5 Brain Changes Underlying the Development of Cognitive Control and Reasoning

SILVIA A. BUNGE, ALLYSON P. MACKEY, AND KIRSTIE J. WHITAKER

ABSTRACT What precisely is changing over time in a child's brain leading to improved control over his or her thoughts and behavior? This chapter investigates neural mechanisms that develop through childhood and adolescence and underlie changes in working memory, cognitive control, and reasoning. The effects of age and experience on specific cognitive functions are discussed with respect to functional brain imaging studies, highlighting the importance of interactions between prefrontal and parietal cortices in cognitive control and high-level cognition.

What precisely is changing over time in a child's brain, leading to improved control over his or her thoughts and behavior? Throughout childhood and adolescence, we improve at organizing our thoughts, working toward long-term goals, ignoring irrelevant information that could distract us from these goals, and controlling our impulses—in other words, we exhibit improvements in *executive function* or
2 *cognitive control* (Diamond, 2002; Zelazo, Craik, et al., 2004; Casey, Tottenham, et al., 2005). By the same token, we exhibit increased facility over this age range in tackling novel problems and reasoning about the world—a capacity referred to as fluid reasoning (Cattell, 1971). Both the capacity to consciously control our thoughts and actions and the capacity to reason effectively rely on *working memory*, or the ability to keep relevant information in mind as needed to carry out an immediate goal.

Neuroscientific research is being conducted to better understand the changes in brain structure and function that underlie improved cognitive control and fluid reasoning during child and adolescent development. More specifically, researchers seek to determine how the neural mechanisms underlying specific cognitive functions change with age, how they differ among individuals, and how they are affected by experience.

We begin this chapter with a brief summary of changes in brain structure, focusing primarily on prefrontal and parietal cortices, the brain regions that have been most closely associated with goal-directed behavior. We then provide an overview of functional brain imaging studies focusing on age-related changes in working memory, cognitive control, and fluid reasoning over childhood and adolescence. Because working memory and cognitive control development have been discussed extensively elsewhere (Munakata, Casey, et al., 2004; Rubia & Smith, 2004; Casey et al., 2005; Bunge & Wright, 2007), a relatively greater emphasis is placed on recent studies focusing on the development of fluid reasoning.

Structural brain development

The brain undergoes major structural and functional changes over childhood and adolescence that may, in part, explain changes in behavior and cognition. As explained in chapter 2, by Kostović and Judaš, rapid changes occur at the neuronal level in the prefrontal cortex (PFC) in the first few years of life, followed by slower, protracted changes through adolescence (Petanjek, Judas, et al., 2008). While brain changes at the cellular level can only be examined in postmortem brain tissue, advances in neuroimaging techniques have made it possible to study gross anatomical development in vivo. Structural magnetic resonance imaging (MRI) methods make it possible to quantify age-related changes in cortical thickness (Sowell, Peterson, et al., 2007), in the volume of specific brain structures (Gogtay, Nugent, et al., 2006), and in the thickness and coherence of white matter tracts connecting distant brain regions to one another (Giedd, Blumenthal, et al., 1999; Klingberg, Vaidya, et al., 1999).

Cortical thickness follows an inverted U-shaped pattern over development. Up to middle childhood (ages 8 to 12), increased thickness of the gray matter at the surface of the brain reflects increased density of neurons and dendrites. Thereafter, decreased gray matter thickness reflects the pruning of excess dendrites and neurons, as well as increased myelination of axonal projections to these neurons (Giedd, 2004).

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1 SILVIA A. BUNGE Helen Wills Neuroscience Institute and Department of Psychology, University of California at Berkeley, Berkeley, California
ALLYSON P. MACKEY, and KIRSTIE J. WHITAKER Helen Wills Neuroscience Institute, University of California at Berkeley, Berkeley, California

The developmental trajectory of changes in cortical thickness varies across brain structures. In PFC and parietal cortex, gray matter volume peaks around age 10–12 (Giedd, 2004). Thereafter, gray matter loss occurs at different rates in different subregions of the PFC, and it is considered one index of the time course of maturation of a region (Sowell, Peterson, et al., 2003). Within the PFC, gray matter reduction is completed earliest in the orbitofrontal cortex, followed by the ventrolateral PFC (VLPFC) and then by the dorsolateral PFC (DLPFC) and rostrolateral PFC (RLPFC) (Gogtay, Giedd, et al., 2004; O'Donnell, Noseworthy, et al., 2005). Differences in maturational time course between prefrontal subregions could help account for differences in the rate of development of distinct cognitive control processes (Bunge & Zelazo, 2006; Crone, Wendelken, et al., 2006).

Developmental changes in interregional connectivity have been studied with an MRI-based method known as diffusion tensor imaging (DTI). Research using DTI has shown that strengthening of frontal-parietal networks is associated with improved performance on working memory tasks (Olesen, Nagy, et al., 2003; Nagy, Westerberg, et al., 2004). An age-related increase in frontostriatal tract coherence has also been associated with more efficient recruitment of cognitive control (Liston, Watts, et al., 2006).

In summary, both cortical pruning within prefrontal and parietal regions and increased neuronal connectivity within and between these and other regions are likely to underlie improvements in cognitive control and fluid reasoning during development. The relationships between behavioral improvements and changes in brain structure and brain function have been explored in recent studies of working memory, as described in the next section.

Working memory development

Working memory is the brain's "mental blackboard," allowing information—either sensory inputs or memories—to be held in mind and manipulated (Miller, Galanter, et al., 1960; Goldman-Rakic, 1992). Considered a central component of human cognition, the maturation of working memory is critical for the development of language comprehension, mental calculation, cognitive control, and fluid reasoning. Although children as young as 5 years do not differ from adults in sensorimotor tasks, performance on tasks that rely on the retention and manipulation of information, such as spatial memory span and Tower of London, improves over childhood (Luciana & Nelson, 1998). Children's performance is critically moderated by task difficulty: their accuracy rapidly declines as the demands of the task become more rigorous and they make more errors. As working memory improves, children likewise improve on tests of cognitive control and fluid reasoning.

Working memory for different types of information is mediated by interactions between domain-specific brain regions and regions in PFC and parietal cortex (D'Esposito, 2007). It is the integration and refinement of these working memory circuits that underlies age improvements in the maintenance and manipulation of mental representations. In the next subsection, we provide a brief overview of fMRI studies examining age-related changes in working memory.

VISUOSPATIAL WORKING MEMORY Most fMRI studies on working memory development have focused on the ability to keep in mind a series of spatial locations (Casey, Cohen, et al., 1995; Thomas, King, et al., 1999; Klingberg, Forssberg, 3 et al., 2002; Kwon, Reiss, et al., 2002; Scherf, Sweeney, et al., 2006). The superior frontal sulcus (SFS) and the intraparietal sulcus (IPS), which have been strongly implicated in adult visuospatial working memory, are increasingly engaged throughout childhood (Klingberg, Forssberg, et al., 2002; Kwon et al.). Across children, the level of fractional anisotropy in the frontoparietal white matter surrounding the SFS and IPS is positively correlated with visuospatial working memory scores (Nagy et al., 2004). Further, the coherence of these white matter tracts in the left hemisphere is greater among children (age 8–18 years) who exhibit the greatest activation in these regions (Olesen et al., 2003). Thus the brain network underlying effective visuospatial working memory is strengthened over development.

At a microscopic level, the increased engagement of SFS and IPS during a BOLD fMRI visuospatial working memory 4 task could be dependent on one or more cellular changes: neuronal pruning, increased myelination, and/or the strengthening of synaptic connections within or between brain regions. Klingberg and colleagues used computational methods to determine which of these processes are likely to support the development of visuospatial working memory (Edin, Macoveanu, et al., 2007). Their computational model of BOLD activation found that strengthened synaptic connectivity within and between brain regions was the most likely candidate for increase in activation in these regions between childhood and adulthood.

Just as core working memory networks are strengthened over childhood and adolescence, supporting networks that are not used by adults for working memory are weakened over this age range. Using a spatial working memory paradigm involving saccadic eye movements, Luna and colleagues showed that increased recruitment of core regions in DLPFC in the left hemisphere and parietal regions was accompanied by a weakening and eventual dismissal of a childhood compensatory circuit involving ventromedial PFC (Scherf et al., 2006). A qualitative shift was observed in comparing children aged 10–13 and adolescents aged 14–17. Comparing adolescents to adults, the changes were more quantitative, evincing refinement of the visuospatial working memory network. This movement away from the childhood circuit to the more mature adult network is a common theme in developmental cognitive neuroscience, and it is further discussed in this chapter's section on cognitive control development.

NONSPATIAL WORKING MEMORY In addition to the fMRI studies of visuospatial working memory development, we would like to highlight a study on the development of nonspatial working memory, in which children aged 8–12, adolescents aged 13–17, and young adults were asked to remember a series of three nameable objects (figure 5.1*A*; Crone et al., 2006). We consider first the pure maintenance condition of this study, in which participants were asked to verbally rehearse the items in the order in which they were presented. All three groups engaged highly overlapping sets of brain regions, indicating that the core working memory network was already in place by middle childhood. However, there was a positive correlation across participants between task accuracy and level of activation in left ventrolateral PFC (VLPFC), bilateral DLPFC, and bilateral superior parietal cortex.

MANIPULATION OF INFORMATION IN WORKING MEMORY This study of nonspatial working memory (Crone et al., 2006) also included a manipulation condition, in which participants were asked to reverse the order of the items in their head. Children aged 8–12 were disproportionately impaired relative to adolescents and adults on this manipulation condition relative to the pure maintenance condition. Further, children failed to engage right DLPFC and bilateral superior parietal cortex, regions linked with working memory manipulation, for this purpose. A qualitative shift in the circuitry underlying manipulation was observed from middle childhood onward, such that adolescents and adults engaged an additional mechanism relative to children aged 8–12. Time-series correlational analyses showed that, for adults, right DLPFC was functionally correlated with bilateral parietal and premotor cortices during manipulation.

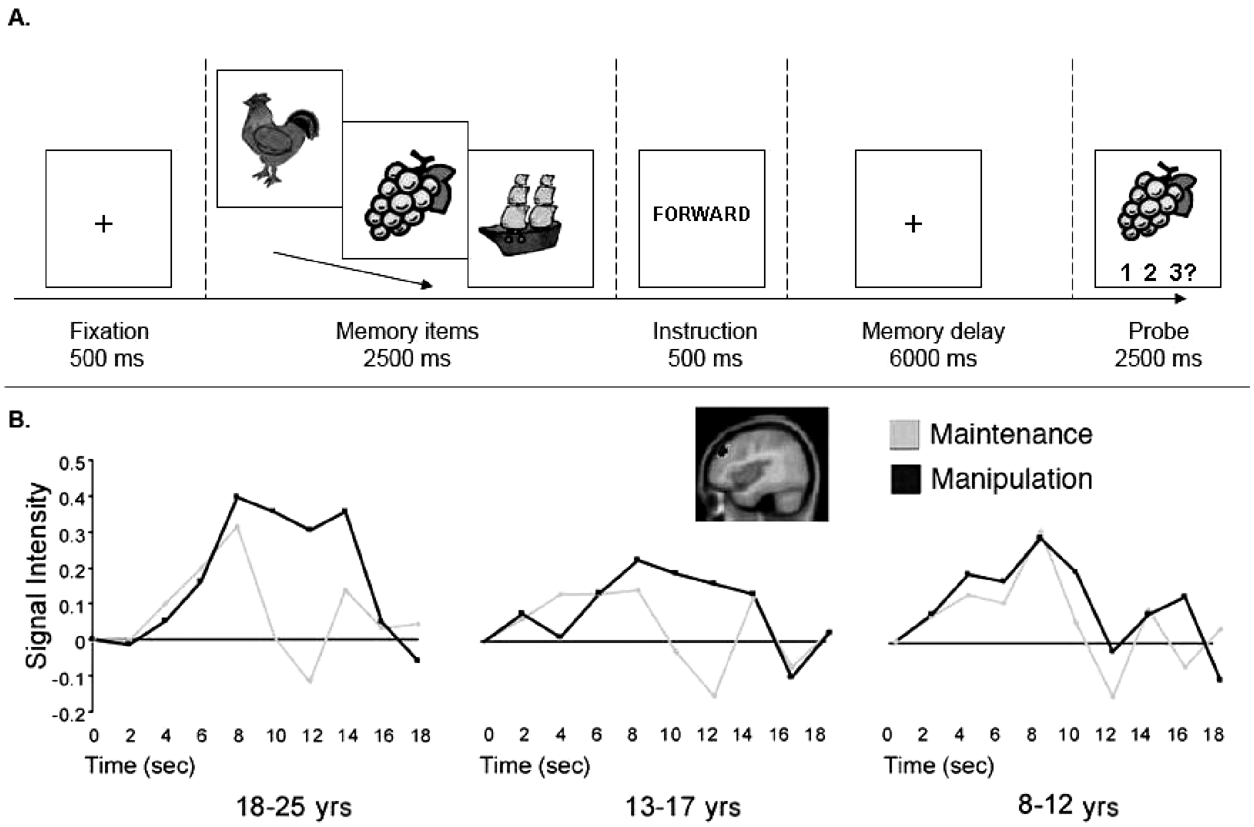

FIGURE 5.1 Development of nonspatial working memory and working memory manipulation. (*A*) Subjects were asked to remember three nameable objects, presented for 750 ms each and separated by a 250-ms fixation cross. After the last object the instruction "forward" or "backward" directed the participant to either mentally rehearse or reorder these objects during the 6,000-ms delay. Finally a probe object was presented and participants indicated with a button press whether it was first, second, or third object in the memorized sequence. Forward trials required pure maintenance, whereas backward trials required manipulation in addition to maintenance. (*B*) Group-averaged time courses for activation in the right DLPFC during the delay period show that adults and adolescents recruited this region more strongly during the harder manipulations trials, whereas children showed the same activation in DLPFC for both "forward" and "backward" tasks. (Reprinted with permission from Crone, Wendelken, et al., 2006, copyright © 2006, National Academy of Sciences, USA.)

In children, by contrast, right DLPFC activation during manipulation was correlated with regions that have not been associated previously with this function (unpublished analyses). Thus the brain network underlying manipulation in adults was not yet engaged by children aged 8–12. Importantly, it is not the case that children failed to engage these brain regions during task performance. Indeed, children engaged DLPFC and parietal cortex at encoding and retrieval of items in working memory; they simply failed to sufficiently engage the circuitry that supports manipulation at the time when it was required to reverse the order of objects in working memory (figure 5.1*B*).

These investigations have shown how the development of PFC and parietal cortex, as well as the connections between them, contributes to increased ability to maintain and manipulate information online. In turn, an increase in working memory capacity contributes to improvements in a variety of cognitive functions, including cognitive control and fluid reasoning.

Cognitive control development

One of the most obvious ways in which children mature behaviorally is that they become increasingly able to ignore irrelevant and distracting information and control their impulses while working toward specific goals. The terms *executive function* and *cognitive control* refer to mental processes associated with the control of thought and action. Thus far, developmental research on cognitive control has been concerned with conscious, deliberate forms of control. Putative cognitive control functions are listed in box 5.1.

COGNITIVE CONTROL DEVELOPMENT: CHANGES IN ONE OR MORE NEURAL CIRCUITS? A key question in developmental research has been whether age-related changes in cognitive control are associated with the development of a single mechanism, such as the capacity to store or process information (Case, 1992; Dempster, 1993), or with a set of mechanisms (Welsh, Butters, et al., 1991). Behavioral studies suggest that some of these abilities may mature at different rates. For example, the ability to inhibit a motoric response matures earlier than the ability to inhibit a response when the task additionally requires selective attention (van den Wildenberg & van der Molen, 2004). Likewise, the ability to switch between task rules develops earlier than the ability to keep a difficult rule online (Crone, Wendelken, et al., 2004). Recent advances using structural equation modeling indicate that working memory, task switching, and response inhibition are separable latent constructs with distinct developmental trajectories (Brocki & Bohlin, 2004; Huizinga, Dolan, et al., 2006). Thus behavioral research provides hints that different cognitive control functions may have separable neurodevelopmental trajectories.

BOX 5.1 Cognitive Control Functions

1. Selectively attending to relevant information (*selective attention*) and ignoring distracting stimuli or thoughts (*interference suppression/resolution*)
2. Selecting between competing response tendencies (*response selection*) and inhibiting inappropriate response tendencies (*response inhibition*)
3. Using contextual information to identify currently relevant information and appropriate responses (*rule/task-set representation*)
4. Reorganizing information currently held in working memory (*manipulation, updating*)
5. Flexibly switching between tasks and performing two tasks concurrently (*task-switching, dual task performance*)
6. Monitoring one's own actions and the consequences of these actions (*performance monitoring, error/feedback processing*)

In a recent study of cognitive network development, Fair, Dosenbach, and colleagues (2007) show that, initially, the strongest connections between frontoparietal gray matter are anatomically close together. As these regions mature, however, the connections become more functionally relevant and reach further afield, presumably to engage the most effective network for cognitive control (figure 5.2).

The protracted myelination of the white matter tracts connecting the regions necessary for cognitive control over childhood and adolescence (Spear, 2007) may explain the compensatory network required for children to complete these tasks. If long-range projections are not sufficiently insulated by the myelin sheath, they will be unable to communicate with the functionally relevant networks utilized by the adult brain. Eventually, during adolescence, the myelination is sufficient to allow a transition from the local, compensatory mechanism to a more diffuse, adult, effective system.

In the following sections, we highlight a few of the many brain-imaging studies that have examined neurodevelopmental changes in cognitive control.

Response selection and inhibition As noted previously, improvements in working memory manipulation—a form of cognitive control—are associated with an increase in lateral PFC activation with age (Crone et al., 2004). For some cognitive control tasks, however, maturation is instead associated with a decrease in lateral PFC recruitment. For example, a large study involving participants between 8 and 27 years of age by Luna and colleagues (Velanova, Wheeler, et al., 2008) examined functional maturational changes associated with performance on an antisaccade task. In this response inhibition task, participants must move their eyes away from a visual stimulus that appears suddenly on the screen, resisting the urge to look toward it. The researchers observed an age-related shift away from reliance on DLPFC, toward

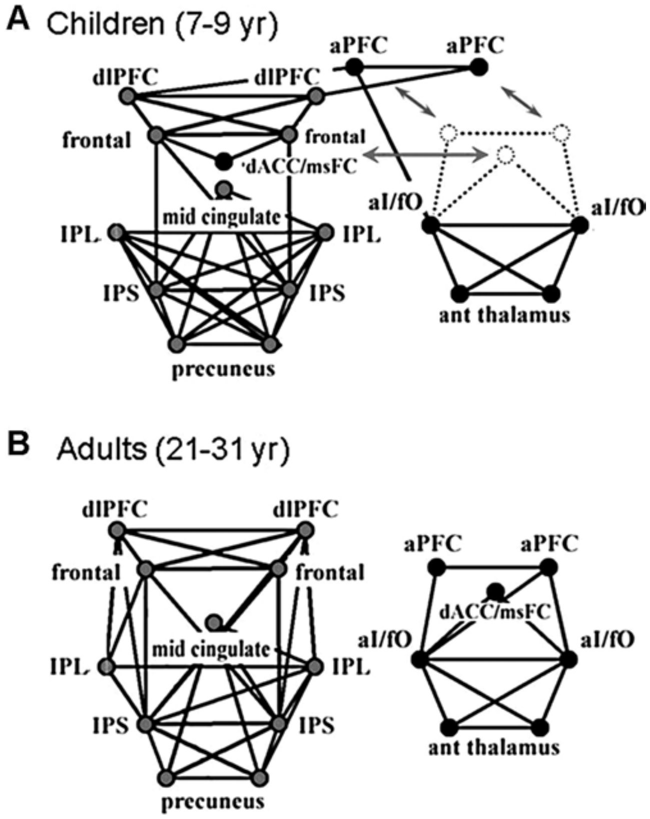

FIGURE 5.2 Development of distinct cognitive control networks through childhood and adolescence. Regions previously identified as pertaining to putative task control were analyzed for pairwise temporal BOLD correlations in (*A*) children and (*B*) adults. Right-side ROIs are displayed on the right of each graph and anterior ROIs at the top of each graph. Whereas adults demonstrate two separate control networks, children show a connection between them. Their networks are connected by a bridge between the anterior PFC and DLPFC, and the dACC and medial superior frontal cortex were incorporated into the frontoparietal network. In addition, children lacked connections between the DLPFC and the IPS and inferior parietal lobule. The two separate networks seen in adults are proposed to interpret cues, implement top-down control, and process bottom-up feedback, but use different mechanisms and over different temporal scales. (Reprinted with permission from Fair, Dosenbach, et al., 2007, copyright © 2007 National Academy of Sciences, USA.)

posterior parietal regions (figure 5.2). Consistent with other work, this finding indicates a shift away from childhood compensatory mechanisms toward the more effective adult networks.

In addition to this antisaccade study, a number of other brain-imaging studies have focused on age-related improvements in the ability to select between competing response choices and inhibit inappropriate response tendencies (see Munakata et al., 2004, and Bunge & Wright, 2007, for reviews). These studies have made use of a variety of paradigms, including the well-known Stroop (Adleman, Menon, et al., 2002; Schroeter, Zysset, et al., 2004; Marsh, Zhu, et al., 2006), go-no-go (Rubia, Smith, et al., in press; Rubia, 6
Russell, et al., 2001; Bunge, Dudukovic, et al., 2002; Durston, Thomas, et al., 2002; Tamm, Menon, et al., 2002; Booth, Burman, et al., 2003; Lamm, Zelazo, et al., 2006), and flanker tasks (Bunge et al.; Lamm et al.; Rubia, Smith, et al., 2006). In task-switching paradigms, the currently relevant task rule changes without warning, and it is necessary to suppress the response to the previous rule and also to retrieve the new rule from memory (Crone et al., 2004). These studies indicate that overlapping but distinct circuits involving regions of PFC, parietal cortex, and basal ganglia are involved in various cognitive control tasks (Rubia, Russell, et al.).

Performance monitoring Luna and colleagues used the antisaccade task to examine not only at the development of response inhibition, but also the development of performance monitoring (Velanova et al., 2008). The dorsal anterior cingulate 7
cortex (dACC), known to play a central role in performance monitoring (Ford, Goltz, et al., 2005; Polli, Barton, et al., 2005), was more strongly engaged on error trials in adults than in children or adolescents (figure 5.3). Increased performance monitoring, supported by dACC, is likely to contribute to the observed improvements in inhibitory cognitive control with age.

In summary, cognitive control is considered to compromise a variety of different putative processes, and a few 8
studies have made attempts to compare the developmental time course of specific control processes (e.g., Bunge et al., 2002; Crone et al., 2006; Rubia et al., 2006). However, it remains to be seen if these different behavioral abilities are in fact different underlying neural substrates and if they develop over separable trajectories. Further work must be undertaken to determine the relative independence and interactions of the many cognitive control capabilities throughout development.

Fluid reasoning development

Fluid reasoning is the capacity to think logically and solve problems in novel situations (Cattell, 1971). The concept of fluid reasoning is integral to theories of human intelligence (Horn, 1967; Cattell, 1987; Horn, 1988; Carroll, 9
1997; McArdle, 1998; Gray, Chabris, et al., 2003). Compared to crystallized, or knowledge-based, abilities it is thought to have a stronger neurobiological and genetic component, leading to the belief that it is less dependent on experience. However, some evidence suggests that it is indeed sensitive to cultural and environmental influences (Flynn, 2007).

The development of reasoning ability is central to understanding cognitive development as a whole, because it serves as scaffolding for many other cognitive functions (Cattell,

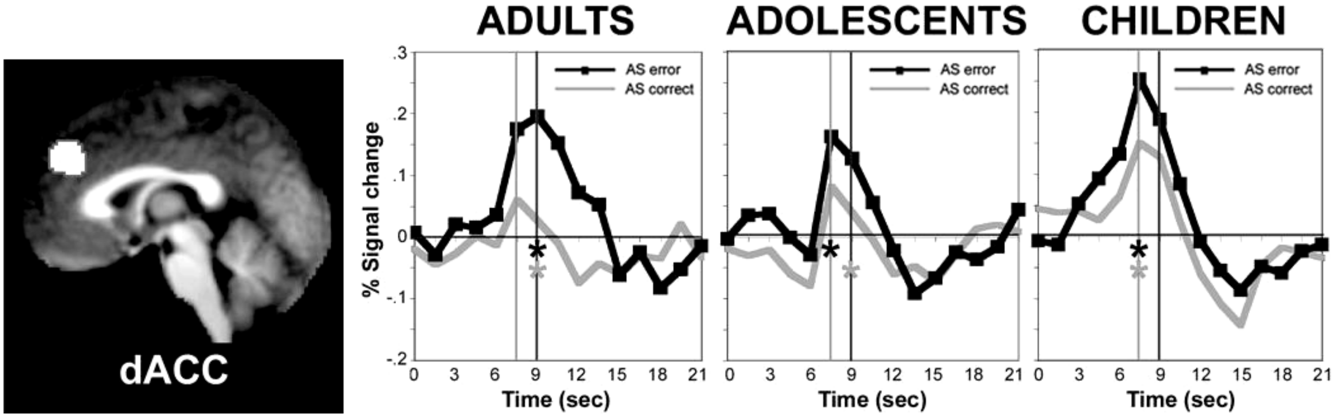

Figure 5.3 Development of response inhibition and performance monitoring. Velanova, Wheeler, and colleagues (2008) demonstrated that dACC showed significantly greater modulation during error versus correct trials in an antisaccade task. The task required subjects to inhibit the prepotent tendency to look toward the stimulus and look in the opposite direction. The time course of activation within the dACC, illustrated here, not only shows the difference between activity during error and correct trials but also that adults exhibit greater differential activity than adolescents and children. For each age group, black asterisks mark the time point showing mean maximal peak activity for error trials, and gray asterisks mark the time point showing mean maximal differences between error and correct trials. (Reprinted with permission from Velanova, 31 Wheeler, et al., 2008, copyright Oxford University Press.)

1987; Blair, 2006). Fluid reasoning has been identified as a leading indicator of changes in crystallized abilities (McArdle, 2001). It strongly predicts changes in quantitative ability
10 (Ferrer & McArdle, 2004) and reading (Ferrer, 2006) among children aged 5 to 10. Fluid reasoning ability even predicts performance through college and in cognitively demanding occupations (Gottfredson, 1997).

One form of fluid reasoning is relational reasoning: the ability to consider relationships between multiple distinct mental representations (Gentner, 1983; Hummel & Holyoak, 1997). Analogical reasoning, more specifically, involves abstracting a relationship between familiar items and applying it to novel representations (Gentner, 1988; Goswami, 1989). In other words, forming analogies allows us to determine general principles from specific examples and to establish connections between previously unrelated pieces of information. Analogical thought is an important means by which cognition develops (Goswami, 1989; R. Brown & Marsden, 1990). For example, children use analogies to learn new words and concepts by association with previously learned information (Gentner, 1983).

When Does Reasoning Ability Develop? Historically, theories of reasoning development focused on children's limitations. Piaget claimed that, before the stage of formal operations around age 11, children are not capable of mentally representing the relations necessary to solve analogies (Inhelder, 1958). When Piaget and his colleagues showed children pictorial problems of the form "A is to B as C is to . . .?" and asked them to find the D term among a set of pictures, he found that children often chose items that were perceptually or semantically related to the C item (Piaget, 1977). Sternberg and colleagues found similar 11
limitations in young children's analogical reasoning, observing an overreliance on lower-order relations during analogical problem solving (Sternberg, 1980, 1982). It has been argued that children as young as 3 years old can solve simple analogies as long as they are familiar with the objects involved and understand the relevant relations (Goswami, 1989), but improvements in analogical reasoning are observed throughout childhood and adolescence (Sternberg & Rifkin, 1979; Richland, Morrison, et al., 2006).

Fluid reasoning ability seems to be a distinct cognitive function, rising and falling at its own rate across the life span (Cattell, 1987). It follows a different developmental trajectory than crystallized abilities, supporting the idea that these are separable cognitive functions (Horn, 1991; Schaie, 1996; McGrew, 1997). Fluid reasoning capacity increases very rapidly until late adolescence and early adulthood, peaking at around age 22 and declining thereafter (McArdle, Ferrer-Caja, et al., 2002).

Assessing Reasoning Ability One of the most commonly used measures of fluid reasoning ability is the Raven's Progressive Matrices test (RPM), a classic visuospatial task that can be administered to both children and adults (Raven, 1941). This test is considered an excellent measure of fluid reasoning ability (Kline, 1993) and of intellectual ability overall (Wechsler & Stone, 1945).

As illustrated in figure 5.4, the RPM includes zero-relational (REL-0), one-relational (REL-1), and two-relational (REL-2) problems. REL-0 problems require only perceptual matching. REL-1 problems require subjects to consider either vertical or horizontal changes (or spatial rela-

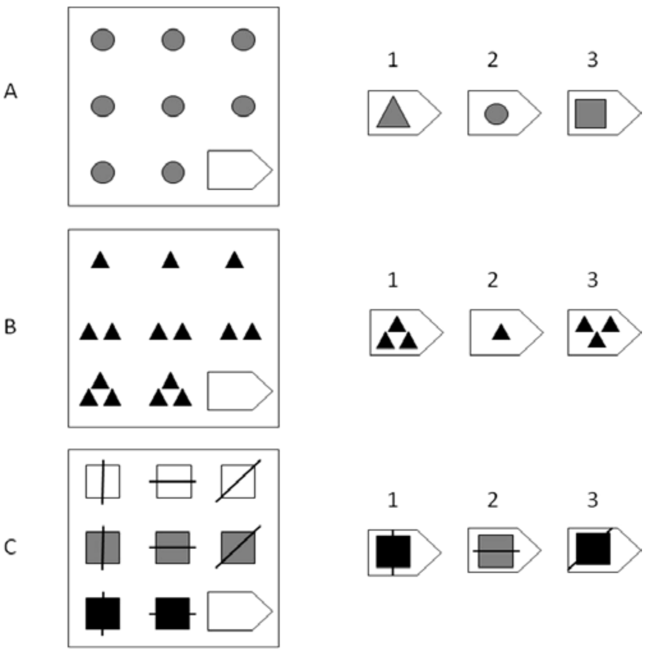

FIGURE 5.4 Sample problem similar to Raven's Progressive Matrices. (*A*) Zero-relational problem (REL-0) that requires only perceptual matching (Answer: 2). (*B*) One-relational problem (REL-1) that involves consideration of change in either the vertical or horizontal direction (Answer: 1). (*C*) Two-relational problem (REL-2) that requires attention to change in both the vertical and horizontal directions (Answer: 3).

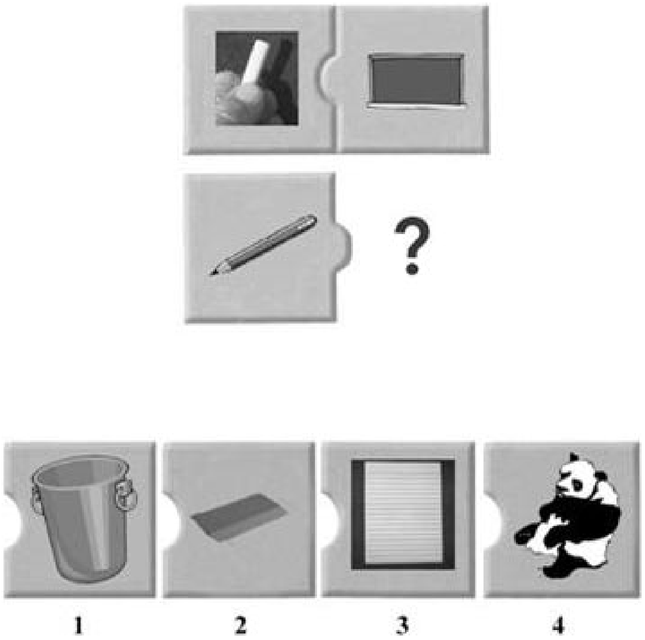

FIGURE 5.5 Sample Visual analogy Problem. On this type of problem, subjects must consider the relationship between the top two images and choose the image that completes the bottom analogy (Answer: 3; 2 is the semantic lure).

tions) across figures in a 3 × 3 grid to infer the missing piece in the bottom right corner. REL-2 problems require subjects to process changes in both the horizontal and vertical directions simultaneously in order to choose the missing piece. These problems are the most difficult because they require the integration of two visuospatial relations.

Analogical reasoning can be assessed behaviorally and in an MRI scanner with propositional analogy problems involving either words or pictures of nameable objects. The visual analogy task used in a recent fMRI study from our
12 laboratory (Wright, 2008) requires children to select which of four pictures completes an analogy. The answer choices for these problems include perceptual and semantic lures (figure 5.5).

NEURAL CORRELATES OF FLUID REASONING Brain regions important for fluid reasoning have been identified through studies of patients with impaired reasoning ability and neuroimaging studies of healthy adults. Research on patients in the early stages of frontotemporal dementia (FTD) has shown that reasoning is differentially affected based on the brain areas most compromised by the disease. Patients with frontal-variant FTD make errors on analogical reasoning problems related to limited working memory and trouble inhibiting inappropriate responses. In contrast, patients with temporal-variant FTD are profoundly impaired on analogical reasoning problems as a result of semantic memory loss (Morrison, Krawczyk, et al., 2004). Another study of patients with prefrontal damage revealed that these patients have a specific deficit in relational integration as compared to patients with anterior temporal lobe damage, who are more impaired on tests of episodic and semantic memory (Waltz, Knowlton, et al., 1999).

Imaging research has narrowed down the region in PFC responsible for relational integration to the most anterior part of lateral PFC (RLPFC). Functional MRI studies of reasoning, including the RPM task (Prabhakaran, Smith, et al., 1997; Christoff, Prabhakaran, et al., 2001; Kroger, Sabb, et al., 2002) and a verbal propositional analogy task (Bunge, Wendelken, et al., 2005), have implicated RLPFC in problems that require joint consideration of multiple relations. The other lateral PFC regions play roles in reasoning that are not specifically associated with relational complexity. DLPFC may support reasoning by organizing representations in working memory, selecting between competing response alternatives, and monitoring performance (Christoff et al.). Depending on the nature of the task, different brain regions contribute to fluid reasoning. Left VLPFC (Broca's area) supports reasoning by retrieving semantic relations on propositional analogy problems (Bunge et al.; Wright, 2008). Likewise, hippocampus and parietal cortex may play a role in reasoning by representing individual

visuospatial relations in visuospatial tasks involving relational
integration, including Raven's Progressive Matrices (Crone,
13 in press) and transitive inference problems (Wendelken,
under review).

Parietal cortex is consistently engaged in high-level cognitive tasks like the RPM (Gray et al., 2003) and shares strong connections with PFC (Petrides & Pandya, 1984; Fuster, 2002). A study of individual differences in reasoning ability in adults showed that stronger prefrontal and parietal recruitment on a difficult working memory task is associated with better fluid reasoning, as measured by an RPM-type task (Gray et al.). The level of activation in left lateral PFC and bilateral parietal cortex accounted for more than 99.9% of the relationship between fluid intelligence and working memory performance in these adults.

Taken together, the preceding studies suggest that maturation of RLPFC should lead to improvements in relational processing, while maturation of Broca's area, hippocampus, and parietal cortex should lead to better reasoning through improved representation of individual verbal and visuospatial relations.

HOW DOES THE BRAIN CHANGE TO ALLOW FOR IMPROVEMENTS IN REASONING ABILITY? The neuroimaging research described so far has identified brain regions that contribute to reasoning in adults. However, researchers are just now beginning to track how these regions develop during childhood and how this development leads to improved fluid reasoning ability. As noted earlier in this chapter, in the section on structural brain development, DLPFC, RLPFC, and parietal cortex develop relatively slowly: cortical gray matter loss continues through the early twenties (Giedd, 2004). A study by Shaw and colleagues showed that the trajectory of changes in cortical thickness in several prefrontal regions differed across children with superior, high, and average intelligence (Shaw, Greenstein, et al., 2006). Surprisingly, children with superior intelligence exhibited a delayed peak of cortical thickness in anterior PFC relative to the other groups, around age 11 as opposed to age 7–8 in children of average intelligence. The precise significance of this intriguing finding is as yet unclear. In particular, the role of environmental factors has not been explored; in this study sample, IQ was correlated with socioeconomic factors. However, this finding indicates that cognitive ability is related to the particular time course of cortical maturation in frontal regions, rather than the size of a given region at a specific age. This finding speaks to the unique insights that can be gained from longitudinal studies of brain development.

While structural imaging has provided critical insight into the neural changes that underlie reasoning development, functional neuroimaging is essential to understand how changes in brain function lead to changes in behavior. This section highlights the first two fMRI studies of reasoning ability in children.

Visual analogies In the first study, our laboratory (Wright, 2008) presented children aged 6–13 and young adults with visual analogy problems (figure 5.5). Children were capable of identifying analogous relationships between pairs of images, but made disproportionately more mistakes than adults on the analogy problems relative to 1-relational problems that required them to select from several images the one that was most semantically related to a cue image (figure 5.5*A*).

In left VLPFC, a region involved in the effortful retrieval of individual semantic relations between items (see, for example, Badre & Wagner, 2007), no consistent differences were observed between children and adults (Wright, 2008). However, older children did engage this region more strongly than younger children, indicating that left VLPFC contributes increasingly to controlled semantic retrieval between the ages of 6 and 13.

In bilateral RLPFC, the time-course analyses provided strong evidence for an immature activation profile in children (figure 5.6). The peak of activation in RLPFC occurred at least 4 seconds later for children than for adults, despite minimal differences in response times between the groups. In fact, for children, RLPFC activation peaked after the motor cortex activation associated with the behavioral response. Overall, consistent with a model whereby relatively more rostral PFC matures later than caudal PFC (Bunge & Zelazo, 2006), larger differences between children and adults were observed in RLPFC than in VLPFC. Changes in the function of RLPFC over childhood and adolescence may contribute to improvements in reasoning ability, and individual differences in RLPFC functioning may explain, at least in part, why some people have a greater capacity for fluid reasoning than others.

Raven's Progressive Matrices In the second study, our laboratory (Crone, in press) presented children aged 8–12 and young adults with problems adapted from the Raven's Progressive Matrices (figure 5.4). Behaviorally, children made a disproportionate number of errors on the REL-2 problems relative to REL-1 problems, and their response times on the REL-2 problems did not differ from those of adults. This finding suggests that children selected responses for these difficult problems before adequately considering both dimensions of relational change.

In adults, RLPFC activation was greater for REL-2 problems than for REL-1 problems. While children also recruited RLPFC, they did not exhibit sustained preferential recruitment of RLPFC for REL-2 problems as compared with REL-1 problems. Together with the response time data, this finding suggests that the children were more likely to treat

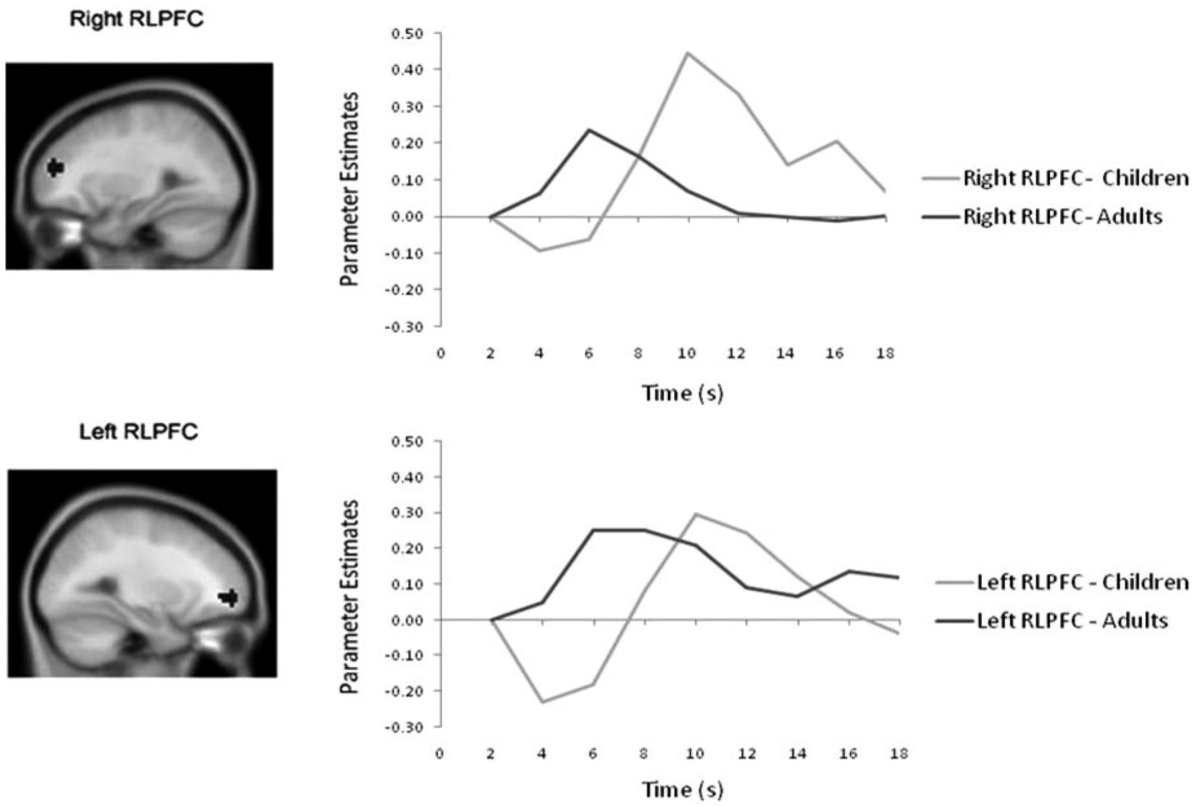

FIGURE 5.6 RLPFC regions of interest and time courses. On the left side of this image, the right and left RLPFC regions of interest are shown in a sagittal view. The right side displays time courses from these regions from baseline at 2 seconds through 18 seconds after trial onset for both children and adults. Bilaterally, the peak of activation occurs about 4 seconds later in children than in adults, and these regions even appear deactivated during the first few seconds of stimulus presentation.

the REL-2 problems similarly to REL-1 problems, considering only a single dimension of change. Activation of RLPFC associated with the REL-2 problems increases with age, indicating that development of RLPFC integration mechanism occurs, at least in part, over the age range (8–12 years) that was studied. Unlike RLPFC, the inferior parietal lobule was sensitive to the number of relations in adults and showed an immature pattern of activation in children. In summary, this study provides evidence that the development of reasoning is associated with functional changes in RLPFC in response to relational integration.

In summary, fluid reasoning ability comes online early in childhood but continues to develop through adolescence and even into adulthood. Intelligence in adults is related to connectivity between PFC and parietal cortex (Shaw et al., 2006). Structural neuroimaging studies (Giedd, 2004) have shown that development of these regions, PFC and parietal cortex, follows a prolonged developmental time course that matches behavioral data on reasoning in childhood (Richland et al., 2006). Initial functional neuroimaging studies have shown that children recruit brain regions similar to those that adults use to solve analogy problems, but with different patterns of activation suggesting functional immaturity (Wright, 2008; Crone, in press).

Conclusions

A growing literature indicates that the increased recruitment of task-related regions in prefrontal and parietal regions contribute to improvements in goal-directed behavior over middle childhood and adolescence. The pattern of developmental changes in brain activation has been generally characterized as a shift from diffuse to focal activation (Durston, Davidson, et al., 2006) and from posterior to anterior activation (Rubia et al., in press; T. Brown, Lugar, et al., 2005). 14 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 on one set of brain regions to another (T. Brown et al., 2005; T. Brown, Petersen, et al., 2006; Rubia et al., in press; Scherf et al., 2006; Badre & Wagner, 2007). Importantly, the precise pattern of change observed depends on the task, the ages being examined, and the brain region in question. By further characterizing neurodevelopmental changes in cognitive control processes within subjects and across a range of tasks, we hope to better understand the development of the human mind.

CURRENT AND FUTURE DIRECTIONS By around age 12, the ability to hold goal-relevant information in mind and use it to select appropriate actions is already adequate, although not fully mature. 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 onward, although the spatiotemporal resolution of this method is suboptimal. It is now possible to acquire fMRI data in children as young as four years of age (Cantlon, Brannon, et al., 2006), although not without challenges like 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 yet 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 allow us to investigate effects of age and effects of practice independently and to test whether inherent age differences in performance and brain activation are still present after substantial practice (Luna & Sweeney, 2004; Qin, Carter, et al., 2004).

Thus far, all but one (Durston et al., 2006) of the published developmental fMRI studies on working memory or cognitive control have compared groups of individuals at different ages. While these cross-sectional studies are valuable, they provide only a coarse indicator of developmental change. It is also important to conduct longitudinal studies to characterize intraindividual changes in brain function with age.

To understand how goal-directed behavior is achieved, it will be necessary to know how PFC and parietal cortices interact with other brain regions. It is the maturation of a specific network, rather than a particular brain region, that determines how effectively a given brain process is carried out. Some information about these interactions can be gleaned from functional connectivity analyses of fMRI data. Another approach is to acquire fMRI and EEG data in the same group of participants, either in separate sessions or simultaneously (Debener, Ullsperger, et al., 2005). An important current and future direction for developmental neuroimaging studies is to examine developmental changes in interactions between brain regions, furthering the work of Fair and colleagues (2007) demonstrated in figure 5.2.

The examination of the normal developmental pathways of distinct control functions will be important for understanding sensitive periods in brain development. For example, damage to PFC in childhood has a much greater impact than does damage in adulthood, likely because this region is important for acquiring skills and knowledge during childhood (Eslinger, Flaherty-Craig, et al., 2004).

Finally, a better understanding of neurodevelopmental changes in healthy children will lead to insights into the reasons for impoverished goal-directed behavior in a number of neurodevelopmental disorders, such as attention-deficit/hyperactivity disorder (Vaidya, Bunge, et al., 2005; Durston, Mulder, et al., 2006) and Tourette syndrome (Peterson, Pine, et al., 2001; Baym, Corbett, et al., 2008).

REFERENCES

Adleman, N. E., Menon, V., et al. (2002). A developmental fMRI study of the Stroop color-word task. *Neuroimage*, *16*(1), 61–75. 15

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, *45*(13), 2883–2901.

Baym, C. L., Corbett, B. A., et al. (2008). Neural correlates of tic severity and cognitive control in children with Tourette syndrome. *Brain*, *131*(1), 165.

Blair, C. (2006). How similar are fluid cognition and general intelligence? A developmental neuroscience perspective on fluid cognition as an aspect of human cognitive ability. *Behav. Brain Sci.*, *29*(2), 109–125; discussion, 125–160.

Booth, J. R., Burman, D. D., et al. (2003). Neural development of selective attention and response inhibition. *Neuroimage*, *20*(2), 737–751.

Brocki, K. C., & Bohlin, G. (2004). Executive functions in children aged 6 to 13: A dimensional and developmental study. *Dev. Neuropsychol.*, *26*(2), 571–593.

Brown, R. G., & Marsden, C. D. (1990). Cognitive function in Parkinson's disease: From description to theory. *Trends Neurosci.*, *13*(1), 21–29. 16

Brown, T. T., Lugar, H. M., et al. (2005). Developmental changes in human cerebral functional organization for word generation. *Cerebral Cortex*, *15*(3), 275–290.

Brown, T. T., Petersen, S. E., et al. (2006). Does human functional brain organization shift from diffuse to focal with development? *Dev. Sci.*, *9*(1), 9–11.

Bunge, S. A., Dudukovic, N. M., et al. (2002). Immature frontal lobe contributions to cognitive control in children: Evidence from fMRI. *Neuron*, *33*(2), 301–311.

Bunge, S. A., Wendelken, C., et al. (2005). Analogical reasoning and prefrontal cortex: Evidence for separable retrieval and integration mechanisms. *Cerebral Cortex*, *15*(3), 239–249.

Bunge, S. A., & Wright, S. B. (2007). Neurodevelopmental changes in working memory and cognitive control. *Curr. Opin. Neurobiol.*, *17*(2), 243–250.

Bunge, S. A., & Zelazo. P. D. (2006). A brain-based account of the development of rule use in childhood. *Curr. Dir. Psychol. Sci.*, *15*(3), 118–121.

Cantlon, J. F., Brannon, E. M., et al. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biol*, *4*(5), e125.

Carroll, J. B. (1997). *The three-stratum theory of cognitive abilities*. New York: Guilford.

Case, R. (1992). The role of the frontal lobes in the regulation of cognitive development. *Brain Cogn.*, *20*(1), 51–73.

Casey, B. J., Cohen, J. D., et al. (1995). Activation of prefrontal cortex in children during a nonspatial working memory task with functional MRI. *2*, 221–229. 17

Casey, B. J., Tottenham, N., et al. (2005). Imaging the developing brain: What have we learned about cognitive development? *Trends Cogn. Sci. 9*(3), 104–110.

Cattell, R. B. (1971). *Abilities: Their structure, growth and action.* Boston: Houghton-Mifflin.

Cattell, R. B. (1987). *Intelligence: Its structure, growth and action.* Amsterdam: North-Holland.

Christoff, K., Prabhakaran, V., et al. (2001). Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage*, *14*(5), 1136–1149.

Crone, E. A., Wendelken, C., et al. (2004). *Contributions of prefrontal subregions to developmental changes in rule use.* San Diego: Society for Neuroscience.

Crone, E. A., Wendelken, C., et al. (2006). Neurocognitive development of the ability to manipulate information in working memory. *Proc. Natl. Acad. Sci. USA*, *103*(24), 9315–9320.

18 Crone, E. A., Wendelken, C., van Leijenhorst, L., Honomichl, R., Christoff, K., & Bunge, S. A. (in press). Neurocognitive development of relational reasoning. *Dev. Sci.*

D'Esposito, M. (2007). From cognitive to neural models of working memory. *Philos. Trans. R. Soc. London [Biol.]*, *362*(1481), 761–772.

Debener, S., Ullsperger, M., et al. (2005). Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. *J. Neurosci.*, *25*(50), 11730–11737.

Dempster, F. N. (1993). Resistance to interference: Developmental changes in a basic processing mechanism. In M. L. H. R. Pasnak (Ed.), *Emerging themes in cognitive development: Vol. 1. Foundations* (pp. 3–27). New York: Springer-Verlag.

19 Diamond, A. (2002). Normal development of prefrontal cortex from birth to young adulthood: Cognitive functions, anatomy and biochemistry. In S. A. Knight (Ed.), *Principles of frontal lobe function* (pp. 466–503). Oxford, UK: Oxford University Press.

Durston, S., Davidson, M. C., et al. (2006). A shift from diffuse to focal cortical activity with development. *Dev. Sci.*, *9*(1), 1–8.

Durston, S., Mulder, M., et al. (2006). Activation in ventral prefrontal cortex is sensitive to genetic vulnerability for attention-deficit hyperactivity disorder. *Biol. Psychiatry*, *60*(10), 1062–1070.

Durston, S., Thomas, K. M., et al. (2002). A neural basis for the development of inhibitory control. *Dev. Sci.*, *5*(4): F9-F16.

Edin, F., Macoveanu, J., et al. (2007). Stronger synaptic connectivity as a mechanism behind development of working memory-related brain activity during childhood. *J. Cogn. Neurosci.*, *19*(5), 750.

20 Eslinger, P. J., Flaherty-Craig, C. V., et al. (2004). Developmental outcomes after early prefrontal cortex damage. *Brain Cogn.*, *55*(1), 84–10320.

Fair, D. A., Dosenbach, N. U., et al. (2007). Development of distinct control networks through segregation and integration. *Proc. Natl. Acad. Sci. USA*, *104*(33), 13507–13512.

Ferrer, E., & McArdle, J. J. (2004). An experimental analysis of dynamic hypotheses about cognitive abilities and achievement from childhood to early adulthood. *Dev. Psychol.*, *40*(6), 935–952.

Ferrer, E. McArdle, J. J., Shaywitz, B. A., Holahan, J. N., Marchione, K., & Shaywitz, S. E. (2006). Longitudinal models of developmental dynamics between reading and cognition from childhood to adolescence. *Dev. Psychol.*, *43*, 1460–1473.

Flynn, J. (2007). *What is intelligence?* New York: Cambridge University Press.

Ford, K. A., Goltz, H. C., et al. (2005). Neural processes associated with antisaccade task performance investigated with event-related fMRI. *J. Neurophysiol.*, *94*(1), 429–440.

Fuster, J. M. (2002). Frontal lobe and cognitive development. *J. Neurocytol.*, *31*(3–5), 373–385.

Gentner, D. (1983). Structure-mapping: A theoretical framework for analogy. *Cogn. Sci.*, *7*, 155–170.

Gentner, D. (1988). Metaphor as structure mapping: The relational shift. *Child Dev.*, *59*, 47–59.

Giedd, J. N. (2004). Structural magnetic resonance imaging of the adolescent brain. *Ann. NY Acad. Sci.*, *1021*, 77–85.

Giedd, J. N., Blumenthal, J., et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neurosci.*, *2*(10), 861–863.

Gogtay, N., Giedd, J. N., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proc. Natl. Acad. Sci. USA*, *101*(21), 8174–8179.

Gogtay, N., Nugent, T. F., 3rd, et al. (2006). Dynamic mapping of normal human hippocampal development. *Hippocampus*, *16*(8), 664–672.

Goldman-Rakic, P. S. (1992). Working memory and the mind. *Sci. Am.*, *267*(3), 110–117.

Goswami, U. (1989). Relational complexity and the development of analogical reasoning. *Cogn. Dev.*, *4*, 251–268.

Gottfredson, L. S. (1997). Why g matters: The complexity of everyday life. *Intelligence*, *24*, 79–132.

Gray, J. R., Chabris, C. F., et al. (2003). Neural mechanisms of general fluid intelligence. *Nature Neurosci.*, *6*(3), 316–322.

Horn, J. L. (1988). Thinking about human abilities. In J. R. N. a. R. B. Catell (Eds.), *Handbook of multivariate experimental psychology* (pp. 645–685). New York: Academic Press. 21

Horn, J. L. (1991). Measurement of intellectual capacities: A review in theory. In K. S. McGrew, J. K. Werder, & R. W. Woodcock (Eds.), *Woodcock-Johnson technical manual* (pp. 197–246). Allen, TX: DLM Teaching Resources.

Horn, J. L., & Cattell, R. B. (1967). Age differences in fluid and crystallized intelligence. *Acta Psychol. (Amst.)*, *26*, 107–129.

Huizinga, M., Dolan, C. V., et al. (2006). Age-related change in executive function: Developmental trends and a latent variable analysis. *Neuropsychologia*, *44*(11), 2017–2036.

Hummel, J. E., & Holyoak, K. J. (1997). Distributed representations of structure: A theory of analogical access and mapping. *Psychol. Rev.*, *10*(3), 427–466.

Inhelder, B. P., J. (1958). *The growth of logical thinking from childhood to adolescence.* New York: Basic Books. 22

Kline, P. (1993). *The handbook of psychological testing.* London: Routledge.

Klingberg, T., Forssberg, H., et al. (2002a). Increased brain activity in frontal and parietal cortex underlies the development of visuospatial working memory capacity during childhood. *J. Cogn. Neurosci.*, *14*(1), 1–10.

Klingberg, T., Forssberg, H., et al. (2002b). Training of working memory in children with ADHD. *J. Clin. Exp. Neuropsychol.*, *24*(6), 781–791.

Klingberg, T., Vaidya, C. J., et al. (1999). Myelination and organization of the frontal white matter in children: A diffusion tensor MRI study. *Neuroreport*, *10*(13), 2817–2821.

Kroger, J. K., Sabb, F. W., et al. (2002). Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: A parametric study of relational complexity. *Cerebral Cortex*, *12*(5), 477–485.

Kwon, H., Reiss, A. L., et al. (2002). Neural basis of protracted developmental changes in visuo-spatial working memory. *Proc. Natl. Acad. Sci. USA*, *99*(20), 13336–13341.

Lamm, C., Zelazo, P. D., et al. (2006). Neural correlates of cognitive control in childhood and adolescence: Disentangling the contributions of age and executive function. *Neuropsychologia*, *44*(11), 2139.

Liston, C., Watts, R., et al. (2006). Frontostriatal microstructure modulates efficient recruitment of cognitive control. *Cerebral Cortex*, *16*(4), 553–560.

Luciana, M., & Nelson, C. A. (1998). The functional emergence of prefrontally-guided working memory systems in four- to eight-year-old children. *Neuropsychologia*, *36*(3), 273–293.

Luna, B., & Sweeney, J. A. (2004). The emergence of collaborative brain function: FMRI studies of the development of response inhibition. *Ann. NY Acad. Sci.*, *1021*, 296–309.

23 Marsh, R., Zhu, H., et al. (2006). A developmental fMRI study of self-regulatory control. *Hum. Brain Mapping*, *27*(11), 848–863.

McArdle, J. J. (2001). A latent difference score approach to longitudinal dynamic structural analysis. In S. d. T. R. Cudeck & D. Sörbom (Eds.), *Structural equation modeling: Present and future: A Festschrift in honor of Karl Jöreskog* (pp. 341–380). Lincolnwood, IL: Scientific Software International.

McArdle, J. J., Ferrer-Caja, E., et al. (2002). Comparative longitudinal structural analysis of growth and decline of multiple intellectual abilities over the lifespan. *Dev. Psychol.*, *38*(1), 113–142.

McArdle, J. J., & Woodcock, J. R. (1998). *Human cognitive abilities in theory and practice*. Mahwah, NJ: Lawrence Erlbaum Associates.

24 McGrew, K. S. (1997). Analysis of the major intelligence batteries according to a proposed comprehensive Gf-Gc framework. In J. L. G. D. P. Flanagan & P. L. Harrison (Eds.), *Contemporary intellectual assessment: Theories, tests, and issues* (pp. 131–150). New York: Guilford.

Miller, G. A., Galanter, E., et al. (1960). *Plans and the structure of behavior*. New York: Holt, Rinehart & Winston.

Morrison, R. G., Krawczyk, D. C., et al. (2004). A neurocomputational model of analogical reasoning and its breakdown in frontotemporal lobar degeneration. *J. Cogn. Neurosci.*, *16*(2), 260–271.

Munakata, Y., Casey, B. J., et al. (2004). Developmental cognitive neuroscience: Progress and potential. *Trends Cogn. Sci.*, *8*(3), 122–128.

Nagy, Z., Westerberg, H., et al. (2004). Maturation of white matter is associated with the development of cognitive functions during childhood. *J. Cogn. Neurosci.*, *16*(7), 1227–1233.

O'Donnell, S., Noseworthy, M. D., et al. (2005). Cortical thickness of the frontopolar area in typically developing children and adolescents. *Neuroimage*, *24*(4), 948–954.

Olesen, P. J., Nagy, Z., et al. (2003). Combined analysis of DTI and fMRI data reveals a joint maturation of white and grey matter in a fronto-parietal network. *Brain Res. Cogn. Brain Res.*, *18*(1), 48–57.

Petanjek, Z., Judas, M., et al. (2008). Lifespan alterations of basal dendritic trees of pyramidal neurons in the human prefrontal cortex: A layer-specific pattern. *Cerebral Cortex*, *18*(4), 915–929.

Peterson, B. S., Pine, D. S., et al. (2001). Prospective, longitudinal study of tic, obsessive-compulsive, and attention-deficit/hyperactivity disorders in an epidemiological sample. *J. Am. Acad. Child Adolesc. Psychiatry*, *40*(6), 685–695.

Petrides, M., & Pandya, D. N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *J. Comp. Neurol.*, *228*(1), 105–116.

Piaget, J. M., J., & Billeter, J. (1977). La formation des correlates. In J. Piaget (Ed.), *Recherches sur l'abstraction reflechissante* (pp. 115–129). Paris: Presses Universitaires de France.

Polli, F. E., Barton, J. J. S., et al. (2005). Rostral and dorsal anterior cingulate cortex make dissociable contributions during antisaccade error commission. *Proc. Natl. Acad. Sci. USA*, *102*(43), 15700–15705.

Prabhakaran, V., Smith, J. A. L., et al. (1997). Neural substrates of fluid reasoning: An fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test. *Cogn. Psychol.*, *33*, 43–63.

Qin, Y., Carter, C. S., et al. (2004). The change of the brain activation patterns as children learn algebra equation solving. *Proc. Natl. Acad. Sci. USA*, *101*(15), 5686.

Raven, J. C. (1941). Standardization of progressive matrices. *Br. J. Med. Psychol.*, *19*, 137–150.

Richland, L. E., Morrison, R. G., et al. (2006). Children's development of analogical reasoning: Insights from scene analogy problems. *J. Exp. Child Psychol.*, *94*(3), 249–273.

Rubia, K., Russell, T., et al. (2001). Mapping motor inhibition: Conjunctive brain activations across different versions of go/no-go and stop tasks. *Neuroimage*, *13*(2), 250–261.

Rubia, K., & Smith, A. (2004). The neural correlates of cognitive 25
time management: A review. *Acta Neurobiol. Exp.*, *64*, 329–340.

Rubia, K., Smith, A. B., et al. (2006). Progressive increase of frontostriatal brain activation from childhood to adulthood during event-related tasks of cognitive control. *Hum. Brain Mapping*, *27*(12), 973–993.

Rubia, K., Smith, A. B., et al. (in press). Development of inhibi- 26
tion and error detection in fMRI. *Hum. Brain Mapping*.

Schaie, K. W. (1996). *Intellectual development in adulthood: The Seattle Longitudinal Study*. New York: Cambridge University Press.

Scherf, K. S., Sweeney, J. A., et al. (2006). Brain basis of developmental change in visuospatial working memory. *J. Cogn. Neurosci.*, *18*(7), 1045.

Schroeter, M. L., Zysset, S., et al. (2004). Prefrontal activation due to Stroop interference increases during development—An event-related fNIRS study. *Neuroimage*, *23*(4), 1317–1325.

Shaw, P., Greenstein, D., et al. (2006). Intellectual ability and cortical development in children and adolescents. *Nature*, *440*(7084), 676–679.

Sowell, E. R., Peterson, B. S., et al. (2003). Mapping cortical change across the human life span. *Nature Neurosci.*, *6*(3), 309–315.

Sowell, E. R., Peterson, B. S., et al. (2007). Sex differences in cortical thickness mapped in 176 healthy individuals between 7 and 87 years of age. *Cerebral Cortex*, *17*(7), 1550–1560.

Spear, L. P. (2007). The developing brain and adolescent-typical 27
behavior patterns: An evolutionary approach. In D. W. Romer (Ed.), *Adolescent psychopathology and the developing brain: Integrating brain and prevention science* (pp. 9–30). New York: Oxford University Press.

Sternberg, R. J., & Rifkin, B. (1979). The development of analogical reasoning processes. *J. Exp. Child Psychol.*, *27*(2), 195–232.

Sternberg, R. J. D., C. (1982). The development of higher-order 28
reasoning in adolescence. *Child Dev.*, *53*, 209–221.

Sternberg, R. J. N., G. (1980). Developmental patterns in the solution of verbal analogies. *Child Dev.*, *51*, 27–38.

Tamm, L., Menon, V., et al. (2002). Maturation of brain function associated with response inhibition. *J. Am. Acad. Child Adolesc. Psychiatry*, *41*(10), 1231–1238.

Thomas, K. M., King, S. W., et al. (1999). A developmental functional MRI study of spatial working memory. *Neuroimage*, *10*(3, Pt. 1), 327–338.

Vaidya, C. J., Bunge, S. A., et al. (2005). Altered neural substrates of cognitive control in childhood ADHD: Evidence from functional magnetic resonance imaging. *Am. J. Psychiatry*. *162*(9), 1605–1613.

van den Wildenberg, W. P. M., & van der Molen, M. W. (2004). Developmental trends in simple and selective inhibition of compatible and incompatible responses. *J. Exp. Child Psychol.*, *87*(3), 201–220.

29 Velanova, K., Wheeler, M. E., et al. (2008). Maturational changes in anterior cingulate and frontoparietal recruitment support the development of error processing and inhibitory control. *Cerebral Cortex*.

Waltz, J. A., Knowlton, B. J., et al. (1999). A system for relational reasoning in human prefrontal cortex. *Psychol. Sci.*, *10*(2), 119–125.

Wechsler, D., & Stone, C. P. (1945). *Wechsler Memory Scale*. New York: Psychological Corporation.

Welsh, K., Butters, N., et al. (1991). Detection of abnormal memory decline in mild cases of Alzheimer's disease using CERAD neuropsychological measures. *Arch. Neurol.*, *48*, 278–281.

Wendelken, C. B., S. A. (under review). Relational processing: Distinct contributions of anterior prefrontal cortex and the hippocampus. *Nature Neurosci.* 30

Wright, S. B., Matlen, B. J., Baym, C. L., Ferrer, E., & Bunge, S. A. (2008). Neural correlates of fluid reasoning in children and adults. *Front. Hum. Neurosci.*, *1*(8).

Zelazo, P. D., Craik, F. I., et al. (2004). Executive function across the life span. *Acta Psychol. (Amst)*, *115*(2–3), 167–183.

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