Structural and functional changes in the prefrontal lobes of the adolescent brain: Implications for executive function

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Abstract
Adolescence is a period of life when profound behavioural and physical changes occur. However, the notion that the brain also undergoes significant changes during this time period is fairly recent, and has arisen due to advances that now make it possible to use (f)MRI and similar imaging techniques in order to track the functioning of specific brain structures. These technical developments have made it possible to safely observe developmental brain changes in children and adolescents. The results of these studies clearly show that the brain matures well into young adulthood. The present article is a review of literature on both structural and functional developmental changes in the prefrontal lobes of the adolescent brain. These studies suggest that the brain areas that are responsible the higher cognitive abilities—which are collectively referred to as the "executive function" are not fully developed in adolescents' brains. Specific components of executive function include response inhibition, working memory and prospective memory. Because executive function plays a major role in decision-making processes, these findings may have serious implications for the appropriate organization of educational systems in which adolescents participate. Some of these implications for educational practice will be discussed in an accompanying article by Pama (2010) in this issue.

Keywords: adolescent brain, prefrontal cortex, developmental cognitive neuroscience, cognition, executive function.

Introduction

Adolescence is the phase of life that covers the transition between childhood and adulthood, and which starts with the onset of puberty around the age of 10 years (Crone, 2009). This period is mainly characterized by significant changes in behavior and appearance. Recent advances in brain imaging techniques, such as magnetic resonance imaging (MRI), made it possible to study structural and functional characteristics of the living brain. The results of neurocognitive studies using these imaging techniques suggest that some areas of the brain, including the prefrontal areas (see figure 1) [INSERT FIGURE 1 NEAR HERE], continue to mature during adolescence and even into young adulthood. These areas are known to be involved in higher cognitive processes, which are usually classified under the general label of the "executive function". This term refers to various higher order cognitive skills such as response inhibition, working memory, planning, and selective attention. Cognitive neuroscientists therefore infer that such cognitive abilities are also still developing in adolescents. These findings strongly suggest that there may be definite limitations as to the skills that adolescents are capable of acquiring.

As Claudia Pama argues in the accompanying article (Pama, 2010), this insight is of great importance for educational practice. She states that, in the Dutch educational system, adolescents of 14 or 15 years of age are required to make decisions which have far-reaching implications for their future. However, several components of executive function are still developing at that age. This means that the persons called upon to make such decisions may experience serious difficulties with regard to the selection of relevant information, the inhibition of impulsive behaviour and planning, all of which highly influence decision-making processes. Pama (2010) therefore questions the extent to which adolescents are aware of the long-term consequences of their decisions.

In addition, this finding has important implications for the expectations and demands that Dutch society imposes on children. The fact that adolescents are required to make decisions regarding their future implicitly shows that adolescents in the Netherlands are expected to be autonomous and to assume full responsibility for their actions and decisions. However, as the studies that will be discussed in this article will show, adolescents lack various abilities, and this fact makes it difficult for them to meet society's demands and expectations. Pama (2010) therefore argues that it is important to find out how society can help children and adolescents to make good decisions, bearing in mind that their decision-making abilities are not fully developed until young adulthood.

This review will first describe the structural brain changes that take place during adolescence. A distinction will be made between the development of white matter and grey matter. Here, the focus will be primarily on the maturation processes that occur in the prefrontal regions of the brain. These regions have consistently been shown to mature in adolescents. Afterward, studies will be examined that investigate the cognitive abilities that rely on the functioning of the prefrontal lobes. The emphasis in this discussion will be on some of the higher cognitive abilities, which are usually classified as specific components of executive function.

Structural changes in the adolescent brain

As previously mentioned, the notion that the brain continues to develop well into young adulthood is very recent. The first studies that showed significant changes in the prefrontal areas of the adolescent brain were conducted in the 1970s and 1980s. According to Blakemore and Choudhury (2006), these studies revealed two main developmental processes of the adolescent brain. The first of these is called myelination, and refers to the production of insulating fatty sheaths. These sheaths, called myelin or white matter, form around the extensions of neurons (see figure 2 at the end of the article). The insulation of these extensions results in an enormous increase in the transmission speed of electrical impulses from one neuron to another. Researchers have proposed that the resulting increase in transmission speed—which can reach 100 times the speed of unmyelinated neurons—leads to the facilitation of cognitive complexity and to the development of the ability to combine information from multiple sources (Giedd, 2004). Yakovlev and Lecours (1967, in Blakemore & Choudhury, 2006) found that myelination processes in the sensory and motor brain areas are completed during the first few years of life. In contrast, myelination in the prefrontal lobes has been shown to continue well into young adulthood.

The second mechanism refers to changes in synaptic density within the brain. Just after birth, the brain starts to form a large number of new connections among neurons, which results in an increase in synaptic density. This process, called synaptogenesis, takes place over the course of several months. After this period, the brain starts to eliminate certain synapses. Although the synaptic density decreases significantly, this elimination process results in the retention of useful connections and the loss of inefficient connections between neurons.

Next, studies in which both processes were investigated using modern brain scanning techniques will be elaborated in more detail. The most important imaging technique in this regard is magnetic resonance imaging (MRI), which produces three-dimensional images of brain structures (Blakemore & Choudhury, 2006).

White matter

One of the first studies that used MRI to investigate structural changes in the brain taking place during childhood and adolescence was performed by a group of researchers led by Elizabeth R. Sowell (Sowell et al., 1999). They recruited nine children aged between 7 and 10 years and nine adolescents aged between 12 and 16 years for participation in this study. The brain images of individuals in the two age groups were compared in order to determine possible age-related differences. Such differences were found in the frontal cortex and the parietal cortex. In both of these areas, a greater volume of white matter was observed in the brains of adolescents than in those of younger children. Conversely, the brain images of the younger children showed a greater density of grey matter than the brain images of adolescents. This suggests that both processes of myelination and synaptic eliminating take place during the transition from childhood to adolescence.

Because these results have been replicated by other research groups in several studies that were based on even greater numbers of subjects (see Blakemore & Choudhury, 2006), this can rightly be considered a robust finding. In general, neuroimaging studies show that linear increases in white matter density occur from childhood through early adulthood. Whereas researchers do not agree on all of the specific brain regions in which white matter density changes occur, the increase in white matter density in the prefrontal cortex seems to be a fairly consistent finding (Blakemore & Choudhury, 2006).

Grey matter

In other studies, neuroscientists concentrated on the developmental differences between children and adolescents with respect to grey matter density. One of the first MRI studies on this topic was carried out by Jay N. Giedd and his colleagues (Giedd et al., 1999). Results were obtained from an ongoing longitudinal pediatric brain MRI study, which at the time of publication involved 145 healthy subjects. Two or more MRI scans, acquired at approximately 2-year intervals, were available for a majority of participants in this study. The age of the participants ranged from 4.2 to 21.6 years old. It was found that changes in cortical grey matter generally tend to be non-linear and region-specific. With respect to the prefrontal lobes, the density of grey matter peaked at around 12 years for males and 11 years for girls. During post-adolescence, the volume of grey matter density in the prefrontal cortex declined and resulted in a net decrease. Even though changes in grey matter density in other areas of the brain follow the same nonlinear pattern as in the prefrontal areas, the peaks in density for those areas were reached at a later age.

Although these findings were replicated in later studies (see Blakemore & Choudhury, 2006), Sowell and her colleagues (Sowell et al., 2001) showed that the developmental changes in grey matter volume possibly continue for a longer period of time than was previously assumed. Their results suggest that the loss of grey matter in the prefrontal lobes continued well into adulthood—right up to the age of 30.

To summarize, the MRI studies described above consistently indicate the occurrence of linear increases in white matter density in prefrontal brain areas along with non-linear and region-specific decreases in grey matter volume.

Functional changes in the adolescent brain

On the basis of the above studies, it seems possible to confidently conclude that the brain is still maturing during later childhood and adolescence. In addition, some studies strongly suggest that certain developmental processes in the brain do not actually end until early adulthood (Sowell et al., 2001). It therefore seems reasonable to conclude that the cognitive abilities that rely on the functioning of these brain areas—especially the prefrontal areas—also go through changes during the same period. The most important method in this type of research is fMRI. Functional magnetic resonance imaging (fMRI) is a relatively recent scanning technique that gives researchers the opportunity to study the brain in action. Whereas magnetic resonance imaging (MRI) techniques map the structure of the brain, functional MRI detects differences in blood flow to particular regions in the brain. This is based on the assumption that active neurons require an increased amount of oxygen, which is delivered to them via blood. The fMRI scanner detects the oxygen through its magnetic properties (Blakemore & Choudhury, 2006). As of the publication date of this paper, only a few studies have been published using fMRI to examine the development of various components of executive function in the adolescent brain.

Executive function

The cognitive abilities that are consistently shown to rely on processes in the prefrontal lobes include response inhibition, working memory, and prospective memory. All of these are specific components of executive function. They play a major role in the control of thought and behavior. For example, they are responsible for the selection of relevant information, planning, and the inhibition of impulses (Blakemore & Choudhury, 2006). Previous findings suggesting that the brain areas responsible for these cognitive functions are still maturing during adolescence led researchers to perform fMRI studies to investigate the development of several components of executive function in adolescence. Several studies on response inhibition, spatial working memory, and prospective memory will be discussed in the following sections.

Response inhibition

The term “response inhibition” refers not only to the inhibition of impulses, but also to the selection of relevant information. One of the first studies that used fMRI to investigate developmental differences in brain activation patterns in the prefrontal cortex during response inhibition was performed by B. J. Casey and her colleagues (Casey et al., 1997). A group of nine children (7-12 years old) and nine adults (21-24 years old) were recruited for this study to perform a “Go-No-Go-task”. This task required the participants to press a button when any alphabetic letter (except for the letter X) was shown. When confronted with the letter X, they had to inhibit themselves from pressing the button.

No differences were observed between the age groups with respect to location of activation in the prefrontal cortex during the No-Go trials. In addition, a significantly higher amount of activation in the prefrontal cortices was observed in children as compared to adults, especially in the dorsolateral regions. Casey et al. (1997) propose the explanation that the increased volume of activation in distinct prefrontal regions is a way to compensate for the ineffective brain regions that are related to response inhibition. This view was based on the observation that the activity in prefrontal cortices of adults was restricted to a more focal region. It should be noted however, that no adolescent participants were included in this study.

However, strong support for this explanation was found in a related study by Tamm, Menon and Reiss (2002). The participants in this study ranged in age from eight to twenty years old. As in the study of Casey and her colleagues (Casey et al., 1997), no age-related differences in task accuracy were found. The results were consistent with the finding of Casey and her colleagues (Casey et al., 1997), in that discrete regions of the prefrontal lobes are more highly activated in younger participants. In addition, fMRI scans of the older subjects showed more focal activation in specific regions that are known to be involved in response inhibition. Furthermore, the negative correlation between age and brain activation supported the hypothesis of the earlier study that increased activation in children is a way to compensate for ineffective neural structures in the prefrontal cortex that are still maturing.

Similar results were obtained in studies that used other types of inhibition tasks. For example, Beatriz Luna and her colleagues (2001) recruited participants for a study involving an "antisaccade task". This task requires participants to deliberately inhibit reflexive eye movements toward new visual stimuli that occur in the visual field, and to instead direct their gaze to the opposite side of the visual field. This study found that there was increased activation in the prefrontal cortex in adolescents as compared to both children and adults. The difference between this finding and that of Casey and her colleagues (Casey et al., 1997), in which increased prefrontal activation in children relative to adults was found during the performance of the response inhibition task, can possibly be accounted for by the difference in task difficulty in the two studies. The "Go-No-Go-task" is generally considered an easier task than the more complex "antisaccade task". The fact that the youngest subjects made more errors in performing the antisaccade task is consistent with this explanation.

These fMRI studies appear to strongly support the conclusion that response inhibition heavily relies on the activation of the prefrontal areas. Furthermore, they showed that the amount of activation during task performance was inversely related to age. A higher degree of activation of the prefrontal cortices was found in both children (Casey et al., 1997; Tamm et al., 2002) and adolescents (Luna et al., 2001), as compared to adults. It therefore seems reasonable to suggest that, during the period from the age of 10 until the age of 30, activity in the prefrontal lobes that is related to response inhibition becomes more focal and specialized, while irrelevant and diffuse activity is reduced (Yurgelun-Todd, 2007).

Working memory

Working memory refers to the capacity to actively maintain information in order to use it in further processing (Baddeley, 1986 in Nelson et al., 2000). Therefore, working memory is assigned a major role in important higher-level cognitive processes such as planning and decision making (Nelson et al., 2000). Improvements in working memory during adolescence were found in a behavioral study by Vicki A. Anderson and her colleagues (2001). Unfortunately, only a few developmental fMRI studies on this topic have been conducted. Developmental changes in visuo-spatial working memory from childhood to adulthood were assessed in an fMRI study by Kwon, Reiss, and Menon (2002). They found that performance on the visuo-spatial working memory task gradually improved with age among subjects ranging in age from 7 to 22. In contrast to the finding in the majority of fMRI studies that concentrated on response inhibition, linear age-related increases in brain activation were found in several parts of the prefrontal areas (Kwon, Reiss & Menon, 2002). The authors concluded that the neural representations of visuo-spatial working memory, as well as this component of working memory itself, continue to mature into young adulthood.

Prospective memory

Prospective memory is a term that refers to the ability to keep in mind the intention to perform some action at a later point in time (Blakemore &

Choudhury, 2006). This type of memory has also been shown to rely on activity in the frontal lobes (Burgess et al., 2000 in Blakemore & Choudhury, 2006). Although no fMRI studies on this topic have been reported in the literature, Blakemore and Choudhury (2006) reported the results of a behavioral study which was presented at a scientific meeting in 2003 by Rachael Mackinlay and her colleagues. They performed a study in which a multitask paradigm was used to assess prospective memory. Adults were found to be significantly more accurate at this task than children ranging from 10 to 14 years old. Because no age-related differences in task accuracy were found in the latter group, the authors concluded that prospective memory primarily develops during late adolescence. Although this explanation has yet to be supported by any results from a study that also includes adolescents as participants, these findings may indicate that adolescents could encounter difficulties with planning. Such a finding has obvious implications with regard to the extent to which adolescents are able to think about the long-term consequences of their actions and decisions. This appears to be an interesting avenue for further investigation.

Limitations

Remember that most of the fMRI studies described above did not show differences in task accuracy between the younger and older participants. On the other hand, several behavioral studies clearly show that adolescents are more impulsive in their decision-making (Crone & Van der Molen, 2004), and that they perform worse than adults on tasks that measure working memory (Anderson et al., 2001) and prospective memory (Mackinlay et al., 2003 in Blakemore & Choudhury, 2006). Essentially, group differences in task accuracy in fMRI studies could impose strict limitations on the interpretation of differences in brain activity. After all, they might be either caused by or be an effect of the task performance differences between the groups. Therefore, researchers performing these kinds of studies in the future should match task performance levels of their study groups in order to avoid interpretation problems (Blakemore & Choudhury, 2006).

On the basis of the studies described above, it remains unclear as to whether there are serious constraints on the cognitive abilities that adolescents can acquire at a certain age or whether they simply lack experience (Crone, 2009). The question that should be addressed is whether or not the age differences in task accuracy and brain activation cease to exist when adolescents engage in interventions to improve their executive functioning. Although a few studies have already addressed this issue, it remains a topic that is still open to debate.

Conclusions

In this article, studies have been reviewed that investigated structural as well as functional developmental changes in the prefrontal lobes during the transition from childhood to adulthood. With regard to structural changes, several studies showed an inverse relationship between increases in white matter and decreases in grey matter in the prefrontal areas. These findings indicate that the maturation of these brain areas take a developmental path that continues into young adulthood. Functional MRI studies have shown that the cognitive abilities that rely on these regions also continue to mature during this time period. This was the case for various components of executive function, particularly response inhibition, working memory, and prospective memory. Because these skills highly influence decision-making processes, the immaturity of executive function could have serious consequences for certain important decisions that adolescents are expected to make. Adolescents were indeed found to be more impulsive in making their decisions. Furthermore, a direct relationship between age and improvements in both working memory and prospective memory in adolescents was also reported. The latter findings may indicate that adolescents have difficulties with planning.

Usually, the findings from developmental cognitive neuroscience have been applied to adolescents' participation in several risk-taking behaviours, including drug and alcohol abuse, unprotected sex, and criminal activities. Nevertheless, these findings may also have profound consequences for other types of decisions that adolescents have to make—for example, decisions in the context of education. Pama (2010) has observed that adolescents are required to make important decisions regarding their future. However, several cognitive abilities that guide decision-making are still maturing within adolescent brains. Therefore, she states that efforts should be made to provide teenagers with the information and experiences needed in order to make thoughtful decisions that will have important future repercussions.

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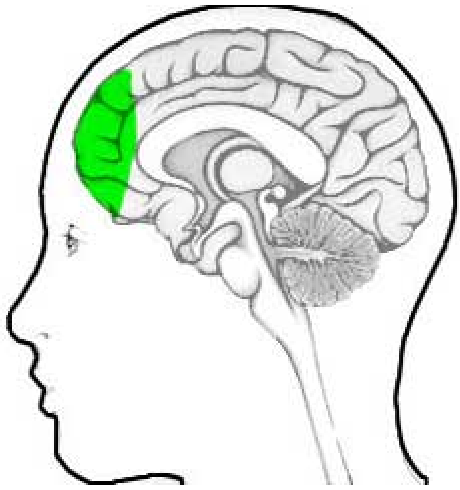

Figure 1
Green area shows the location of the prefrontal cortex in the human brain
(Source: Mind Trip, 2009)

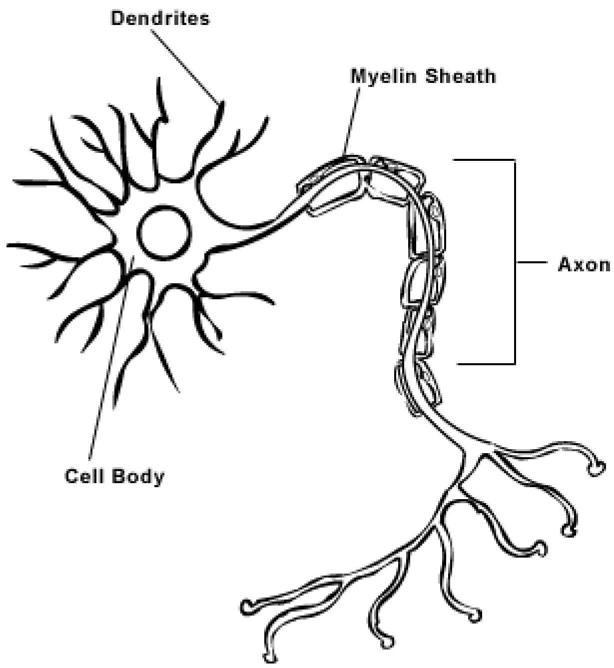

Figure 2
An axon surrounded by myelin sheaths
(Source: Journal of Young Investigators, 2009)