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What have we learned about cognitive development from neuroimaging?

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Abstract

Changes in many domains of cognition occur with development. In this paper, we discuss neuroimaging approaches to understanding these changes at a neural level. We highlight how modern imaging methods such as functional magnetic resonance imaging (fMRI) and diffusion tensor imaging (DTI) are being used to examine how cognitive development is supported by the maturation of the brain. Some reports suggest developmental changes in patterns of brain activity appear to involve a shift from diffuse to more focal activation, likely representing a fine-tuning of relevant neural systems with experience. One of the challenges in investigating the interplay between cognitive development and maturation of the brain is to separate the contributions of neural changes specific to development and learning. Examples are given from the developmental neuroimaging literature. The focus is on the development of cognitive control, as the protracted developmental course of this ability into adolescence raises key issues. Finally, the relevance of normative studies for understanding neural and cognitive changes in developmental disorders is discussed.

Keywords: Cognition; Development; Functional MRI; DTI; ADHD

Over the last decade, investigators have become increasingly interested in how cognitive development is supported by the maturation of the brain (Casey, Tottenham, Liston, & Durston, 2005). Investigators interested in the interplay between the two have used a host of paradigms and methods to investigate this association. In the following paper, we review some of the methods that have been used to examine the behavioral and neural basis of the development of cognition. This paper is not intended as an exhaustive review of the literature, but rather as a discussion of how the study of development may benefit from neuroimaging approaches. We will focus largely on cognitive control, as the protracted developmental course of this ability into adolescence is relevant to a number of developmental disorders, such as attention deficit hyperactivity disorder (ADHD), childhood-onset schizophrenia, and childhood-onset obsessive–compulsive disorder. Illustrative examples from the developmental literature of other cognitive functions will also be discussed. In the final section of this manuscript, we will discuss some points from the ADHD-literature, as an example of how atypical development may be relevant to our understanding of typical developmental processes.

Cognitive control may be defined as the flexible regulation of thoughts and actions in the presence of competing ones, and is involved in many cognitive functions, including motor inhibition, interference inhibition, cognitive flexibility and attentional control. In recent years, the ability to flexibly adapt behavior has played a critical role in theories of cognitive development. These theories have characterized immature cognition as being particularly susceptible to interference (e.g., Brainerd & Reyna, 1993; Dempster, 1992; Munakata, 1998), with younger children having difficulties in overriding competing attentional or behavioral responses. This susceptibility to interference during childhood is illustrated by studies showing that performance on Stroop, flanker, and go no-go tasks continues to develop over childhood and does not reach full maturity until roughly 12 years or later (e.g., Carver, Livesey, & Charles, 2001; Diamond, Cruttenden, & Nederman, 1994; Diamond & Taylor, 1996; Enns & Akhtar, 1989; Enns & Cameron, 1987; Enns, Brodeur, & Trick, 1998; Gerstadt, Hong, & Diamond, 1994; Luria, 1961; Passler, Isaac, & Hynd, 1985; Ridderinkhof

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& Van der Molen, 1997; Ridderinkhof, Van der Molen, & Band, 1997; Tipper, Bourque, Anderson, & Brehaut, 1989; Van der Meere & Stemerdink, 1999). This work shows a developmental trend in the ability to suppress information and actions over the ages of 4–12 years, as indexed by mean reaction times and accuracy rates. Importantly, age-related differences in accuracy are not observed on these tasks in the absence of interfering information (e.g., Enns et al., 1998) illustrating the differential developmental trajectories for cognitive control relative to more simple, target detection tasks.

1. Structural brain development

Although pediatric neuroimaging is a relatively young field, several studies have begun to track the anatomical course of normal brain development (see, Durston et al., 2001, for a review). These structural MRI studies have shown an increase in brain volume over the first few years and then relative stability in brain volume by later childhood (Caviness, Kennedy, Richelme, Rademacher, & Filipek, 1996; Courchesne et al., 2000; Giedd et al., 1996, 1999; Reiss, Abrams, Singer, Ross, & Denckla, 1996; Thompson et al., 2000). The relative stability of total brain volume in later development belies a dynamic interplay of simultaneously occurring progressive and regressive events, with different regions following different time courses. Significant changes occur in regional cortical and subcortical gray matter volumes (Caviness et al., 1996; Giedd et al., 1996, 1999; Jernigan, Trauner, Hesselink, & Tallal, 1991; Sowell, Thompson, Holmes, Jernigan, & Togan, 1999; Sowell et al., 2003). Perhaps the most informative studies to date have been those tracking changes over time within individuals. These studies have shown differential development between different regions of the brain, where increases in cortical gray matter followed by volume loss apppear to occur first in sensori-motor and last in higher-order association cortices such as the dorsolateral prefrontal cortex (see Giedd, 2004 for a review; Gogtay et al., 2004). In another example of this approach, Sowell et al. (2004) tracked changes in cortical gray matter thickness longitudinally in preadolescent children, and showed regionally specific increases in classical language regions, accompanied by more widespread thinning in other cortical areas. Interestingly, they were also able to show a relationship between cortical thinning and improvements in language ability.

Simultaneous with ongoing changes in gray matter, white matter shows linear increases in volume during childhood and into adulthood, with changes appearing to follow a pattern from caudal to more rostral (Giedd et al., 1999; Jernigan et al., 1991; Paus et al., 1999; Pfefferbaum et al., 1994). Diffusion tensor imaging (DTI), a relatively new technique offers greater detail than conventional structural MRI techniques, as it provides information on the directionality and regularity of myelinated fiber tracts. Initial studies using this method have confirmed changes in cortical white matter pathways during development (e.g., Klingberg, Vaidya, Gabrieli, Moseley, & Hedehus, 1999). These changes presumably reflect the ongoing myelination of axons by oligodendrocytes, enhancing neuronal conduction and communication. The direct application of this methodology to examining development of cognitive control will be discussed in a subsequent section of this paper.

2. Structural brain changes and cognitive development

By definition, developmental changes in cognition coincide with changes in the brain. In order to inform us about the functional organization of the brain, investigators have begun to link neuroanatomical development to cognitive changes. For example, the basal ganglia have a number of projections to and from the prefrontal cortex and both brain regions mature relatively late (Sowell et al., 1999). As this circuitry has been implicated in goal-directed actions, development of this circuitry has been suggested to relate to the development of cognitively driven actions throughout childhood and adolescence. Reiss et al. (1996) have shown that the largest increase in prefrontal volume, in fact, takes place during this period of development consistent with this claim. However, these parallel changes could be coincident. A number of studies have begun to link developmental changes in brain anatomy to behavior (e.g., Olesen, Nagy, Westerberg, & Klingberg, 2003; Sowell et al., 2004). In one such example, Casey, Castellanos et al. (1997) showed correlations between performance on measures of impulse control and volumetric measures of the prefrontal cortex and basal ganglia in healthy children relative to children with ADHD. Such correlational analyses are intriguing as they suggest a possible causal relationship between brain and behavior. However, they provide only an indirect link between the two, whereas advances in current imaging methods allow for more direct assessment of this relationship using non-invasive measures.

3. Functional brain changes and cognitive development

More direct investigations of structure–function associations and their development have been performed using functional magnetic resonance imaging (fMRI). These studies suggest different developmental trajectories of brain regions involved in cognitive control. A number of investigators have examined differential maturation of this function in frontal and parietal cortices (e.g., Booth et al., 2003; Luna et al., 2001; Rubia et al., 2000). For example, Adleman et al. (2002) used a Stroop task to show that increases in activation associated with improved cognitive performance occurred by adolescence for the parietal lobe, whereas increases in prefrontal activation continued into adulthood. Similar findings have been reported for the development of working memory, where increased capacity is supported by higher levels of activation in prefrontal and parietal cortices in adolescents compared to children (Casey et al., 1995; Klingberg, Forssberg, & Westerberg, 2002). A number of investigators have suggested that maturation is not only associated with enhanced activation in areas that are critical for task performance, but also with attenuation of activation in non-critical areas. For example, Tamm, Menon, & Reiss (2002) showed that maturation was associated with more focal activation in areas critical for task performance on a go no-go task.