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DEVELOPMENTAL SCIENCE REVIEW

Executive functions in adolescence: inferences from brain and behavior

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Abstract

Despite the advances in understanding cognitive improvements in executive function in adolescence, much less is known about the influence of affective and social modulators on executive function and the biological underpinnings of these functions and sensitivities. Here, recent behavioral and neuroscientific studies are summarized that have used different approaches (cognition, emotion, individual differences and training) in the study of adolescent executive functions. The combination of these different approaches gives new insight into this complex transitional phase in life, and marks adolescence as not only a period of vulnerabilities, but also great opportunities in terms of training possibilities and interventions.

Introduction

Adolescence is a highly important transition phase between childhood and adulthood, marked by significant physical, social, cognitive and emotional changes (Dahl & Gunner, 2009; Steinberg, Albert, Cauffman, Banich, Graham & Woolard, 2008). The onset of adolescence is characterized by the start of pubertal maturation around the age of 10 years, during which children undergo rapid physical growth and experience the onset of sexual maturation (Shirtcliff, Dahl & Pollak, 2009). One of the most salient characterizations of adolescence is a steady increase in executive functioning; during adolescence children increasingly master the ability to control their thoughts and actions to make them consistent with internal goals. Executive functions are thought to be central to human cognition, and therefore adolescence can be seen as a period of significant cognitive advancements.

However, around the same time as the start of pubertal maturation, adolescents become increasingly self-conscious, they get involved in risky and sometimes reckless behavior and they become increasingly sensitive to the opinions and evaluations of others (Steinberg, 2005). Thus, adolescence is an age of advantages (improvements in executive function), but also sensitivities (such as vulnerability to risk-taking and social evaluation). Despite these well-known developmental transitions, the neural substrates that support these developmental changes in cognitive, emotional and social behavior are still largely unknown. A fundamental question in current research on child and adolescent development concerns how these changes in cognitive, emotional and social behavior are linked to brain development.

Longitudinal research examining changes in brain structure over development within individuals has shown that cortical white matter increases approximately linearly with age throughout childhood and adolescence, and differs little across regions (Gogtay, Giedd, Lusk, Hayashi, Greenstein, Vaituzis, Nugent, Herman, Clasen, Toga, Rapoport & Thompson, 2004; Sowell, Thompson, Leonard, Welcome, Kan & Toga, 2004). In contrast, cortical gray matter, which reflects neuronal density and the number of connections between neurons, follows an inverted-U shape over development, peaking at different ages depending on the region. Therefore, gray matter loss is considered an index of the time-course of maturation of a region (Sowell *et al*., 2004). In the last decade, considerable progress has been made in identifying the neural correlates of age-related change in executive function. A number of brain imaging studies in recent years have been conducted using event-related potentials (ERPs: a method to measure brain potentials from the scalp) or functional magnetic resonance imaging (fMRI: a safe and non-invasive brain imaging technique) which have identified neural correlates of age-related improvement in executive function. In this article, I will review several highly interesting and promising studies, some of which have recently been published in *Developmental Science*. These studies highlight the important interplay between studying changes in behavior under various experimental conditions. Subsequently, those changes that show largest developmental differences are related to changes in brain function in a specific

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experimental context. This approach, by which complex behavioral paradigms and specific experimental brain studies go hand in hand, proves most fruitful in constraining developmental theories.

Changes in executive functions

Traditionally, changes in cognitive functions during adolescence have been examined in the context of improving executive functions (Huizinga, Dolan & Van der Molen, 2006). For example, during childhood and adolescence, children gain increasing capacity for inhibition and mental flexibility, as is evident from, for example, improvements in the ability to switch back and forth between multiple tasks (Crone, Bunge, Van der Molen & Ridderinkhof, 2006; Cragg & Nation, 2008; Michel & Anderson, 2009).

The Wisconsin Card Sorting Task (WCST) is probably one of the most widely used executive function tasks, both in clinical and research contexts. The task requires participants to sort stimuli according to color, shape or number on the basis of feedback, and after a number of correct consecutive sorts, rules are shifted without warning. Patients with damage to the prefrontal cortex have difficulty switching between different tasks, because they perseverate on the previous rule (Barcelo & Knight, 2002). Developmental studies converged on the conclusion that errors observed in the performance of young children resemble those observed by prefrontal cortex patients, because they also have difficulty switching between rules based on performance feedback. Somsen (2007) noted that although these results provide us with more insight into the development of executive functions in childhood and adolescence, more careful analyses of response patterns are necessary to dissociate between different components of executive functions.

Somsen analyzed WCST performance of 259 children between ages 6 and 18 years and showed that different developmental trajectories could be observed for sorting performance and feedback attendance. Specifically, she showed that the number of errors that participants made decreased with age, whereas the number of completed sorting rules increased linearly until approximately age 11, after which it reached a plateau. In contrast, when examining error inspection time (as indexed by the time participants took to process performance feedback before starting the new trial), the results showed an increase in the inspection time to negative feedback relative to positive feedback, and age differences were present until late adolescence. This increase in inspection time to negative feedback was enhanced in good performing children, suggesting that increased monitoring may result in better behavioral performance. In her concluding remarks, the author warned against using perseverative errors as an index of frontal lobe function and executive function monitoring. Perseverative errors may result from guessing, failure to switch behavioral response tendencies, or failure to inspect feedback. In addition, these broad dependent measures may mask late occurring developmental changes, and careful analysis of separable executive function categories is necessary to correctly describe developmental changes in executive function. Similar conclusions were obtained in a study by Crone, Ridderinkhof, Worm, Somsen and Van der Molen (2004) using a spatial version of the WCST. These authors showed that age differences in failure to switch set (as indexed by perseverative errors) was most pronounced between ages 8–9 and 11–12, whereas adult levels in ability to maintain set (as indexed by distraction errors) were not reached until age 13–15.

The neural correlates of changes in executive functioning across adolescence, in particular error monitoring, have been nicely demonstrated in an ERP study by LaDouceur, Dahl and Carter (2007) using an action monitoring task. Participants from three age groups, early adolescents (mean age 12), late adolescents (mean age 16) and adults (mean age 29 years), performed an Eriksen Flanker task under speed instructions. In this task, participants were asked to respond to a target arrow which appeared in the center of the screen by pressing a left- or a right-hand key. The arrow could be flanked with arrows pointing in the same direction (congruent) or in the opposite direction (incongruent). On average, young adolescents made 11% errors, whereas late adolescents made approximately 7% errors on the task. Event-related potentials (ERP) which were averaged around the errors yielded a negative ERP component in adults, which occurred approximately 80–100 ms after the erroneous response. This negative potential was referred to as the Error Related Negativity (ERN). A similar ERN was observed in the late adolescents. In the younger adolescents, however, this ERN response was significantly reduced, which was interpreted as immature error monitoring. Importantly, all participants showed a later positive ERP component following the error, showing that the errors were processed by all age groups. Source localization results showed that the neural generators of the ERN were located in, or very near to, the anterior cingulate cortex (ACC). The changes that occurred between early and late adolescence could therefore be associated with maturation of the ACC. The results reported by LaDouceur *et al.* (2007) are consistent with results obtained using fMRI. These studies have reported that adolescence is characterized by more focal and increased magnitude of activation in brain regions which are important for cognitive control in adults, including the lateral prefrontal cortex, parietal cortex and medial prefrontal cortex (for a review, see Bunge & Wright, 2007).

The modulating influence of affect and social context

Besides changes in cognitive control functions, adolescence is also the time period of changes in affect and emotion; therefore several researchers have hypothesized that adolescent change in executive functions may be modulated by affective or social context. For example, Huizenga, Crone and Jansen (2007) used a modified version of the Iowa Gambling Task to examine changes in affective learning in adolescence. In this task, participants can select decks which result in different amounts of rewards, and occasionally the card selection is accompanied by a punishment. The participants need to learn across multiple trials that those decks which result in large rewards are also associated with high punishments, and therefore these decks are disadvantageous in the long run. In contrast, those decks which result in smaller rewards also result in smaller punishments, and therefore these decks are advantageous in the long run. The basic requirements of this task require successful self-regulation, or the ability to inhibit the temptation to respond to immediate gratification, with the goal of obtaining long-term reward. The authors demonstrated an age-related shift in self-regulation, such that young children were more inclined to choose for immediate high rewards, whereas adults learned to adopt a long-term advantageous strategy. These changes in choice behavior were observed until late adolescence, indicating that affective self-regulation develops slowly across adolescent development. Huizinga *et al.* (2007) further demonstrated that the choice behavior could be classified according to different response rules. Whereas young children mostly used a guessing strategy with a small focus on frequency of punishment, young adolescents adopted a more complex strategy and choices were generally driven by the frequency with which they received punishment. It is not until early adulthood that participants take both the frequency as well as the magnitude of probabilistic loss into account. Apparently, changes in executive functions in adolescence are also present under the context of affective (reward and punishment) conditions. Interestingly, the authors concluded that even though this task is often presented as a ‘hot’ affective task, in this context behavior can also be classified based on reasoning rules.

Next, the question arises whether executive function development is also modulated by social context. One of the most salient social functions in everyday interaction is probably the ability to interpret emotions in facial expressions. Thomas, De Bellis, Graham and LaBar (2007) studied the developmental changes in ability to interpret facial expressions related to fear and anger across adolescence, to study if adolescents still improve in the ability to understand these complex social stimuli. They compared performance of three age groups, children aged 7–11, adolescents aged 14–18 and adults aged 25–57 years, while they rated Eckman face morphs which ranged on a 6-point scale from neutral to anger, neutral to fear, and fear to anger. Participants were asked to judge the faces by making judgments between two responses (neutral or angry, neutral or fearful, angry or fearful). The data showed that all age groups were able to discriminate between the facial emotions, as their ratings approached the 6-point scale. However, recognition data from adults were qualitatively different from those of children and adolescents. Overall, adults showed greater sensitivity to the target emotion. Second, sensitivity to fear emotions increased linearly with age, whereas sensitivity to anger showed a quadratic trend, with a large increase between adolescence and adulthood. The authors interpreted these findings in terms of the increased cognitive control that is necessary for the processing of angry faces. The combination of emotion processing and cognitive control changes in late adolescence may have caused this slow developmental trajectory. Thus, possibly affective social stimuli do not only modulate executive function, but improvements in executive functions may also aid in the recognition of facial expressions.

The relation between processing of emotional faces and executive functions was further examined in a neuroimaging study. In this study, Wang, Huettel and De Bellis (2007) showed that emotional processing may interfere with executive attention in adolescents. In this study, adolescents aged 10–15 years performed an emotional odd-ball task during fMRI scanning. In this version of the oddball task, participants were presented with four stimulus types: circles (3.33%, targets), sad photographs (3.33%, emotional distractors), neutral photographs (3.33%, neutral distractors) and phase-scrambled photographs (90%, neutral stimuli). Participants were instructed to press a response button only when a circle was presented. Hemodynamic response functions were modeled for each stimulus type and compared in contrasts. These contrasts revealed involvement of the attentional control network in response to target circles (target–neutral), including the anterior medial frontal gyrus (aMPFC) and the ACC. In contrast, the sad distractions (sad–neutral) activated the affective neural circuitry, including the amygdala and ventral medial prefrontal cortex (VMPFC). Interestingly, those individuals who showed more activation in the VMPFC to sad distractors also showed reduced activation in the aMPFC to target distractors. The authors interpreted this result as an imbalance between the attention and affective networks, where emotional distractors can have a detrimental effect on executive function. It should be noted that in this study no comparison age groups were included. Therefore, it is possible that the fragile cognition–emotion balance is a general pattern which is observed for all ages. Nonetheless, the involvement of separable neural networks for cognitive regulation (aMPFC and ACC) and affective regulation (amygdala, VMPFC) informs the behavioral results presented in prior work, by showing that one system can affect the other also at the neural level. It is therefore possible that modulations in executive function in adolescence are the result of an imbalance between cognitive and affective brain networks, which would also explain why adolescent behavior is often erratic. These hypotheses have received initial support in brain imaging studies examining emotion processing in different age groups (Galvan, Hare, Parra, Penn, Voss, Glover & Casey, 2006; Hare, Tottenham, Galvan, Voss, Glover & Casey, 2008).

Individual differences and their relation to brain and behavior

Even though comparison between age groups is highly informative for understanding common age patterns in behavior and brain activation, it is also evident that adolescence is a period characterized by individual differences in how fast children develop, how often they engage in risky situations, and how sensitive they are to social influences (Steinberg, 2005; Paus, Keshavan & Giedd, 2008). Taking into account these individual differences can be informative for revealing patterns that are present only for a subgroup of a certain age group (for example, adolescents who are more prone to risk-taking), but also to have better understanding of the neural correlates of a specific cognitive function by demonstrating brain–behavior relations.

The approach of individual differences was nicely demonstrated in a study by Galvan, Hare, Voss, Glover and Casey (2008). These researchers showed that those adolescents who are at risk for impulsive behavior that can have fatal outcomes also show larger responses to monetary rewards in reward-related neural circuits. Using a pirates cartoon task, Galvan *et al.* (2008) asked participants to press the button at the location where a pirate appeared, which was then followed by a monetary reward (finding the treasure). Three different pirates resulted in three different reward magnitudes (small, medium, large). In response to receiving rewards, mid-adolescents (13–17 years) showed enhanced responses in the nucleus accumbens, which is part of the neural reward circuitry, relative to children (7–11 years) and adults (23–29 years). When correlating these responses to real-life risk-taking indices, such as the cognitive appraisal of risk activities scale and Connor's impulsivity scale, they demonstrated that those individuals who are likely to engage in risky activities in real life show enhanced neural responses to reward in the nucleus accumbens. The authors interpreted this effect as indicating that those individuals who are prone to risky behavior are at further risk in adolescence when neural systems underlying risky behavior go through developmental changes.

It has also been demonstrated that there may be a genetic factor in the display of adolescent executive function, especially in the social domain. This relation was demonstrated using a task which targeted one of the greatest changes in adolescence, namely behavior in social interactions. Gregory, Light-Hausermann, Rijsdijk and Eley (2008) used a twin model to examine the genetic, non-shared environment and shared environment predictors of pro-social ratings in a longitudinal study, involving children between ages 13 and 17. In general, they reported more pro-social ratings for girls than for boys. In addition, they provided evidence for the heritability of pro-social behavior and genetic continuity in adolescence across a 2-year-period. It should be noted that the genetic heritability was larger for parent ratings of pro-social behavior than for self-ratings. Non shared, but not shared, environmental factors were also related to pro-social behavior, suggesting an important role of peers and friendships in adolescence. Together, these results demonstrate that in future studies it will be important to not only identify general patterns of task-related neural activation, but also to use phenotypes and individual characteristics to understand the complex relation between behavior, brain and genetic head start.

Training and intervention

One of the foremost questions with regard to age differences in executive function and associated brain function is whether there is potential to improve. For example, the finding of lower engagement of dorsolateral prefrontal cortex (DLPFC) during working memory in 8–12-year-old children relative to adults has been interpreted as the maturation of an additional neural circuit that aids in the performance of cognitive tasks (Bunge & Wright, 2007). However, it remains to be determined to what extent the observed age differences in behavior and associated brain activation reflect hard developmental constraints (as suggested by an immature anatomical network at a given age) or a lack of experience with a given type of task or cognitive strategy.

Holmes, Gathercole and Dunning (2009) examined training potential in children with low working memory scores by using an adaptive and non-adaptive working memory training program. The authors trained 42 10-year-old children, half of whom received the adaptive training and half of whom received the non-adaptive training. All children scored in the bottom 15% of working memory performance based on normative scores prior to the training program. The results showed that adaptive training was associated with sustained gains in working memory performance. Importantly, besides working memory mathematical ability also improved. The authors interpreted these results in terms of flexibility of the executive control system, especially for those individuals who are initially in the lower range of performance. Similar results were also reported by Thorell, Lindqvist, Bergman Nutley, Bohlin and Klingberg (2009) in pre-school children, in which working memory training also resulted in better performance with transfer to other executive function domains.

In a different context, Kohls, Peltzer, Herpetz-Dahlmann and Konrad (2009) showed that executive control functions can also be modulated by reinforcement. They presented children aged 8–12 years with an incentive go-nogo task, which required them to respond to all letter stimuli with a button press except when the letter was an X. Successful inhibition trials were followed by feedback stimuli in three different blocks: a neutral block in which the feedback consisted of a meaningless image, a social reward block in which the feedback consisted of a smiling face, and a monetary reward block in which the feedback consisted of a monetary reward. Both social and monetary rewards resulted in better inhibition scores, but the reduction of inhibition errors was largest for the monetary reward. These findings demonstrate that improvement in executive functions can also be achieved by attractive motivators.

One of the challenging questions for the future is to investigate how these changes in behavior are associated with changes at the neural level. Does working memory result in increased activation in DLPFC or do children recruit different neural networks to enhance task performance? Are there sensitive periods in which children benefit most from training and intervention? And does training also work for affective functions by reducing sensitivity to emotional distractors or showing enhanced cognitive control to emotional stimuli?

Conclusion and future directions

In conclusion, different behavioral and neuroimaging studies have examined executive function improvements in adolescence. These studies demonstrate that adolescence is a time period of significant advancements in executive control functions, but is also marked by vulnerabilities to affective input or social context.

Several event-related fMRI studies have now shown that the regions that are involved in executive functions in adults, including the ACC, parietal cortex and DLPFC, are increasingly engaged over childhood. Future training and intervention studies should investigate whether improvements which can be achieved by extensive practice of reinforcement contingencies can also modulate activation in these brain networks, or if children need to rely on other neural circuits to perform the task.

Although improvements in the ability to perform cognitive tasks are observed between childhood and adulthood, the developmental changes in emotion regulation and social competence have been found to follow complicated non-linear age patterns. In particular, functional neuroimaging studies have shown that adolescent development is typically characterized by immature prefrontal cortex activity (important for cognitive control and intelligent behavior) and enhanced responses in subcortical affective systems (important for emotional responses), suggesting an intensification of emotional experience and an immature capacity of affective regulation and self-control in adolescence (Galvan *et al.*, 2006; Hare *et al.*, 2008).

It was recently suggested that the heightened sensitivity of subcortical brain regions in adolescence is associated with specific biological changes that affect brain functioning (Nelson, Leibenluft, McClure & Pine, 2005). Specifically, gonadal hormones associated with the onset of puberty may have a modulating effect on subcortical brain regions resulting in increased approach and/or avoidance behavior, whereas cortical development and function follows a developmental pattern independent of hormonal changes (Steinberg *et al.*, 2008). There is compelling evidence from animal models showing that gonadal hormone changes in puberty induce a (second) organizational period, serving to guide the remodeling of the adolescent brain in sex-appropriate ways (Sisk & Zehr, 2005; Spear, 2009). Literature from rodent studies indicates a remodeling of the dopaminergic system within the affective subcortical brain network which involves an initial postnatal rise starting in pre-adolescence and a subsequent reduction of dopamine receptor density in the striatum and prefrontal cortex; a pattern which is more pronounced in males than females. As a result, dopaminergic activity increases significantly in early adolescence and is higher in this period than before or after (Sisk & Zehr, 2005). Given the important role of dopamine in the brain's reward circuitry, this redistribution of dopamine receptors may increase reward-seeking behavior in puberty and therefore affect executive functions. Thus, adolescents who perform at adult level on most executive function tasks may fail to perform at this level under conditions of risk, arousal or social influence. One of the challenges for future research is to further understand why, when and how behavior is more erratic in adolescence compared to other stages in life, and to identify not only the risks, but also the opportunities, of this high potential developmental period in life.

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