





Neurodevelopmental changes in working memory and cognitive control

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One of the most salient ways in which our behavior changes during childhood and adolescence is that we get better at working towards long-term goals, at ignoring irrelevant information that could distract us from our goals, and at controlling our impulses - in other words, we exhibit improvements in cognitive control. Several recent magnetic resonance imaging studies have examined the developmental changes in brain structure and function that underlie improvements in working memory and cognitive control. Increased recruitment of task-relevant regions in the prefrontal cortex, parietal cortex and striatum over the course of development is associated with better performance in a range of cognitive tasks. Further work is needed to assess the role of experience in shaping the neural circuitry that underlies cognitive control.

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Introduction

If you ask a young child to choose between having one cookie now and two cookies in fifteen minutes, it is likely that he or she will initially attempt self-restraint in favor of the larger snack, but ultimately request the single cookie before the time is up $[1,2^{\circ}]$. Indeed, one of the most obvious ways in which our behavior changes during childhood and adolescence is that we get better at working towards long-term goals, ignoring irrelevant information that could distract us from these goals, and controlling our impulses - in other words, our cognitive control improves [3,4[•]].

What precisely is changing in a child's brain over time, enabling him or her to better control his or her thoughts and behavior? To what extent do these neural changes result from experience and practice, and to what extent do they result from predictable developmental changes in brain structure? What are the elemental control processes that develop during childhood?

Several brain imaging studies have been conducted in recent years in an effort to tackle these and other difficult questions about the developing brain [5–7]. Compared with what is known about changes in brain structure during development (Box 1), far less is known about the resulting changes in brain function. In this review, we focus on event-related functional magnetic resonance imaging (fMRI) studies from the past year that examine age-related changes in working memory and cognitive control.

Visuospatial working memory

Since the first fMRI study of working memory in children just over a decade ago [8], most such studies have focused on pure maintenance of memory, and specifically on visuospatial working memory (VSWM) [9-11,12[•]]. Event-related fMRI studies have shown that regions that have been strongly implicated in VSWM in adults — the superior frontal sulcus (SFS) and the intraparietal sulcus (IPS) — are increasingly engaged as childhood progresses [10,11]. Moreover, increased fractional anisotropy in frontoparietal white matter is positively correlated with blood oxygen level dependent (BOLD) activation in the SFS and IPS, and with VSWM capacity [13]. These data indicate that increased interaction between the SFS and IPS over development is important for improvements in VSWM.

Although these regions are increasingly engaged over childhood and adolescence, others are less so. For instance, Scherf et al. [12[•]] found that children weakly recruited core working-memory regions (the dorsolateral prefrontal cortex [DLPFC] and parietal regions) and instead relied primarily on ventromedial regions (the caudate nucleus and anterior insula). In adolescence, by contrast, they observed refinements of the specialized network found in adults [3,12°,14°°,15]. These results suggest that the maturation of adult-level cognition involves first an integration of childhood compensatory network with that of the more mature performanceenhancing regions, and next an increase in localization within those necessary regions (Figure 1).

At the cellular level, three possible developmental changes could account for the developmental increases in SFS and IPS activation that are observed during fMRI: pruning of excess neurons, myelination and increased strength of connections within or between brain regions.

Box 1 Developmental changes in brain structure and function

By the time a child starts primary school, the shape and size of his or her brain is roughly comparable to that of an adult. However, structural differences are evident upon closer examination [45] Cortical gray matter volume, which reflects neuronal density and the number of connections between neurons, peaks at around age 10-12 in both prefrontal and parietal cortices - regions that have been strongly implicated in working memory and cognitive control [46]. Thereafter, gray matter loss occurs at different rates in different subregions of the brain, and is considered an index of the timecourse of maturation of a region [47]. The dynamics of gray matter increases and decreases, particularly in the prefrontal cortex (PFC). are associated with differences in intellectual ability [48]. Within the PFC, grav matter reduction is completed earliest in the orbitofrontal cortex, followed by the ventrolateral PFC (VLPFC) and then by the dorsolateral PFC (DLPFC) [49]. It has been argued that differences in maturational time-course between prefrontal subregions partially account for differences in the rate of development of distinct cognitive control processes [19,27,50].

Unlike gray matter, white matter volume increases with age, reflecting myelination and increased axon thickness [46]. Diffusion tensor imaging (DTI) studies have shown greater coherence of white matter tracts in adults than in children, as measured by an index of fractional anisotropy [51]. Importantly, greater coherence is associated with better performance on tasks that require interaction between regions that are connected by these tracts [13,52,53*]. In summary, both cortical pruning within brain regions and increased neuronal connectivity within and between regions could underlie improvements in cognitive control over development, as discussed in the main text with reference to a recent study by Edin, Klingberg and colleagues [16**].

In a cutting-edge study, Klingberg and colleagues [16^{••}] took a computational approach to determine which of these changes could contribute to the developmental changes observed in their VSWM studies. They concluded that the greater prefrontal and parietal activation and interactions that are observed in adults relative to children could result from increased strength of connectivity between regions, but not from pruning, myelination or the strength of connectivity within regions (Figure 2).

Interference suppression during performance of a VSWM task

A further VSWM study by Olesen, Klingberg and colleagues [17[•]] included a period of distraction, during which participants were asked to ignore stimuli appearing in various locations on a screen. Children around the age of 13 exhibited greater SFS activation than did adults during this period of distraction, despite having shown reduced activation in this region in VSWM studies that did not involve distraction. Given that SFS is involved in spatial working memory, this finding suggests that the children were less effective at ignoring the irrelevant spatial stimuli.

By contrast, adults engaged the right DLPFC and bilateral intraparietal cortex more strongly than children did while maintaining relevant information online. This finding is potentially significant in light of a prior study in adults by Sakai, Rowe and Passingham [18]. Using a similar task with adults, Sakai *et al.* showed that engagement of a slightly anterior region of the right DLPFC was associated with better performance on the working-memory task. Thus, in the study by Olesen *et al.* [17[•]], children showed weaker activation during VSWM in a region of the right DLPFC that adults might rely on to create a distractor-resistant memory trace. It would be of great interest to examine developmental changes in the functional interactions between the DLPFC, SFS and IPS, and how these changes affect the ability to suppress interference [18].

Non-spatial working memory

Although the majority of developmental fMRI studies of working memory have focused on VSWM, a recent study by Crone, Bunge and colleagues [19[•]] focused on development of non-spatial working memory. Participants had to remember a series of three nameable objects; children made more errors than adolescents and adults, but engaged highly overlapping brain regions during task performance. Positive correlations between accuracy and activation across the entire group were observed in all regions of interest: the ventrolateral prefrontal cortex (VLPFC), the DLPFC and the superior parietal cortex. These correlations remained significant after controlling for age, suggesting that the level of engagement of these regions itself has an impact on performance. Taken together with the aforementioned VSWM studies, these findings indicate not only that the basic working-memory circuitry is in place by middle childhood (see also [20]), but also that working-memory circuitry is strengthened during middle childhood.

Manipulation of items in working memory

As we have already noted, improvements in the ability to maintain information on-line are observed during childhood, and — when highly sensitive measurements are used — throughout adolescence [7]. However, developmental changes are more dramatic when one must manipulate, or work with, information held in working memory [21].

The aforementioned working-memory study by Crone *et al.* [19[•]] provided evidence for protracted neurodevelopmental changes in regions involved in manipulating items in working memory relative to regions involved in simply maintaining items in working memory. Prior imaging research in adults had implicated the DLPFC and superior parietal cortex in manipulation [22]. In the Crone *et al.* study [19[•]], adolescents and adults, but not 8–12year olds, engaged the right DLPFC and bilateral superior parietal cortex when it was necessary to reverse the order of items held in working memory (Figure 3). Unlike the older age groups, 8–12-year olds did not recruit additional regions for manipulation above and beyond



Figure 1

Scherf *et al.* [12*] graphically depicted developmental shifts in the location of active voxels during performance of a visuospatial working memory (VSWM) task. (a) The three group-averaged functional maps of percentage signal change illustrate differences in both the magnitude and extent of activation. Children showed strongest activation bilaterally in the caudate nucleus, the thalamus and the anterior insula. Adolescents showed strongest activation in the right dorsolateral prefrontal cortex (DLPFC), and adults showed concentrated activation in the left prefrontal and posterior parietal regions. Additional abbreviations: AC, anterior cingulate; rINF PCS, right inferior precuneus; rSTG, rostral superior temporal gyrus. (b) Differences between the three age groups in the extent of activation, as measured by the proportion of total active voxels in each region of interest. Although the proportion of voxels that were active in the was consistent across the age groups, the groups showed large differences in the proportions of these active voxels across the regions of interest. Reproduced, with permission, from p. 1054 of [12*] (D MIT Press.

what they would use for pure maintenance; this reliance on maintenance circuitry was associated with suboptimal manipulation ability. Such lower engagement of the DLPFC in children than in adults has also been observed in other studies of working memory and cognitive control [15,17[•]].

These data do not address the issue of whether children fail to recruit brain regions that are involved in manipulation because of maturational constraints associated with immature neural circuitry, and/or because of limited practice with this type of task. Interestingly, in the study by Crone *et al.* [19•], the children did recruit these DLPFC and superior parietal regions during encoding and response selection — just not during the delay period, when manipulation was required. A pattern of mature DLPFC activation has also been observed in 8–12-year olds performing a simple gambling task, even though agerelated differences associated with the processing of uncertainty and negative feedback were observed in anterior cingulate cortex and lateral orbitofrontal cortex, respectively [23].

These observations highlight a general point about developmental changes in brain function: a region can exhibit adult-like patterns of activation in one task but not in another. As another example, VLPFC showed a mature pattern of activation in the non-spatial working-memory task [19[•]], but not in tasks that involved response inhibition [24–26] or rule representation [27[•]]. Thus, a region might contribute effectively to a neural circuit that underlies one task or cognitive function, but not to a neural circuit that underlies another.

Response control: inhibition and selection

Improvements are observed over childhood in the ability to control our actions [4[•]]. Control is needed when one must inhibit a tendency to respond to a stimulus (i.e. 'response





Cellular mechanisms underlying increased engagement of working-memory circuitry over development. (a) Edin *et al.* [16^{••}] sought to determine the underlying structural changes over development that could explain why BOLD activation in the superior frontal sulcus (SFS) and the intraparietal sulcus (IPS) during VSWM performance is greater for adults (shown in green) than for children (black). (b) They used a model of VSWM to determine which of the known neural changes across development — pruning, myelination and/or increased strength of connection between neurons within (w) or between (b) brain regions — could contribute to the developmental changes observed in BOLD activation during VSWM performance. Based on these known changes, Edin *et al.* put forth five hypotheses (H_1 – H_5) regarding the structural development of the VSWM network, and simulated the consequences of each of these structural changes on BOLD activation levels. For each hypothesis, a 'child' (black) and 'adult' (green) version of the network was created. The strengths of connections within a region are indicated by the connection curves inside the circles (which represent the parietal and frontal pyramidal cell populations), whereas the curves between the circles show connection curves between regions. By comparing these simulated outcomes with their empirical data, Edin *et al.* concluded that their data could be explained by increased strength of connectivity between regions (H₂) but not by increased strength of connectivity within a region (H₁), synaptic pruning (H₃ and H₄) or myelination (H₅). See [16^{••}] for more details. Reproduced, with permission, from [16^{••}] © MIT Press.

inhibition'); this ability is typically measured using Go-No-Go and stop-signal paradigms [24–26,28–30,31^{••}]. Control of responses is also needed when one must select between competing response alternatives ('response selection'). Neurodevelopmental changes in response control have been studied using various paradigms, including the Simon task [32[•]], antisaccade task [9], Eriksen flanker task [24,30,32[•]] and Stroop task [33–35]. Although these tasks differ in many ways and are therefore likely to rely on distinct cognitive processes, many of them test common underlying neural substrates that support controlled responding.

As such, to understand better the development of brain networks that underlie response control, it is crucial to determine which age-related differences are task-specific



Figure 3

Crone *et al.* [19*] examined age-related differences in activation of the DLPFC during working-memory manipulation. (a) Each trial of the working-memory task started with 250 ms fixation of a cross, followed by three nameable objects that were presented for 750 ms each, with a 250 ms presentation of the fixation cross between each nameable object. Forward trials required pure maintenance, whereas backward trials required manipulation in addition to maintenance. After the last object, the instruction 'forward' or 'backward' was presented for 500 ms (a forward trial is shown here). Participants were instructed to mentally rehearse or reorder the names of the three objects during the 6000 ms delay, and then to indicate using a button press whether the probe object was the first, second or third object in the forward or backward sequence. (b) Activation of regions of interest in the right DLPFC (Brodmann area 9) was functionally defined during the 6000 ms memory delay period; signal intensity was identified from a contrast of all conditions relative to fixation for all participants. Unlike adolescents and adults, children aged 8–12 failed to recruit the DLPFC and DLPFC on forward and backward trials are presented for each age group. The group-averaged time courses illustrate the finding that adults and adolescents, but not children aged 8–12, showed clear sustained DLPFC activity during the delay period. Reproduced, with permission, from pp. 9316–9317 of [19*] () National Academy of Sciences.

and which generalize across several paradigms [24,30,32[•]]. An earlier fMRI study [24] combining elements of the Go-No-Go and flanker tasks revealed that children aged 8–12 failed to engage a region in the right VLPFC that young adults recruited for both response selection and inhibition. It has since been shown that adults with damage to the right VLPFC have difficulty in several tasks that involve response control [36], and a developmental study by Rubia *et al.* [26] further shows a positive correlation between activation of the right VLPFC and age (between 10–42 years) during successful versus unsuccessful inhibitions on the stop-signal paradigm (Figure 4; for a similar correlation in a developmental Stroop study, see [35]). These findings indicate that suboptimal response control in children and adolescents stems from insufficient recruitment of the right VLPFC and functionally connected regions, including the thalamus, caudate and cerebellum [26].

Another recent study by Rubia *et al.* [32[•]] combined three tasks that involve response control: Go–No-Go, Simon and attentional set-shifting tasks. The investigators compared activation on all three tasks for youths aged 10–17 and adults aged 20–43. In all three tasks, adults recruited portions of the prefrontal cortex, anterior cingulate cortex and striatum more strongly than the youths, and there was a positive linear correlation with age in task-relevant frontal and striatal regions. Additionally, adults engaged the inferior parietal cortex more strongly than youths on the Simon and set-shifting tasks [32[•]], and a similar finding has previously been reported for the Go–No-Go task [24].





Rubia et al. [31**] examined developmental changes in activation during response inhibition on a stop-signal paradigm. (a) Horizontal arrows were presented one at a time on the screen, and the participant pressed one of two buttons to indicate which direction the arrow was facing. However, 20% of the time, the horizontal arrow was followed by a vertical arrow, which signaled that the participant should inhibit their response. The interval of time between the presentation of the horizontal and vertical arrows was adjusted so the participant successfully inhibited their responses ${\sim}50\%$ of the time. (b) Brain regions of increased activation in adults compared with children and adolescents (P < 0.01) during successful stop trials contrasted with unsuccessful stop trials. Depicted here in threedimensional and horizontal sections is increased activation in right prefrontal cortex (Brodmann areas 44, 45 and 47), a region for which a greater difference between successful trials as compared with unsuccessful trials is observed in adults. From left to right, the slices correspond to z-coordinates of +4, 10, 14, 20 and 24. Reproduced, with permission, from [31**].

However, the lateralization and precise location of these age-related changes depended on the task at hand, further highlighting the need to seek converging evidence from multiple tasks.

Conclusions

In summary, a growing literature indicates that increased recruitment of task-related areas in frontal, parietal and striatal regions underlies improvements in working memory and cognitive control over the course of middle childhood and adolescence. The pattern of developmental changes in brain activation has been generally characterized as a shift from diffuse to focal activation [14^{••}] and from posterior to anterior activation [32[•],37]. Differences can be quantitative, with one age group engaging a region more strongly or extensively than another, and/or qualitative, with a shift in reliance from one set of brain regions to another [12[•],32[•],37,38]. Importantly, the precise pattern of change observed depends on the task, the ages being examined and the brain region in question.

By middle childhood, the ability to hold goal-relevant information in mind and use it to select appropriate actions is already adequate. It is of great interest to track brain function associated with working memory and cognitive control earlier in childhood, when these abilities are first acquired. Optical imaging studies can be conducted from infancy onwards [20,39], although the spatiotemporal resolution of this method is suboptimal (but see [40]). It is now possible to acquire fMRI data in children as young as four years of age [41[•]], although this is not without challenges such as head motion, low accuracy and poor attention span.

An important future direction is to determine the extent to which observed age differences in brain activation reflect hard developmental constraints (e.g. the required anatomical network is simply not in place at a given age) as opposed to lack of experience with a given type of task or cognitive strategy. Training studies involving several age groups would enable us to investigate effects of age and effects of practice independently, and to test whether age differences in performance and brain activation are still present after substantial practice [42-44]. So far, all but one [14^{••}] of the published developmental fMRI studies on working memory or cognitive control have compared groups of individuals at different ages. These cross-sectional studies are valuable, but it is also important to conduct longitudinal studies to characterize intraindividual changes in brain function with age.

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