rules that apply across diverse settings and may themselves influence the choice of other rules for behavior. Yet, despite its centrality for everyday—indeed every minute—functioning, we know very little about how the human brain accomplishes hierarchical cognitive control or how it is impaired by accident, disease, and disorder.

Patients with diminished capacity for cognitive control commonly find hierarchical cognitive control problems particularly challenging. For example, these patients have trouble planning and completing tasks requiring multiple steps that progress to an end point (Shallice and Burgess, 1991; Duncan et al., 1996; Zanini et al., 2002; Gouveia et al., 2007; Goel et al., 2013). Yet, often these deficits in everyday function are not captured by widely used neuropsychologic assessments of executive function (Eslinger and Damasio, 1985; Shallice and Burgess, 1991). This paradox likely arises from the gap between basic mechanisms studied in the lab, like inhibition or set shifting, and the open-ended complexity confronted in everyday life (Burgess et al., 1998; Manchester et al., 2004; Royall et al., 2002; Chaytor et al., 2006; Chan et al., 2008).

More ecologically valid neuropsychologic tests, like the multiple errands test (Dawson et al., 2009), are better at predicting outcomes in everyday life. However, these tests are themselves quite complex, and so they are not suitable for the mechanistic analysis of basic neural mechanisms that leads to understanding of these systems. Further, cognitive control itself is not one faculty and its implementation is multifaceted. So, different patients may perform poorly on the same tests of executive function, but for different reasons. Thus, though one can predict from these tests that a patient might have difficulty in the activities of daily living, they do not provide insight into the causes of a given patient's deficit or how best to therapeutically intervene.

Basic research that leads to a better understanding of the neural basis of cognitive control in the human brain—particularly in its ability to scale up to the complex settings for which it evolved—promises far-reaching impact by transforming treatment and rehabilitation of a wide range of neurologic disorders. In recent years, there have been a growing number of attempts to study complex cognitive control in tractable ways by identifying scalable variables in simple cognitive control tasks. By observing how the system responds to systematic changes in complexity along these dimensions, it is possible to draw stronger inferences about how the brain manages the control problems it confronts in the real world.

This chapter will consider two such forms of complexity that require hierarchical cognitive control. First, we will discuss a line of work on the problem of policy abstraction, which concerns rules of higher order contextual contingency. Second, we will address the problem of serial order of task control, wherein an overall goal is pursued over time while other subgoals are being addressed in the interim. In both of these cases, we will discuss how the functional organization of the frontal lobe, particularly along its rostral-to-caudal axis, may support these hierarchical cognitive control functions.

CONTROL BASED ON MULTIPLE CONTINGENCIES

The basic cognitive control problem concerns how a person behaves according to behavioral "policies." A policy refers to the relationship between a context and a course of action in the context of a desired outcome (i.e., a goal; Fig. 9.1A). For example, as children, we learn policies like speak softly when indoors (indoor voice), but outside, it is okay to shout. Here, an element of the context (i.e., indoor) constrains one's manner of speaking. A policy can increase its complexity such that higher-order policies specify the relationship between a context and a class of simpler policies rather than directly mapping a context to a response. For example, older children may eventually learn that the "indoor voice" rule is a member of a class of rules that only apply when a parent is around. By structuring the policy in this way, the "parent" provides an overarching contextual element that determines which other policies are appropriate. Thus, demands on hierarchical control can be manipulated in the lab in terms of the "order" of policy, whereby higher-order policy requires selecting over sets of other policies and so traversing a deeper decision tree (Fig. 9.1B).

How does the brain support this type of control? One influential hypothesis has been that areas in caudal frontal cortex, starting with motor cortex, represent the rules and contexts required for the lowest order and concrete kinds of policies, such as those relating simple stimulus inputs with responses (see Badre and D'Esposito, 2009 for a review). As one progresses to more rostral areas of frontal cortex, there is a corresponding increase in policy abstraction, with the most rostral areas of PFC
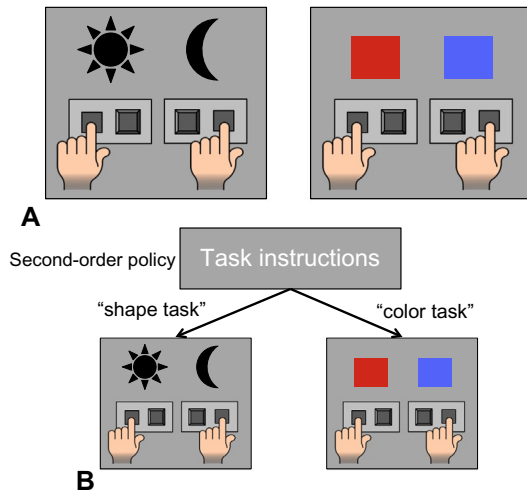
Fig. 9.1. Schematic illustration of policy abstraction. In the laboratory, a policy can be implemented in terms of a mapping from a context, such as a stimulus, and a response. (A) Two sets of simple policies are shown that map either shape stimuli to a button press response (*left*) or a color to a button press (*right*). These are first-order policies because the motor response is directly determined by the stimulus. (B) Based only on our first-order policy, conflict would arise if we encountered a *red moon*, for example, because the color and shape contexts map to different responses. However, if we maintain an additional context, like a "task instruction" we are given to either do the shape or color task, we can use this context to select the right set of first-order mappings. The instruction is a second-order policy because it does not contextualize the response but rather how to interpret other contexts that map to the response.

supporting the most abstract kinds of control. It is further proposed that this pattern may not reflect a mere descriptive functional organization, but rather a true processing hierarchy whereby anterior regions of frontal cortex exert influence and organize processing in more posterior areas.

The hypothesis that the frontal lobes are organized along a rostro-to-caudal hierarchy has been a consistent theme among theories of frontal lobe function. Early theorists noted a number of anatomic features across species that suggested the rostral forebrain might be important for the integrative processing of abstract, higher-order information en route to a response. These features included reduced cell density (Finlay, 2016; Thiebaut de Schotten et al., 2017), intraareal connectivity (Finlay, 2016), and laminar differentiation (Sanides, 1972), accompanied by greater dendritic spines (Jacobs et al., 2001) and longer connectional and synaptic distance from sensory input regions (Yeterian et al., 2012; Margulies et al., 2016).

Citing these features along with physiological evidence of "memory cells" capable of supporting working memory in PFC, Fuster first proposed that the frontal lobes were primarily organized to support hierarchical control (Fuster, 2001). Fuster's perception-action cycle proposed that progress from concrete to abstract perceptual processing in posterior neocortex was mirrored by abstract to concrete processing of action in the frontal lobes. In other words, highly concrete visual input to the retina is transformed over the course of perceptual processing to abstract object and semantic representations. Conversely, abstract action representations in the form of goals and plans, like "make lunch," are transformed into more concrete and temporally realized action plans that are most concrete in motor output. The progression from temporally extended, abstract goals to immediate concrete actions is processed in a series of loops between frontal and posterior neocortical areas running from rostral to caudal in frontal cortex. Notably, for Fuster, the critical variable was temporal rather than policy abstraction. Contexts associated with higher-order rules must remain in working memory longer in order to bridge the longer temporal gaps over which they are relevant. So, more rostral frontal cortex is required in these cases in order to maintain them. The consequence of this, however, is that more abstract policy depends upon more rostral frontal cortex.

A series of functional magnetic resonance imaging (fMRI) studies, first by Koechlin et al. (2003) and then Badre and D'Esposito (2007), provided specific evidence that was seemingly in line with Fuster's proposal. In the Badre and D'Esposito (2007) experiment, participants followed rules that progressively increased in policy abstraction. Each level added a contextual contingency, such that colors simply mapped to responses at the lowest level, and in three additional progressive steps, color mapped to feature then response, then color-to-dimension-to-feature-to-response, and finally, episode-to-color-to-dimension-to-feature-to-response. Controls were included at each level for choice difficulty, so that it was possible to distinguish effects of harder choices from higher-order policy. As participants made choices about higher-order policies, fMRI activation was observed in dorsal premotor (PMd), anterior dorsal premotor (prePMd), dorsolateral PFC (DLPFC), and finally rostrolateral PFC (RLPFC), a caudal-to-rostral progression.

As fMRI cannot provide evidence that these regions of PFC are necessary for performance of these complex rule tasks, subsequent studies sought to test whether patients with focal damage to prefrontal cortex showed deficits consistent with a hierarchical architecture. Badre et al. (2009) tested this hypothesis in two groups of stroke patients whose lesions included the DLPFC and prePMd areas that Badre and D'Eposito (2007) observed to be engaged during second- and third-order policy choices, respectively.

These patients exhibited a pattern of deficits consistent with a hierarchical organization. Each group showed deficits in rule following at a level of policy consistent with the rostrocaudal locus of their lesion and higher levels, but not lower levels. In other words, the patients with damage to DLPFC were impaired at third-order control and also at fourth-order control, but were unimpaired at second- and first-order control. This basic pattern was subsequently replicated and extended to a more rostral lesion focus by a separate group using different hierarchically ordered tasks based on the Koechlin et al. (2003) fMRI study (Azuar et al., 2014).

Taken together, the fMRI and lesion results provided strong evidence that more rostral frontal cortex might support more abstract forms of cognitive control. However, research building off these initial studies started to paint a more complex picture. Badre (2008) noted that several different forms of abstraction covaried in these studies beyond policy abstraction. Not only was policy abstraction increasing at higher rule levels, but also demands on maintaining contexts over time (temporal abstraction) and the demand to relate more than one feature to each other (relational integration) tended to increase in these tasks. Further, other studies suggested that rostral PFC might support more domain general representations, whereas caudal PFC was related to specific input domains, like verbal or spatial information (Courtney et al., 1997; Sakai and Passingham, 2003). Thus if there was a rostrocaudal gradient in frontal cortex, it was not clear what specific type of abstraction ranked the hierarchy. This was an obstacle to generalization of this organization beyond the specific tasks in which they were observed.

Subsequent investigation sought to identify what type of abstraction might rank the rostrocaudal hierarchy in frontal cortex (e.g., Barbalat et al., 2009; Nee et al., 2014; Bahlmann et al., 2015; Nee and D'Esposito, 2016). Though these experiments replicated the rostrocaudal differences in frontal cortex across different tasks and manipulations, there was also no single dimension of abstraction that appeared to rank the hierarchy. Indeed, even when abstraction was held constant, factors like when and how working memory is updated appeared to affect rostro-to-caudal locus more than the level of rule (Reynolds et al., 2012; Nee and Brown, 2013; Chatham et al., 2014).

Furthermore, it is clear that the rostrocaudal organization is not unique to loci within frontal cortex. Rather, these functional differences map onto networks rather than specific areas. Choi et al. (2018) quantified the overlap of functional activations associated with four levels of cognitive control from Badre and D'Esposito (2007) with distributed association networks identified from resting state data (Yeo et al., 2011). This analysis found that three networks, a sensorimotor network and two frontoparietal association networks, distinguished between the rostrocaudal differences associated with increasing policy order (Fig. 9.2A). Further, these same networks also accounted for differences in the functional activation across levels of policy observed in parietal cortex. Thus, rather than a gradient along a dimension of abstraction in PFC, there may be a set of functional networks that interact hierarchically with one another.

In an updated and systematic review of the literature concerning the rostrocaudal organization of frontal cortex, Badre and Nee (2018) conducted a meta-analysis of fMRI studies reporting differences along lateral frontal cortex in hierarchical control tasks (Fig. 9.2B). Based on this analysis, Badre and Nee (2018) suggested that there are at least three distinct functional zones of lateral frontal cortex that are distinguished from caudal to rostral. Rather than forming a "gradient," however, these zones are members of networks that are engaged by distinct control demands.

The most caudal zone encompasses motor and premotor cortex and supports sensorimotor control. It is engaged in tasks that require choices among different movements based on simple cues and rules. For example, a choice RT task, in which one or another button must be pressed based on a particular stimulus feature, like the color of a box, would engage this network. Within this network, there is a hierarchical relationship between premotor and motor cortex in terms of movement plans and simple rule representation.

More rostral is the "contextual control zone." This area encompasses the anterior premotor cortex as well as traditional DLPFC along the dorsal bank of the inferior frontal sulcus up into middle frontal gyrus. Regions in this zone are activated in cases where one or more simple policies must be selected on the basis of higher-order contexts, or the contexts themselves must be selected. This selection occurs in order to guide control in the current moment based on these higher-order contingencies.

The Badre and Nee (2018) analysis further indicated that within this zone there is an additional functional distinction between the more rostral DLPFC site and the more caudal prePMd site. For example, the selection of rules on the basis of a context (second-order rule) might require prePMd but not DLPFC. However, the choice of which context to use based on another context (third-order rule) may require DLPFC. Importantly, however, these decisions are all made in the moment based on higher-order rules and so require regions in the contextual control zone (Fig. 9.3).

Finally, Badre and Nee (2018) associated the most rostral zone of lateral PFC with "schematic control." We will discuss RLPFC more in the next section on sequential control. But, in general, the RLPFC or lateral frontal polar cortex is found to be active in a wide range of tasks that involve reference to an internal model of the
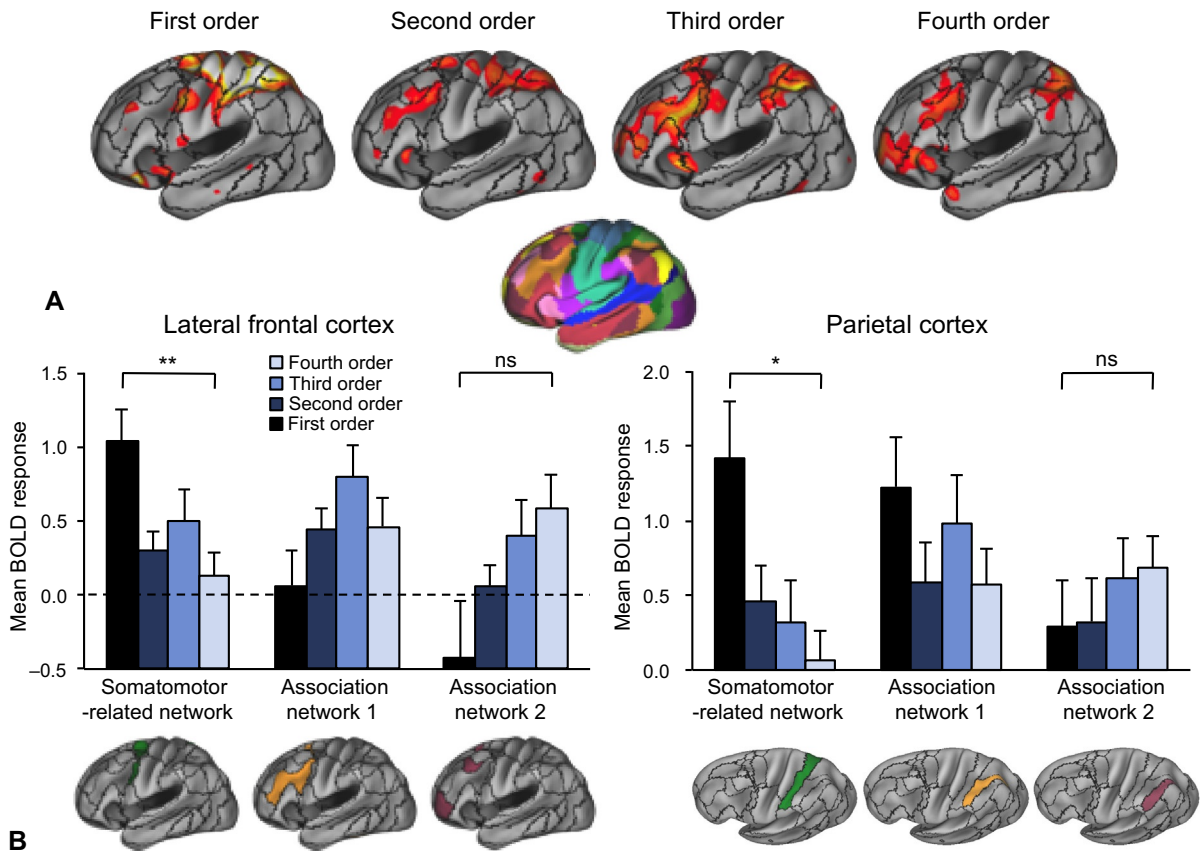
Fig. 9.2. Relationship of rostrocaudal activations due to increased policy and networks defined in resting state from Choi et al. (2018). (A) The activations from Badre and D'Esposito (2007) related to first- through fourth-order control are plotted at a low threshold to emphasize their extent. These are rendered on surfaces showing the boundaries of functional networks defined in the resting state as reported by Yeo et al. (2011). For reference, the color-coded networks for these bounds are plotted below the activation plots. (B) Quantification of the activation associated with each level of control that overlapped the sensorimotor network and two associative frontoparietal networks. The rostrocaudal association of activation with each network is evident in both frontal and parietal cortex. Reprinted from Choi, E.Y., Drayna, G.K., Badre, D., 2018. Evidence for a functional hierarchy of association networks. J Cogn Neurosci 30, 722–736. doi: 10.1162/jocn_a_01229 with permission from MIT Press. © 2018 by the Massachusetts Institute of Technology.

world. For example, it is active in tasks requiring pending or future tasks to be held in wait while other tasks are being performed (Koechlin et al., 1999; Nee and D'Esposito, 2016). Likewise, it has been shown to track hypothetical, counterfactual, or alternative courses of action (Badre et al., 2012; Mansouri et al., 2017). RLPFC is also active during tasks requiring integrative or relational reasoning (Parkin et al., 2015).

These demands have in common a demand to access an explicit model of the world whether hypothetical or informed by explicit memory systems. As this type of explicit and generative internal model is often referred to as a schema, Badre and Nee (2018) characterized this region as playing a role in schematic control, as in when control requires access to a schema representation. As such, though most rostral and arguably abstract, RLPFC is not necessarily more active for higher-order policy. To the degree that monitoring of a pending subtask is

required, for example, RLPFC is even activated for simple, relatively concrete rules. Thus, though functionally distinct from the more caudal frontal zones, the RLPFC is not well characterized as the extreme of a single dimension of policy abstraction starting in motor cortex.

Beyond these functional differences in lateral PFC, a critical question has concerned how these regions might work together to support hierarchical cognitive control. As already noted, a corollary of the abstraction gradient in lateral PFC has been the hypothesis of a processing hierarchy, whereby higher-order, rostral regions or networks organize processing in lower-order, caudal ones (Fuster, 2001; Badre and D'Esposito, 2009). Given that the tasks required for testing hierarchical control are often only testable in human beings, it has been hard to test this hypothesis rigorously. However, there have been some notable recent attempts that have begun to make progress.
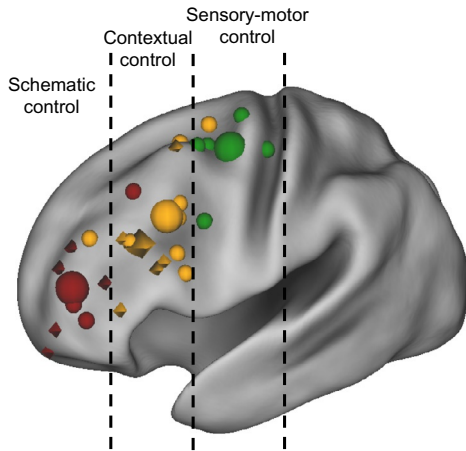
Fig. 9.3. Meta-analysis plot of studies locating differences in the frontal lobe during hierarchical tasks from Badre and Nee (2018). *Small shapes* plot the locus of activation of individual studies. *Large shapes* represent mean locations. The color and shape codes are as follows: *Green spheres* are first-order policy, *yellow spheres* are second-order policy, *yellow pyramids* are third-order policy, *maroon spheres* involve schematic control regardless of the policy level. Though no single dimension of abstraction ranks the hierarchy in frontal cortex, functional distinctions are consistently found for three main lateral cortical zones from rostral to caudal: schematic control (*maroon*), contextual control (*yellow*), and sensory-motor control (*green*). A further rostrocaudal distinction is evident within the contextual control zone between second- (*yellow spheres*) and third- (*yellow pyramids*) order policy. Reprinted with permission from Badre, D., Nee, D.E., 2018. Frontal cortex and the hierarchical control of behavior. Trends Cogn Sci 22 (2), 170–188.

Voytek et al. (2015) tested 4 patients undergoing electrocorticographic (ECoG) monitoring for epileptic seizure, using the task from Badre and D'Esposito (2007). This experiment allowed a rare glimpse of the neural dynamics of hierarchical control in the human brain. The results were initially consistent with a processing hierarchy. As patients performed rules at higher orders of policy, the relationship between signal oscillations related to neural processing changed: lower frequency oscillations from rostral PFC electrodes exerted greater influence over high frequency oscillations (high gamma) in posterior electrodes overlying premotor and motor cortex. In other words, there appeared to be greater communication among these rostral and caudal recording sites that increased with hierarchical control. And, this communication was directional such that signals from rostral prefrontal cortex influenced processing in posterior frontal cortex—a rostral-to-caudal hierarchical processing relationship.

Importantly, however, Voytek et al. (2015) required averaging across several electrodes in two general groups, prefrontal versus premotor, and so provided little insight into the specific locus of these hierarchical influences or their relationship to the more fine-grained functional distinctions discussed previously. A recent series of experiments by Nee and D'Esposito (2016, 2017) tested the more specific hypothesis of a processing hierarchy along lateral frontal sites.

In an initial experiment, Nee and D'Esposito (2016) scanned participants with fMRI while they performed a hierarchical control task. Regions along rostral-caudal PFC showed activation differences that corresponded to the regional differences in schematic, contextual, and sensory-motor control. Further, dorsal (human frontal eye fields—FEF) and ventral (inferior frontal junction—IFJ) frontal regions within the caudal sensory-motor zone activated differentially when the tasks involved spatial versus verbal information, respectively.

To determine the direction of influence each of these areas had on one another, the authors applied effective connectivity analysis to the fMRI data, using dynamic causal modeling. Hierarchical strength was defined on the basis of greater outward than inward effective connectivity at baseline (in the absence of control demands). In other words, this quantified the concept proposed by Badre and D'Esposito (2009) that areas higher in a hierarchy should have a broader influence on lower-order areas than the reverse. So defined, hierarchical strength progressed from an "input" pattern (greater inward than outward connectivity) for the most caudal sensory-motor regions to positive for the caudal midlateral regions (prePMv and prePMd) to maximal for rostral DLPFC. However, in RLPFC, hierarchical strength reversed with greater inward than outward connectivity, an inverse hierarchical strength comparable to the caudal sensory-motor regions.

These baseline relationships were then modulated by cognitive control demands incurred by the tasks the participants performed. Overall, the regions acted as a hierarchy, with mid-DLPFC at its apex exerting a domain-general influence on prePMd and prePMv regions. These caudal regions, still within the contextual control zone, received domain-specific input from the sensory-motor input regions. Analogously, the RLPFC provided input to the mid-DLPFC during conditions of schematic control. A subsequent fMRI/transcranial magnetic stimulation (TMS) experiment not only replicated these findings from effective connectivity, but also observed behavioral changes consistent with this apical organization following brain stimulation of these sites (Nee and D'Esposito, 2017).

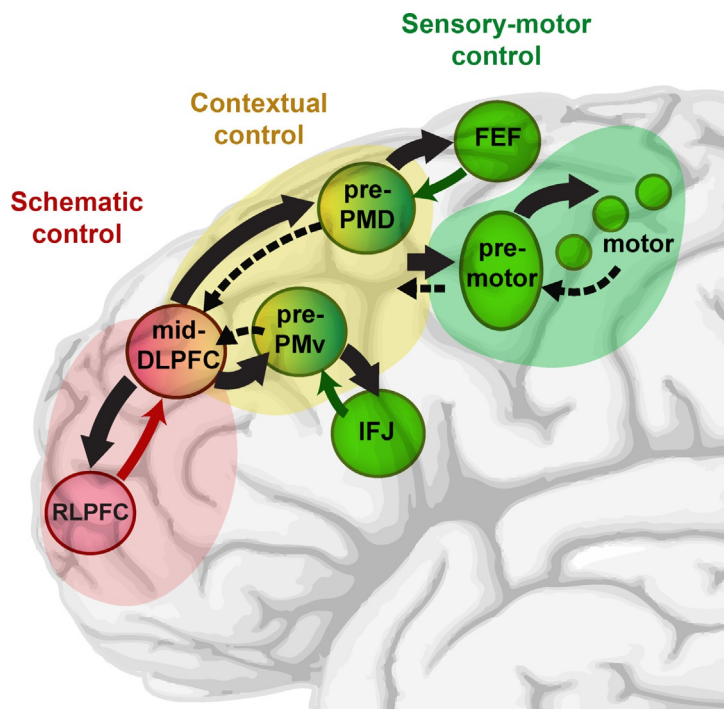Collectively, these results provide evidence for a processing hierarchy in lateral frontal cortex, with rostral

Fig. 9.4. Schematic of the hierarchical processing architecture of lateral frontal cortex from Badre and Nee (2018). Regions within the sensory-motor control (*green*), contextual control (*yellow*), and schematic control (*maroon*) zones are connected by *arrows* summarizing their processing influences. *Larger arrows* indicate a greater directional influence than thin arrows. *Colored arrows* represent domain-specific information (*green* are perceptual either spatial [dorsal] or verbal [ventral], *maroon* shows schema information). Anterior mid-DLPFC is the highest-level controller, but it exerts its influence via more domain-specific lower-order controllers in anterior premotor cortex. Rostrolateral prefrontal cortex (RLPFC), mid-dorsolateral prefrontal cortex (mid-DLPFC), ventral anterior premotor cortex (pre-PMv), dorsal anterior premotor cortex (prePMd), inferior frontal junction (IFJ), and frontal eye fields (FEF). Reprinted with permission from Badre, D., Nee, D.E., 2018. Frontal cortex and the hierarchical control of behavior. Trends Cogn Sci 22 (2), 170–188.

DLPFC at its apex (Fig. 9.4). Specifically, regions along the midlateral contextual zone of frontal cortex receive input about verbal and spatial information from domain-specific areas of caudal frontal cortex, and information from internal memory and schematic representations from RLPFC. These can be used as contextual information to guide selection of responses by premotor and motor cortex. Importantly, however, this does not make areas within this contextual control zone a "hub," whereby a single area acts as the brain's CPU for cognitive control. Rather the organization is hierarchical, such that more rostral areas, like rostral DLPFC, are engaged for higher-order rules and influence lower-order areas, like prePMd, to the degree that higher-order contexts might influence contextual control by these regions.

In future work, it will be critical to understand the mechanisms by which these hierarchical interactions among separate frontal regions and networks take place. For example, initial investigation using fMRI has indicated that hierarchical interactions among these separate networks may depend crucially on gating functions carried out by the basal ganglia (Chatham et al., 2014; Chatham and Badre, 2015), and may support learning, transfer, and generalization of complex rules to novel settings (Badre et al., 2010; Badre and Frank, 2012; Frank and Badre, 2012; Collins and Frank, 2013). Further, the integration of value and control signals by a parallel functional organization of medial frontal cortex may interact with this lateral frontal system to allow motivation to modulate contextual control (Kouneiher et al., 2009; Venkatraman et al., 2009; Alexander and Brown, 2011; Zarr and Brown, 2016; Korb et al., 2017). The emerging picture, then, is of a distributed hierarchical processing organization among association networks of the frontal and parietal cortex, coordinated through interactions with the basal ganglia. Complex dynamics in this system allow us to integrate sensory, memory, and motivational signals in the service of behaving according to multiple contextual contingencies. The loss of any component of this system makes this highest-order cognition particularly vulnerable to deficits across a wide range of underlying causes.

SEQUENTIAL TASK CONTROL

As discussed in the previous section, the complexity of the world demands that we integrate multiple signals in a given moment so we can behave according to higher-order contingencies. Importantly, however, the temporal structure of our world also requires controlling behavior in time, oriented to the future, and managing a series of transitions from one state to the next depending on the actions we take. It is evident that we are capable of using and planning according to abstract goals that leave a specific realization in terms of a concrete behavior unspecified. One would not typically think to oneself: "I'm going to go grind beans, place the filter, scoop the grounds, pour water, and press the button." Instead, we would envision this task in the abstract, such as "I'm going to go make a cup of coffee." Such temporal abstractions can be defined as contexts that are sustained through time and abstracted over individual, component tasks and/or episodes (e.g., grind beans, pour water).

Most tasks we enact in daily life are sequential. Beyond managing multiple goals in time, sequential tasks are often further challenged because we do not always have explicit cues as to where we are in a sequence. For example, keeping track of whether or not you already washed your face or added salt to the pot on the stove does not benefit from any cues in the world itself. Rather, one must keep track internally, presumably by relying on memory systems.

How does the brain support these sequential tasks? In light of the discussion in the preceding section, it is reasonable to hypothesize that schematic control systems, supported by RLPFC, would be crucial for this type of control. The RLPFC has been implicated in representing high-level, abstract, hierarchical information (Badre and D'Esposito, 2007; Nee et al., 2014; Rahnev et al., 2016), maintaining multiple alternative courses of action (e.g., Koechlin et al., 1999; Braver and Bongiolatti, 2002), integrating verbal and spatial information in working memory (Chahine et al., 2015), and supporting temporal abstraction (Nee and D'Esposito, 2016). Recent work has provided evidence for a specific role of the RLPFC in monitoring sequential tasks as well, but with dynamics that hint at a more nuanced functional role.

Desrochers et al. (2015) asked participants to repeatedly complete simple, four-item task sequences (Desrochers et al., 2015) (based on Schneider and Logan, 2006). The tasks were binary categorizations, either deciding about the shape (circle or square) or color (red or blue) of a presented stimulus (Fig. 9.5A). Importantly, there was no instruction about which task to perform on every trial. Rather, participants knew which categorization they should make from the task sequence instruction at the beginning of a block of trials, e.g., color–color–shape–shape (Fig. 9.5B). This instruction would indicate that on the first trial participants should make a color judgment, on the second trial a color categorization, on the third trial a shape categorization, and so on. Participants repeated the same sequence of tasks or categorizations several times until the block ended.

This behavioral task captures several key elements that are common in real-world task sequences. First, participants could not predict the identity of the stimulus that would be presented on each trial, only the categorization that should be made. As a consequence, the specific response could not be planned in advance, and as the stimulus categories were random, so was the sequence of responses. Thus, the task sequence was independent of the specific motor actions that must be completed. Second, as there were no external cues to guide the participants, the internal structure and boundaries of the sequence had to be internally monitored. Third, this task involves selecting and switching between different subtasks at each serial position of the sequence. Rarely in real life does one maintain a single task multiple times to complete a sequence (pouring water four times would not make coffee).

Using fMRI, the authors found a network of brain areas, including the RLPFC, DLPFC, presupplementary motor area (pre-SMA), and medial frontal cortex, that responded with dynamics specifically related to the serial positions in the task sequence (Fig. 9.5C). Specifically, activity in these areas gradually increased or "ramped" through the four-item task sequence (Fig. 9.5D). Other areas in the frontal cortex, such as prePMd in the caudal part of the contextual control zone, showed responses that were not contingent on sequence position and did not exhibit the ramping pattern of activation. This result dissociated these caudal areas from the dynamics observed in the RLPFC.

The fMRI results suggested a unique role for the RLPFC and its associated network in sequential task control. To determine if the RLPFC is necessary for task sequences, the authors used TMS to manipulate the functioning of this area and its associated network. Single pulse TMS to the RLPFC during the sequential task (Fig. 9.5E) caused an increasing number of errors at later positions in the sequence, mirroring the ramping pattern observed in fMRI (Fig. 9.5D). These effects in RLPFC dissociated from the effects of stimulation in the prePMd and a second control region, the rostromedial prefrontal cortex (RMPFC), and were replicated in two separate experiments.

Together, these fMRI and TMS results suggest that RLPFC is necessary during sequential control, but not consistently throughout a sequence. This contrasts with models of RLPFC function that indicate it is needed to
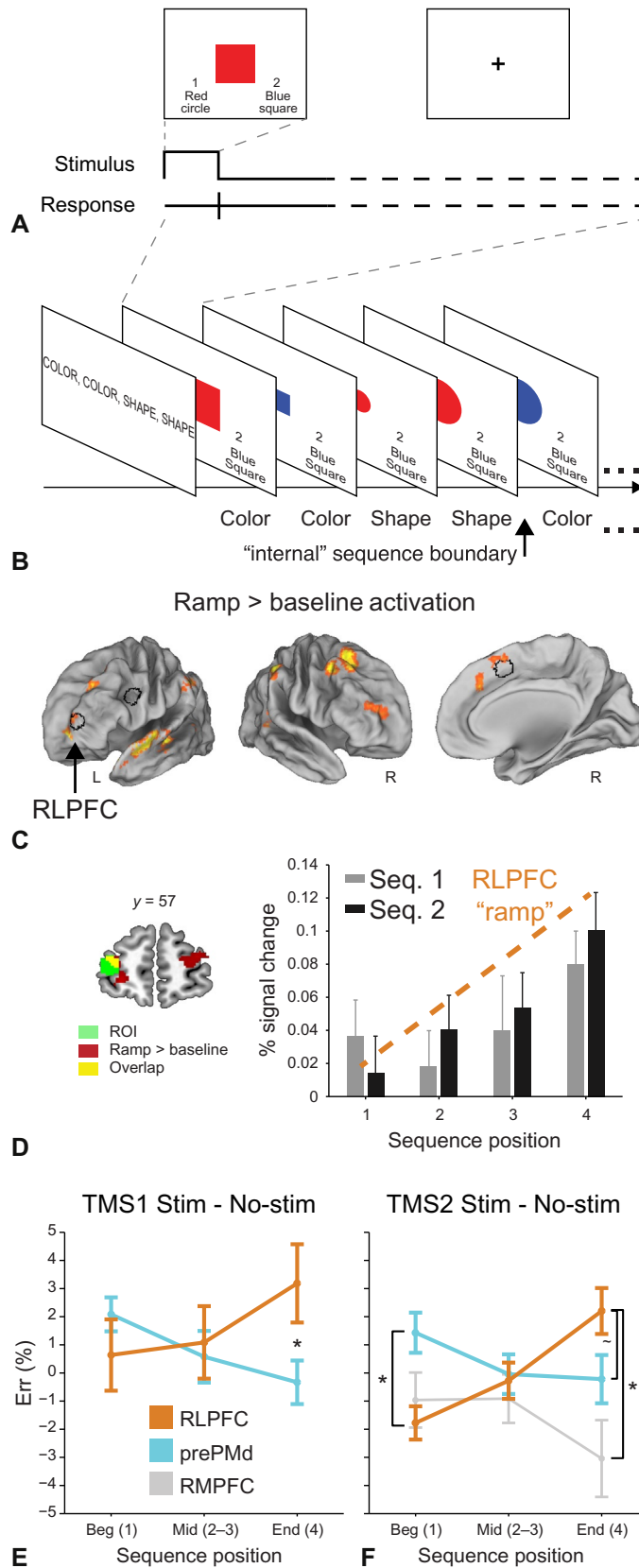
A

B

"internal" sequence boundary

Ramp > baseline activation

RLPFC

C

D

y = 57

ROI
Ramp > baseline
Overlap

E

F

RLPFC
prePMd
RMPFC

Fig. 9.5. See legend on next page.

continuously provide control signals from temporal or episodic context, as these contexts were demanded at every sequence position in this task, not just at the last sequence position. Rather, this result indicates that RLPFC plays an important role only at specific points in time, such as near the boundary of a sequence. However, what this role might be remains unclear from this study.

To better understand the functional contribution of RLPFC to sequential control, it is necessary to isolate the key component of the sequential task that drove the observed ramping dynamic. As previously described, there are several components of task sequences that the behavioral paradigm captured beyond the demand to perform a task sequence. To review, these were: (1) independence of task from motor actions, (2) internal monitoring of the sequence without external cues, and (3) serial task selection. A combination of two follow-up fMRI experiments (Desrochers et al., 2019) examined activity in the RLPFC during sequential tasks, while manipulating the final two components.

In the first experiment (Desrochers et al., 2019), the degree to which internal sequence monitoring was required was manipulated by the addition of "clue" stimuli to the behavioral paradigm from Desrochers et al. (2015). These clues were presented on approximately a third of the trials and removed ambiguity as to the correct task to perform by presenting a stimulus that could only have one eligible response. For example, if all the non-clue stimuli were red/blue circles/squares, then a green circle would indicate the participant must answer according to the shape, as "green" was not a response option for the color task. If the ramping activity in the RLPFC depended on consistent internal monitoring of the task sequence and potentially played a role in resolving uncertainty about the sequence position as the sequence progressed, it should be modulated by the presence or absence of clues. However, while the ramping activation in the RLPFC was replicated during this sequential task, no significant differences were observed between clue and no-clue trials. Thus, task-level uncertainty did not seem to modulate the activity pattern in RLPFC.

The second experiment further investigated the necessity of internal monitoring, or monitoring without external cues, and whether serial task selection was necessary to drive RLPFC engagement (Desrochers et al., 2019).

This experiment used a simplified task that eliminated the categorization decisions on each trial based on sequence position, and rather asked participants to simply monitor the sequential order of presented images either as presented (visible) or internally tracked (occluded). Ramping activity in the RLPFC was again present in this simplified sequential task and was not significantly modulated by whether the monitored sequences were visible or had to be internally monitored.

Together, these experiments establish a consistent pattern of ramping activation in the RLPFC during sequential tasks that is independent of the availability of external cues or the requirement to select tasks. Rather, the main component is the approach of a boundary, when one chunk of predictable transitions of state to state give way to another chunk of predictable states. RLPFC may selectively represent the top-down monitoring demands that are required at these bounds, such as access to the "overall plan" or overarching goal. Along these lines, beyond its functional association across tasks with schematic control, RLPFC is also the area of lateral frontal cortex most directly connected with medial frontal networks associated with explicit long-term memory retrieval. In line with this hypothesis, a recent high-resolution fMRI study has shown that when humans perform a virtual navigation task, the hippocampus represents future goals and the entire trajectory to reach them (Brown et al., 2016). Critically, the stronger the representation of the end goal in hippocampus, as measured using multivariate classification methods, the stronger the activation in RLPFC. Thus, RLPFC is well positioned to input, maintain, and transmit information about these higher-order goals and contexts to the rest of the control system at critical junctures, like the boundary of a task chunk or sequence.

CONCLUSION

This chapter has provided an overview of current research on the problem of hierarchical cognitive control. Hierarchical control problems are those in which multiple sources of contextual information must be updated, maintained, and related to one another separately in order to generate appropriate responses. Arguably, the capacity

Fig. 9.5. RLPFC is necessary during sequential task control. (A) Example trial of sequential task from Desrochers et al. (2015). (B) Partial example block showing the instruction screen and the first five trials in the block. The categorization task to be performed on each trial, as remembered from the instruction screen, is indicated below. (C) Whole-brain contrast showing ramping activation (cluster corrected $P < 0.05$). RLPFC region of interest (ROI) outlined in *black*. (D) Ramping activation in RLPFC ROI across the four positions in two different types of sequences. (E) Difference in error rate (Err) between stimulated and nonstimulated trials during single-pulse transcranial magnetic stimulation (TMS) targeting two different sequential control regions: RLPFC and prePMd. The effect of stimulation significantly increased across the sequence positions in the RLPFC, in contrast to the prePMd. (F) Second replication TMS experiment that also showed no effect of stimulation to the RMPFC. Reprinted with permission from Desrochers, T.M., Chatham, C.H., Badre, D., 2015. The necessity of rostrolateral prefrontal cortex for higher-level sequential behavior. Neuron 87, 1357–1368.

for hierarchical control is central to managing the complexity of the world outside the laboratory. And, it follows this capacity is most vulnerable to deficits in patients across a wide range of neurologic and psychiatric problems. These deficits present a significant obstacle to successful, independent living.

We have reviewed research related to two cases of hierarchical control problems: the ability to traverse multiple contextual contingencies and the ability to control and sustain behavior in an extended sequence. From this review, it is evident that the lateral frontal cortex, along with medial frontal and basal ganglia systems, support a processing hierarchy with DLPFC at its apex and motor cortex its final output. However, rather than a strict gradient of processing, there are at least two networks, a contextual control network and a sensorimotor network, that are related to each other hierarchically. Further, within each network, regions like anterior DLPFC and more caudal prePMd hold a hierarchical relationship to one another. Thus, the processing architecture supporting cognitive control is best characterized as hierarchical rather than hub-like. There is no single convergence zone for control in the brain, just as there is no homunculus or CPU for all of cognitive control.

Second, the most rostral portion of lateral frontal cortex, RLPFC, appears to support a distinct role that has been labeled schematic control. This part of frontal cortex receives inputs, likely from medial frontal and medial temporal networks, that contain information from explicit memory and planning systems about the past, future, and hypothetical alternatives to the current course of action. Held in RLPFC, this information can be transmitted to the lateral frontal control hierarchy depending on task demands. This is illustrated in the case of sequential control, where the involvement of RLPFC is more necessary towards the boundaries of sequences, potentially when there is the most uncertainty and reference to higher-order plans is most required.

Future work will no doubt yield further revisions to this basic framework. There are still relatively few experiments directly testing hierarchical cognitive control demands. Further, as these hierarchical control dynamics are not readily observable in simpler tasks that are easily trained in animal models, there is still limited data on the neural representations and dynamics that support hierarchical control. Parallel work between human and animal experiments, including drawing direct functional analogies where possible, is essential for progress in this domain. The ramping patterns observable during even simple sequential tasks in RLPFC may be one promising case for such parallel work.

Finally, research into the basic mechanisms of hierarchical control and how this function arises from this functional organization are required. Computational models of hierarchical control have placed an emphasis on working memory gating functions carried out by cortico-striatal interactions (Chatham and Badre, 2015). These interactions can regulate when and what contextual representations are updated by separate frontal networks and can control which of these exert top-down control signals, and when. Control over the control signals themselves is essential for hierarchical tasks that require managing multiple levels of contingency over time. As reviewed here, some experiments have begun to test predictions from these models. However, many more are needed to constrain theory and gain a mechanistic understanding of the neural mechanisms of hierarchical control. Beyond its basic science implications, a mechanistic understanding will allow for informed diagnosis of the sources of control problems in everyday life, and potentially, the best ways to intervene.

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