Emergence of Higher Cognitive Functions: Reorganization of Large-Scale Brain Networks During Childhood And Adolescence

Pedro M. Paz-Alonso, Silvia A. Bunge, and Simona Ghetti

Abstract

In the present chapter, we first provide an overview of *neurodevelopmental changes in brain structure and function*, which have implications for the development of higher cognitive functions as well as for other areas of research within developmental cognitive neuroscience. Second, we highlight neuroimaging evidence regarding the *development of working memory and cognitive control processes*, and the main neural mechanisms and brain networks supporting them. Third, we review behavioral and neuroimaging research on the *development of memory encoding and retrieval processes*, including *episodic memory* and *mnemonic control*. Finally, we summarize important current and future directions in the study of the neurocognitive mechanisms supporting the development of higher cognitive functions, noting that multidisciplinary approaches, different level of analyses, and longitudinal designs are needed to shed further light on the emergence and trajectories of these functions over development.

Keywords: developmental cognitive neuroscience, episodic memory, mnemonic control, working memory, cognitive control.

Children frequently face situations in which they must select among competing choices, such as eating a snack now or saving room for dinner, or focusing on finishing homework before playing a videogame. In making such decisions, it is necessary to reconcile the conflict between competing options available in the context with a specific set of expectations and rules as well as to inhibit impulses for immediate gratification in the service of a choice that is less immediate and automatic. Similarly, children often come across challenging cognitive operations that may

require, for instance, adding a series of numbers, ordering several pieces of information to build a logical argument, or trying to remember something the teacher said. These operations require retrieving, maintaining, and updating relevant information that is accessible and available for manipulation.

Higher cognitive functions refer to multidimensional executive and control processes characterized by being voluntary and highly effortful. These functions include the ability to evaluate, organize, and reach goals as well as the capacity to flexibly adapt behavior when confronted with novel problems and situations. Selective and executive attention, cognitive control, and working memory have been considered as some of the main higher cognitive functions, with developmental improvements in these abilities promoting concurrent improvements in other cognitive domains.

Research evidence from developmental cognitive neuroscience has consistently linked improvements on these executive functions with prefrontal cortex (PFC) maturation. However, the PFC does not function alone. Improvements on higher cognitive functions from childhood to adulthood reflect the integration of complex, widely distributed brain systems that are subject to structural and functional changes over development (Fair et al., 2009; Lebel, Walker, Leemans, Phillips, & Beaulieu, 2008). In recent years, developmental scientists have begun to examine how brain *networks,* rather than merely isolated brain regions, develop over time. The ultimate goal of developmental cognitive neuroscientists is to characterize how the concerted effort of these networks gives rise, during development, to high-level human cognition functions.

In so doing, developmental cognitive neuroscientists are now drawing on multiple imaging methods and analytic approaches allowing for assessing cross-sectional differences and longitudinal changes over development in brain structure, function, and interactions between

structure and function. In the present chapter, we first review evidence of *neurodevelopmental changes in brain structure and function* derived from the use of these advanced neuroscientific tools, which have implications not only for the development of higher cognitive functions but also for other areas of research within developmental cognitive neuroscience. Second, we highlight the main neuroimaging evidence on the *development of working memory and cognitive control processes,* which implicates a number of neural mechanisms and brain networks. Third, we review behavioral and neuroimaging research on the *development of memory encoding and retrieval processes*, including *mnemonic control*. Finally, we summarize important current and future directions in the study of the neurocognitive mechanisms supporting the development of higher cognitive functions, underscoring the importance of multidisciplinary approaches, different levels of analysis, and longitudinal designs to shed further light on the emergence and trajectories of these functions over development.

Neurodevelopmental Changes in Brain Structure and Function

To date, developmental cognitive neuroscience research has focused on regional and network changes in *structure* and *function*, which are strong candidates for determining behavioral improvements in higher cognitive functions observed during childhood and adolescence. These domains of investigation are briefly reviewed below.

Cortical Thinning

Thanks to the development of powerful analytic tools for measuring longitudinal changes in brain structure, we now have detailed information about within-person changes in cortical thickness over development (e.g., Gogtay & Thompson, 2010; Tamnes et al., 2010). These data reveal piecemeal cortical thinning over childhood and adolescence, with association cortices—including but not limited to PFC—maturing later than primary sensory cortices. Within PFC,

medial and ventral regions mature earlier than the dorsolateral PFC (dlPFC), which matures steadily during the adolescent and postadolescence (e.g., Shaw et al., 2008).

There are several important caveats related to this research. First, these developmental changes are not yet understood at the cellular level. Cortical thinning is likely to reflect multiple changes at the cellular level, including decreased gray matter due to synaptic pruning and increased white matter as a result of myelination and/or increased axon diameter (Giedd, 2008; Tamnes et al., 2010). Indeed, recent structural MRI analyses by Gotgay and Thompson (2010) and Hua et al. (2009) suggest that there is white matter growth underlying areas of thinning gray matter.

Second, the functional significance of these changes in cortical thickness is not yet clear, in most cases (e.g., Lu et al., 2009). It is possible to find evidence for positive and/or negative relationships between cortical thickness and cognitive performance. Further complicating the story, these brain-behavior relationships can be influenced by age, sex (Christakou et al., 2009; Lenroot & Giedd, 2010), and cognitive aptitude (Karama et al., 2009). However, structural equation modeling has been used successfully to assess the contributions of changing structure to changing function. For example, one combined structural and functional MRI study has reported increased functional specificity in a region in lateral PFC (lPFC) over childhood and adolescence; it has shown that this change cannot be explained by cortical thinning in this region but *can* be explained—in small part—by cortical thinning in a functionally connected region in the parietal cortex (Wendelken, O'Hare, Whitaker, Ferrer, & Bunge, 2011). These results suggest that increased neural efficiency within the parietal cortex, mediated by synaptic pruning and/or myelination, reduces the demands on the affiliated PFC region.

Regional Changes in Function

Developmental functional MRI studies on executive control typically show that the core regions of a circuitry underlying specific functions are in place early in development (e.g., Luna, Padmanabhan, & O'Hearn, 2010). Nevertheless, important refinements in the recruitment patterns and functional specialization of regions associated with executive control functioning occur across middle childhood and adolescence years. For instance, research evidence on response inhibition has revealed age-related increases in the activation of the inferior frontal gyrus and premotor regions across different tasks (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Marsh et al., 2006; Rubia et al., 2006). In contrast, some of these and other studies on inhibitory control also showed age-related decreases in the recruitment of middle/superior frontal gyrus regions. Decreases with age in the activation of a relevant region within a circuitry are thought to reflect a reduced effort in executing a specific cognitive process relevant for the task (e.g., Tamm, Menon, & Reiss, 2002).

Developmental cognitive neuroscience has also underscored substantial changes in the patterns of activation between relevant brain regions underlying the performance of executive functions. For instance, Luna et al.'s (2001) study on response inhibition revealed that adolescents exhibited an increased recruitment of dlPFC relative to adults and middle childhood children, suggesting that the engagement of additional PFC regions allow to achieve an adultlike behavioral performance pattern in developmental groups still subjected to further refinements in brain functioning. Similarly, parallel to the important changes in prefrontal function over development, research evidence on PFC-dependent tasks has consistently shown age-related changes in widespread activation of regions outside the PFC, including parietal, temporal, subcortical, and cerebellar regions. These age-related changes in regional patterns of activation on higher cognitive functioning are influenced by developmental trajectories in long-range

connections, which become more consistent during late middle childhood and adolescence and are associated with more effective neural processing (Bunge et al., 2002; Crone, Wendelken, Donohue, van Leijenhorst, & Bunge, 2006; Rubia et al., 2006; Velanova, Wheeler, & Luna, 2008).

Despite the relevant contributions made by functional magnetic resonance imaging (fMRI) studies over the last years in our understanding of age-related changes in the neural processes underlying higher cognitive functions, there are still important challenges to be addressed in terms of neuroimaging data interpretation and analytic methods. First, in fMRI studies the dependent measure is the blood oxygen level dependent (BOLD) response, and it is not yet well established yet what differences in BOLD response mean in the context of development. The BOLD response is the microvascular response in blood flow resulting from fluctuations in the metabolic needs of a population of neurons as they become involved in a task (Luna et al., 2010). Maturational changes in brain structure, including myelination and synaptic pruning and plasticity, as well as hormonal changes and refinements in neurotransmitter processing, may all contribute to the observed differences in BOLD response over development (e.g., Bunge et al., 2005; Geier & Luna, 2009).

Second, developmental changes in function supporting similar levels of performance can indicate that the younger groups are exerting a greater effort, that compensatory neural processes are implemented due to limitations in accessing the adult circuitry, or that different strategies are engaged by the different age groups (Luna et al., 2010). Further developmental research specifically aimed at disentangling these interpretation issues is strongly needed in the study of the development of higher cognitive functions.

Third, together with the necessary increase in methodological rigor in functional MRI studies (e.g., corrections for multiple comparisons) (Bennett, Wolford, & Miller, 2009), the use of more robust analytic methods will allow the field to move beyond the prevailing focus on localization of function (Poldrack, 2012). Connectivity modeling (e.g., Smith et al., 2011), multivariate analytical approaches (e.g., Kriegeskorte, Goebel, & Bandettini, 2006), combining neurophysiology and fMRI (e.g., David et al., 2008), or multimodal imaging techniques (e.g., Supekar et al., 2010) are some of the advanced methods that can substantially contribute to a better understanding of the relation between the development of cognitive processes and brain function.

Strengthening of White Matter Pathways

Diffusion tensor imaging (DTI) provides an indirect measure of white matter tracts in vivo in the human brain (Fields, 2008). A recent postmortem study has validated DTI probabilistic tractography of a specific neural pathway with tissue samples of the medial temporal lobes (MTL) (Augustinack et al., 2010). The development of DTI has made it possible to measure within-individual changes in white matter tracts over development and their relationship to changes in cognition. In a longitudinal study, Giorgio and colleagues (2010) have shown that white matter volume increases over development, likely due to increasing axon diameters within developing tracts. Thus far, however, most developmental DTI research has been cross-sectional, comparing participants of different ages. Lebel and colleagues (2008) have published a large cross-sectional DTI dataset characterizing the developmental trajectories of a number of important white matter tracts (Lebel et al., 2008). Although white matter maturation takes place throughout the brain, it is possible to link cognitive performance to the strength of specific tracts

(Johansen-Berg, 2010; Madsen et al., 2010; Niogi, Mukherjee, Ghajar, & McCandliss, 2010; Olson et al., 2009).

We have learned a lot over the last few years about the typical developmental trajectory of cortical thickness and white matter tracts. However, we still know very little about how these changes relate to developmental changes or individual differences in brain function or behavior. Recently, Niogi et al. (2010) have provided evidence of a triple dissociation in the brain-behavior relationships of the integrity (fractional anisotropy, or FA) of three white matter tracts to the three attention components identified with the Attention Network Task (ANT): alerting, orienting, and executive attention (specifically, conflict resolution; see Figure 1). Consistent with previous functional imaging evidence indicating that these components of attention are subserved by dissociable networks, this study revealed structure–function positive correlations between alerting and the anterior limb of the internal capsule, orienting and the splenium of the corpus callosum, and conflict resolution and the anterior corona radiata. Thus it is clear that the examination of changes in white matter integrity holds great promise to further characterize the developmental trajectories of the pathways connecting distributed cortical regions and their relationship to the development of higher cognitive functions.

- Insert Figure 1 around here -

Developmental Changes in Functional Networks

While techniques like DTI help us to characterize the development of white matter tracts, research on patterns of correlated brain activation provide a complementary picture of developing cortical networks. Functional connectivity analyses identify regions with strongly correlated patterns of BOLD activation over time, either during performance of a cognitive task

or at rest. Brain regions that are not directly connected to one another via white matter tracts may nonetheless act in concert as part of a distributed network. Conversely, two brain regions that are anatomically connected may not yet be fully integrated into a shared network (Biswal et al., 2010). Therefore a promising approach is to integrate these complementary measures of brain connectivity (Rykhlevskaia, Gratton, & Fabiani, 2008). Over the last few years there have been a number of studies characterizing changes in network connectivity in typically and atypically developing populations (Cao et al., 2009; Church et al., 2009; Fan et al., 2011; Gao et al., 2009; Superkar et al., 2010; Thomason et al., 2008; see Stevens, 2009, for a review).

One of the central developmental findings in recent functional connectivity work is the progression from short-range connections within cortical areas to longer-range cortico-cortico connections (Church et al., 2009; Fair et al., 2009; Jolles, van Buchem, Crone, & Rombouts, 2011; Stevens, Pearlson, & Calhoun, 2009). As children grow older, short-range functional connections become weaker and long-range connections strengthen (Figure 2). At first, the distributed network comprises many weak connections, but as children move into adolescence and adulthood, functional connections tend to become stronger but sparser, reflecting the increasing specificity of emerging functional networks (Fair et al., 2009; Superkar et al., 2010). Indeed, Schlaggar, Petersen, and colleagues have shown that it is possible to predict the age of an individual within 2 years based purely on the patterns of functional connectivity measured in a resting-state fMRI scan using vector machine-based multivariate pattern analysis based (Dosenbach et al., 2010). Thus functional connectivity measures strongly correlate with age, providing a plausible snapshot of the changes in the state of brain networks across childhood and adolescence.

Insert Figure 2 around here –

Each of these measures provides a complementary perspective on brain development. Any one measure considered in isolation, such as cortical thickness (Lenroot & Giedd, 2010), regional changes in brain function (Crone et al., 2006), white matter integrity (Lebel et al., 2008), or functional connectivity (Dosenbach et al., 2010) can provide only an incomplete view of brain maturation.

Relationships Between Structural and Functional Brain Changes over Development

Task-related adjustments of regional gray matter function are determined by the properties of anatomical connections between relevant cortical regions (e.g., Burzynska et al., 2011). In fact, the differences between children and adults in patterns of functional connectivity are consistent with the trajectories of gray and white matter development. At the same time that local functional connections within the cortex are weakening, cortical gray matter is thinning—and, as long-range white matter tracts are getting stronger, so is long-range functional connectivity. Supekar et al. (2010) found that only some of the changes in functional connectivity had obvious anatomical correlates. For example, children, who exhibited significantly lower functional connectivity between the posterior cingulate cortex and medial PFC than young adults, also displayed higher gray matter volume and lower white matter density in these regions relative to young adults. On the other hand, while children and adults displayed equally strong functional connectivity between the posterior cingulate cortex and the left MTL, children exhibited weak direct anatomical connectivity between these two regions as measured by DTI. Such findings support the view that these structural and functional measures provide valuable and complementary views of brain development.

Development of Higher Cognition: Working Memory and Cognitive Control

Long-range connections support developmental achievements in higher cognitive functions, such as working memory and cognitive control. Notwithstanding conceptual differences, a general consensus holds regarding working memory and cognitive control as some of the canonical higher cognitive functions in most cognitive developmental theories. *Working memory* refers to the ability to maintain, attend to, and update information that is currently relevant and available online for evaluation and manipulation (Baddeley, 1998). *Cognitive control* refers to a set of mental processes responsible for executing, guiding, and monitoring goal-directed behaviors while inhibiting inappropriate or disadvantageous ones (Braver, Paxton, Locke, & Barch, 2009).

Neuroimaging evidence has shown that frontoparietal circuits implicated in simple *working memory* tasks are already established by middle childhood (e.g., Geier, Garver, Terwilliger, & Luna, 2009; Scherf, Sweeney, & Luna, 2006). Nevertheless, compared with adults, older children and adolescents recruit a more extensive distributed frontoparietal circuitry during working memory maintenance (Geier et al., 2009; Klingberg, 2006) and fail to effectively recruit frontoparietal regions during their performance on more challenging working memory tasks, such as those requiring online manipulation of information (Crone et al., 2006) or maintaining attention on the task by ignoring irrelevant information (Olesen, Macoveanu, Tegner, & Klingberg, 2007). Thus maturation of the neural circuits supporting working memory processes is characterized by a more consistent recruitment of cortical regions and a refinement in the long-range frontoparietal network connecting these cortical regions.

The cognitive processes of response inhibition, attentional regulation, and the monitoring of conflict and error are engaged in the service of *cognitive control*. In adults, cognitive control

relies on broad cortical areas, including the anterior cingulate cortex, dlPFC, and ventrolateral PFC (vlPFC)/lateral orbitofrontal cortex as well as temporal and parietal regions, all of which have connections with the striatum (e.g., Rubia et al., 2006). The striatum contains several subcortical structures implicated in cognitive control, receives major projections from the main dopaminergic and serotonergic complexes, and it is heavily connected with the thalamus and PFC in neuroanatomical cascading series of serial and parallel circuitries (Haber, Fudge, & McFarland, 2000). Performance on tasks that require suppression of an automatic behavior to perform a less automatic one—such as the Go/No-Go, Stop-Signal, Stroop, and Simon tasks—does not approach adult levels until late childhood or early adolescence (Davidson, Amso, Anderson, & Diamond, 2006). Evidence from developmental neuroimaging studies suggest that behavioral improvements on cognitive control with age are associated with increasing activation of frontostriatal circuits (Marsh et al., 2006), with a shift from diffuse to focal activation and from posterior to anterior activation (Durston et al., 2006; Rubia et al., 2006). Moreover, dysregulation or immature frontostriatal control systems has been documented in children, adolescents, and adults with disorders related to inhibitory control, such as Tourette's syndrome, Obsessive Compulsive Disorder, and eating disorders (see Marsh, Maia, & Peterson, 2009, for a review); as well as in risk-taking behavior in adolescence paired with increased sensitivity to rewards (Somerville, Hare, & Casey, 2011; van Leijenhorst et al., 2010).

Development of Episodic Memory and Mnemonic Control

To evaluate, organize, and adapt behavior and thoughts to reach goals often requires cognitive control mechanisms that permit the codification and use of accessible relevant information while ignoring irrelevant information. The term *mnemonic control* refers to a set of control processes

that, central to higher cognition and key to multiple cognitive operations, determine how relevant information is encoded and retrieved from memory.

Developmental research has revealed strong improvements from early childhood to adolescence in the ability to encode relevant information and to limit interference from irrelevant information (Kail, 2002; Schneider & Pressley, 1997). These developmental achievements are related to control processes at encoding, such as efficient engagement of selective attention to relevant information and elaborative encoding processes leading to a better organization of information in memory (Bauer, 2006). Improvement in memory retrieval processes, including more effective monitoring of the accessed information and better strategic regulation of hippocampal-dependent operations, are usually characterized as showing a slightly more protracted developmental trajectory, especially during the early and middle childhood years.

In behavioral research, however, it is difficult to tease apart the contribution of specific encoding and retrieval processes because dependent measures are obtained principally at retrieval (Bauer, 2006; Ghetti & Bauer, 2012. In contrast, with neuroimaging techniques, it is possible to measure brain activation at these specific memory stages separately. Thus developmental neuroscientific research holds much promise for a comprehensive theory of memory and its development, allowing us to characterize the neural basis of memory-related processes and to extant previous evidence from behavioral research in elucidating age-related improvements on mnemonic processes at both encoding and retrieval. Below we describe behavioral research and recent fMRI studies examining age-related changes in activation at encoding and retrieval.

Development of Memory Encoding Processes

Developmental research combining behavioral and electrophysiological measures has underscored that age-related changes in episodic memory during early childhood are especially attributable to developmental improvements in encoding and consolidation processes (Bauer, 2006). For instance, increases in short-term memory span are evident during early childhood and continue during middle childhood years, indicating that children become increasingly more effective at keeping task-irrelevant information out of short-term memory (Bauer, 2008; Oakes & Bauer, 2007). Also, with age there are increases in the use of rehearsal to maintain to-be-remembered information over time, reflecting a more organized processing of relevant information (e.g., Bjorklund, Dukes, & Brown, 2009; Schneider & Bjorklund, 1998). During middle childhood, children also become increasingly efficient at encoding verbal information, exhibiting gains in remembering verbatim forms, and extracting gist information (Brainerd, Holliday, & Reyna, 2004). For instance, Ghetti and Angelini's (2008) study underscored the role of elaborative processing during encoding, showing that age-related improvements in episodic recollection were observed only when children encoded content semantically. In contrast, episodic recollection did not differ as a function of age following perceptually encoded information.

Given these results, it is expected that brain regions supporting cognitive control are heavily involved in supporting memory encoding and retrieval either in isolation or in connection with other relevant regions. This evidence is reviewed next.

Increased PFC Engagement During Encoding over Childhood and Adolescence

Improvements in memory encoding are associated with age-related changes in the temporocortical network that subserves long-term memory. PFC and MTL regions interact

during encoding and, as a consequence, structural and functional age-related changes in both regions are likely to contribute to developmental changes in episodic memory. Recent neuroimaging evidence has showed increased activation and selective recruitment of vlPFC and dlPFC regions in encoding processes leading to successful memory formation during middle childhood and adolescence (Ghetti, DeMaster, Yonelinas, & Bunge, 2010; Ofen et al., 2007). Also, increases in the coupling between left dlPFC and left MTL regions during encoding has been observed from middle childhood to adolescence, suggesting that increased functional interactions between the PFC and MTL underlie the development of more effective memory encoding strategies (Menon, Boyett-Anderson, & Reiss, 2005).

Nevertheless, although the involvement of MTL regions in encoding processes across development is widely demonstrated, there is still debate in regard to developmental changes in the pattern of activations in this region during encoding processes. Recent evidence from a cortical pattern matching study examining maturational changes in cortical thickness between ages 4 and 25 revealed cortical thickness reductions in the anterior hippocampus over development, with concomitant increases in the posterior hippocampus (Gogtay et al., 2006). These findings support the idea that MTL regions do not mature as early as previously thought. Also, developmental fMRI studies have shown increasing functional specialization with age of hippocampus and the posterior parahippocampal gyrus for recollective details (Ghetti et al., 2010) and also of the posterior parahippocampal gyrus for scenes of high complexity (Chai, Ofen, Jacobs, & Gabrieli, 2010; but see Ofen et al., 2007).

Evidence for Neurodevelopmental Increases in Mnemonic Control over Encoding

Despite of the importance of the previously reported neurodevelopmental studies in elucidating the role of different MTL and PFC regions and their interactions during memory encoding, there is sparse neuroimaging research examining developmental changes in mnemonic control processes at encoding. A recent study by Wendelken, Baym, Gazzaley, and Bunge (2011) investigated age-related changes in selective attention processes associated with committing relevant information to memory while ignoring competing or irrelevant stimuli (Bjorklund & Harnishfeger, 1990).

Results from Wendelken et al.'s study revealed that top-down recruitment of the bilateral parahippocampal place area (PPA) increased from middle childhood to adolescence when participants specifically attended to scene stimuli. Moreover, while younger children appeared to differ markedly from young adults in terms of their capacity to modulate the recruitment of PPA, these differences have practically disappeared by age 14. Children's age-related increases in PPA enhancement were also matched by age-related increases in the selective activation for attention to scenes versus passive viewing of lateral dlPFC (Figure 3). These findings are consistent with previous evidence showing age-related increases in the selective activation of lPFC on cognitive control tasks (Crone et al., 2006; Konrad et al., 2005) and the role of dlPFC as a primary locus of top-down control (Gazzaley et al., 2007). Additional neuroimaging research on developmental trajectories in mnemonic control processes at encoding is needed to further characterize the neural mechanisms underlying the formation of relevant memories for goal-directed thought and behavior.

- Insert Figure 3 around here –

Development of Control and Monitoring Processes over Retrieval

The development of retrieval processes can largely contribute to age-related changes in episodic memory performance observed across childhood and adolescence. Overall, there is extensive behavioral evidence showing age-related improvements during middle childhood in the ability to use cues flexibly in aiding retrieval (Ashcraft, Kellas, & Keller, 1976; Emmerich & Ackerman, 1978). Even assuming that relevant information is successfully encoded and stored across ages as compared with older children and adults, younger children are more heavily dependent of the cues presented in the original context to reinstate encoded information (Ackerman, 1982). Moreover, there is evidence showing that the detrimental effects on memory performance resulting from changing cues between encoding and retrieval decrease from middle childhood to adulthood, even for materials that, after encoding, have been repeatedly reinforced in association with their original cues (Paz-Alonso, Ghetti, Matlen, Anderson, & Bunge, 2009).

Similarly, developmental changes in the ability to use strategies and reasoning processes during retrieval may also explain the age-related improvements typically observed in episodic memory during the school years. For instance, clustering to-be-remembered information as a function of semantic categories during free recall is a helpful strategy that, relying on a knowledge base about the world, improves across the childhood years and correlates positively with metamemory skills (Hasselhorn, 1990; Schneider & Pressley, 1997). In fact, together with age-related improvements in the ability to flexibly use different type of cues and strategies to aid memory retrieval, the development of metamemory abilities has an important impact on the final memory output, allowing individuals to monitor the accuracy of the retrieved information (e.g., Ghetti, 2008; Ghetti, Lyons, Lazzarin, & Cornoldi, 2008) and to evaluate accessible contextual information to locate memories as a function of place and time (Johnson, Hashtroudi, & Lindsay, 1993; Mitchell & Johnson, 2009).

Neurodevelopmental Correlates of Memory Retrieval Processes

Developmental achievements in episodic memory retrieval are frequently described as PFC-dependent strategic processes and, as a consequence, have been linked to PFC maturation (Nelson, 1997; Schwenck, Bjorklund, & Schneider, 2009). Cognitive neuroscience research with adults has underscored the role of lPFC in episodic memory retrieval, with vlPFC being implicated in processing item-related cues across different representational domains (e.g., Badre & Wagner, 2007) and dlPFC aiding monitoring and response selection processes (e.g., Ranganath, Heller, & Wilding, 2007).

We have also shown differentiated patterns of activation with age in vlPFC and dlPFC retrieval, reflecting, respectively, the development of semantic elaboration processes and decision operations during memory retrieval (Paz-Alonso, Ghetti, Donohue, Goodman, & Bunge, 2008). Together with evidence indicating that developmental changes in PFC cortical thickness occur throughout childhood and adolescence (Gogtay & Thompson, 2010; Tamnes et al., 2010), these findings support the hypothesis that the structural and functional development of the PFC mediates the development of episodic memory retrieval.

Developmental Changes in Mnemonic Control over Retrieval

Sometimes it is possible to suppress the process of memory retrieval, which allows us to focus on goal-relevant memories and to limit the influence of interfering information. Evidence from previous behavioral research using directed-forgetting paradigms has suggested increases in memory inhibitory control during the middle childhood years (Sahakyan & Kelley, 2002; Wilson & Kipp, 1998). However, directed-forgetting effects can be explained by alternative interpretations to mnemonic control over retrieval, including selective encoding and rehearsal of

the to-be-remembered items and contextual shifts (Paz-Alonso et al., 2009; Wilson & Kipp, 1998).

We have recently used the Think/No-Think (TNT) paradigm (Anderson & Green, 2001) to examine developmental changes in mnemonic control over retrieval. The TNT paradigm makes it possible to measure active online attempts to prevent and encoded memory to enter consciousness and their effects in long-term memory. Results from this study revealed age-related improvements in memory suppression (i.e., higher percent recalled for Baseline relative to No-Think items) over middle childhood (Figure 4). Moreover, improvements in memory suppression from ages 8 to 12 were observed against a backdrop of overall improvements in declarative memory for to-be-remembered items over this age range.

- Insert Figure 4 around here –

Several neuroimaging studies with adults using this paradigm have shown that lPFC modulates hippocampal activation during attempts to suppress memory retrieval (e.g., Anderson et al., 2004; Depue, Burgess, Willcutt, Ruzic, & Banich, 2010; Depue, Curran, & Banich, 2007). Thus it is likely that developmental improvements in the ability to stop memory retrieval are due to age-related refinements in the ability to engage specific lPFC regions or, complementarily, perhaps a larger mnemonic control network that modulates activation in MTL areas is involved in episodic retrieval. Moreover, the main anatomical fiber tracts that could support lPFC-MTL interactions are the cingulum bundle and the uncinate fasciculus (Figure 5A). Compared with other white matter tracts, these dorsal and ventral frontotemporal anatomical pathways have the most protracted maturation, reaching 90% of their development only after 25 years of age (Lebel et al., 2008; see Figure 5B & C). Current research is testing these hypotheses on the neural

mechanisms determining age-related changes in mnemonic control over retrieval in a large fMRI study including children aged 8 to 9 and 11 to 12 and also young adults (Paz-Alonso, Bunge, Anderson, & Ghetti, 2013).

- Insert Figure 5 around here -

Important Current and Future Directions in Developmental Cognitive Neuroscience

There is still much to be discovered regarding the neural mechanisms that support the emergence of higher cognitive functions over childhood and adolescence. An endeavor of this level of complexity necessitates a multidisciplinary approach with large research teams, large sample sizes, and data collection at multiple time points per individual. At the same time, it will be important in the coming years for developmental cognitive neuroscience to strike the right balance between high-throughput, data-driven research, or "discovery science" (Biswal et al., 2010) and hypothesis-driven research grounded in theories of cognitive development. Below we highlight several important areas for further research.

Cellular Basis Underlying Macroscopic Structural Changes Observed over Development

Before it was possible to measure brain function, anatomical research was the only recourse for a budding neuroscientist. As functional brain imaging techniques have surged, there has been a steady decline in well-trained neuroanatomists. The pendulum must swing back in the other direction if we are to understand the neural basis of developmental changes in brain function and behavior. Structural MRI imaging can provide astonishingly detailed images of the brain; used in

combination with sophisticated anatomical techniques in post mortem tissue (Augustinack et al., 2010), it is now possible to begin to explore the cellular underpinnings of macroscopic structural changes over development and how they determine higher cognitive functioning improvements over development.

Early Brain Development

Although most of the behavioral literature on cognitive development has focused on the period of rapid changes observed during early childhood, most of the developmental cognitive neuroscientific studies to date have, for practical reasons, focused on older children and adolescents (Poldrack, 2010). In recent years, researchers have refined pediatric imaging protocols (Nordahl et al., 2008; Raschle et al., 2009) that make it possible to obtain high-quality structural and functional MRI data from infants (Dehaene-Lambertz et al., 2010; Fan et al., 2011; Gao et al., 2009) and young children (Cantlon, Pinel, Dehaene, & Pelphrey, 2011). This advance makes it possible to measure the functional organization of the newborn brain and to examine the neural changes that support the emergence of new cognitive abilities over early childhood.

Longitudinal Research

To examine—and interrelate—developmental trajectories for cognition, brain structure, and brain function, it is necessary to acquire data at multiple time points per individual. Longitudinal research can provide important insights regarding typical and atypical cognitive development (Reichenberg et al., 2010). Although there are few published longitudinal MRI studies of children (Giedd et al., 2009; Gogtay & Thompson, 2010) and even fewer that include functional as well as structural measures (Fan et al., 2011; Shaw et al., 2009), a number of research groups are conducting this important work now. Longitudinal research in the field of developmental cognitive neuroscience holds much promise in identifying specific developmental trajectories of

higher cognitive functions from within-subjects changes in brain function and structure, allowing us to model complex patterns of interrelations between these measures (Shaw et al., 2006) as well as to evaluate their predictive value of individual's performance at a later time (Hoeft et al., 2007).

External Influences on Cognitive and Brain Development

An important next step in developmental cognitive neuroscience is the elucidation of genetic, physical, physiological, and environmental factors that interact during the development of higher cognitive functions. There has been research on gene × environmental influences on behavior during development (Wiebe et al., 2009). Until recently, this work has left the brain out of the equation, but developmental cognitive neuroscience is beginning to examine the influence of physical changes (e.g., pubertal hormone levels) on cognition and brain function (Blakemore, Burnett, & Dahl, 2010) and genetic and/or environmental influences on brain structure and function (Casey, Soliman, Bath, & Glatt, 2010; Chiang et al., 2009; Hackman & Farah, 2009; Lenroot et al., 2009; Thomason et al., 2010). For instance, certain allelic variants of serotonin- and dopamine-related genes are associated to attentional biases to emotional stimuli (e.g., SLC6A4; Thomason et al., 2010), attentional control, working memory performance, and stronger neural activation in the frontal regions (e.g., DRD4, COMT) (Bishop, Cohen, Fossella, Casey, & Farah, 2006; Fan, Fossella, Sommer, Yanghong, & Posner, 2003). Future research in behavioral and imaging genetics can strongly contribute to our understanding of the neurodevelopmental mechanisms involved in cognitive function and to develop therapeutic interventions for atypically developed children.

Acknowledgments

The authors thank Henna Mishra, Carter Wendelken, Kirstie Whitaker, Jessica Church, and Mario Bunge for contributions to the review. The authors were supported by consolider-ingenio 2010 (CSD2008-00048) and PSI2012-32093 grants from the Spanish Ministry of Economy and Competitiveness, and grant PI2012-15 from the Department of Education, University and Research from the Basque Government (P.M.P.-A.), a grant from the National Institute of Neurological Disorders and Stroke (S.G., S.B.), and the James S. McDonnell Foundation (S.B., S.G.).

References

Ackerman, B. P. (1982). Retrieval variability: The inefficient use of retrieval cues by young children. *Journal of Experimental Child Psychology, 33*, 413–428.

Anderson, M. C., & Green, C. (2001). Suppressing unwanted memories by executive control. *Nature, 410*, 366–369.

Anderson, M. C., Ochsner, K. N., Kuhl, B., Cooper, J., Robertson, E., Gabrieli, S. W., . . . Gabrieli, J. D. (2004). Neural systems underlying the suppression of unwanted memories. *Science, 303*, 232–235.

Ashcraft, N. H., Kellas, G., & Keller, D. (1976). Retrieval processes in fifth graders and adults. *Journal of Experimental Child Psychology, 21*, 264–276.

Augustinack, J. C., Helmer, K., Huber, K. E., Kakunoori, S., Zöllei, L., & Fischl, B. (2010). Direct visualization of the perforant pathway in the human brain with ex vivo diffusion tensor imaging. *Frontiers in Human Neuroscience, 4*, 42, 1–13.

Baddeley, A. (1998). Recent developments in working memory. *Current Opinion in Neurobiology, 8*, 234–238.

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia, 45*, 2883–2901.

Bauer, P. J. (2006). Constructing a past in infancy: A neuro-developmental account. *Trends in Cognitive Neuroscience, 10*, 175–181.

Bauer, P. J. (2008). Toward a neuro-developmental account of the development of declarative memory. *Developmental Psychobiology, 50*, 19–31.

Bennett, C. M., Wolford, G. L., & Miller, M. B. (2009). The principled control of false positives in neuroimaging. *Social Cognitive & Affective Neuroscience, 4*, 417–422.

Bishop, S.J, Cohen, J. D., Fossella, J., Casey, B. J., & Farah, M. J. (2006). COMT genotype influences prefrontal response to emotional distraction. *Cognitive, Affective, & Behavioral Neuroscience, 6*, 62–70.

Biswal, B. B., Mennes, M., Zuo, X. N., Gohel, S., Kelly, C., Smith, S. M., . . . Milham, M. P. (2010). Toward discovery science of human brain function. *Proceedings of the National Academy of Science USA, 107*, 4734–4739.

Bjorklund, D. F., Dukes, C., & Brown, R. D. (2009). The development of memory strategies. In M. Courage and N. Cowan (Eds.), *The development of memory in childhood* (2nd edition), *Studies in developmental psychology* (pp. 145–175). New York: Psychology Press.

Bjorklund, D., & Harnishfeger, K. (1990). The resource construct in cognitive development: Diverse sources of evidence and a theory of inefficient inhibition. *Developmental Review, 10*, 48–71.

Blakemore, S. J., Burnett, S., & Dahl, R. E. (2010). The role of puberty in the developing adolescent brain. *Human Brain Mapping, 31*, 926–933.

Brainerd, C. J., Holliday, R. E., & Reyna, V. F. (2004). Behavioral measurement of remembering phenomenologies: So simple a child can do it. *Child Development 75*, 505–522.

Braver, T. S., Paxton, J. L., Locke, H. S., & Barch, D. M. (2009). Flexible neural mechanisms of cognitive control within human prefrontal cortex. *Proceedings of the National Academy of Sciences USA, 106*, 7351–7356.

Bunge, S. A., Dudukovic, N. M., Thomason, M. E., Vaidya, C. J., & Gabrieli, J. D. (2002). Immature frontal lobe contributions to cognitive control in children: Evidence from fMRI. *Neuron, 33*, 301–311.

Bunge, S. A., Wallis, J. D., Parker, A., Brass, M., Crone, E. A., Hoshi, E., & Sakai, K. (2005). Neural circuitry underlying rule use in humans and nonhuman primates. *Journal of Neuroscience, 25*, 10347–10350.

Burzynska, A. Z., Nagel, I. E., Preuschhof, C., Li, S. C., Lindenberger, U., Bäckman, L., Heekeren, H. R. (2011). Microstructure of frontoparietal connections predicts cortical responsivity and working memory performance. *Cerebral Cortex, 21*, 2261–2271.

Cantlon, J. F., Pinel, P., Dehaene, S., & Pelphrey, K. A. (2011). Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cerebral Cortex, 21*, 191–199.

Cao, X., Cao, Q., Long, X., Sun, L., Sui, M., Zhu, C., . . . Wang, Y. (2009). Abnormal resting-state functional connectivity patterns of the putamen in medication-naive children with attention deficit hyperactivity disorder. *Brain Research, 1303*, 195–206.

Casey, B. J., Soliman, F., Bath, K. G., & Glatt, C. E. (2010). Imaging genetics and development: Challenges and promises. *Human Brain Mapping, 31*, 838–851

Chai, X. J., Ofen, N., Jacobs, L. F., & Gabrieli, J. D. E. (2010). Scene complexity: Influence on perception, memory, and development in the medial temporal lobe. *Frontiers in Human Neuroscience, 4*, 21, 1–10.

Chiang, M. C., Barysheva, M., Shattuck, D. W., Lee, A. D., Madsen, S. K., Avedissian, C., . . . Thompson, P. M. (2009). Genetics of brain fiber architecture and intellectual performance. *Journal of Neuroscience, 29*, 2212–2224.

Christakou, A., Halari, R., Smith, A. B., Ifkovits, E., Brammer, M., & Rubia, K. (2009). Sex-dependent age modulation of frontostriatal and temporo-parietal activation during cognitive control. *Neuroimage, 48*, 223–236.

Church, J. A., Fair, D. A., Dosenbach, N. U., Cohen, A. L., Miezin, F. M., Petersen, S. E., & Schlaggar, B. L. (2009). Control networks in paediatric Tourette syndrome show immature and anomalous patterns of functional connectivity. *Brain, 132*, 225–238.

Crone, E., Wendelken, C., Donohue, S., van Leijenhorst, L., & Bunge, S. A. (2006). Neurocognitive development of the ability to manipulate information in working memory. *Proceedings of the National Academy of Sciences USA, 103*, 9315–9320.

David, O., Guillemain, I., Saillet, S., Reyt, S., Deransart, C., Segebarth, C., & Depaulis, A. (2008). Identifying neural drivers with functional MRI: An electrophysiological validation. *PLoS Biology, 6*, 2683–2697.

Davidson, M. C., Amso, D., Anderson, L. C., & Diamond, A. (2006). Development of cognitive control and executive functions from 4 to 13 years: Evidence from manipulations of memory, inhibition, and task switching. *Neuropsychologia, 44*, 2037–2078.

Dehaene-Lambertz, G., Montavont, A., Jobert, A., Allirol, L., Dubois, J., Hertz-Pannier, L., & Dehaene, S. (2010). Language or music, mother or Mozart? Structural and environmental influences on infants' language networks. *Brain and Language, 114*, 53–65.

Depue, B. E., Burgess, G. C., Willcutt, E. G., Ruzic, L., & Banich, M. T. (2010). Inhibitory control of memory retrieval and motor processing associated with the right lateral prefrontal cortex: Evidence from deficits in individuals with ADHD. *Neuropsychologia, 48*, 3909–3917.

Depue, B. E., Curran, T., & Banich, M. T. (2007). Prefrontal regions orchestrate suppression of emotional memories via a two-phase process. *Science, 37*, 215–219.

Dosenbach, N. U., Nardos, B., Cohen, A. L., Fair, D. A., Power, J. D., Church, J. A., . . . Schlaggar, B. L. (2010). Prediction of individual brain maturity using fMRI. *Science, 329*, 1358–1361.

Durston, S., Davidson, M. C., Tottenham, N., Galvan, A., Spicer, J., Fossella, J. A., & Casey, B. J. (2006). A shift from diffuse to focal cortical activity with development. *Developmental Science, 9*, 1–8.

Emmerich, H. J., & Ackerman, B. P. (1978). Developmental differences in recall: Encoding or retrieval? *Journal of Experimental Child Psychology, 25*, 514–525.

Fair, D. A., Cohen, A. L., Power, J. D., Dosenbach, N. U., Church, J. A., Miezin, F. M., . . . Petersen, S. E. (2009). Functional brain networks develop from a "local to distributed" organization. *PLoS Computational Biology, 5*, e1000381.

Fan J, Fossella J, Sommer T, Yanghong, W., & Posner (2003). Mapping the genetic variation of executive attention onto brain activity. *Proceeding of the National Academy of Science USA*, 100, 7406–7411.

Fan, Y., Shi, F., Smith, J. K., Lin, W., Gilmore, J. H., & Shen, D. (2011). Brain anatomical networks in early human brain development. *Neuroimage, 54*, 1862–1871.

Fields, R. D. (2008). White matter in learning, cognition and psychiatric disorders. *Trends in Neuroscience, 31*, 361–370.

Gao, W., Zhu, H., Giovanello, K. S., Smith, J. K., Shen, D., Gilmore, J. H., & Lin, W. (2009). Evidence on the emergence of the brain's default network from 2-week-old to 2-year-old healthy pediatric subjects. *Proceeding of the National Academy of Science USA, 106*, 6790–6795.

Gazzaley, A., Rissman, J., Cooney, J., Rutman, A., Seibert, T., Clapp, W., & D'Esposito, M. (2007). Functional interactions between prefrontal and visual association cortex contribute to top-down modulation of visual processing. *Cerebral Cortex, Suppl. 1*, i125-i135.

Geier, C. F., Garver, K., Terwilliger, R., & Luna, B. (2009). Development of working memory maintenance. *Journal of Neurophysiology, 101*, 84–99.

Geier, C., & Luna, B. (2009). The maturation of incentive processing and cognitive control. *Pharmacology, Biochemistry and Behavior, 93*, 212–221.

Ghetti, S. (2008). Rejection of false events in childhood: A metamemory account. *Current Directions in Psychological Science, 17*, 16–20.

Ghetti, S., & Angelini, L. (2008). The development of recollection and familiarity in childhood and adolescence: Evidence from the dual-process signal detection model. *Child Development, 79*, 339–358.

Ghetti, S. & Bauer, P. J. (2012). *Origins and development of recollection: Perspectives from psychology and neuroscience.* New York: Oxford University Press.

Ghetti, S., DeMaster, D. M., Yonelinas, A. P., & Bunge, S. A. (2010). Developmental differences in medial temporal lobe function during memory encoding. *Journal of Neuroscience, 30,* 9548–9556.

Ghetti, S., Lyons, K. E., Lazzarin, F., & Cornoldi, C. (2008). The development of metamemory monitoring during retrieval: The case of memory strength and memory absence. *Journal of Experimental Child Psychology, 99,* 157–181.

Giedd, J. N. (2008). The teen brain: Insights from neuroimaging. *Journal of Adolescent Health 42*, 335–343.

Giedd, J. N., Lalonde, F. M., Celano, M. J., White, S. L., Wallace, G. L., Lee, N. R., & Lenroot, R. K. (2009). Anatomical brain magnetic resonance imaging of typically developing children and adolescents. *Journal of the American Academy of Child Adolescent Psychiatry, 48,* 465–470.

Giorgio, A., Watkins, K. E., Chadwick, M., James, S., Winmill, L., Douaud, G., . . . James, A. C. (2010). Longitudinal changes in grey and white matter during adolescence. *Neuroimage, 49*, 94–103.

Gogtay, N., Nugent, T. F., Herman, D. H., Ordonez, A., Greenstein, D., Hayashi, K. M., . . . Thompson, P. M. (2006). Dynamic mapping of normal human hippocampal development. *Hippocampus, 16,* 664–672.

Gogtay, N., & Thompson, P. M. (2010). Mapping gray matter development: Implications for typical development and vulnerability to psychopathology. *Brain and Cognition, 72*, 6–15.

Haber, S. N., Fudge J. L., & McFarland, N.R. (2000). Striatonigrostriatal pathways in primates form an ascending spiral from the shell to the dorsolateral striatum. *Journal of Neuroscience, 20,* 2369–2382.

Hackman, D. A., & Farah, M. J. (2009). Socioeconomic status and the developing brain. *Trends in Cognitive Science, 13,* 65–73.

Hasselhorn, M. (1990). The emergence of strategic knowledge activation in categorical clustering during retrieval. *Journal of Experimental Child Psychology, 50,* 59–80.

Hoeft, F., Ueno, T., Reiss, A. L., Meyler, A., Whitfield-Gabrieli, S., Glover, G. H., . . . Gabrieli, J. D. (2007). Prediction of children's reading skills using behavioral, functional, and structural neuroimaging measures. *Behavioral Neuroscience. 121,* 602–613.

Hua, X., Leow, A. D., Levitt, J. G., Caplan, R., Thompson, P. M., & Toga, A. W. (2009). Detecting brain growth patterns in normal children using tensor-based morphometry. *Human Brain Mapping, 30,* 209–219.

Johansen-Berg, H. (2010). Behavioural relevance of variation in white matter microstructure. *Current Opinion in Neurology, 23,* 351–358

Johnson, M. K., Hashtroudi, S., & Lindsay, D. S. (1993). Source monitoring. *Psychological Bulletin, 114,* 3–28.

Jolles, D. D., van Buchem, M. A., Crone, E. A., & Rombouts, S. A. (2011). A comprehensive study of whole-brain functional connectivity in children and young adults. *Cerebral Cortex, 21,* 385–391.

Kail, R. (2002). Developmental change in proactive interference. *Child Development, 73,* 1703–1714.

Karama, S., Ad-Dab'bagh, Y., Haier, R.J., Deary, I. J., Lyttelton, O. C., Lepage, C., . . . Brain Development Cooperative Group (2009). Positive association between cognitive ability and cortical thickness in a representative US sample of healthy 6 to 18 year-olds. *Intelligence, 37*, 145–155.

Klingberg, T. (2006). Development of a superior frontal-intraparietal network for visuo-spatial working memory. *Neuropsychologia, 44*, 2171–2177.

Konrad, K., Neufang, S., Thiel, C. M., Specht, K., Hanisch, C., Fan, J., . . . Fink, G. R. (2005). Development of attentional networks: An fMRI study with children and adults. *Neuroimage 28*, 429–439.

Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Science USA, 103*, 3863–3868.

Lebel, C., Walker, L., Leemans, A., Phillips, L., & Beaulieu, C. (2008). Microstructural maturation of the human brain from childhood to adulthood. *Neuroimage, 40,* 1044–1055.

Lenroot, R. K., & Giedd, J. N. (2010). Sex differences in the adolescent brain. *Brain and Cognition, 72*, 46–55.

Lenroot, R. K., Schmitt, J. E., Ordaz, S. J., Wallace, G.L., Neale, M. C., Lerch, J. P., . . . Giedd, J. N. (2009). Differences in genetic and environmental influences on the human cerebral cortex associated with development during childhood and adolescence. *Human Brain Mapping, 30*, 163–174.

Lu, L. H., Dapretto, M., O'Hare, E.D., Kan, E., McCourt, S. T., Thompson, P. M., . . . Sowell, E. R. (2009). Relationships between brain activation and brain structure in normally developing children. *Cerebral Cortex, 19*, 2595–2604.

Luna, B., Padmanabhan, A., & O'Hearn, K. (2010). What has fMRI told us about the development of cognitive control through adolescence? *Brain and Cognition, 72,* 101–113.

Luna, B., Thulborn, K. R., Munoz, D. P., Merriam, E. P., Garver, K. E., Minshew, N. J., . . . Sweeney, J. A. (2001). Maturation of widely distributed brain function subserves cognitive development. *Neuroimage, 13,* 786–793.

Madsen, K. S., Baaré, W. F., Vestergaard, M., Skimminge, A., Ejersbo, L. R., Ramsøy, T. Z., . . . Jernigan, T. L. (2010). Response inhibition is associated with white matter microstructure in children. *Neuropsychologia, 48,* 854–862.

Marsh, R., Maia, T. V., & Peterson, B. S. (2009). Functional disturbances within frontostriatal circuits across multiple childhood psychopathologies. *American Journal of Psychiatry, 166,* 664–674.

Marsh, R., Zhu, H., Schultz, R. T., Quackenbush, G., Royal, J., Skudlarski, P., & Peterson, B. S. (2006). A developmental fMRI study of self-regulatory control. *Human Brain Mapping, 27,* 848–863.

Menon, V., Boyett-Anderson, J. M., & Reiss, A. L. (2005). Maturation of medial temporal lobe response and connectivity during memory encoding. *Cognitive Brain Research, 25,* 379–385.

Mitchell, K. J., & Johnson, M. K. (2009). Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory? *Psychological Bulletin, 135,* 638–677.

Nelson, C. A. (1997). The neurobiological basis of early memory development. In N. Cowan (Ed.), *The development of memory in childhood* (pp. 41–82). Hove, England: Psychology Press.

Niogi, S., Mukherjee, P., Ghajar, J., & McCandliss, B. D. (2010). Individual differences in distinct components of attention are linked to anatomical variations in distinct white matter tracts. *Frontiers in Neuroanatomy, 4*, 2, 1–12.

Nordahl, C. W., Simon, T. J., Zierhut, C., Solomon, T. J., Rogers, S. J., & Amaral, D. G. (2008). Brief report: Methods for acquiring structural MRI data in very young children with autism without the use of sedation. *Journal of Autism and Developmental Disorders, 38*, 1581–1590.

Oakes, L. M., & Bauer, P. J. (Eds.) (2007). Short-and long-term memory in infancy and early childhood: Taking the first steps toward remembering. New York: Oxford University Press.

Ofen, N., Kao, Y.-C., Sokol-Hessner, P., Kim, H., Whitfield-Gabrieli, S., & Gabrieli, J. D. E. (2007). Development of the declarative memory system in the human brain. *Nature Neuroscience, 10*, 1198–1205.

Olesen, P. J., Macoveanu, J., Tegner, J., & Klingberg, T. (2007). Brain activity related to working memory and distraction in children and adults. *Cerebral Cortex, 17*, 1047–1054.

Olson, E. A., Collins, P. F., Hooper, C. J., Muetzel, R., Lim, K. O., & Luciana, M. (2009). White matter integrity predicts delay discounting behavior in 9- to 23-year-olds: A diffusion tensor imaging study. *Journal of Cognitive Neuroscience, 21*, 1406–1421.

Paz-Alonso, P. M., Ghetti, S., Donohue, S., Goodman, G. S., and Bunge, S. A. (2008). Neurodevelopmental correlates of true and false recognition. *Cerebral Cortex, 19,* 2208–2216.

Paz-Alonso, P. M., Ghetti, S., Matlen, B. J., Anderson, M. C., & Bunge, S. A. (2009). Memory suppression is an active process that improves over childhood. *Frontiers in Human Neuroscience, 3,* 24, 1–6.

Paz-Alonso, P. M., Bunge, S. A., Anderson, M. C., & Ghetti, S. (2013). Strength of coupling within a mnemonic control network differentiates those who can and cannot suppress memory retrieval. *Journal of Neuroscience, 33,* 5017–5026.

Poldrack, R. A. (2010). Interpreting developmental changes in neuroimaging signals. *Human Brain Mapping, 31,* 872–878.

Poldrack, R. A. (2012). The future of fMRI in cognitive neuroscience. *Neuroimage, 62,* 1216–1220.

Ranganath, C., Heller, A. S., & Wilding, E. L. (2007) Dissociable correlates of two classes of retrieval processing in prefrontal cortex. *Neuroimage, 35,* 1663–1673.

Raschle, N. M., Lee, M., Buechler, R., Christodoulou, J. A., Chang, M., Vakil, M., . . . Gaab, N. (2009). Making MR imaging child's play—pediatric neuroimaging protocol, guidelines and procedure. *Journal of Visualized Experiments, 29,* pii: 1309.

Reichenberg, A., Caspi, A., Harrington, H., Houts, R., Keefe, R. S., Murray, R. M., . . . Moffitt, T. E. (2010). Static and dynamic cognitive deficits in childhood preceding adult schizophrenia: A 30-year study. *American Journal of Psychiatry, 167,* 160–169.

Rubia, K., Smith, A. B., Woolley, J., Nosarti, C., Heyman, I., Taylor, E., & Brammer, M. (2006). Progressive increase of frontostriatal brain activation from childhood to adulthood during event-related tasks of cognitive control. *Human Brain Mapping, 27*, 973–93.

Rykhlevskaia, E., Gratton, G., & Fabiani, M. (2008). Combining structural and functional neuroimaging data for studying brain connectivity: A review. *Psychophysiology 45*, 173–187.

Sahakyan, L., & Kelley, C. M. (2002). A contextual change account of the directed forgetting effect. *Journal of Experimental Psychology: Learning, Memory and Cognition, 28*, 1064–1072.

Scherf, K. S., Sweeney, J. A., & Luna, B. (2006). Brain basis of developmental change in visuospatial working memory. *Journal of Cognitive Neuroscience, 18*, 1045–1058.

Schneider, W., & Bjorklund, D. F. (1998). Memory. In W. Damon (Ed.), *Handbook of child psychology* (5th ed., Vol. 2, pp. 467–521). New York: John Wiley and Sons.

Schneider, W., & Pressley, M. (1997). Memory development between two and twenty (2nd ed.). Mahwah, NJ: Lawrence Erlbaum Associates.

Schwenck, C., Bjorklund, D. F., & Schneider, W. (2009). Developmental and individual differences in young children's use and maintenance of a selective memory strategy. *Developmental Psychology, 45*, 1034–1050.

Shaw, P., Geenstein, D., Lerch, J. P., Clasen, L., Lenroot, R., Gogtay, N., . . . Gieed, J. (2006). Intellectual ability and cortical development in children and adolescents. *Nature, 30*, 676–679.

Shaw, P., Kabani, N. J., Lerch, J. P., Eckstrand, K., Lenroot, R., Gogtay, N., . . . Wise, S. P. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *Journal of Neuroscience, 28,* 3586 –3594.

Shaw, P., Lalonde, F., Lepage, C., Rabin, C., Eckstrand, K., Sharp, W., . . . Rapoport, J. (2009). Development of cortical asymmetry in typically developing children and its disruption in attention-deficit/hyperactivity disorder. *Archives of General Psychiatry, 66,* 888–896.

Smith, S. M., Miller, K. L., Salimi-Khorshidi, G., Webster, M., Beckmann, C. F., Nichols, . . . Woolrich, M. W. (2011). Network modelling methods for fMRI. *Neuroimage 54,* 875–891.

Somerville, L. H., Hare, T., & Casey, B. J. (2011). Frontostriatal maturation predicts cognitive control failure to appetitive cues in adolescents. *Journal of Cognitive Neuroscience, 23,* 2123–2134.

Stevens, M. C. (2009). The developmental cognitive neuroscience of functional connectivity. *Brain and Cognition, 70,* 1–12.

Stevens, M. C., Pearlson, G. D., & Calhoun, V. D. (2009). Changes in the interaction of resting-state neural networks from adolescence to adulthood. *Human Brain Mapping, 30,* 2356–2366.

Supekar, K., Uddin, L. Q., Prater, K., Armin, H., Greicius, M. D., & Menon, V. (2010). Development of functional and structural connectivity within the default mode network in young children. *Neuroimage, 52,* 290–301.

Tamm, L., Menon, V., & Reiss, A. L. (2002). Maturation of brain function associated with response inhibition. *Journal of the American Academy of Child and Adolescent Psychiatry, 41,* 1231–1238.

Tamnes, C. K., Østby, Y., Walhovd, K. B., Westlye, L. T., Due-Tønnessen, P., & Fjell, A. M. (2010) Brain maturation in adolescence and young adulthood: Regional age-related changes in cortical thickness and white matter volume and microstructure. *Cerebral Cortex, 20*, 534–548.

Thomason, M. E., Dougherty, R. F., Colich, N. L., Perry, L. M., Rykhlevskaia, E. I., Louro, H. M., . . . Gotlib, I. H. (2010). COMT genotype affects prefrontal white matter pathways in children and adolescents. *Neuroimage, 15*, 926–934.

Thomason, M. E., Chang, C. E., Glover, G. H., Gabrieli, J. D., Greicius, M. D., & Gotlib, I. H. (2008). Default-mode function and task-induced deactivation have overlapping brain substrates in children. *Neuroimage, 41*, 1493–1503.

van Leijenhorst, L., Gunther, M. B., Op de Macks, Z. A., Rombouts, S. A., Westenberg, P. M., & Crone, E. A. (2010). Adolescent risky decision-making: Neurocognitive development of reward and control regions. *Neuroimage, 15*, 345–355.

Velanova, K., Wheeler, M. E., & Luna, B. (2008). Maturational changes in anterior cingulate and frontoparietal recruitment support the development of error processing and inhibitory control. *Cerebral Cortex, 18*, 2505–2522.

Wendelken, C., Baym, C. L., Gazzaley, A., & Bunge, S. A. (2011). Neural indices of improved attentional modulation over middle childhood. *Developmental Cognitive Neuroscience, 1*, 175–186.

Wendelken, C., O'Hare, E. D., Whitaker, K. J., Ferrer, E., & Bunge, S. A. (2011). Increased functional selectivity over development in rostrolateral prefrontal cortex. *Journal of Neuroscience, 31*, 17260–17268.

Wiebe, S. A., Espy, K. A., Stopp, C., Respass, J., Stewart, P., Jameson, T. R., . . . Huggenvik, J. I. (2009). Gene-environment interactions across development: Exploring DRD2 genotype and prenatal smoking effects on self-regulation. *Developmental Psychology*, *45*, 31–44.

Wilson, S. P., & Kipp, K. (1998). The development of efficient inhibition: Evidence from directed-forgetting tasks. *Developmental Review*, *18*, 86–123.

Figure 1.

In this study, McCandliss and colleagues provide evidence for a triple dissociation in the interindividual relationships between white matter integrity of three tracts and cognitive performance on the alerting, orienting, and conflict resolution components of the Attention Network Task (ANT). On this task, participants must decide as quickly as possible whether the central arrow of an array points to the left or to the right. On each trial, one of three cue types is presented, followed closely by a target (sample cues and targets illustrated in gray). Alerting cues indicate that a trial is about to begin, and spatial cues indicate whether the target stimulus is most likely to appear above or below the fixation cross. On incongruent target stimuli, participants must resolve conflict between the responses indicated by the central and flanking arrows. Each of three white matter tracts—the posterior limb of the internal capsule, the splenium of the corpus callosum, and the anterior corona radiata—exhibited a positive correlation between fractional anisotropy (FA) and cognitive performance on one of the three components of the ANT. Modified with permission from Niogi et al. (2010).

Figure 2.

Red lines indicate functional connections that are stronger in children than in adults; blue lines indicate the connections that are stronger in adults. The inlaid graph shows age-related changes

in functional connectivity between the intraparietal sulcus (IPS) and dorsolateral prefrontal cortex (dlPFC) over age. Modified with permission from Church et al. (2009).

Figure 3.

(A) Mean familiarity rating for adults and children as a function of condition (attended, passive, ignore). Dotted line represents mean familiarity ratings for new scenes presented only during the retrieval phase. (B) Coronal view of the left dorsolateral prefrontal cortex (dlPFC) functional region-of-interest (ROI), identified from the scene > passive contrast across all participants, showing a positive correlation for dlPFC selective enhancement (Scene-Passive cue) with age. Modified with permission from Wendelken et al. (2011).

Figure 4.

Subsequent memory recall on the Same-Probe task for Think, No-Think, and Baseline items as a function of age group from our previous behavioral study including a total of 70 participants (twenty 8- to 9-year-olds, twenty 11- to 12-year-olds, and 30 young adults. Modified from Paz-Alonso et al. (2009).

Figure 5.

The cingulum bundle (*dark blue*) and the uncinate fasciculus (*yellow*) are the two white matter tracts connecting medial temporal lobe (MTL) and lateral PFC (lPFC) regions. (A) The cingulum bundle connects posterior hippocampus with posterior parietal cortex and lPFC via the parahippocampal gyrus. The uncinate fasciculus, on the other hand, connects anterior hippocampus with ventral lPFC. (B) Age-related fractional anisotropy (FA) increases from age 5 to 30 measured by tractography in the cingulum bundle (*dark blue*) and the uncinate fasciculus (*yellow*). (C) Magnitude and timing of development in these frontotemporal white matter tracts. The length of the colored bar indicates the age at which the region reached 90% of its

development plateau from 5 years, as measured by fitting parameters in the exponential equation. The color of each bar represents the percent increase of FA. Modified with permission from Lebel et al. (2008).