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Review

Neural Perspectives on Cognitive Control Development during Childhood and Adolescence

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Since the discovery that patients with damage to the prefrontal cortex (PFC) show similar deficits in cognitive control as young children, the PFC model of cognitive control development has been a popular description of how cognitive control emerges over time. In this review, we show that not only do many studies support this model, but also that more specific models of PFC development can be formulated, according to the functional roles of subregions and by taking into account the distinctions within ventral–dorsal and lateral–medial PFC. We also reveal that the functional development of dorsolateral PFC supports the development of deliberative processes, whereas that of the medial PFC supports the development of internalized decisions. These new conceptualizations may provide better descriptions of the complexity of cognitive control development.

Trends

Developmental patterns of activation in PFC in response to cognitive control tasks have shown a remarkable and unexplained heterogeneity.

Conventional classifications of cognitive control (i.e., basic versus complex) can be extended to rule-based versus internalized processes.

Novel classifications of cognitive control can offer a new perspective for accounting for specific developmental patterns of findings.

The Prefrontal Cortex Hypothesis of Cognitive Control Development

Cognitive control refers to the ability to control our thoughts and actions for the purpose of future goals. Over the past decades, a wealth of results has shown that the ability to exert cognitive control increases from early childhood to late adolescence [1,2]. These improvements can be observed across a range of tasks, such as working memory, inhibition, and making complex decisions between options varying in their associated costs and benefits [2,3]. A key question is how different cognitive control functions develop with respect to one another. For example, using **latent class models** (see Glossary), it was observed that working memory shows a more protracted developmental time course compared with cognitive switching and inhibition [4]. Recent studies in cognitive neuroscience have made important progress in understanding how cognitive control functions rely upon overlapping and different neural regions and processes.

Ever since the discovery that patients with damage to the PFC show deficits in cognitive control [5,6], many theoretical models have suggested that cognitive control development is closely tied to the development of the PFC [1,7,8]. Subsequent and increasingly refined models have taken the heterogeneity of the PFC into account and suggest that the developmental time course of separable cognitive control functions is related to the maturation of subregions of the PFC [9]. This hypothesis was tested more directly in recent years with the rise of *in vivo* brain-imaging methods, including fMRI [10,11], which have consistently shown that the PFC is important for cognitive control in adults [12–14] and were applied to aid our understanding of the neural basis of cognitive control development in children and adolescents.

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Developmental neuroimaging studies initially focused on mapping single cognitive control functions to the maturation of specific areas within the PFC. For example, a large literature on working memory development has demonstrated that increases in working memory performance during adolescent development are related to stronger recruitment of the dorsolateral and ventrolateral PFC [15–17]. Inhibitory control is also often mapped to increased activity in the PFC with increasing age [18,19]. Furthermore, error monitoring was linked to increased activity in the anterior cingulate cortex [20,21]. Taken together, a large body of literature points to developmental changes in the neural recruitment of the PFC, consistent with the hypothesis of a functional role of protracted PFC maturation in the development of cognitive control.

However, the complexity of these neurodevelopmental patterns is highlighted by the heterogeneous responses elicited by variations in tasks and approaches across studies and how these inform about the significance for performance. For example, whereas some studies report increased activation with age in specific regions, others find age-related decreases in activation in other regions [22–24], and it is currently not clear how this is mapped to performance changes. One of the largest studies in the developmental neuroimaging literature tested how developmental progression in working memory updating performance related to neural activity in dorsolateral PFC (N=951, ages 8–22 years) [15]. This study reported that activity increase in dorsolateral PFC mediated the relation between age and performance, explaining 38% of the shared variance of age and performance [15]. Many studies have confirmed that neural activity increases are related to performance improvements across the domains of working memory [17], inhibition [25], feedback learning [26], and delay of gratification [27,28]. However, studies reporting age-related decreases in neural activity have also linked these to behavior progressions [24], showing that both decreases and increases can be meaningfully linked to developmental changes in cognitive control. So far, there have been few systematic reviews of what this could mean (see also Box 1). Children may be using different strategies compared with adults, which is associated with different patterns of neural activity. In this review, we suggest that new conceptualizations of cognitive control and mapping these to subregions within PFC may inform about the way that different types of cognitive control are developing.

Here, we provide two perspectives on cognitive control development, each offering several interpretations of the current literature of how constructs of cognitive control are represented in the human brain: (i) basic, stimulus-driven versus complex, deliberative cognitive control functions [29,30]; and (ii) rule-based versus internalized cognitive control [31,32]. These are discussed with view to providing a starting point for a better understanding of cognitive control development (Figure 1). Both perspectives take the complexity of cognitive control as a multifaceted construct into account, and make separable predictions about the patterns of change over development, although these are not complete dichotomies and some overlap will exist between the concepts. As we discuss, these conceptualizations constitute a powerful approach to synthesizing divergent patterns of results into a potentially unifying theoretical framework.

A Hierarchical Representation (Basic to Complex) of Cognitive Control

Researchers often conceptualize cognitive control by dividing it into several subprocesses [33,34]. This approach is based on the assumption that cognitive control is an umbrella term for several different executive functions. The basic executive functions comprise working memory, inhibition, cognitive flexibility, and error monitoring [1], which are thought to be supported by different underlying neural regions within the PFC, and each have separate developmental time courses [9]. These processes need to work well in concert, thereby contributing to performance in more complex cognitive control tasks [29]. Complex executive function tasks rely more on

Glossary

Delay discounting: the monotonic decline in reward value with an increased time delay of its receipt (i.e., choice outcomes are reweighted to take the delay into account).

Interference control: the suppression of responses that are triggered by competing events and responses.

Latent class models: models that rely on a statistical method for identifying unmeasured class membership among observed variables.

Latent variables: variables that are not directly observed but can be inferred through a mathematical model based on other variables that are observed.

Response inhibition: the suppression of habitual behavioral actions, which supports flexible and goal-directed behavior

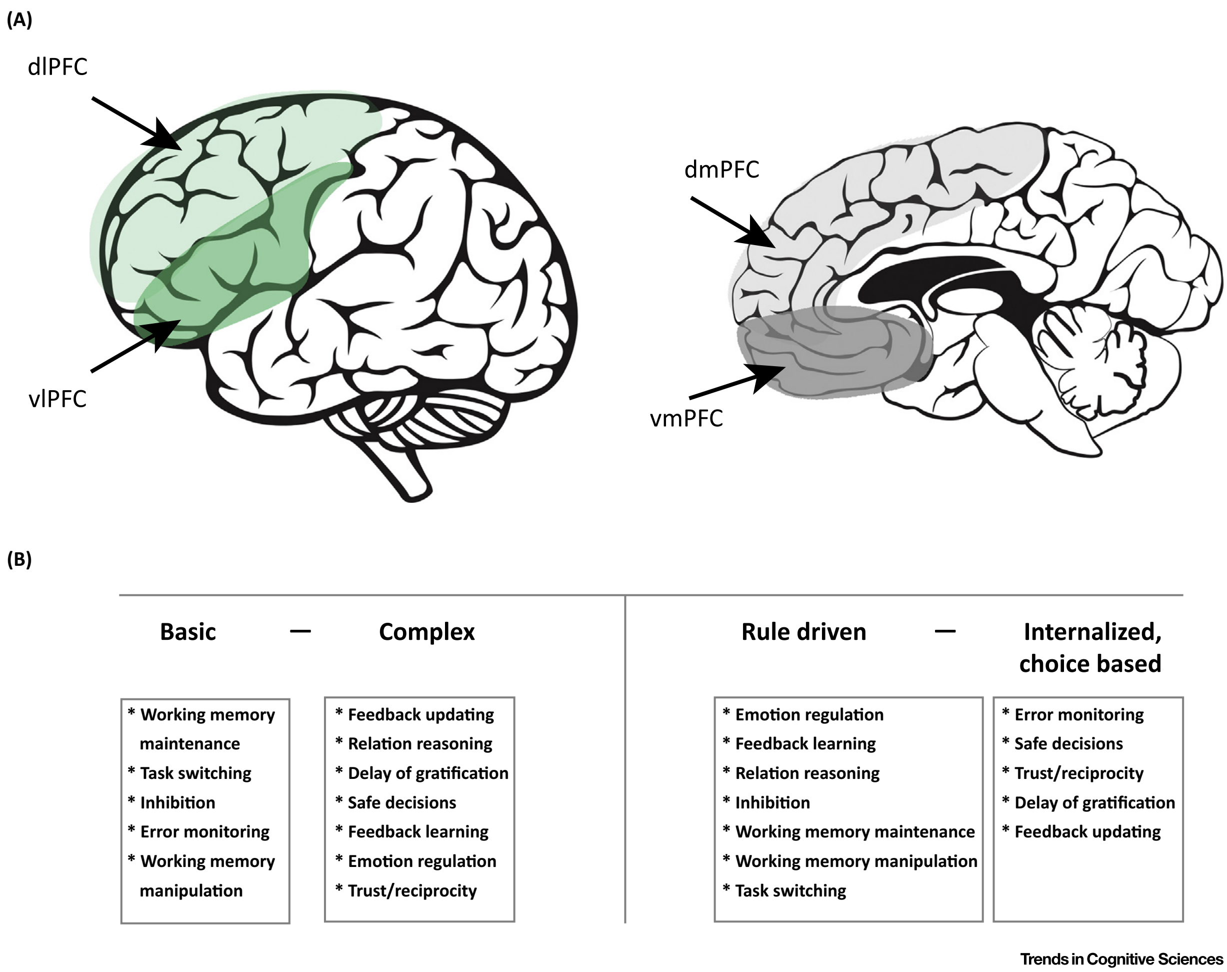

Figure 1. Overview of Proposed Distinctions within Prefrontal Cortex (PFC). (A) Conceptual overview of the distinctions within PFC related to basic and complex and/or deliberative processes, and rule-based (lateral) to internalized (medial) processes. (B) How different cognitive control tasks can be subdivided along these processes. Abbreviations: dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; vlPFC, ventrolateral prefrontal cortex; vmPFC, ventromedial prefrontal cortex.

deliberative processes than do basic, stimulus-driven processes. Deliberative cognitive control refers to processes that are potentially prone to strategy use (i.e., planning, emotion regulation, and feedback learning) [35].

Research to date has focused mainly on the developmental time course of basic and complex cognitive control functions separately. Working memory is often studied using delay or span tasks, and these studies consistently report improvements in performance until late adolescence [36], especially for tasks that require updating [37]. For **response inhibition** (i.e., go/nogo tasks and stop-signal inhibition tasks) or **interference control** tasks (i.e., flanker or Simon tasks), improvements are reported during childhood, but no large additional improvements are observed during adolescence [4,38]. Cognitive flexibility is often examined using task-switching paradigms, which report improvements until early adolescence [4,39]. Finally, error monitoring is an internal process that does not result in an immediate behavioral output, but studies have examined post-error slowing as an index of the maturation of error monitoring. Studies have reported that young children (from the age of 7 years) already show evidence for post-error slowing [40]. Other studies revealed developmental decreases in post-error slowing, suggesting that more efficient error monitoring occurs as children get older [41].

Using the unity and diversity model suggested by Miyake *et al.* [29], it has been tested whether **latent variables** derived from a battery of basic executive function tasks predicted performance on more complex cognitive control tasks that rely on a mixture of basic executive functions, such as performance on the Wisconsin Card Sorting Task (WCST) or the Tower of London Task (ToL). Indeed, there was some evidence that the development of working memory contributed to performance on the WCST and the development of interference control contributed to performance on the ToL [4,42–44]. It should be noted that the unity versus diversity model is focused primarily on cognitive functions and devotes less attention to affective control processes. Prior studies have suggested that cognitive and affective components of cognitive control have dissociable developmental trajectories [2], and that basic executive functions, such as inhibition, also contribute to complex tasks, such as economic decision-making (e.g., **delay discounting**) [28].

What are the implications of the above results for the basic–complex distinction for understanding the neural development that supports cognitive control development? One assumption based on the behavioral data is that neural activity in brain regions that are typically associated with the basic executive functions (working memory, inhibition, cognitive flexibility, and error monitoring) in adults should show increases in recruitment, as children get older. Prior research in adults points to a role of the ventrolateral and dorsolateral PFC supporting working memory performance [14]. Inhibitory control is often linked to the right inferior frontal gyrus and dorsolateral PFC based on patient research and functional neuroimaging studies [13,45] (but see [46] for recent debates on the precise locus of inhibitory control). Finally, cognitive flexibility is mostly related to activity in the pre-supplementary motor area and the inferior frontal junction [47,48] and error monitoring to the anterior cingulate cortex [49].

Developmental studies have subsequently tested whether these regions show protracted functional maturation during child and adolescent development. Developmental fMRI studies show most consistent patterns for working memory development. Working memory updating in particular has been consistently related to increases in dorsolateral PFC across studies throughout adolescence [15,17,50–53]. Likewise, there are consistent findings for error monitoring showing developmental increases in activity in the anterior cingulate cortex and medial PFC, especially between childhood and early adolescence [20,21,40]. Less consistency is observed in studies that examined the development of response inhibition and switching, both in the direction (i.e., age-related increases and decreases) as well as the regions involved (e.g., [20,22,54,55]). It might be that younger children call upon more diverse processes to perform well on these tasks.

The second assumption of the basic–complex model is that improvements in complex cognitive control tasks rely on the same regions as the basic executive functions that underlie these complex processes, and that there is a larger concomitant increase between PFC regions as children grow up. Given the variability in the developmental results from the basic executive function tasks, it is difficult to relate these directly to activity during more complex cognitive control tasks. Nonetheless, the general pattern suggests that neural activity during more complex cognitive control tasks shows age-related increases in multiple PFC regions. These developmental increases were observed in research using feedback-learning task (mirroring the WCST) [26,56], relational reasoning [57,58], delay of gratification [27,28,59], and emotion regulation [60,61].

We visualized the developmental progressions in cognitive control according to this distinction (Figure 2). Figure 2A presents a categorization of cognitive control processes in terms of basic and complex deliberative processes. Both behavioral and neural studies report that deliberative processes have a more protracted developmental trajectory compared with basic cognitive

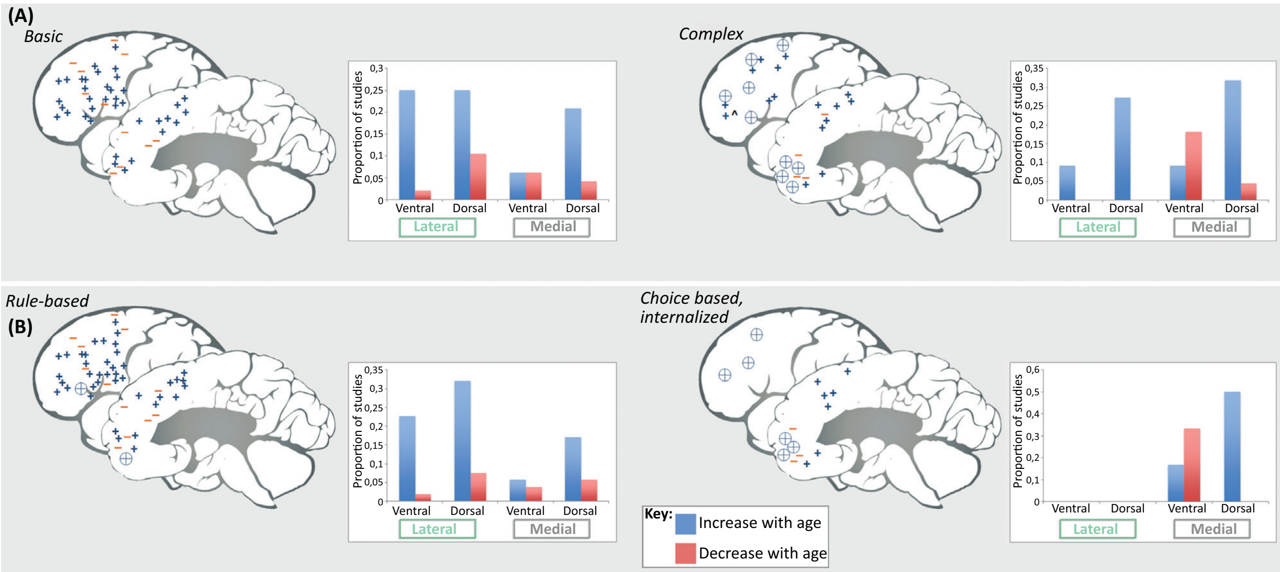

Figure 2. Overview of Empirical Findings in Prefrontal Cortex (PFC). An overview of increases and decreases in activity based on studies that are presented in this review, according to the distinctions presented in Figure 1 (main text). Studies that show age-related increases (blue) or decreases (red) in (A) basic (left [15–18,20–25,48,50–55,95–101]) and complex (right [26–28,56,57,59–62,68–73,75,102–104]) cognitive control tasks and in (B) rule-based (left [15–18,20,22–26,48,50–57,60–62,95–100,102–104]) and internalized, choice-based (right [20,21,27,28,59,68–73,75,101]) cognitive control tasks. Increases are presented as + (blue) and decreases as − (red). In cases where there was a change in connectivity reported, a ⊕ is used. Nonlinear patterns are displayed as '^'. The bar graphs present relative increases and decreases according to lateral (coordinates outside x=−15 and x=15) and medial (coordinates within x=−15 and x=15) regions, for ventral and dorsal PFC. The ventral and dorsal distinction was based on the way in which this was presented in the specific studies. In cases where studies reported multiple activity foci within one brain area, the one with the largest intensity was plotted on the cartoon brain. Given that some studies overlapped, the activities may differ slightly from the location in the original paper for visibility and clarity of this figure.

control processes. Developmental improvements in response inhibition [4], task switching [39], error monitoring, and probability updating [62] are typically observed until late childhood and/or early adolescence. By contrast, developmental improvements in working memory manipulation [36,63], delay discounting [64], emotion regulation [61], and feedback learning [63] are observed throughout adolescence until early adulthood.

Some studies also show decreases with increasing age, mostly in dorsal regions, and mainly for basic processes, such as response inhibition and working memory maintenance [19,22,23,54]. This might indicate that young children use additional strategies in basic tasks more often than do adults (i.e., recruit dorsal regions associated with deliberative processes for a stimulus-driven task) to compensate for potential capacity limitations. Alternatively, a new conceptualization of how cognitive control can be divided in subprocesses may help in understanding the developmental time courses of these functions (Fig. 1).

Rule-Based versus Internalized Cognitive Control

An alternative way in which cognitive control processes can be distinguished is based on the extent to which the processes are rule-based or internalized decision processes. With rule-based processes, we refer to the cognitive processes that rely on specific predefined rules or instructions. By contrast, internalized processes refer to those decisions where there is no specific instruction, and choices are based on internal deliberations. Examples of internal deliberations are 'deciding to restrain from acting on impulses' (i.e., safe decision-making or delay of gratification), or 'updating values based on prior experiences' (prediction updating or error monitoring). Several theoretical models based on brain-imaging data in adults show that

Box 1. On the Significance of Neural Activation for Behavior

An interesting question concerns the issue of developmental change in neural activity that is unrelated to task performance. For example, several studies reported additional change in neural activity related to age, while keeping performance constant [87] or when accounting for performance [88]. One possibility is that these neural activities represent a certain readiness for change. For example, even when a child is performing at level x, this child may be more likely to make the transition soon to progress to level x+1 compared with another child who also performs at level x (Figure I). This idea of readiness is well conceptualized in the developmental psychology literature that describes children's task performance in the overlapping waves theory. This theoretical framework shows that children may have several strategies available and differ in the strategy that they use [89,90]. Children who show stronger neural activity during task performance may have more strategies available, or may be more likely to progress to the next (more advanced) strategy soon, despite showing currently similar performance levels as children who have fewer strategies available. Some evidence for this assumption comes from longitudinal studies that show that stronger activity in PFC at a first time point is predictive for longitudinal improvement in cognitive performance from the first to the second time point, over and above behavioral measures [91].

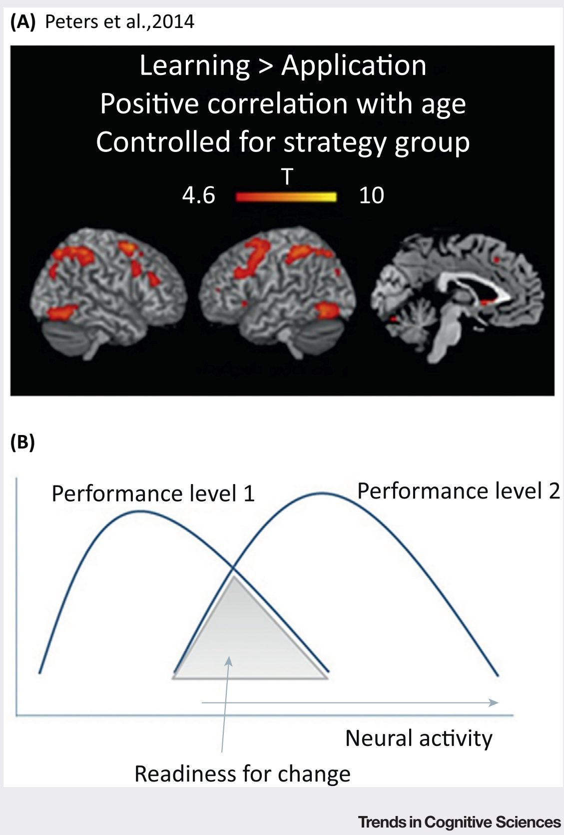

Figure I. Brain Regions That Show Age-Related Increases When Controlling for Performance May Signal Potential for Change. (A) Brain regions that show age-related changes when controlling for performance levels [88]. (B) An illustration of how performance-corrected age-related activity may reflect 'readiness' for change to the next performance level.

rule-based cognitive control relies on lateral prefrontal regions, whereas internalized control relies on medial regions, as recruited by intentional decisions [32], tracking motivation of others [65], or internal processing of emotions [30]. It is assumed that, for example, the medial frontal cortex (specifically the dorsal anterior cingulate cortex) monitors our environment for task difficulty, and signals the lateral PFC when control needs to be exerted [31].

Following this lateral–medial distinction, Figure 2B presents a categorization of cognitive control processes in terms of rule-based and internalized processes. Whereas rule-based processes are associated with developmental increases in both medial and lateral regions of the PFC, internalized processes are associated with changes mainly in medial regions of the brain. Interestingly, the studies that reported age-related changes in neural activity in lateral regions only did so for connectivity findings (circles in Figure 2). The changes in connectivity are related to connectivity with ventromedial PFC [28], and the ventral striatum [27,59]. Thus, similar to the basic and complex and/or deliberative distinction, there appears to be an early functional specialization in PFC areas to support processes of rule-based and internalized cognitive control, albeit on a gradient from lateral to medial regions. Both rule-based and internalized cognitive control processes show developmental changes over time in behavioral tasks, such as protracted development of both rule-based working memory manipulation [36,66] and internalizing delay discounting [64] or giving trust [67], but these behavioral patterns are possibly associated with the maturation of different regions within the PFC (Box 2).

The distinction between dorsomedial and ventromedial PFC deserves additional attention. Cognitive control processes that are associated with changes in dorsomedial PFC consistently show increases in activity related to trust [68], delay of gratification [69], and error monitoring [20,21]. However, age-related changes in ventromedial PFC show a less-consistent pattern. In this region, age-related increases are observed in activity and connectivity for updating of decision-making parameters [70–72] and delay of gratification choices [28,59]. However, some studies also report age-related decreases in neural activity, specifically decreases are observed for trust [68], reciprocity [73], refraining for risk taking [74], and positive prediction errors [75].

It has recently been argued that ventromedial PFC supports highly complex functions, such as valuation, affect regulation, and social cognition [76]. Given that the studies reporting both increases and decreases in activity (delay discounting, trust, and feedback updating) used paradigms that are related to social and affective cognitive control, this possibly indicates that ventromedial PFC is, in some cases, more active in adolescent participants because these signals have different personal value to them [77]. Social-affective learning signals may be more significant for children and young adolescents, whereas cognitive-affective learning signals are possibly more significant for older adolescents and adults [78].

Connectivity and Functional Specialization of Prefrontal Cortical Regions

It would be simplistic to assume that there is a general maturational pattern, driven by a predetermined maturational time course across childhood and adolescence, of such a large and heterogeneous brain area as the PFC. Behavioral developmental studies also consistently show that not all cognitive control functions develop at the same pace. It is more likely that developmental changes, especially in higher-level cognitive skills, result from interactive specialization within the PFC and its connections to other regions in the brain [79]. Therefore, there is a need for a better conceptual understanding of how cognitive control development is associated with functional changes in the PFC and collaborating brain regions.

Box 2. Linking Brain Structure and Brain Function

Recently, studies of the development of cognitive control have begun to combine both functional and structural data. Such approaches follow from the assumption that brain function is rooted in the anatomy and connectivity of a specific brain structure (for two recent demonstrations of this in fusiform face and visual form area, see [92,93]). In one study, age-related changes in structural connectivity between the striatum and the right dorsolateral PFC predicted the extent of functional connectivity between these two regions, which in turn accounted for developmental differences in delay discounting [27]. By contrast, recent studies combining cortical thickness and functional activation showed that developmental differences in each contributed unique portions of variance in explaining social behaviors that rely on inhibitory control [94]. This suggests that structural and functional connectivity are more tightly coupled than are anatomy and functional activation. Combining brain structure and function in explaining the emergence of cognitive control constrains what might be expected in terms of the associated variability in task-related activation patterns.

Several studies have made use of advanced data-driven methods to discover meaningful connectivity patterns in the developing brain [80,81]. Dosenbach *et al.* introduced this analysis based on resting-state connectivity patterns [82,83]. They distinguished between a network that was defined as the cingulo-opercular network, and a network that was defined as the frontoparietal network. These networks were associated with set maintenance and control adjustment, respectively, which builds upon the idea that the medial frontal cortex monitors for internalized task processes and sends signals to the lateral PFC to signal task adjustment [31]. Using advanced resting-state connectivity analyses (including graph theory and hierarchical clustering, and using independent component analyses), Dosenbach *et al.* reported support for this distinction, but argued that these regions are hubs in a much larger network involved in the maintenance of task setting and the adjustment of control. Interestingly, the network analyses showed differential development of set-maintenance networks and task adjustment networks. Our review suggests that the development of functional distinctions in the PFC in response to cognitive control tasks differing in the extent to which they draw on rule-based versus internalized processes is already present at least in middle childhood and undergoes further functional refinement with age.

Concluding Remarks and Future Directions

Here, we have explored new ways of categorizing developmental progressions in cognitive control during childhood and adolescence. We have argued that neural activity patterns provide insight into how children and adolescents perform tasks, thereby informing the formulation of more sophisticated models of cognitive control development.

By starting with a basic–complex model [29,43,44], we showed that behavioral performance on tasks that rely on complex deliberative processing has a more protracted development compared with basic stimulus-driven performance. This pattern was associated with a more protracted development of dorsolateral PFC in terms of activity, structure, and connectivity to other regions in the cortex. Interestingly, patterns were most consistent (i.e., showed consistent increases throughout childhood and adolescence) when the tasks relied on complex deliberative processes, whereas tasks that relied on basic, stimulus-driven processes showed a more complex pattern of increases and decreases in different regions of PFC. One possibility is that younger children use compensatory strategies when they perform stimulus-driven tasks. Basic stimulus-driven tasks may require more strategy compensation than was previously believed.

Additionally, there was convincing evidence for a distinction between rule-based and internalized decision processes, such that internalized decision processes in particular were associated with activity changes in medial PFC. The lateral–medial distinction has only recently received more attention in developmental cognitive neuroscience, with reviews focusing on internalized inhibition processes [84] and mentalizing processes [85]. This will be a fruitful avenue to explore in future, especially given that the patterns of increases and decreases in ventromedial PFC show the most protracted time courses and task-dependent patterns of change. It is likely that this is associated with the connections that this area has with subcortical brain regions, which show dramatic changes during adolescence [86].

A challenging but critical task for the future will be to decompose executive functions to understand not only their developmental time courses, but also how children and adolescents are capable of combining these skills to predict high-stake behaviors, such as performing well in school, planning their future, and developing meaningful social relationships.

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Outstanding Questions

To what extent is increased variability in functional recruitment of brain regions for cognitive control a result of differences in strategy use?

Is intraindividual variance related to interindividual variance for specific cognitive control functions?

How can the structural maturation of brain regions and pathways connecting different regions account for different patterns of variability in functional activation?

Do age-related differences in brain activity reflect readiness for change?

What is the role of motivation in the recruitment of cognitive control across different stages of development?

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