

Development of the Teenage Brain

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ABSTRACT—Adolescence is a time characterized by change—hormonally, physically, and mentally. We now know that some brain areas, particularly the frontal cortex, continue to develop well beyond childhood. There are two main changes with puberty. First, there is an increase in axonal myelination, which increases transmission speed. Second, there is a gradual decrease in synaptic density, indicating significant pruning of connections. These neural changes make it likely that cognitive abilities relying on the frontal cortex, such as executive functions and social-cognitive abilities, also change during adolescence. Here, we review recent research that has demonstrated development during adolescence of a variety of social-cognitive abilities and their neural correlates.

INTRODUCTION

Although it has long been recognized that adolescence is a time when children undergo very significant social and cognitive development, until recently, little consideration was given to any role that brain maturation might play in these developments. However, research has begun to suggest that the human brain may be adaptive to the behaviorally demanding social environment during adolescence. In recent years, there has been an increase in research into adolescent behavior and cognition. This may in part be due to new data about brain development during this period and, on the other hand, may relate to broader social issues concerning reports of relatively high rates of psychiatric morbidity during adolescence evidenced epidemiologically and anecdotally and documented in popular media (Green, McGinnity, Meltzer, Ford, & Goodman, 2004). Although adolescence presents a period of

maturation in terms of cognitive control, reaction speed, reasoning, and decision-making skills, compared with childhood, it also marks a period of increased rates of depression, substance abuse, suicide, eating disorders, and other risky behaviors (Dahl, 2004; Spear, 2000). It is likely that this paradox arises due to developmental trajectories of cognitive skills that do not occur in sync. For example, certain abilities, such as emotion regulation, may develop later than others, such as motor control, during adolescence. What can knowledge about brain development tell us about the underlying reasons for strengths in certain abilities and vulnerabilities of others and the possibilities for interventions in the clinic, in the classroom, and in general? Indeed, social, cultural, and family life become increasingly complex in late childhood and adolescence and are likely to present new and challenging contexts for adolescents and a sensitive developmental period. It is likely that interactions between social and neural influences underpin behaviors linked to emotional and cognitive control that emerge in adolescence. The role of brain development in particular, however, remains relatively understudied.

In the past few years, several pioneering experiments have investigated the development of the brain and cognitive processes during this period of life. Even though brain adaptation can occur throughout the life span, the maturational phases during early life, that is, during fetal development, childhood, and adolescence, are thought to be the most dramatic (Toga, Thompson, & Sowell, 2006). Recent brain imaging studies suggest that cortical plasticity during adolescence is associated with cognitive development, particularly in executive function and social cognition. The first section of this article summarizes the cellular studies that first demonstrated anatomical brain developments during adolescence. We then go on to describe how recent brain imaging techniques have supported these findings and have shed some light on the trajectories of maturational processes in the brain during adolescence. The final section discusses research on social-cognitive processing in adolescence and suggests that brain maturation may play a role in at least some of these changes, which in turn are likely to be linked to the large shifts in social behavior that characterize this period. We suggest that this brain development may facilitate sociocultural learning over the life span.

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BRAIN DEVELOPMENT DURING ADOLESCENCE

Histological Studies of the Adolescent Brain

The notion that the brain continues to develop after childhood is relatively new. Experiments on animals, starting in the 1950s, showed that sensory regions of the brain go through “sensitive periods” soon after birth, during which time environmental stimulation appears to be crucial for normal brain development and for normal perceptual development to occur (e.g., Hubel & Wiesel, 1962). It was not until the late 1970s that research on postmortem human brains revealed that some brain areas continue to develop well beyond early childhood, which in turn suggested that sensitive periods for the human brain may be more protracted than previously thought. It was shown that cellular events take different trajectories in different areas of the human brain (Huttenlocher, 1979). Synaptic density in the visual cortex reaches a peak during the fourth postnatal month and is followed by the elimination of synapses and the stabilization of synaptic density to adult levels before the age of 4. In contrast, the structure of the prefrontal cortex (PFC), the area of the brain associated with understanding other minds (social cognition) and coordinating thoughts and behaviors (executive function), undergoes significant changes during puberty and adolescence. Two main changes were revealed in the brain before and after puberty. As neurons develop, a layer of myelin is formed around their extension, or axon, from supporting “glial” cells. Myelin acts as an insulator and massively increases the speed of transmission (up to 100-fold) of electrical impulses from neuron to neuron. Whereas sensory and motor brain regions become fully myelinated in the first few years of life, although the volume of brain tissue remains stable, axons in the frontal cortex continue to be myelinated well into adolescence (Yakovlev & Lecours, 1967). The implication of this research is that the transmission speed of neural information in the frontal cortex should increase throughout childhood and adolescence.

The second difference in the brains of prepubescent children and adolescents pertains to changes in synaptic density in the PFC. Early in postnatal development, the brain begins to form new synapses, so that the synaptic density (the number of synapses per unit volume of brain tissue) greatly exceeds adult levels. This process of synaptic proliferation, called synaptogenesis, can last up to several months or years depending on the species of animal and brain region. These early peaks in synaptic density are followed by a period of synaptic elimination (or pruning) in which frequently used connections are strengthened and infrequently used connections are eliminated. This experience-dependent process, which occurs over a period of years, reduces the overall synaptic density to adult levels.

However, histological studies of monkey and human PFC have shown that synaptogenesis and synaptic pruning in

this area have a particularly protracted time course. These studies show that there is a proliferation of synapses in the subgranular layers of the PFC during childhood and again at puberty, followed by a plateau phase and a subsequent elimination and reorganization of prefrontal synaptic connections after puberty (Huttenlocher, 1979; Woo, Pucak, Kye, Matus, & Lewis, 1997). According to these data, in the human brain, synaptic pruning occurs throughout adolescence and results in a net decrease in synaptic density in the PFC during this time.

Magnetic Resonance Imaging Studies of Adolescent Brain Development

The scarcity of postmortem child and adolescent brains meant that knowledge of the adolescent brain was until recently extremely scanty. However, since the advent of magnetic resonance imaging (MRI), a number of brain imaging studies, using large samples of participants, have provided further evidence of the ongoing maturation of the cortex into adolescence and even into adulthood. In the past few years, several MRI studies have been performed to investigate the development of the structure of the brain during childhood and adolescence in humans (cf. Paus, 2005). The brain areas that undergo pronounced development during adolescence, in particular medial PFC and parietotemporal cortex, form parts of the “social brain,” that is, the network of brain regions involved in understanding other people.

Gray Matter and White Matter in the Adolescent Cortex

One of the most consistent findings from these MRI studies is that there is a steady linear increase in white matter (WM) in certain brain regions during childhood and adolescence. This change has been highlighted both in frontal and in temporoparietal regions (Sowell et al., 1999). Myelin appears white in MRI scans, and therefore, the increase in WM and decrease in gray matter (GM) with age was interpreted as reflecting increased axonal myelination in frontal cortex. The increased WM and decreased GM density in frontal as well as temporal and parietal cortex throughout adolescence has now been demonstrated by several studies carried out by a number of different research groups with increasingly large groups of participants (e.g., Giedd et al., 1996, 1999).

Although the increase in WM in certain brain regions seems to be linear across all brain areas, the changes in GM density appear to follow a region-specific, nonlinear pattern. MRI data demonstrate that changes in the frontal and parietal regions are similarly pronounced (Giedd et al., 1999). The study by Giedd and colleagues showed that the volume of GM in the frontal lobe increased during preadolescence with a peak occurring at around 12 years for boys and 11 years

for girls, followed by a decline after adolescence. Similarly, parietal lobe GM volume increased during the preadolescent stage to a peak at around 12 years for boys and 10 years for girls, again followed by decline during postadolescence. GM development in the temporal lobes was also nonlinear, but the peak was reached later at about 17 years. Although frontal and parietal cortex development is relatively rapid during adolescence (Sowell, Thompson, Tessner, & Toga, 2001), GM volume in the superior temporal cortex, including superior temporal sulcus (STS), steadily declines during adolescence and across the lifetime, following an inverted U curve and reaching maturity relatively late (Gogtay et al., 2004; Toga et al., 2006).

In a study of participants between 4 and 21 of age, frontal lobe maturation was shown to occur in a back-to-front direction, starting in the primary motor cortex (the precentral gyrus), then extending anteriorly over the superior and inferior frontal gyri (Gogtay et al., 2004). The PFC was shown to develop relatively late. In the posterior half of the brain, the maturation began in the primary sensory area, spreading laterally over the rest of the parietal lobe. Lateral temporal lobes were the last to mature. It has been proposed that those brain areas associated with more basic cognitive skills, such as motor and sensory functions matured first, followed by brain areas including parietal cortex linked to spatial orientation and attention and finally the regions related to executive function and social cognition (PFC).

The MRI results demonstrating a nonlinear decrease in GM in various brain regions throughout adolescence have been interpreted in two ways. First, it is likely that axonal myelination results in an increase in WM and a simultaneous decrease in GM as viewed by MRI. A second additional explanation is that the GM changes reflect the synaptic reorganization that occurs at the onset of and after puberty. Thus, the increase in GM apparent at the onset of puberty might reflect a wave of synapse proliferation at this time. In other words, the increase in GM at puberty has been interpreted to reflect a sudden increase in the number of synapses. At some point after puberty, there is a process of refinement such that these excess synapses are eliminated (Huttenlocher, 1979). It is speculated that this synaptic pruning is reflected by a steady decline in GM density seen in MRI (cf. Blakemore & Choudhury, 2006).

What do these developments of cortical structure mean for cognitive development? Some of the areas that undergo pronounced development during adolescence, in particular medial PFC and STS, are involved in social cognition, that is, understanding and interacting with others. Recent behavioral and neuroimaging studies have investigated the development of social cognition during adolescence. This research points to continued development of certain social-cognitive processes during this period of life. This research is described in the following section.

SOCIAL-COGNITIVE DEVELOPMENT DURING ADOLESCENCE

Behavioral and functional imaging studies consistently demonstrate maturation in executive functions during adolescence. These studies show improvements in reaction speeds, accuracy, and changes in functional activation in associated frontal regions of the brain with age in tasks that involve attentional control, cognitive flexibility, and problem solving (e.g., Anderson, Anderson, Northam, Jacobs, & Catroppa, 2001; Casey, Trainor, & Orendi, 1997; Tamm, Menon, & Reiss, 2002; see Blakemore & Choudhury, 2006, for review). There is less empirical data, however, relating to the association between social development and brain maturation in adolescence. Indeed, the period of adolescence involves new social encounters with peers and heightened awareness and interest in other people. The importance of evaluating other people may be associated with increased attention to socially salient stimuli, particularly faces, and the processing of emotional information and mental states. There is a rich literature on the development of social cognition in infancy and childhood pointing to stepwise changes in mentalizing (i.e., the attribution of mental states) during the first 5 years of life (Frith & Frith, 2006). However, although the early development of mentalizing has been well studied, there has been surprisingly little empirical research on social-cognitive development beyond childhood. In the following section, we summarize some of the key findings from studies investigating the implications of brain development for social cognition. There have been a relatively small number of experiments investigating the development of social cognition during adolescence, most of which have focused on face processing and mentalizing.

Development of Face Processing During Adolescence

Some of the earliest empirical studies on cognitive development during adolescence focused on the effect of puberty on face recognition. In one study, female participants 6–16 years of age performed a face recognition task (Carey, Diamond, & Woods, 1980). Although performance improved steadily during the first decade of life, this was followed by decline at around age 12. Puberty is implicated in this decline: A later study showed that midpubertal girls performed worse than prepubertal or postpubertal girls matched for age (Diamond, Carey, & Back, 1983). A more recent study also found evidence of a pubertal dip on a match-to-sample task in which emotional faces had to be matched to emotion words (McGivern, Andersen, Byrd, Mutter, & Reilly, 2002). Participants ranged in age from 10 to 17 years. A 10–20% increase in reaction time on the match-to-sample task occurred in the children of pubertal age (10- to 11-year-old girls and 11- to 12-year-old boys) compared with younger children.

Performance then improved, reaching its earlier level by about 16–17 years.

There is some indication that, for face processing tasks, activity in the frontal cortex increases between childhood and adolescence and then decreases between adolescence and adulthood. In a functional magnetic resonance imaging (fMRI) study of adolescents 13–17 years of age, the perception of happy faces compared with neutral was associated with significant bilateral amygdala activation (Yang, Menon, Reid, Gotlib, & Reiss, 2003). The effect of age was addressed by Thomas et al. (2001) in their investigation of amygdalar response to fearful facial expressions in two groups: a group of children (*M* age 11 years) and adults (*M* age 24 years). Adults relative to children demonstrated greater amygdala activation to fearful facial expressions, whereas children relative to adults showed greater amygdala activation to neutral faces. It was argued that the children perceived the neutral faces as more ambiguous than the fearful facial expressions, with resulting increases in amygdala activation to the neutral faces. Sex differences in amygdala-mediated cognitive development have also been reported to occur during adolescence. In an fMRI study that investigated the recognition of fearful faces, female (but not male) participants showed increased activation in dorsolateral PFC in response to fearful faces between childhood and adolescence (Killgore, Oki, & Yurgelun-Todd, 2001). Another study reported increased activity in PFC (bilaterally for girls and right sided for boys) in response to fearful faces between age 8 and 15 (Yurgelun-Todd & Killgore, 2006). In a recent study of face processing, when attention was directed to a nonemotional aspect of fearful faces (relative to neutral faces), activity was found to increase in orbitofrontal cortex in adolescents compared to adults (Monk et al., 2003).

Development of Mentalizing During Adolescence

fMRI studies of mental state attribution also show decreases in activity between adolescence and adulthood. A recent fMRI study investigated the development of communicative intent using an irony comprehension task. A group of 12 adults (6 men), ranging in age from 23 to 33 years, and a group of 12 children (6 boys), ranging in age from 9 to 14 years, were scanned (Wang, Lee, Sigman, & Dapretto, 2006). Children engaged medial PFC and left inferior frontal gyrus more than did adults in this task. The authors interpreted the increased medial PFC activity in children as reflecting the increased processing demands of this task (compared to adults) of needing to integrate several cues to resolve the discrepancy between the literal and the intended meaning of an ironic remark.

A similar region of medial PFC was more highly activated by children than by adults in a recent fMRI study that involved thinking about one's own intentions (Blakemore, den Ouden, Choudhury, & Frith, 2007). Thinking about your

own, or someone else's intentions to act, requires mental state representation, so this task was expected to activate the mentalizing network. A group of 19 female adolescents (age range 12–18 years) and a group of female adults (age range 22–38 years) were presented with scenarios about causes and effects. In both adults and adolescents, the intentional causality relative to the physical causality condition activated the classic mentalizing network including medial PFC and posterior STS. However, the interaction between group and condition resulted in differential activity within the mentalizing network. Medial PFC was activated more by adolescents than by adults when thinking about intentions relative to thinking about physical causality. Conversely, a region in right STS was more active in adults than in adolescents when thinking about intentions relative to thinking about physical causality. These results suggest that the neural strategy for thinking about intentions changes between adolescence and adulthood. Although the same neural network is active, the relative roles of the different areas change, with activity moving from anterior (medial PFC) regions to posterior (STS) regions with age.

Although as yet there have only been a handful of developmental neuroimaging studies of social cognition, there does seem to be some consistency with respect to the direction of change in frontal activity. Overall, the studies reviewed above have found that activity in PFC decreases during adolescence. This might be because adolescence represents a time in which the frontal cortex is being fine-tuned by synaptic pruning. Thus, with age, less activity (as seen in fMRI) is associated with carrying out the task in question. An alternative, or additional, explanation is that there is a change in the cognitive strategy for mentalizing, which will result in different brain regions being recruited.

Whichever explanation turns out to be the correct one, the data might have implications for learning and behavior during adolescence. It is proposed that synaptic pruning in early development fine-tunes neural circuitry in an input-dependent manner. Synaptic pruning is thought to underlie sound categorization, for example. Learning one's own language initially requires categorizing the sounds that make up language. Newborn babies are able to distinguish between all speech sounds. Sound organization is determined by the sounds in a baby's environment in the first 12 months of life—by the end of their 1st year, babies lose the ability to distinguish between sounds to which they are not exposed (see Kuhl, 2004). The ability to distinguish certain speech sounds depends on being exposed to those distinct sounds in early development. Before about 12 months of age, babies brought up in the United States can detect the difference between certain sounds common in the Hindi language, which after 12 months, they cannot distinguish (Werker, Gilbert, Humphrey, & Tees, 1981). In contrast, babies brought up hearing the Hindi language at the same age become even

better at hearing this distinction because they are exposed to these sounds in their language. This fine-tuning of sound categorization is thought to rely on the pruning of synapses in sensory areas involved in processing sound.

It is unknown whether the pruning of synapses in frontal cortex during adolescence is similarly influenced by the environment. If this turns out to be the case, it would have profound implications for the kinds of experiences and environments that are optimal for teenage brain development.

CONCLUSION AND IMPLICATIONS FOR TEENAGERS

In this article, we have reviewed evidence that certain brain regions undergo substantial development during adolescence. Recent studies of social-cognitive development, coupled with neuroanatomical findings, during this period of life suggest that there is a peak in activity within PFC during early adolescence, which reflects the peak in synaptic density and GM in this region. It has been suggested that the functioning of PFC is temporarily perturbed by the wave of synaptogenesis that occurs at puberty. Only later in adolescence does synaptic pruning render this region more efficient, such that less neural activity will correlate with the same task performance.

Research into the cognitive implications of continued brain maturation beyond childhood may be relevant to understanding the social development and educational attainment of adolescents. Further studies are necessary to reach a consensus about how axonal myelination and synaptic proliferation and pruning impact on social, emotional, linguistic, mathematical, and creative development. Several important questions deserve to be investigated: Which skills undergo perturbation? Which undergo sensitive periods for learning? How does the quality of the environment interact with brain changes in the development of cognition? Whether greater emphasis on social and emotional cognitive development would be beneficial during adolescence is unknown, but research will provide insights into potential intervention schemes in secondary schools.

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