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Neural perspectives on cognitive control development during childhood and adolescence

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Abstract

Since the discovery that patients with damage to the prefrontal cortex show similar deficits in cognitive control as young children, the prefrontal cortex model of cognitive control development has been a popular description of how cognitive control emerges over time. In this review, we show that many studies support this model, but also that more specific models of prefrontal cortex development can be formulated, according to the functional roles of subregions and by taking into account the distinctions within ventral-dorsal and lateral-medial prefrontal cortex. Here we show that functional development of dorsal lateral prefrontal cortex supports the development of deliberative processes, whereas medial prefrontal cortex supports the development of internalized decisions. These new conceptualizations may provide better descriptions of the complexity of cognitive control development.

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. In the last decades, a wealth of findings 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 it was observed that working memory shows a more protracted developmental time course than cognitive switching and inhibition [4]. Recent studies in the field of cognitive neuroscience have made important progress in understanding how cognitive control functions rely on overlapping and different neural regions and processes.

Ever since the discovery that patients with damage to the prefrontal cortex show deficits in cognitive control [5, 6], many theoretical models have suggested that cognitive control development may be closely tied to the development of the prefrontal cortex [1, 7, 8]. Subsequent and increasingly refined models have taken the heterogeneity of the prefrontal cortex into account and suggest that the developmental time course of separable cognitive control functions are possibly related to maturation of subregions of the prefrontal cortex [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 prefrontal cortex is important for cognitive control in adults [12-14] and were applied to the understanding of the neural basis of cognitive control development in children and adolescents.

Developmental neuroimaging studies have initially focused on mapping single cognitive control functions to the maturation of specific areas within the prefrontal cortex. 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 dorsal and ventral lateral prefrontal cortex [15-17]. Inhibitory control is also often mapped to increased activity in the prefrontal cortex 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 neural recruitment of the prefrontal cortex, consistent with the hypothesis of a functional role of protracted prefrontal cortex 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 us about the significance for performance. For example, whereas some studies

report increased activations with age in specific regions, others find age-related decreases in activations 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 progressions in working memory updating performance related to neural activity in dorsolateral prefrontal cortex ($n=951$, ages 8-22-years). This study reported that activity increase in dorsolateral prefrontal cortex 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, also studies reporting age-related decreases in neural activity linked these to behaviour progressions [24], showing that both decreases and increases can be meaningfully linked to developmental changes in cognitive control. So far, there is little systematic review of what this could mean. Children may be using different strategies compared to 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 prefrontal cortex may inform us about the way that different types of cognitive control are developing.

This review will 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. These perspective comprise the distinctions of (1) basic, stimulus-driven versus complex, deliberative cognitive control functions [29, 30], and (2) 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 (see 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 it should be noted that these are not complete dichotomies and some overlap will exist between the concepts. It will emerge that these conceptualizations constitute a powerful approach to synthesize 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 consist of working memory, inhibition, cognitive flexibility and error monitoring [1], which are thought to be supported by different underlying neural regions within the prefrontal cortex, and each have separate developmental time courses [9]. These processes need to work well in concert and thereby contribute to performance on more complex cognitive control tasks [29]. Complex executive function tasks rely more on deliberative processes than basic, stimulus-driven processes. Deliberative cognitive control refers to processes that are potentially prone to strategy use (i.e. working memory manipulation, 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 (go/nogo tasks and stop-signal inhibition tasks) or interference control tasks (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 immediate behavioural output, but studies have examined post-error slowing as an index of the maturation of error monitoring. Studies report that already young children (from the age of 7 years) show evidence for post error slowing [40]. Other studies reported developmental decreases in post-error slowing suggesting more efficient error monitoring as children get older [41].

Using the unity and diversity model suggested by Miyake et al. (2000), it has been tested if 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, like delay discounting [28].

What are the implications for the basic-complex distinction for understanding the neural development that supports cognitive control development? One assumption based on the behavioural data is that neural activity in brain regions that are typically associated with the basic executive functions (working memory, inhibition, cognitive flexibility, error

monitoring) in adults should show increases in recruitment, as children get older. Prior research in adults points to a role of the ventral and dorsal lateral prefrontal cortex supporting working memory performance [14]. Inhibitory control is often linked to the right inferior frontal gyrus and dorsolateral prefrontal cortex 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-SMA and the inferior frontal junction [47, 48] and error monitoring to the anterior cingulate cortex [49].

Developmental studies have subsequently tested if these regions show protracted functional maturation over child and adolescent development. Developmental fMRI studies show most consistent patterns for working memory development. Especially working memory updating has been consistently related to increases in dorsolateral prefrontal cortex across studies over the whole period of 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 frontal cortex 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]). Possibly younger children call upon more diverse processes to perform well on these tasks.

The second assumption of the basic-complex model is that improvements on 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 prefrontal cortex regions as children grow up. Given the variability in the developmental findings on the

basic executive function tasks, it is difficult to relate these directly to activity on more complex cognitive control tasks. Nonetheless, the general pattern suggests that neural activity on more complex cognitive control tasks are showing age related increases in multiple prefrontal cortex 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 according to this distinction. Figure 2- top panel 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 than basic cognitive control processes. Developmental improvements for response inhibition [4], task switching [39], error monitoring and probability updating [62] are typically observed until late childhood/ early adolescence. In contrast, developmental improvements in working memory manipulation [36, 63], delay discounting [64], emotion regulation [61] and feedback learning [63] are observed over the whole period of adolescence up to early adulthood.

Some studies also show decreases with increasing age, mostly in dorsal regions, and mostly for basic processes such as response inhibition and working memory maintenance [19, 22, 23, 54]. Possibly, this indicates that young children use additional strategies in basic tasks more often than 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 in how cognitive control can be divided in subprocesses may help in understanding the developmental time courses of these functions.

Rule-based versus internalized cognitive control

An alternative way, in which cognitive control processes can be distinguished, is according to the extent to which the processes are rule-based or internalized decision processes. With rule-based, we refer to the cognitive processes that rely on specific predefined rules or instructions. In 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, delay of gratification), or ‘updating values based on prior experiences’ (prediction updating, error monitoring). Several theoretical models based on brain imaging data in adults show that 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 prefrontal cortex when control needs to be exerted [31].

Following this lateral-medial distinction, Figure 2-lower panel 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 prefrontal cortex, internalized processes are associated with changes mainly in medial regions of the brain. Interestingly, the studies that report age-related changes in neural activity in lateral regions, only report this for connectivity findings (circles in Figure 2). The changes in connectivity are related to connectivity with ventral medial prefrontal cortex [28], and the ventral striatum [27, 59]. Thus, similar to the basic and complex/deliberative distinction, there appears to be an early functional specialisation in prefrontal cortical 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 on behavioural 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 behavioural patterns are possibly associated with the maturation of different regions within the prefrontal cortex.

The distinction between dorsal and ventral medial prefrontal cortex deserves additional attention. Cognitive control processes that are associated with changes in *dorsal* medial prefrontal cortex consistently show increases in activity related to trust [68], delay of gratification [69], and error monitoring [20, 21]. However, age related changes in *ventral* medial prefrontal cortex show a less consistent pattern. There, 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 vmPFC 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, feedback updating) used paradigms that are related to social and affective cognitive control, this possibly indicates that ventral medial PFC is in some cases more active in adolescent participants because these signals have different personal value for 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 specialisation 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 prefrontal cortex. Behavioural developmental studies also consistently show that not all cognitive control functions develop with the same pace. It is more likely that developmental changes, especially in higher-level cognitive skills, result from interactive specialization within the prefrontal cortex and its connections to other regions in the brain [79]. There is, therefore, a need for a better conceptual understanding of how cognitive control development is associated with functional changes in the prefrontal cortex and collaborating brain regions.

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 cingular-opercular network, and a network that was defined as the frontal-parietal 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 prefrontal cortex 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. report support for this distinction, but argue that these regions are hubs in much larger network involved in the maintenance of task-set and the adjustment of control. Interestingly, the network analyses show differential development of set-maintenance networks and task adjustment networks. Our review suggests that the development of

functional distinctions in the prefrontal cortex in response to cognitive control tasks differing in the extent to which they draw on rule-based vs internalized processes is already present at least in middle childhood and undergoes further functional refinement with age.

Future directions

The goal of this review was to explore new ways of categorizing developmental progressions in cognitive control during childhood and adolescence. We argued that neural activity patterns provide insight into how children and adolescents perform tasks, and thereby inform the formulation of more sophisticated models of cognitive control development.

By starting out with the basic-complex model [29, 43, 44], we showed that behavioural performance on tasks that rely on complex deliberative processing has a more protracted development than basic stimulus-driven performance. This pattern was associated with a more protracted development of dorsal lateral prefrontal cortex in terms of activity, structure and connectivity to other regions in the cortex. Interestingly, patterns were most consistent (i.e. showing consistent increases over the whole course of 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 in prefrontal cortex. One possibility is that younger children employ compensatory strategies when they perform stimulus-driven tasks. Basic stimulus-driven tasks may require more strategy compensation than previously believed.

Additionally, there was convincing evidence for a distinction between rule-based and internalized decision processes, such that especially internalized decision processes were associated with activity changes in medial prefrontal cortex. The lateral-medial distinction

only recently received more attention in developmental cognitive neuroscience, with reviews focusing on internalized inhibition processes [84] and mentalizing processes [85]. This will prove to be a fruitful avenue to explore in future, especially given that the patterns of increases and decreases in ventral medial prefrontal cortex 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 their developmental time courses, but also to understand how children and adolescents are capable of combining these skills to predict high stake behaviours such as performing well in school, planning their future, and developing meaningful social relationships.

Text box 1: On the significance of neural activation for behaviour

An interesting question concerns the issue of developmental change in neural activity that is unrelated to task performance. For example, several studies report 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 to another child who also performs at level x (see Figure 3). 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]. Possibly, 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 prefrontal cortex at a first time point is predictive for longitudinal improvement in cognitive performance from the first to the second time point, over and above behavioural measures [91].

Figure: Brain regions that show age-related increases when controlling for performance may signal potential for change. (A) Peters et al. 2014, brain region that show age-related changes when controlling for performance levels. (B) Brain activity that predicts change in reading and arithmetic two years later. (C) An illustration of how performance-corrected age-related activity may reflect 'readiness' for change to the next performance level.

Text box 2: Linking brain structure and brain function

Recently, studies on the development of cognitive control have begun to combine both functional as well as 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 DLPFC predicted the extent of functional connectivity between these two regions, which in turn accounted for developmental differences in delay discounting [27]. On the other hand 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 might be more tightly coupled than 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.

Figure Captions

Figure 1: **Overview of proposed distinctions within prefrontal cortex.** Conceptual overview of the distinctions within prefrontal cortex related to basic and complex/deliberative processes, and rule-based (lateral) to internalized (medial) processes. dlPFC=dorsal lateral prefrontal cortex, vlPFC=ventral lateral prefrontal cortex, dmPFC=dorsal medial prefrontal cortex, vmPFC=ventral lateral prefrontal cortex. The bottom half of the Figure shows how different cognitive control tasks can be subdivided along these processes.

Figure 2: **Overview of empirical findings in prefrontal cortex.** An overview of increases and decreases in activity based on studies that are presented in in this review, according to the distinctions presented in Figure 1. The first horizontal row describes studies that show age-related increases (blue) or decreases (red) in 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. The second horizontal row describes these for 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. The increases are presented as + (blue) and decreases as – (orange). In case there was a change in connectivity reported, a circled + is presented. Non-linear 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 this was presented in the specific studies. In case 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 the figures.

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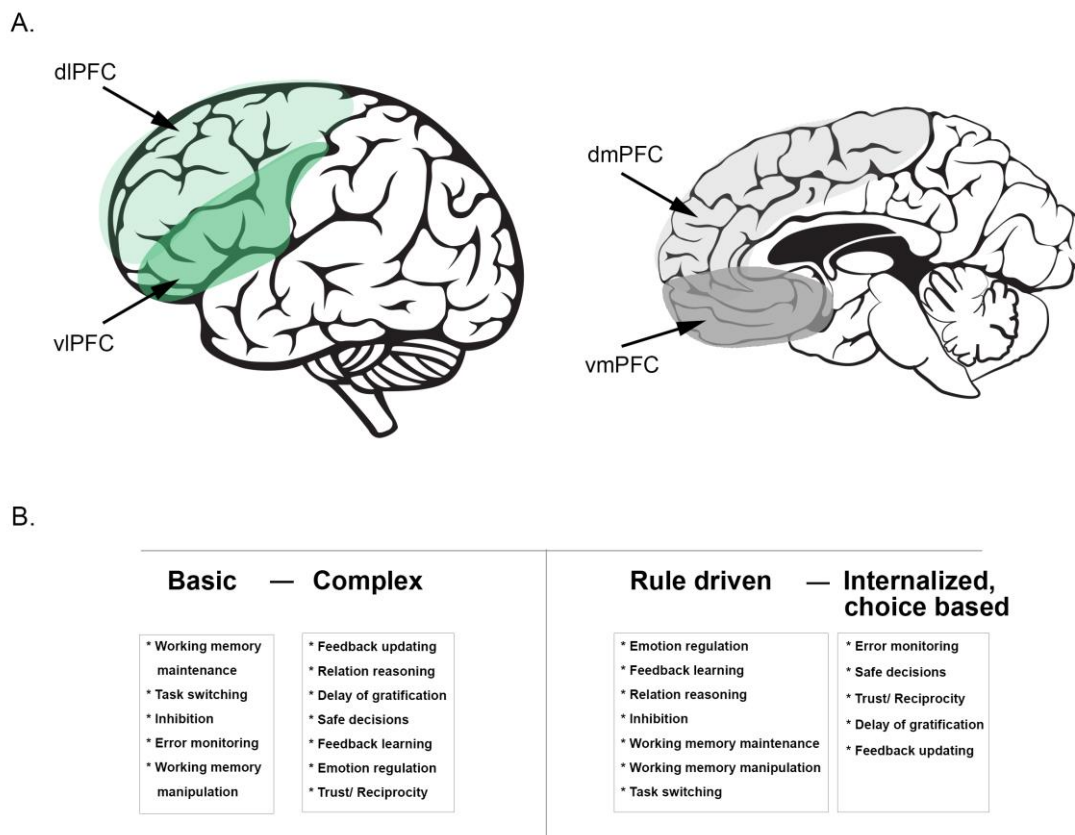


Figure 1

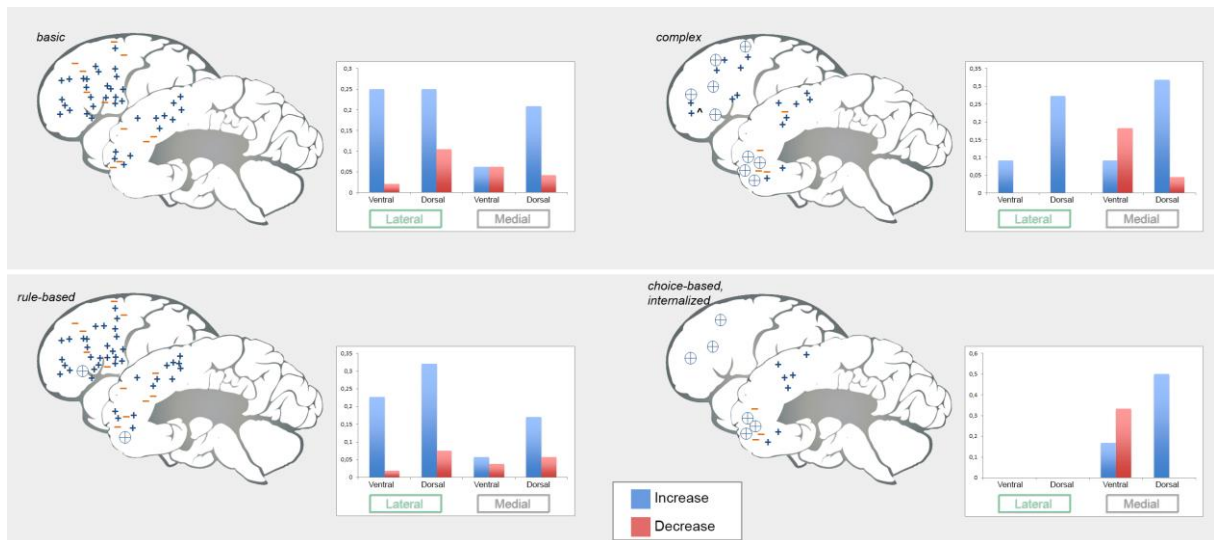
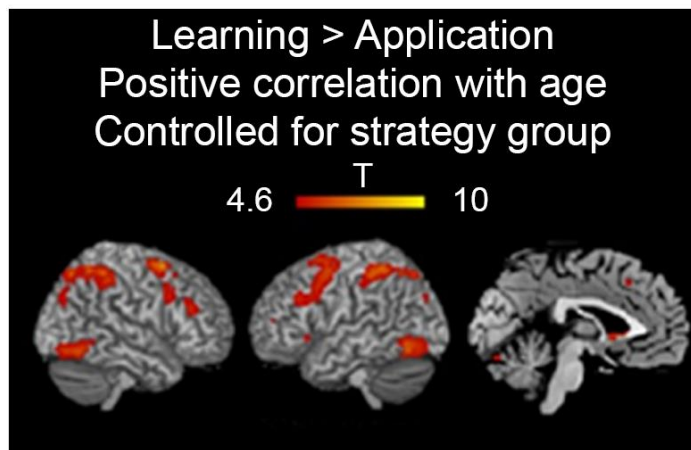


Figure 2

A: Peters et al., 2014



B:

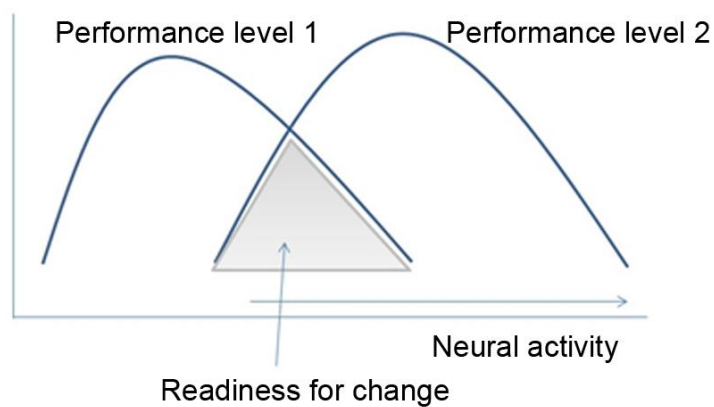


Figure 3