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Cognitive control, hierarchy, and the rostro–caudal organization of the frontal lobes

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Cognitive control supports flexible behavior by selecting actions that are consistent with our goals and appropriate for our environment. The prefrontal cortex (PFC) has an established role in cognitive control, and research on the functional organization of PFC promises to contribute to our understanding of the architecture of control. A recently popular hypothesis is that the rostro–caudal axis of PFC supports a control hierarchy whereby posterior-to-anterior PFC mediates progressively abstract, higher-order control. This review discusses evidence for a rostro–caudal gradient of function in PFC and the theories proposed to account for these results, including domain generality in working memory, relational complexity, the temporal organization of behavior and abstract representational hierarchy. Distinctions among these frameworks are considered as a basis for future research.

Introduction

Cognitive control permits selection of actions that are consistent with our goals and context. The prefrontal cortex (PFC) is a central component in the network of brain regions supporting cognitive control [1–9]. Thus, a fruitful approach to understanding the architecture of control has been to investigate the functional organization of the PFC. In recent years, functionally selective PFC sub-regions have been associated with distinct forms of control [10–15]. However, it remains an important goal to understand these isolated control functions in context of broader functional and neuroanatomical organizing principles [2,13,16]. This review considers one such organizing hypothesis: that the rostro–caudal axis of the frontal lobes is organized hierarchically, whereby posterior frontal regions support control involving temporally proximate, concrete action representations, and the anterior PFC supports control involving temporally extended, abstract representations [5,16–24] (Figure 1). Of course, there are diverse ways of defining 'abstraction' and, likewise, many processing schemes by which these levels might interact, including non-hierarchical ones. Here, the evidence and associated theories of a frontal rostro–caudal gradient of function are reviewed.

Hierarchy in action and the action system

Hierarchical structures occur throughout artificial and natural systems. The defining properties of hierarchy depend on whether one is emphasizing processing or representation. Processing hierarchies require that superordinate levels, operating over longer time scales, asymmetrically modulate subordinate processing [25,26]. Representational hierarchies require that superordinate representations form abstractions over subordinate representations, favoring generality over detail and allowing information to be inherited asymmetrically from higher to lower levels [26,27].

The representation and control of action is often conceptualized hierarchically in both processing and representational senses [28–31]. Lashley [28] first noted that behaviorist theories of chaining – whereby an action (e.g. grinding coffee) triggers the next in sequence (e.g. put grounds in machine) – could not account for several observations about sequential action, such as errors of omission (e.g. starting the coffee machine having forgotten to add grounds). Without an abstract, temporally extended representation of the task context (e.g. coffee making), an action chain would terminate following an omission. Similarly, the task-switching literature has indicated that selection of task sets and task sequences can occur without being influenced by the subordinate constituents of those sets [32–34]. Thus, representations of complex actions can apparently be maintained simultaneously at multiple levels ranging from abstract goals (e.g. make coffee) to sub-goals (e.g. grind beans) to concrete motor outputs.

However, the fact that a task can be represented hierarchically does not require that the action system itself consist of structurally distinct processing levels. Single-level neural networks can represent both general and specific information [35]. And, Botvinick and Plaut [36] have demonstrated that goals and sub-goal representations of sequential actions can be represented simultaneously in a single layer neural network. Thus, the neural data become crucial in distinguishing whether structurally and spatially distinct neural processors support hierarchical representation and control of action [37].

Fuster's perception–action cycle [21–23] was among the first to directly relate a hierarchical theory of action to the organization of the brain. Fuster proposed a series of loops between perceptual hierarchies in posterior neocortex and regions along the rostro–caudal axis of the frontal lobes.

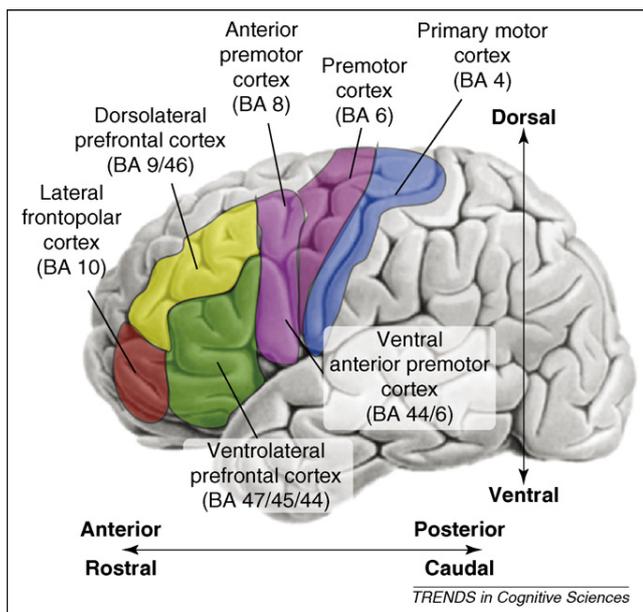*Corresponding author:* Badre, D. (David_Badre@brown.edu).

Figure 1. Schematic of major anatomical sub-divisions in the frontal lobes. Boundaries and Brodmann areas (BA) are only approximate. Arrows indicate anatomical directions of anterior/rostral (front) versus posterior/caudal (back) and dorsal (up) versus ventral (down). From caudal to rostral, labeled areas include motor cortex, dorsal (PMd) and ventral premotor cortex, dorsal (pre-PMd) and ventral aspects of anterior premotor cortex, ventro- (VLPFC) and dorsolateral PFC (DLPFC), and lateral frontal polar cortex (FPC).

According to the theory, as actions are specified from abstract plans to concrete responses, progressively posterior regions of lateral frontal cortex are responsible for integrating more concrete information over more proximate time intervals. Critically, this rostro–caudal hierarchy does not reflect stages of processing but, rather, describes how action representations are selected, maintained and inhibited at multiple levels of abstraction. Thus, the perception–action cycle proposes that the hierarchical structure of action might be represented in the organization of cortical areas and the interactions between the rostro–caudal axis of the frontal lobes and posterior neocortex. The basic properties of the perception–action cycle are reflected in the recent frameworks discussed in the remainder of this review.

The rostro–caudal axis of PFC and working memory: domain generality

Working memory refers to active maintenance and manipulation of information over a brief interval in the service of a task. Initial evidence for rostro–caudal distinctions within the PFC comes from experiments designed to test regional differences based on working memory domain. In general, regional distinctions based on the content of maintained information, such as spatial or object, remain controversial [38–40]. However, when content-based distinctions are evident, they are typically observed in caudal PFC structures [24,41–44]. By contrast, rostral PFC regions seem to be capable of maintaining information from multiple domains, such as object and spatial, in addition to integrated cross-domain information, such as an object in a particular location [44–49].

Based on this and other evidence, domain generality versus domain specificity has been hypothesized to

distinguish rostral from caudal PFC [18,20,24,41,50] (Figure 2a), and this distinction is supported by a double dissociation between posterior and mid-dorsolateral PFC (DLPFC) regions [24,51,52]. In particular, lesions to areas 6 and 8 (periarcuate area) in the monkey disrupt performance of domain-specific conditional motor tasks but not that of a domain-general monitoring task. By contrast, lesions to the mid-DLPFC impair performance of monitoring but not of conditional motor behavior.

This distinction of domain generality versus specificity does not provide evidence that the processors involved hold a hierarchical relationship to one another, and the double dissociation might argue otherwise (see later). However, there is evidence that these regions do interact hierarchically. Sakai and Passingham [53,54] have demonstrated that activation during a preparatory interval in the anterior DLPFC/frontal polar cortex (FPC) correlates with activation in the caudal superior frontal gyrus (BA 8) or caudal inferior frontal gyrus (BA 44) depending on whether an upcoming task is spatial or verbal, respectively. These data were interpreted as indicating that regions in anterior PFC maintain domain general rules that instantiate task sets among posterior neocortical regions. However, a recent experiment [55] has demonstrated that patients with damage to the anterior DLPFC/FPC, and who exhibit task-switching deficits, are still capable of establishing normal pre-task activation in the preserved regions of posterior PFC. Notably, functional connectivity among the full network of task-related regions is disturbed, indicating that maintenance of higher-order rules in anterior DLPFC might serve to establish effective network dynamics among task-related regions.

The rostro–caudal axis of PFC and abstract thought: relational complexity

Christoff and colleagues [20,56,57] (also see Refs [2,58,59]) have proposed a framework for the rostro–caudal gradient in the frontal lobe that is also based on the content of working memory representations. But, rather than emphasizing domain, abstraction derives from relational complexity [56] (Figure 2b). The number of variable dimensions that must be integrated to determine a response determines the order of relational complexity [60,61].

First-order relational complexity, associated with ventrolateral PFC (VLPFC), maintains rules involving item properties (e.g. 'what is the color?') [56]. By contrast, second-order relational complexity derives from simple relationships between concrete properties (e.g. 'do the colors match?') and is associated with DLPFC, which is consistent with neurophysiological evidence [62,63]. This distinction between DLPFC and VLPFC follows from classical distinctions between dorsal and ventral PFC in working memory processes [13,45], and is supported more recently by a dissociation between attention to items in VLPFC versus item categories in DLPFC [64].

Higher, third-order relational complexity is associated with FPC and entails evaluation of relationships among relationships [56–58,65]. For instance, subjects decide whether the mismatching dimension (texture or shape) of a target pair matches the mismatching dimension of a
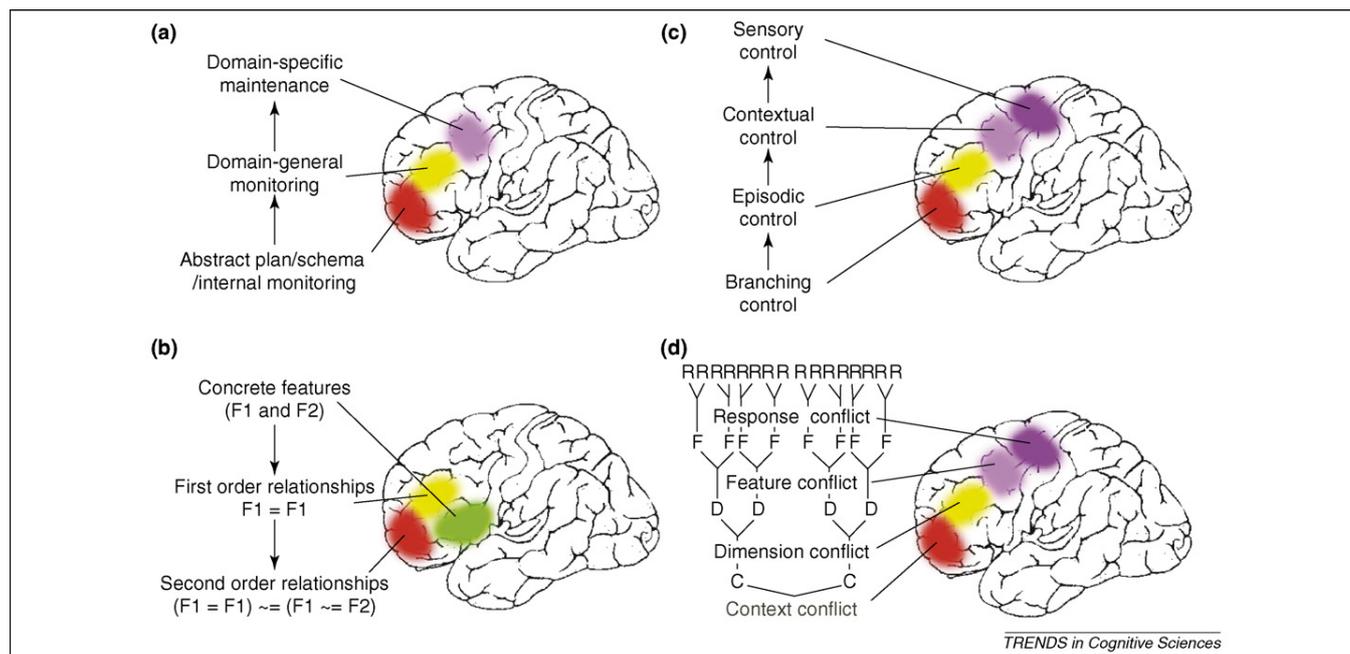
Figure 2. Theoretical accounts of the rostro–caudal gradient in the PFC. **(a)** From a working memory perspective, rostral and caudal PFC can be distinguished on the basis of processing domain general versus specific representations [20,24,41]. Hierarchical versions of this perspective propose that domain-specific posterior frontal regions can be modulated by the maintenance domain general rules in anterior DLPFC and FPC [50,54]. **(b)** Relational complexity proposes a gradient in the PFC with respect to evaluation of simple stimulus properties, first-order relationships among the properties, and second-order relationships among relationships [56,57]. **(c)** The cascade model proposes four levels of control that are distinguished by temporally disparate control signals, either sensory, context, episodic or branching [5]. **(d)** Abstract representational hierarchy proposes that regions of the PFC are distinguished by the level of abstraction at which representations compete in a hierarchy of action representations [74].

subsequently presented target pair [57]. Responding requires evaluation of the relationship of two relationships. Evaluating this third-order relationship is associated with activation in FPC. In a review of the FPC literature, Ramnani and Owen [59] noted that many tasks engage FPC, such as sub-goaling or episodic recognition, that do not obviously involve third-order relationships in the strict sense described here. Thus, Ramnani and Owen [59] broadened the proposed role of FPC to include integrating the outcomes of multiple cognitive operations, including relational ones.

Relational complexity proposes that the rostro–caudal organization of PFC can be viewed as a progression in the level of abstraction of working memory representations. Reasoning and problem solving are hypothesized to require the ability to integrate multiple relationships simultaneously [60,61], and so the theory indicates that FPC is central to the highest levels of reasoning and thought [56,57]. However, as higher-order relationships depend on lower-order relationships, higher levels need not asymmetrically influence lower-levels. Indeed, modulation could reasonably be assumed to occur in both directions [56]. Thus, relational complexity is heterarchical, requiring neither modulation nor inheritance of information asymmetrically from higher to lower levels. This feature might distinguish this framework from the hierarchical perspectives described in the following section.

The rostro–caudal axis of PFC and cognitive control: representational hierarchy

Cognitive-control theories propose that the PFC maintains contextual information to bias selection of relevant representations over competitors [6,66–69]

(Box 1). Within a uniform computational control structure, there is opportunity for hierarchy among both the representations that compete for processing and the representations that are maintained to provide a control signal.

Representational hierarchy ranked by the control signal

The 'cascade model' [5,70,71] is an elegant cognitive control framework that makes predictions about the rostro–caudal organization of the PFC (Figure 2c). In cascade, control resolves competition among alternative action representations based on mutual information with contextual information, also termed control signals. Crucially, the control signals relate to one another hierarchically, in that information is inherited from superordinate to subordinate levels, and separate signals are processed by spatially distinct regions along the rostro–caudal axis of the PFC. At the lowest level, sensory control is supported by premotor cortex and selects a motor response based on a sensory input. Next, contextual control, supported by posterior PFC, selects an action based on an environmental contextual cue. Episodic control, supported by anterior DLPFC, selects an action based on an ongoing temporal context. Finally, a highest level, branching control, supported by FPC, selects action representations based on a pending temporal context. Thus, from caudal to rostral, regions of the PFC are distinguished based on their reliance on control signals that differ temporally, from immediate environment (sensory and context), to current temporal frame (episodic), to a pending frame (branching).

An influential study by Koechlin *et al.* [71] provided functional magnetic resonance imaging (fMRI) evidence for the lower three levels of the cascade model. In separate

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Box 1. Mechanisms of hierarchical control

Formal models of cognitive control make explicit how control might be implemented within a hierarchy. One influential class of connectionist models of control derives from the assumptions of biased competition [66–69,76,77]. Competition arises when bottom-up input produces activation of multiple response pathways. This competition can be quantified as Hopfield energy, which is the sum of the products of all the nodes in a layer weighted by their competitive, lateral inhibitory connections [66,78]. Assuming mutually equivalent competition, at a given overall level of activation, energy in the network will be maximal when all units are equivalently active. In response to competition, a recurrent layer that maintains task-relevant contextual information biases task-relevant responses over competitors.

A sophisticated biased competition framework by O'Reilly and colleagues [69,76,79] implements hierarchical control through multiple contextual layers at different levels of abstraction and recursion. An early variant of the model [79], motivated by a double dissociation in the intra–extra-dimensional switching task [80], included two hierarchically related working memory buffers that separately maintain the recently rewarded dimension (e.g. a category of shapes) or feature (e.g. a particular shape). These buffers independently bias dimension or feature in a common representational space and are rapidly updated in response to conflict between predicted and actual outcomes. 'Lesioning' each of these layers simulated a double dissociation between reversals at feature or dimension levels. More recent versions of the model are capable of modeling different cognitive control tasks and even show generalization to novel tasks [76]. O'Reilly and colleagues have suggested that this hierarchical architecture reflects the gradient of abstraction along the rostro–caudal axis of the PFC [69,76].

The cascade model [5,71] shares fundamental properties with the biased competition framework. The primary control demand is uncertainty or entropy. Uncertainty increases with the number of candidate responses. For any number of responses, uncertainty will be maximal when the response probabilities are equivalent. Given that relative activation among competing response units in a network relates directly to the probability distributions of those responses [81], entropy will exhibit similar dynamics as Hopfield energy when all responses are equally likely. Control is expressed as the reduction in uncertainty (mutual information) given some additional signal (sensory, context or episodic). Different regions of the PFC are specialized for different types of control signals and signals sum from super- to sub-ordinate levels [5,71].

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experiments, subjects selected one of two button-press responses based on a colored cue (sensory control), or one of two letter-judgment tasks based on a colored cue (contextual control). A third manipulation arranged the color mappings in both experiments such that a given color mapped to a different response or task across different blocks of the experiments. Thus, the appropriate color mapping had to be selected based on an ongoing temporal frame (episodic control).

Consistent with the control signal distinctions of the cascade model, the dorsal premotor cortex (PMd) was active across all three levels, the anterior premotor (pre-PMd)/posterior DLPFC was active across sensory and context levels, and the anterior DLPFC was active only for the highest episodic level. Finally, effective connectivity revealed that activation in posterior regions co-varied with activity in more anterior regions but not vice versa, which is potentially consistent with an anterior-to-posterior inheritance of information.

Evidence for the highest level, branching control, comes from a separate experiment in which FPC was activated when performance of one task had to be interrupted during performance of an intervening task [72]. Such sub-goaling effects in FPC are highly replicable across various paradigms [1,73]. From the cascade perspective, this activity reflects the maintenance of a more temporally distant event than the ongoing episode, and so ranks higher in the temporal organization of PFC.

Representational hierarchy ranked by the control demand

Recently, Badre and D'Esposito [74] proposed a related alternative to a control signal account of hierarchy in PFC. We suggested that the rostro–caudal hierarchy can be better understood in terms of differences in control demands, defined based on the form of the representations that compete during action selection (Figure 2d). As noted earlier, action representations might be organized hierarchically, such that more abstract action representations designate a set of more specific representations. For example, a task-set can be said to be abstract because it generalizes across a set of specific stimulus–response mappings. As representations at progressively abstract levels compete, distinct control processors along the rostro–caudal axis of the PFC might resolve the competition.

Koechlin and Summerfield [5] suggested that selecting responses versus classes of responses might distinguish the sensory and context levels of the cascade model. And, based on an experiment that increased the response sequence chunking over three levels [70], they argued that such a progression should be confined to premotor cortex and posterior DLPFC. However, activation associated with the highest level of this experiment (the third order of abstraction) seemed to be close to the episodic site from Koechlin *et al.* [71], albeit more ventral. Thus, could differences in control demands rather than control signals account for the rostro–caudal gradient?

To distinguish between these hypotheses, we tested control demands at increasing orders of abstraction while also being explicit about the form of the control signal [17] (Box 2):

(i) the response experiment required selection of a stimulus-response mapping, a first-order abstraction, based on a perceptual cue (context and/or sensory control);

(ii) the feature experiment required selection of a set of stimulus–response mappings, a second-order abstraction, based on a perceptual cue (context and/or sensory control);

(iii) the dimension experiment required selection of a set of sets of stimulus–response mappings, a third-order abstraction, based on a perceptual cue (context and/or sensory control);

(iv) the context experiment required selection of a set of sets of sets of stimulus–response mappings, a fourth-order abstraction, based on information from a current temporal frame (episodic control).

Frontal hierarchy ranked by the control signal predicted that the response, feature and dimension experiments should be confined to the posterior frontal sector, and the context experiment should activate anterior DLPFC. By

Box 2. Testing hierarchy ranked by the control demand

In a recent experiment, Badre and D'Esposito [74] tested whether the rostro–caudal frontal gradient is ranked by the level of abstraction at which representations compete. Four fMRI experiments tested control demands by increasing the number of competing alternatives parametrically at four levels of abstraction. In each experiment, the number of alternatives varied between blocks. Subjects were aware of the number of alternatives on each block.

In the 'response experiment' (Figure Ia), subjects saw one colored square at a time and then selected a response based on a learned mapping between the color and response. The number of candidate responses could increase from one to four, thereby increasing competition. In the 'feature experiment' (Figure Ib), subjects saw objects presented inside colored squares. The subject made a positive response whenever a particular feature was represented in the object, such as a particular texture, and made a negative response to other features. On a given trial, the feature that cued a positive response depended on the colored cue. The number of candidate features that could potentially cue a positive response increased from one to four and so increased competition. In the 'dimension experiment' (Figure Ic), subjects saw two objects inside a colored square; four dimensions (i.e. texture, shape, size and orientation) of the objects varied from trial to trial. Subjects decided if the objects matched along one of the four dimensions. The relevant dimension was cued by the color of the square. Increasing the number of potentially relevant dimensions (from one to four) resulted in increased competition. Finally, in the 'context experiment' (Figure Ic), the task was identical to the dimension experiment, except that there were always two dimensions from which to choose. In this experiment, competition was manipulated among overlapping color-to-dimension mappings using the frequency manipulation described by Koechlin *et al.* [71]. The results of these experiments (see Figure 3 in main text) support a rostro–caudal hierarchy that is ranked by the level of abstraction of competing action representations.
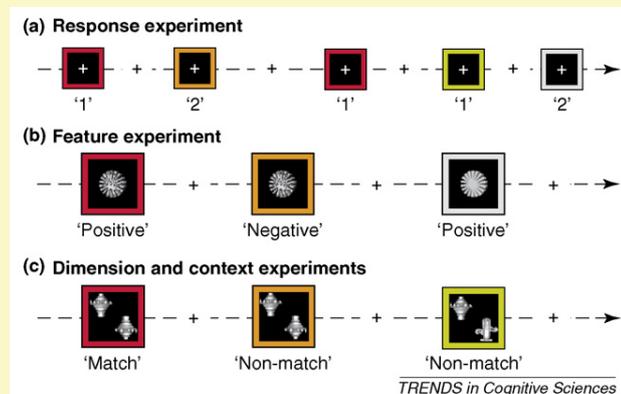

Figure I. Task schematics depicting trial events in the four tasks used to test representational hierarchy from Badre and D'Esposito [74]. **(a)** In the response experiment, subjects responded with key presses (number in quotes) to colored squares. Conflict was manipulated based on the number of key-press alternatives within a block of trials. **(b)** In the feature experiment, subjects made positive or negative responses to specific features of objects, such as a texture of the central object, with a positive response dependent on the colored square. Conflict was manipulated by increasing the number of alternative features within a block of trails that could cue a positive response. **(c)** In both the dimension and context experiments, subjects decided if two objects matched along a perceptual dimension determined by the colored square. Conflict in the dimension experiment was manipulated by increasing the number of alternative dimensions within a block, and conflict in the context experiment was manipulated by varying the frequency of sets of color to dimension mappings.

contrast, hierarchy ranked by the control demand predicted that the dimension experiment (third order) would produce activation in anterior DLPFC and the context experiment (fourth order) in FPC.

The results from this experiment support a rostro–caudal gradient distinguished by the control demand (Figure 3a). A clear progression was evident in PMd, pre-PMd, inferior frontal sulcus/DLPFC, and FPC based on the parametric manipulation of competition in the response, feature, dimension and context experiments, respectively. The context experiment required episodic control but resulted in activation in the FPC, rostral-to-anterior DLPFC (Figure 3b). By contrast, the dimension experiment did not require episodic control but resulted in activation in the anterior DLPFC (Figure 3b). Thus, anterior DLPFC and FPC are inconsistently activated based solely on the presence of an episodic control signal. Likewise, anterior DLPFC, pre-PMd or PMd were all activated when using the same sensory control signal. By contrast, the abstract rank of the competing representations seemed systematically related to which regions of the frontal lobe were activated.

Distinguishing theories of rostro-caudal function

Progressively anterior regions of the frontal cortex support increasingly complex, abstract representations and processes. On this point, the frameworks reviewed here agree. However, there are several points of divergence among the frameworks that are theoretically significant for our understanding of frontal-lobe function and cognitive control.

Hierarchy versus non-hierarchy

A key point to resolve is whether the gradient of function in the frontal lobes truly reflects a hierarchical system. Not all of the frameworks are hierarchical. For instance, the domain generality versus specificity distinction [24] is non-hierarchical and the relational complexity perspective is heterarchical. The cascade [5], Sakai and Passingham [53,54], and Badre and D'Esposito [74] frameworks are hierarchical in that superordinate, anterior regions are hypothesized to asymmetrically modulate processing in posterior, subordinate regions and/or to operate on hierarchically abstract representations. Evidence from explicit hierarchical control manipulations [71,74] and functional connectivity analyses [53,71] strongly support these perspectives. Still, the double dissociation in the monkey [24] leaves such an organization in doubt. In a hierarchical system, damage to posterior processors should impair behavior even when anterior processors are intact. Thus, it will be crucial to further investigate this important result to verify a hierarchical organization of the frontal lobes.

Hierarchical views also suffer from the limitation that higher-order representations could be generated indefinitely. Obviously, PFC cannot extend rostrally without limit. Future research should investigate the significance of this limitation for the proposed frameworks, such as whether higher-order structures become chunked or if there exists some fundamental capacity limitation for the control of action [75,76].

Ranking the functional gradient

A second critical point to resolve is what factor distinguishes regions of the PFC. One principal difference among the frameworks, perhaps captured directly between
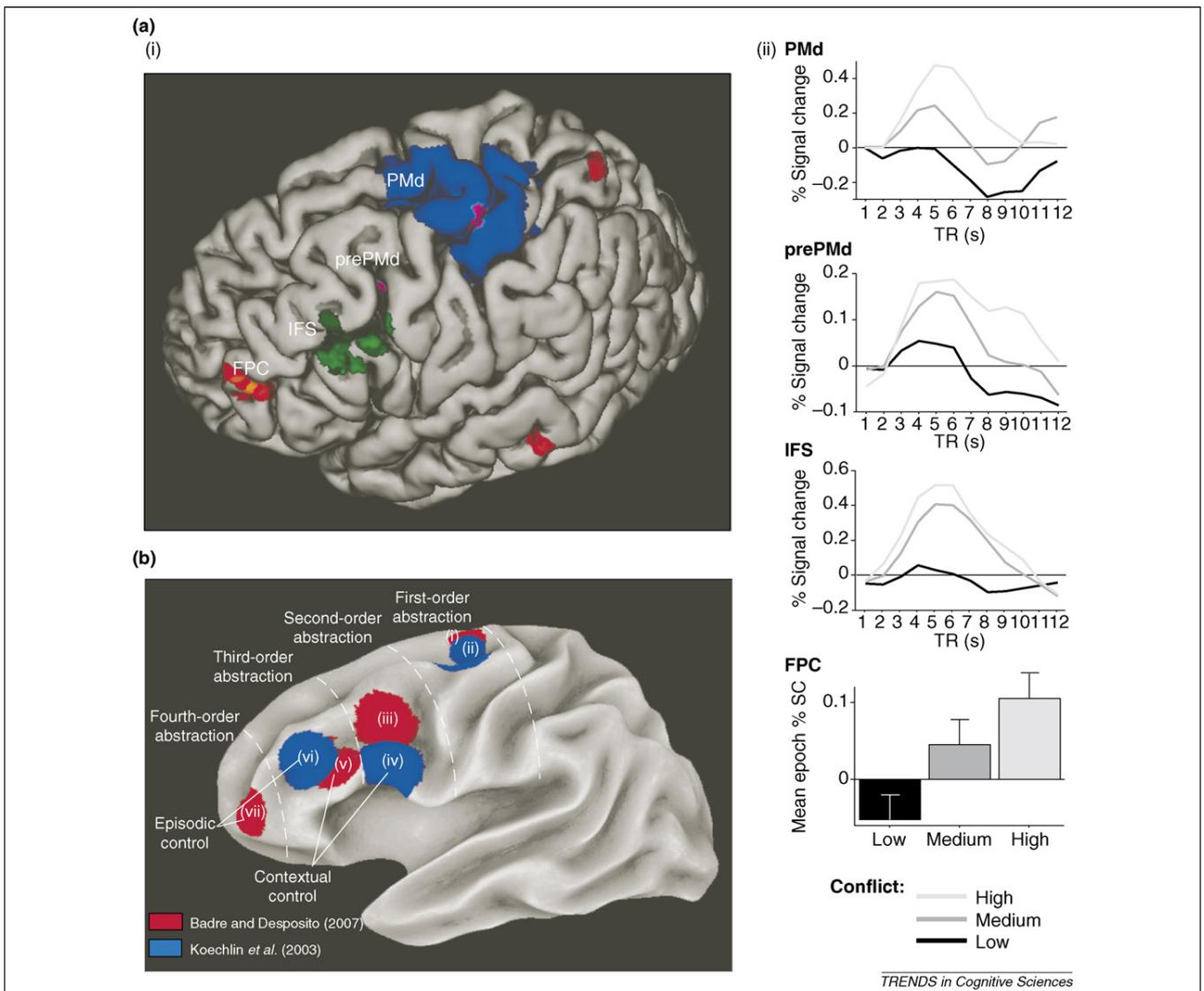
Figure 3. Results from the response, feature, dimension and context experiments and comparison to the model of Koechlin et al. [71]. **(a)** The whole-brain analysis [74] (i) shows a clear caudal-to-rostral progression in activation as conflict was manipulated in the response (blue; PMd), feature (purple; prePMd), dimension [green; inferior frontal sulcus (IFS)/DLPFC] and context (red; FPC) experiments. These activations reflect the parametric manipulation of conflict at each level, derived from the event-related signal change or, in the case of FPC, in the sustained signal over the block of trials (ii). Note that this parametric manipulation rules out certain alternative accounts. For example, the inclusion of a match decision or two stimuli in the dimension experiment does not account for activation in IFS/DLPFC because, when only one dimension is relevant, a match decision is still required and two stimuli are still present but activity is at baseline. **(b)** Abstract relational hierarchy seems to provide a parsimonious account of rostro–caudal gradient across the models of Koechlin et al. [71], and Badre and D'Esposito [74]. Spheres with diameters of 8 mm (within the smoothing kernel of each experiment) were centered on maxima from response (i), feature (iii), dimension (v) and context (vi) manipulations of D'Esposito and Badre [74] (red), and on the sensory (ii), context (iv) and episodic (vi) manipulations of Koechlin et al. [71] (blue). These spheres were rendered on an inflated Talairach surface. Note that the spheres are for precise illustration of proximity but do not represent actual spread of activation in each experiment. Broken lines separate manipulations at equivalent levels of abstraction in a representational hierarchy. Equivalent episodic and contextual control manipulations across the two experiments are also labeled. Parts (a) (i) and (b) adapted, with permission, from Ref. [74].

the cascade model and Badre and D'Esposito views, is whether the abstractness of control signal or control demand determines regional differences in the frontal lobes. As noted, it seems to be difficult to account for the Badre and D'Esposito [17] results from a strict control signal perspective. However, Koechlin et al. [71] found that anterior DLPFC and pre-PMd were active under conditions of episodic control when only a response had to be selected. Thus, why did selection at an apparent second-order abstraction require DLPFC?

One potential account of this result is that heteromodal cortex in the PFC has access to more information, including mnemonic information, than the premotor cortex

does. This does not mean that PFC organization is determined by the form of the control signal *per se*, but it does predict limitations on the extent to which premotor cortex can enact control.

Temporal versus representational abstraction
The frameworks can be further distinguished by their emphasis on temporal versus representational abstraction. For example, anterior PFC might maintain information over longer intervals, as with episodic or branching control [72], or might differentially rely on information from memory versus the environment [20,24,71]. To some extent, representations that are more

Box 3. Questions for future research

- Is the rostro–caudal gradient in the frontal lobe a hierarchical system?
- What factor governs functional distinctions along the rostro–caudal gradient?
- Is there a fundamental distinction between temporal and representational abstraction within the PFC?
- How is the number of hierarchical levels constrained?
- How does PFC represent non-hierarchical action structures (e.g. heterarchical)?
- Does hierarchy extend to the control of memory, which, like action, exhibits hierarchical properties?
- How are novel tasks and rule structures acquired within this architecture?
- How does the rostro–caudal frontal lobe development impact a child's ability to reason and organize their behavior?

abstract are relevant for longer, so it remains to be seen whether a strong distinction can be made between temporal and representational abstraction. However, apart from FPC, it does seem that anterior PFC has both sensory and mnemonic information available for control, rather than demonstrating a unique preference for remembered information.

Concluding remarks

The fact that behavior can be organized hierarchically does not require that the system itself be structured hierarchically. Nevertheless, growing evidence supports spatially distinct regions of the frontal lobe that process differentially abstract components of action selection. Considerable controversy persists regarding the factors that distinguish this functional gradient and whether these processors interact hierarchically. Resolving these points of controversy will be fundamental to our understanding of frontal-lobe function and the control of action (Box 3).

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