Adolescent development of functional brain networks of selective and divided attention

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Tiivistelmä – Referat – Abstract

Tämän tutkimuksen tavoitteena on selvittää valikoivan ja jaetun tarkkaavaisuuden kehitystä nuoruusiässä aivojen toiminnallisen magneettikuvantamisen (fMRI) sekä behavioraalisten mittareiden avulla. Tarkkaavaisuudelle ja toiminnanohjaukselle tärkeä etuotsalohko kehittyy vielä aikuisiän saavuttamisen jälkeen, mutta nuoruusiässä tapahtuvasta kehityksestä on hyvin vähän tutkimuksia. Jaetun tarkkaavaisuuden kehitystä ei ole tutkittu aiemmin fMRI:llä. Tässä tutkimuksessa tarkkaavaisuuden kehitystä tarkastellaan sekä pitkittäis- että poikittaisasetelmilla. Lähes kaikki aiemmat tutkimukset aiheesta ovat poikittaistutkimuksia, joten on kiinnostavaa selvittää myös mahdollisia eroja tutkimusasetelmien tuottamissa tuloksissa.

Aivojen aktivaatiota tehtävän aikana mitattiin 103:lta 13–22-vuotiaalta koehenkilöltä, jotka oli jaettu kolmeen kohorttiin. Kaksi nuorinta kohorttia mitattiin uudelleen 1,5 vuoden jälkeen pitkittäistutkimusta varten. Skannerissa koehenkilöt tekivät tehtävää, jossa he arvioivat lauseiden semanttista johdonmukaisuutta. Heitä ohjeistettiin tarkkailemaan joko puhe- tai tekstiärsykkeitä tai jakamaan tarkkaavaisuutensa näiden kesken. Poikittaistulosten mukaan tehtäväsuoriutuminen oli parempaa vanhemmissa kohorteissa (16–17v. ja 20–22v.) kuin nuorimmassa kohortissa (13–14v.), mutta vanhempien kohorttien välillä ei ollut eroa. Pitkittäistutkimuksessa ei kuitenkaan havaittu selkeää kehitystä valikoivan tai jaetun tarkkaavaisuuden tehtävätilanteissa.

Pitkittäisten fMRI-tulosten mukaan aivojen aktivaatio väheni valikoivassa tarkkaavaisuudessa erityisesti etuotsalohkon sisäpinnalla 13–14-vuotiaasta 15–16 vuoden ikään, ja aktivaatio lisääntyi hieman päälaenlohkon alueella. Jaetussa tarkkaavaisuudessa taas aktivaatio väheni pääasiassa etuotsalohkon ulkopinnalla. 16–17-vuotiaasta 18–19-vuotiaaksi aktivaatio lisääntyi kummassakin tehtävässä motorisilla alueilla sekä etukiilassa (precuneus), jotka on liitetty toiminnanohjaukseen. Yleisesti efektit olivat kuitenkin varsin pieniä johtuen mahdollisesti lyhyestä mittausvälistä ja pienehköstä otoskoosta. Poikittaistuloksissa taas kehitys näytti hyvin erilaiselta ja aktivaatio keskittyi niissä enemmän temporaalialueille. Erot asetelmien tuloksissa korostavat pitkittäistutkimusten tärkeyttä kehityksen tutkimuksessa, erityisesti käytettäessä fMRI:tä.

Vaikka aktivaation muutokset olivat pieniä, pitkittäistulokset olivat silti linjassa aiempien toiminnanohjauksen tutkimusten kanssa, joiden mukaan iän myötä aktivaatio vähenee etuotsalohkolla ja lisääntyy muilla tehtävälle keskeisillä alueilla. Tämän tutkimuksen tulokset viittaavat siihen, että joitain muutoksia toiminnanohjaukseen liittyvässä verkostossa tapahtuu vielä nuoruusiästä varhaisaikuisuuteen, kun etuotsalohko ja sen yhteydet kypsyvät.

Avainsanat – Nyckelord – Keywords

Valikoiva tarkkaavaisuus, jaettu tarkkaavaisuus, kehitys, fMRI, nuoret, pitkittäistutkimus

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Tiivistelmä – Referat – Abstract

The aim of this study is to examine the development of selective and divided attention in adolescence using functional magnetic imaging (fMRI) and behavioral measures. Although the prefrontal cortex, a key area for attention and cognitive control, is thought to mature well into adulthood, few studies have examined the development of attention in adolescents and young adults. No fMRI studies have been conducted on the development of divided attention. In this study, development was examined both cross-sectionally and longitudinally to also assess the possible differences in the results they produced, as nearly all previous studies have been cross-sectional.

Brain activity was measured from 103 participants aged 13–22 who were divided into three age cohorts. The youngest two cohorts were measured again after 1.5 years for the longitudinal study. While in the scanner, participants performed a sentence congruence task where they were instructed either to attend to only the speech or text stimulus or divide their attention between both modalities simultaneously. The cross-sectional results showed improvement in task performance between the youngest cohort (13–14y.) and the older cohorts in both selective and divided attention tasks. No difference was found between the older two cohorts (16–17y. and 20–22y.) However, the longitudinal results did not indicate clear performance improvement with age in either task type.

According to the longitudinal fMRI results from age 13–14 to 15–16, in the selective attention task brain activity decreased mainly in the medial prefrontal area and activity increased slightly in parietal regions. In the divided attention task, the decreased prefrontal activity was more lateral. From age 16–17 to 18–19, increased activity in motor regions and precuneus was found in both tasks. In general, the effects were very subtle, possibly due to a short measurement interval and relatively small cohort sizes. The cross-sectional results indicated quite a different pattern of change in brain activity, concentrated on temporal areas. This difference in results emphasizes the importance of conducting longitudinal developmental studies in the future. Although the effects were not large, the longitudinal fMRI results were in line with some previous findings that prefrontal areas are recruited less with age, so that activity in more posterior task-related areas increases. The current results suggest that some fine-tuning of the attention and cognitive control -related network still occurs from adolescence to early adulthood, as the prefrontal cortex and its connections mature.

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selective attention, divided attention, executive functions, fMRI, development, adolescents, longitudinal study

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1. Intro

Attention is one of the core functions of human cognition, enabling us to extract relevant information from the constant stream of stimuli from our surroundings. The aim of this thesis is to examine the age-related development of attention from adolescence to early adulthood using modern brain imaging (functional magnetic resonance imaging; fMRI). The focus is specifically on the development of selective and divided attention and the functional brain networks associated with them. The study examines this development both longitudinally and cross-sectionally to also assess possible differences in the results they produce.

Research on the development of adolescent attention is needed, as the maturation of the frontal cortex and complex executive functions continues throughout adolescence (Casey, Tottenham, Liston, & Durston, 2005) but developmental research with adolescents has so far been scarce. Longitudinal studies on the development of executive functions, that underlie goal-directed behavior, are necessary because nearly all studies thus far have compared children to adults cross-sectionally. Especially the functional development of divided attention has not yet been examined with functional magnetic resonance imaging. Studying the normal development of attention can also help to understand more about its deviations, such as attention deficit and hyperactive disorder (ADHD) which has already been subject to a number of research. Investigating age-related changes in executive functions in adolescence complements the developmental research of human cognition that is often restricted to either childhood or old age.

1.1 Motivation for the current study

Previous research own the development of executive functions has focused mainly on young children and quite narrow age groups, instead of adolescents and larger age spans (Best & Miller, 2010). More research on adolescents is needed, as basic mechanisms of inhibition and attention emerge already in early childhood, but performance in different complex tasks of cognitive control continues to mature until early adulthood (Best & Miller, 2010; Casey et al., 2005). This maturation could be best understood by combining behavioral measures with neuroimaging techniques such as MRI and fMRI that can detect changes in brain volume and function, because as Best and Miller (2010) point out, even dramatic neural changes might translate to only subtle behavioral changes. The current study examines the development of attention from both perspectives.

In the developmental research of executive functions, there is also a clear lack of longitudinal studies that track development within individuals. Nearly all studies on this subject have been cross-sectional, with the exception of Durston and colleagues (2006), who used both cross-sectional and longitudinal designs in their study of cognitive control development. The problems in cross-sectional studies are, however, quite well understood. Cross-sectional studies can falsely show change in time or distort the magnitude of actual change in either direction, especially with smaller sample sizes (Casey et al., 2005; Giedd et al., 1999). In MRI studies, an important reason for this distortion is the large variability in brain structures between individuals, which can be taken into account only with longitudinal studies (Mills & Tamnes, 2014). For these reasons, cause-effect conclusions cannot be drawn from cross-sectional results.

When comparing developmental results from longitudinal and cross-sectional data, Durston and colleagues (2006) found that the longitudinal design revealed larger changes in brain activation, and was more sensitive to changes that were left hidden in the cross-sectional study design. However, the age range in their study was only 9–12 years, and the study was conducted with a total sample size of 14. The current study aims to investigate a broader age span (13–22 years), with more participants per age group. Another methodological issue in developmental research is the interpretation of change: all differences are easily interpreted as age-related when they could be due to differences in performance. This can be minimized for example by measuring behavioral data together with neural data (Casey et al., 2005).

1.2 Executive functions

Executive functions are essential for any complex human behavior requiring cognitive control, from driving a vehicle to everyday social interaction. Executive functioning can be described as voluntary, deliberate action towards a certain goal (Luna, Padmanabhan, & Hearn, 2010). Executive functioning or cognitive control is required especially in situations where there are several possible options for behavior, or several sources of input (Miller & Cohen, 2001). Multiple components have been classified in the literature under executive functions, but most models of executive functions include at least inhibition, set shifting and working memory as the main components (Luna et al., 2010; Miyake et al., 2000). Other executive functions related to these main components include selective attention, and divided attention or dual tasking (Miyake et al., 2000). The concept of 'unity and diversity of executive functions' (Miyake et al., 2000) best describes the nature of executive functions in general: its components are somewhat correlated, but can still be separated.

Different components of executive functions each serve a certain purpose for achieving the goal of the action. According to Luna and colleagues (2010), working memory is a system for manipulating and storing information short-term, which is crucial for executive functioning as the desired goal has to be kept active and updated in the brain. Selecting and attending to relevant sources of information in the environment requires attention, and inhibition is needed to block the irrelevant information and restrain inappropriate responses. Set shifting refers to the ability to flexibly change mental sets according to task requirements, which seems to be separate from simply shifting the focus of attention (Miyake et al., 2000). According to Miyake and colleagues (2000), dividing attention might also require executive functions that are somewhat independent from the components of working memory, shifting, and inhibition. Although the current study will focus on attentional networks and their development, it should be noted that clearly separating attention from other executive functions using experimental manipulations is extremely difficult. This is because most complex executive function tasks are "impure" and tap several functions, and the components are somewhat correlated with each other (Lehto, Juujärvi, Kooistra, & Pulkkinen, 2003).

In the brain, the frontal lobe and especially the prefrontal cortex (PFC) is involved in all executive functioning (eg. Best & Miller, 2010). The prefrontal cortex can even be seen as a unified but adaptive system that can adjust its function according to task requirements (Duncan, 2001). According to Duncan (2001) certain areas in the prefrontal cortex are recruited in multiple executive functions such as working memory, attention, and cognitive control. This overlap could be seen as evidence for the adaptability of prefrontal cortex. Duncan argues that instead of perceiving PFC activity as a group of specified functions, some PFC functions could be broad enough to contribute to different task types. Miller and Cohen (2001) also propose that the role of the prefrontal cortex is to control and modulate activity in other brain regions according to task requirements and goals of behavior. These goals and the means to achieve them would be represented in PFC's activity patterns. Although these models act as a framework for PFC's role in executive functions on a larger scale, for the purposes of this study it is relevant to focus on a few specific functions: selective attention, inhibition, and divided attention.

1.3 Selective attention and inhibition

The concept of attention can be better understood by breaking it down to different components. One way to conceptualize attention is using three dimensions: arousal, capacity and selectivity (Desimone & Duncan, 1995; Posner & Boies, 1971). *Arousal* refers to the level of alertness of the processing system, *capacity* to the assumption that human attentional resources are limited, and *selectivity* to the ability to direct these resources to relevant information. In the current study, we are particularly interested in the dimension of selectivity.

As attentional resources are limited, processing effort has to be either focused on a single target, or divided among several targets (Plude, Enns, & Brodeur, 1994). With selective attention, only the stimuli that are relevant to the goal of the behavior are processed further, and the unattended stimuli are not processed or identified beyond basic physical properties (Lachter, Forster, & Ruthruff, 2004). However, according to Lachter and colleagues (2004) most attention tasks enable attention to slip to the to-be-ignored stimuli, so that they are sometimes processed further, causing interference.

This kind of selective attention where task relevant targets have to be discriminated from distractors according to their different attributes is often referred to as filtering (Lachter et al., 2004; Plude et al., 1994). Filtering paradigms, where the attended and unattended stimuli are separated clearly, have been used both in the visual and auditory modalities. Visual filtering can be examined for example with visual search tasks (e.g. Booth et al., 2003) where the participant is asked to search for a feature conjunction target in a field of distractors. Another example is the flanker task, where participants respond to a target stimulus in the presence of a distractor (the flanker) that is either congruent or incongruent with the target, usually causing the congruence effect where the target is responded to faster when the distractor is congruent (Shimamura, 2000). In the auditory modality, a classical filtering task is the dichotic listening task (Cherry, 1953), where two streams of speech are presented simultaneously and the participant is asked to attend to only one of them. The unattended speech is processed only at the level of physical characteristics such as timbre, unless attention is captured by relevant stimuli like one's own name (Lachter et al., 2004).

In both visual and auditory modalities, filtering seems to require successful inhibition of the irrelevant stimuli, showing how the functions of selective attention and inhibition are closely related. According to Miller and Cohen (2001) selective attention and inhibition can even be seen as "two sides of the same coin", as task-relevant information is biased in the processing system while other information is inhibited. Inhibition refers to deliberately suppressing a pre-potent or automatic response, or limiting interference of irrelevant stimuli (Barkley, 1997; Miyake et al., 2000). The Stroop-task (1935), for example, requires the subject to inhibit the automatic processing of semantic meaning of a word and focus attention only on its color. The congruence effect (or Stroop-effect) causes the color to be named faster when the word is congruent with the color than incongruent. Another common task that requires inhibition of a pre-potent response is the Go/No-go task, where one category of stimuli have to be reacted to e.g. by pressing a button, while with others the response has to be inhibited (e.g. Booth et al., 2003).

According to Casey, Durston and Fossella's (2001) model, inhibition activates a basal ganglia thalamo-cortical network in the brain, where basal ganglia are involved in response inhibition, and the prefrontal cortex is involved in limiting interference and maintaining a response set. In their model, the basal ganglia form circuits via thalamus back to different parts of the cortex, for example the pre/motor and prefrontal cortex. These circuits process different types of information (e.g. oculomotor or emotional), but have the same inhibitory mechanism.

In fMRI studies of selective attention, attending to a stimulus seems to increase activation in the sensory areas processing the attended input, and decrease activation in the areas processing the unattended input, regardless of the modality of the task (Alho et al., 1999; Johnson & Zatorre, 2005; Shomstein & Yantis, 2004). Johnson and Zatorre (2005) suggest that top-down attentional effects modulate activations in sensory processing areas by gating sensory input. The idea of prefrontal cortex being a modulator of activations in other brain areas is postulated in the biased competition theory (Desimone & Duncan, 1995; Miller & Cohen, 2001) according to which information processing is either biased or inhibited by bottom-up stimulus salience, or top-down goals represented in the PFC.

Evidence for this kind of top-down modulation has been found in neuroimaging studies, in frontal as well as parietal areas. Regions in the posterior parietal and superior prefrontal cortex have been connected to shifts of attention from one modality to another in a bimodal attention task (Shomstein & Yantis, 2004). The frontal cortex has also been associated with the top-down modulation and control of attention in a spatial auditory attention task (Alho et al., 1999). In several visuospatial attention studies, parietal areas like the intraparietal sulcus (IPS) and superior parietal lobule (SPL), as well as frontal areas (e.g. middle frontal gyrus, frontal eye fields) have been connected to attentional modulation of activity in the visual cortex (see review by Pessoa, Kastner, & Ungerleider, 2003).

1.4 Divided attention

Divided attention, also called dual tasking, occurs when two tasks are performed simultaneously. Divided attention has been studied with different tasks ranging from simple to more complex. One example of a dual tasking paradigm is presenting the same task simultaneously in two different modalities, for example an n-back working memory task in both the auditory and visual modality (Yoo, Paralkar, & Panych, 2004). A more complex task can be, for example, listening to novel melodies while viewing abstract shapes (Johnson & Zatorre, 2006).

Dividing attention between two tasks usually causes performance decrements in reaction times or error rates in one or both tasks, compared to performing only a single task (Pashler, 1994; Szameitat, Schubert, Mu, & Cramon, 2002). This decrement is called *dual task interference*, possibly requiring some form of executive control of the concurrent processing (Saxena, Cinar, Majnemer, & Gagnon, 2017; Szameitat et al., 2002). Dual task interference can be measured with *dual task cost*: the difference in performance between single and dual tasks (Saxena et al., 2017).

Several models of the source of dual task interference have been created. One source of interference has been suggested to be a bottleneck in the processing mechanism, which would allow only one task to be processed at a time (Pashler, 1994; Szameitat et al., 2002). When two tasks are performed closely in time, the bottleneck causes the mechanism to switch between tasks, requiring executive control and resulting in performance decrements (Pashler, 1994; Szameitat et al., 2002). According to Pashler (1994), another explanation is the *capacity sharing model*. Capacity sharing refers to the idea of limited processing resources that are allocated to tasks, causing performance decrements in dual tasking when less capacity is available for each single task.

When discussing the brain areas involved in dual tasking, the central dispute is whether dual tasking recruits separate executive control areas or not. According to some studies, dual tasking causes activation also outside the task specific areas: the dorsolateral prefrontal cortex (DLPFC) (Johnson, Strafella, & Zatorre, 2007; Johnson & Zatorre, 2006) as well as the inferior frontal sulcus (IFS) (Schubert & Szameitat, 2003), the middle frontal gyrus (MFG), and the intraparietal sulcus (IPS) and the precuneus (PrC) (Szameitat et al., 2002). These results indicate the involvement of executive control or specialized dual tasking–areas, which can be seen as support for the bottleneck model of dual tasking. Performance decrements would thus be due to limitations in the executive processing that recruits the frontal and parietal areas mentioned above.

Other studies, however, have not found any additional activations during dual tasking outside the task specific areas. A study by Adcock, Constable, Gore, and Goldman-Rakic (2000) revealed that all the areas that activated in a dual task also activated during the component tasks, with dual task activity resembling the sum of the two independent tasks'. Activation increases caused by dual tasking have also been found: according to Moisala and colleagues (2015), dividing attention did not recruit any additional areas compared to selective attention, but caused an increase of activation in the same areas. They concluded this activation increase (in combination with performance decrements) to be a result of a competition of resources, as the tasks utilized the same brain areas.

These types of results give support to the capacity sharing model and question the involvement of additional executive control.

As discussed the previous three sections, executive functions seem to be closely connected to each other in most tasks but can be separated into a few components (Miyake et al., 2000). Attention is an essential part of human cognition, as makes it possible to select relevant information for further processing. Equally important is the ability to limit the interference of irrelevant stimuli via inhibition. The mechanisms of attention could to be partially different in the cases of selective and divided attention– for example, inhibition seems to be involved more during selective attention (filtering**).** Next, we will look into the development of attention and inhibition from behavioral and neuroimaging perspectives.

1.5 Development of executive functions in adolescence

In the development of human cognition, adolescence is an important period, as the ability to behave in a goal-directed manner continues to evolve. This is connected to the maturation of executive functions and their related brain networks. The explanation for the late maturation of executive functions comes mainly from the development of the prefrontal cortex. Brain maturation consists of both progressive and regressive changes: synaptic pruning and myelination process occurs first in the sensorimotor cortex, followed by parietal and temporal cortices, and lastly the prefrontal cortex (Casey et al., 2005; Gogtay et al., 2004). In terms of brain function, several studies have suggested that brain activity becomes more efficient and focal with age, so that task-correlated areas are recruited more precisely while other activity decreases (Best & Miller, 2010; Casey et al., 2005; Durston et al., 2006). The use of prefrontal cortex in different executive function tasks has been found to decrease with age, which could be caused by increased processing effort and immaturity of the network in children and adolescents compared to adults (Konrad et al., 2005; Luna et al., 2010; Tamm, Menon, & Reiss, 2002). Luna, Padmanabhan, & Hearn (2010) suggest that integration from PFC to other brain areas improves with age, which would lead to a more distributed pattern of activation and less reliance on PFC. Indeed, Liston and colleagues (2006) found in their diffusion tensor imaging study that increased myelination from PFC to striatum correlated with better performance on an inhibition task.

1.6 Development of inhibition and attention

The development of performance in executive function tasks varies with different functions (Best & Miller, 2010), suggesting that the brain networks they recruit do not develop concurrently. According to the review by Luna, Padmanabhan, & Hearn (2010), what seems to improve behaviorally in adolescence is the rate of correct responses in multiple tasks of response inhibition, because the ability to make a correct response has already emerged in childhood. They propose that this is because children's less efficient inhibitory mechanisms cannot sustain a high rate of correct responses. Studies investigating age-related functional changes in inhibition tasks have produced alternating results, with both decreases and increases in frontal activation (Luna et al., 2010; Rubia et al., 2006). Booth and colleagues (2003) found increased fronto-striatal activation in children compared to adults during a Go/No-go task. In a similar task, Tamm, Menon, and Reiss (2002) investigated 8–20 year-olds, and found both developmental increases in the inferior frontal gyrus (IFG), as well as decreases in middle and superior frontal gyri.

In addition to frontal changes, age and performance in inhibitory tasks has been found to correlate with changes in fronto-striatal, fronto-temporal and fronto-parietal activity, suggesting better integration to other brain areas with age (Rubia et al., 2006). The only longitudinal developmental study of cognitive control has been conducted by Durston and colleagues (2006). Using a variation of the Go/No-go task, they found age-related decreases in the DLPFC as well as increased focal activation in the right IFG. This study investigated subjects only from age 9 to age 11, so the results might not be completely comparable to other studies with older adolescents.

The immature inhibitory mechanisms of children also affect task performance in filtering tasks of selective attention. Larger effects of interference on children have been found in studies of visual and auditory selective attention tasks (Konrad et al., 2005; Plude et al., 1994). A diminishing of the Stroop effect from childhood to early adulthood was already discovered in the early studies of Comalli Jr., Seymour, and Werner (1962). These results have been replicated in later studies (see review by Plude, Enns, & Brodeur, 1994). Similar age-related improvements in selectively attending to a stimulus have been found in dichotic listening studies. Takio and colleagues (2009) studied the effect of age on top-down attentional modulation in dichotic listening with subjects aged 5-79 years. They found that the ability to control auditory processing with attention emerged at around age 11, but fully matured in early adulthood (age 19–32). Results from both visual and auditory studies suggest that children are less efficient than adults in focusing on relevant information and inhibiting distractors, which require top-down control abilities.

Only a few neuroimaging studies have investigated developmental changes in brain function in inhibitory and selective attention tasks, and the results are inconclusive. Adleman and colleagues (2002) performed a developmental study of the Stroop-task, comparing school-age children, adolescents, and adults with fMRI. They found that Stroop-related activation in the left lateral prefrontal cortex, anterior cingulate, and parietal cortices correlated positively with age. Between-group comparisons revealed that parietal areas seemed to develop functionally by adolescence, but there was an increase in frontal cortex MFG activation after adolescence up to early adulthood. They attributed these changes to better recruiting abilities of focal task-related areas with age.

In addition to the Stroop task, which requires a broader range of executive functions like inhibition and conflict resolution (Adleman et al., 2002), selective attention has been examined with fMRI in flanker and visual search tasks. Konrad and colleagues (2005) found that in executive attentional control (measured with reaction time in a flanker task) children recruited IFG and superior parietal cortex less than adults, but SFG and temporal areas more than adults. They concluded that children had immature and less defined fronto-parietal and temporo-parietal top-down systems compared to adults. In a visual search task, Booth and colleagues (2003) found only minor differences between school-age children and adults: the anterior cingulate and thalamus activated slightly more in children than in adults. They attributed these results to the relatively early development of simple visual search skills. In conclusion, development of selective attention has been researched little, and the neuroimaging studies have produced quite diverse results. Gathering from studies of the development of these executive functions, it could be hypothesized that brain activity becomes more focal and concentrated on task-relevant areas with age, while the activity not related to the task decreases. More research is needed on the role of adolescence in this developmental process.

So far the only review on developmental studies of divided attention has been conducted by Saxena, Cinar, Majnemer and Gagnon (2017), in which they reviewed 31 studies on the development of behavioral dual tasking performance. They focused especially on the effect of age on the degree of dual task cost (difference in performance between single and dual tasks). They concluded from these studies that there is weak evidence that dual tasking causes less interference with age, but this applied only to difficult or complex tasks. The development also seemed to be somewhat nonlinear. Some methodological challenges were identified in the reviewed studies: all studies were cross-sectional and task difficulty of the single tasks was not equated in most studies. Neuroimaging methods could elucidate the functional changes behind the development of dual tasking performance. However, no fMRI studies on the age-related changes related to divided attention have been conducted.

1.7 Study questions and hypotheses

The aim of this study is to advance the understanding of the adolescent development of selective and divided attention by using functional magnetic resonance imaging in both cross-sectional and longitudinal study designs. The aim is to also examine the possible differences in the longitudinal and cross-sectional results, and whether their results lead to similar conclusions.

The topic is examined with the following study questions:

i. How do selective and divided attention develop behaviorally and in terms of brain function from adolescence to early adulthood?
ii. How is the development of attention captured by cross-sectional and longitudinal studies, and do their results lead to similar conclusions?

Based on prior research the subsequent hypotheses were formulated:

Hypothesis 1*: Behavioral performance improves with age in both selective and divided attention tasks.* In tasks of attention and inhibition, the behavioral development in adolescence is often manifested as a larger percentage of correct responses on the task, as the ability to inhibit interference matures (e.g. Luna et al., 2010).

Hypothesis 2: *Brain activity decreases with age in the prefrontal cortex and increases in more posterior areas that are associated with attention and cognitive control, such as the parietal cortex.* Several previous studies have suggested that brain activity becomes less dependent on the PFC and more concentrated on other task-relevant areas (Best & Miller, 2010; Casey et al., 2005; Durston et al., 2006) possibly caused by the maturation of the PFC and its connections.

Hypothesis 3*: The cross-sectional and longitudinal fMRI results indicate change in similar brain areas but the affected areas are larger in the longitudinal comparison.* There have not been many studies in developmental neuroimaging that would have used both longitudinal and cross-sectional study designs. This tentative hypothesis was postulated on the basis of the study by Durston and colleagues (2006), in which they found that the number of affected voxels was greater for the longitudinal comparison, although the areas were the same.

1.8 Functional magnetic resonance imaging (fMRI)

Non-invasive neuroimaging methods such as magnetic resonance imaging (MRI) and fMRI has been used to track development both in brain structure and activity (Casey et al., 2005). In developmental studies, MRI has been used to detect age-related changes in brain morphometry such as grey matter volume and cortical thickness, as the method is sensitive to different tissue types (e.g. Gogtay et al., 2004). Functional magnetic imaging in turn detects changes in brain activity that are associated with certain cognitive functions (Paus, 2005). fMRI is based on the blood-oxygen-level dependent (BOLD) signal that can follow changes in the oxygenation level of blood in the brain, because deoxygenated and oxygenated hemoglobin have different magnetic properties. These local changes in blood flow and volume are thought to be indirectly connected to changes in brain activity in that area, as neuronal activity is coupled with brain's energy metabolism (Logothetis & Pfeuffer, 2004). fMRI has a high spatial resolution compared to e.g. electroencephalography (EEG) which provides better temporal information but poor spatial resolution (Logothetis & Pfeuffer, 2004). For this reason, fMRI has been used to localize developmental changes in brain function related to e.g. inhibition (Adleman et al., 2002; Tamm et al., 2002) and attention (Konrad et al., 2005).

2. Methods

2.1 Participants

Participants were selected from a sample of 2977 subjects, who had answered a questionnaire about their media use as a part of a research project called Mind the Gap Between Digital Natives and Educational Practices (2013–2016) funded by the Academy of Finland. Participants with learning difficulties, poor school performance and those ineligible for fMRI were screened out. 173 healthy volunteers were measured in the fMRI in total. Out of these participants, 103 (54 females) were selected for this present study. The participants were divided into three cohorts based on their age at the first measurement point (Figure 1). From cohorts 1 and 2 only those who participated in the follow-up study were included in the present analyses. Only the youngest 35 participants were selected from Cohort 3 to balance the cohort sizes and bring the average age of Cohort 3 closer to that of the second longitudinal measurement. All participants were native Finnish speakers, right-handed, had normal or corrected-to-normal vision and normal hearing. The participants had no self-reported psychiatric or neurological illnesses. Each participant gave an informed written consent before the experiment, as did the parents of underage participants.

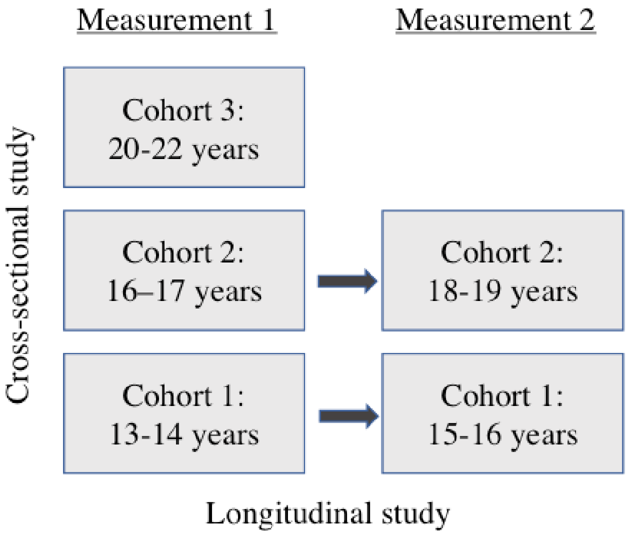

Figure 1. Age cohorts in the cross-sectional (vertical) and longitudinal (horizontal) studies. Cohort 1 n=33, Cohort 2 n=35, Cohort 3 n=35.

As shown in Figure 1, participants in Cohort 1 (n=33, 17 females) were aged 13–14 years (mean age 13) at the time of the first measurement. In Cohort 2 (n=35, 19 females) participants were aged 16–17 years (mean age 17). From the original Cohort 3 (age 20-24 years), only the youngest participants aged 20–22 (mean age 20, n=35, 18 females) were selected for further analyses to make the cross-sectional results more comparable with the longitudinal results. Participants in cohorts 1 and 2 were measured again in the follow-up study after 1.5 years. Mean age of Cohort 1 at the second measurement point was 15.1 years, and 18.4 years in Cohort 2.

2.2 Stimuli

The stimuli used in the experiment were semantically congruent and incongruent sentences in Finnish, presented as speech through headphones and as text on a computer screen. The congruent sentences could be e.g. “In the morning, I ate a bowl of cereal”. The incongruent written sentences were created by combining the beginning of a congruent sentence with a syntactically correct but semantically incongruent last word (e.g. “In the morning, I ate a bowl of *shoes*.”). Each participant saw a total of 108 incongruent and 144 congruent sentences. Each sentence was presented only once, and the incongruent and congruent versions of the same sentence were never presented within the same run. In the written sentences, the last word of the sentence was covered with x-letters for the first two seconds of the trial, and then revealed for two seconds. The participants viewed the written sentences (font Arial, size 14) projected on a mirror attached to the MRI head coil from ~40 cm viewing distance with angular size of ~1.4° vertically and ~24° horizontally.

Spoken sentences were spoken by a native Finnish speaker. The sentences were constructed in the same way as the written sentences by combining either an incongruent or congruent last word with the beginning of a sentence. The participants heard in total 72 incongruent and 108 congruent sentences. The last word of the recorded sentence was presented simultaneously with the written last word, two seconds after the beginning of the trial. The auditory stimuli were presented binaurally in the scanner through Sensimetrics headphones (Sensimetrics model S14; Sensimetrics, Malden, MA USA). Volume was set individually at a pleasant but sufficiently loud level at about 80 decibels. Spoken sentences were low-pass filtered with a cut-off at 7000 Hz and high-pass filtered at 100 Hz. Music distractors were 2.5 second clips of different music genres that were obtained from a free-source online music website. 48 music excerpts were used in total and they were preprocessed in the same way as the spoken sentences.

2.3 fMRI data acquisition

In the current study, functional brain imaging was performed with a 3T Magnetom Skyra whole body scanner (Siemens Healthcare, Erlangen, Germany) at AMI Centre, Aalto Neuroimaging, Aalto University School of Science. A head coil with 20 channels was used. There were three functional runs per participant, each with 222 volumes. The duration of one run was 11 minutes and the total of three runs lasted 33 minutes. The EPI (echo planar) imaging area was 43 contiguous oblique axial slices (TR 2500 ms, TE 32 ms, flip angle 75º, field of view 20 cm, voxel matrix 64 x 64, slice thickness 3 mm, in-plane resolution 3.1mm x 3.1mm). Image acquisition was asynchronized with stimulus onsets but performed at a constant rate. High resolution anatomical images were obtained after the last functional run (voxel matrix 256 x 256, in plane resolution 1 mm x 1mm x 1mm).

2.4 Procedure

The procedure has been previously described by Moisala and colleagues (2016). The original experimental protocol was approved by the Ethics Committee for Gynecology, Pediatrics and Psychology of The Hospital District of Helsinki and Uusimaa, Finland. Six out of nine task conditions were used in the analyses for the current study. One block of rest was also included in every run.

The task conditions used in the current study are represented in Figure 2. Two out of six conditions were **undistracted attention** conditions, where either auditory or visual stimuli were presented alone with no distractor in the other modality. When only speech stimuli were presented, a fixation cross was shown in the middle of the computer screen for the duration of the trial. Selective attention was examined with three **selective attention** conditions where participants were told to ignore a distractor stimulus and focus on the target stimulus. Spoken sentences were presented simultaneously with written sentence distractor, and written sentences with a music distractor or a speech distractor. The last condition was a **divided attention** condition, in which both speech and text were presented at the same time and participants were told to attend to both stimuli.

Each task block began with instructions for the task for 3.5 seconds. Each block contained 12 sentences or sentence pairs, depending on the task, that were presented for 2.5 seconds. A 1 second response window with a question mark on the screen followed every sentence. During the response window the participant was instructed to press a button (with the right index or middle finger) as quickly as possible according to the task instructions. In the undistracted attention condition the participant was instructed to answer whether or not the presented sentence (either auditory or visual) was congruent. In the selective attention condition, the participant was instructed to answer whether the to-be-attended sentence had been congruent or not. In the divided attention condition, the participant had to answer whether both sentences had been congruent, or whether one of the sentences had been incongruent (both sentences were never incongruent). Half of the sentences in each block were always congruent and half were incongruent. At the end of the task block, the percentage of correct answers was displayed on the screen for 2 seconds, followed by a blank screen for 4 seconds before the next block.

There were three functional runs during one measurement with 11 task blocks in each run: one block for each task condition (except two for divided attention condition) and one rest block. In total, there were 36 trials for each task condition, except for the divided attention condition. For the divided attention condition, there were 72 trials in order to have an equal number of incongruent trials in all conditions. The order of the task blocks within a run was randomized (the rest block was always in the middle) as well as the order of the stimuli within a block.

Figure 2: The sentence congruence judgement task for the undistracted, selective, and divided attention conditions. The red circle represents the modality that the participant was instructed to attend.

2.5 Behavioral analyses

The percentage of correct responses on the sentence task was used as a behavioral measure of attention. Behavioral performance in the undistracted attention task was calculated by averaging the percentages of correct answers from both visual and auditory modalities together to form one variable. The same average was calculated for the three selective attention conditions (with speech, music and text distractors). The undistracted attention task was included in the behavioral analyses as a baseline for task performance. In the cross-sectional design, all three age cohorts were included in the analysis. The difference in the amount of correct responses was analyzed with a repeated-measures ANOVA with the three task conditions (undistracted, selective attention and divided attention) as within-subject variables. Age cohort and Gender (both categorical variables) were selected as between-subject variables.

In the longitudinal design, only Cohorts 1 and 2 were included in the analysis. The longitudinal data was also analyzed with repeated-measures ANOVA, with two levels for the two measurement points and three levels for the attention tasks as within-subject variables, and Age cohort and Gender as between-subject variables.

Greenhouse-Geisser correction was used for all the ANOVAs as Mauchly's tests of sphericity were significant. The ANOVAs were calculated at a 95% confidence level. Bonferroni post-hocs were calculated if the p-value of the ANOVA was significant. The analyses were conducted with IBM SPSS 21 (IBM SPSS, Armonk, NY, USA).

2.6 fMRI analyses

The fMRI preprocessing and analyses were performed with SPM8 (Wellcome Department of Cognitive Neurology, London, UK). In pre-processing the data was high pass filtered (cut-off at 1/128 Hz), motion corrected and spatially smoothed with a 6mm Gaussian kernel. To correct for the interaction of susceptibility artefacts and head movements the EPI images were un-warped and intra-individually realigned to the middle image in each time series.

To study the effects of the three different task conditions, statistical parametric maps (averaged across participants within each age cohort separately) were compared between contrasts for tasks and rest. In the cross-sectional design, these contrasts were then compared using t-test contrasts between age cohorts, whereas in the longitudinal design they were compared between the two measurement points. The contrast for undistracted attention was not compared between cohorts or measurement points, as it acted only as a baseline for the behavioral task performance. The undistracted attention task required mostly semantic processing, while the focus of this study is to examine the development of selective and divided attention. A voxel-wise height t-value threshold was set at 1.0 and cluster-size threshold at 50 voxels at an uncorrected $p<.01$. The relatively low thresholds were chosen to show the extent of the changes. Although multiplicity correction is usually applied, the age effects in the current study were very subtle and did not survive the correction. The uncorrected results are nevertheless reported to examine potential effects that could be replicated later with a larger sample size.

3. Results

3.1 Behavioral results

Cross-sectional results

The estimated marginal mean percentages of correct responses for the three task types and age groups are shown in Figure 3. The ANOVA revealed a significant main effect for Task type ($F(1.727, 170.998)=450.52$, $p<.001$). Post-hocs for the three task types showed that all task performances differed significantly from each other ($p<.001$ in all comparisons), with the largest amount of correct responses in the undistracted attention task. The amount of correct responses decreased in selective attention task, and task performance was the poorest in the divided attention task. There was also a significant main effect for Gender ($F(1, 99)= 11.13$, $p<.001$) and Age cohort ($F(2, 99)=18.27$, $p<.001$) on performance. Females performed better than males across all age cohorts. Post-hoc tests for the age cohorts showed that performance was significantly better in Cohort 2 (16–17 years) and Cohort 3 (20–22 years) compared with Cohort 1 (13–14 years) ($p<.001$). No significant difference was found between Cohorts 2 and 3 ($p<1{,}000$). There were no statistically significant interactions between the Gender, Age cohort and Task type variables.

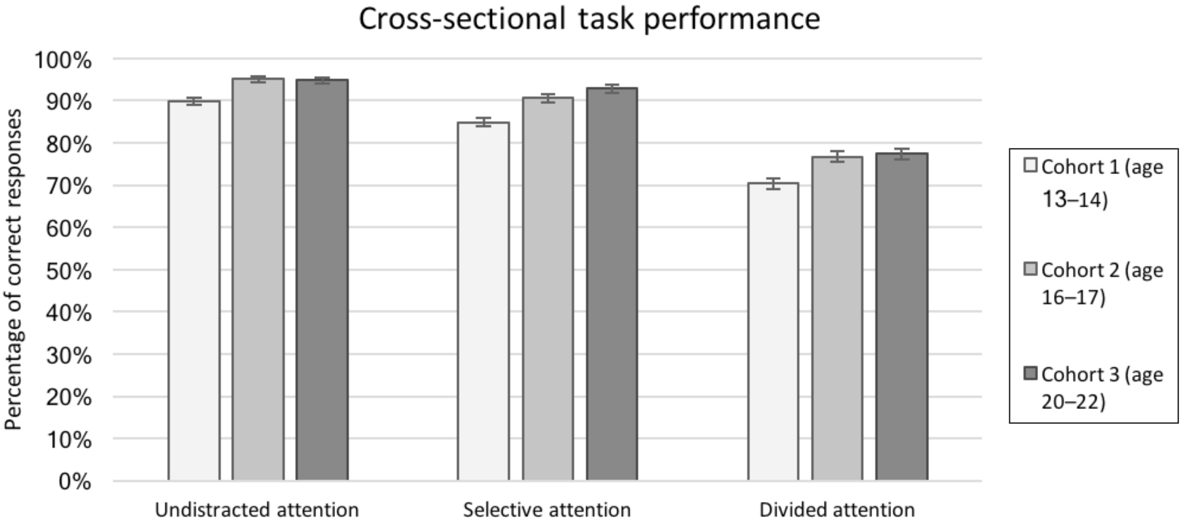

Figure 3: Percentages of correct responses of three age cohorts in the undistracted, selective, and divided attention tasks in the cross-sectional study. Error bars indicate SEMs.

Longitudinal results

The estimated marginal mean percentages of correct answers for the three task types at two time points are shown in Figure 4 for both Cohort 1 and Cohort 2. In the longitudinal design, the repeated measures ANOVA revealed a significant main effect for Task type (F(1.983, 126.992)=216.293, p<.001). Post-hoc tests for Task type showed that all comparisons between the task types were significant (p<.001).

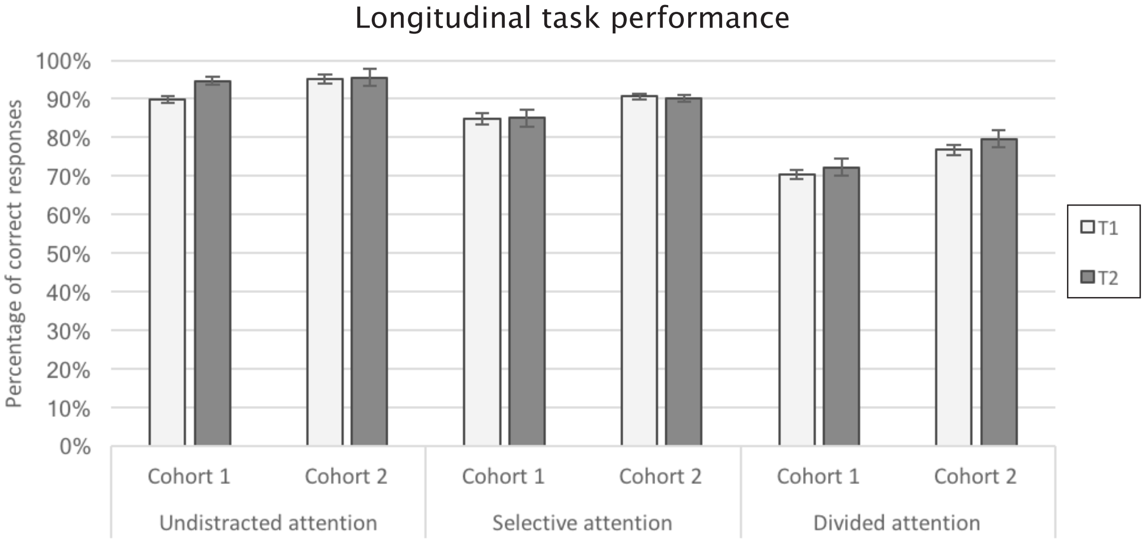

Figure 4: Percentages of correct responses of cohort 1 (age at T1: 13–14y. and T2: 15–16y.) and cohort 2 (age at T1: 16–17y. and T2: 18–19y.) at two time points (1.5 years apart) in the undistracted, selective, and divided attention tasks in the longitudinal study. Error bars indicate SEMs.

The results were similar to the cross-sectional design: performance was best in the undistracted attention task, deteriorated in the selective attention task, and was worst in the divided attention task. There was also a significant main effect for Age cohort (F(1, 64)=13.471, p<.001), with Cohort 2 performing better than Cohort 1. The main effect of Time point (effect of time between two measurements within the same participant) was not quite statistically significant (F(1,64)=3.815, p=.055). No interaction between the variables was detected.

3.2 fMRI results

Cross-sectional results

In the **selective attention** task, both increases and decreases of activation were found when comparing the activations of Cohort 1 (13–14 -years) to those of Cohort 2 (16–17-years). The exact locations and sizes of main clusters (p<.01, uncorrected) are reported in Table 1. As can be seen in Figure 5, activation increased slightly with age bilaterally around temporal and parietal areas such as the superior temporal gyrus and paracentral lobule. Small decreases of activation were found in the supramarginal gyrus and prefrontal cortex. When comparing age Cohort 2 (16–17 years) to Cohort 3 (20–22 years), increases of activation were found mostly around the left postcentral gyrus, but no significant activation decreases were detected.

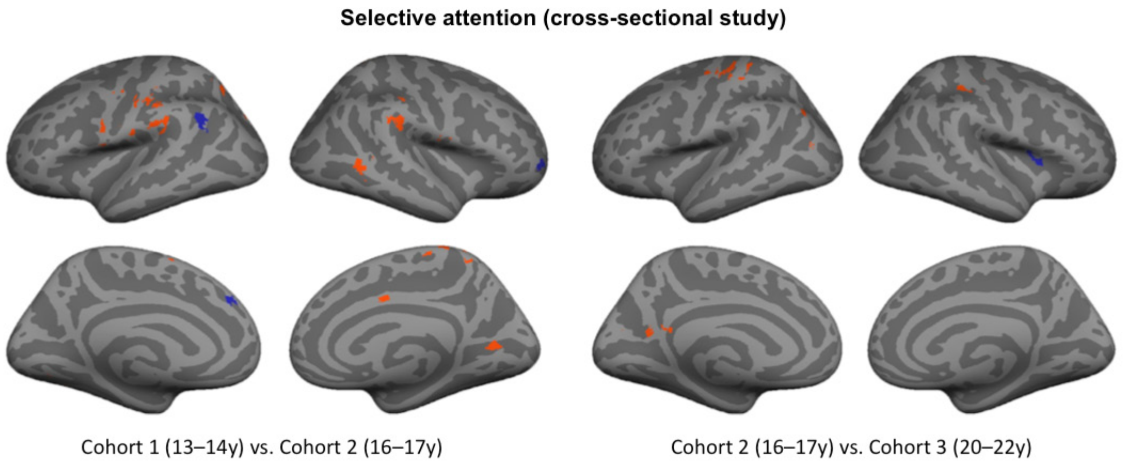

Figure 5: Significant changes of activation in the selective attention task in the cross-sectional study. Areas that increased activity with age are colored red, and areas of decreased activity are marked with blue. Voxel-wise threshold t = 1, cluster size > 50 vox, uncorr. p<0.01.

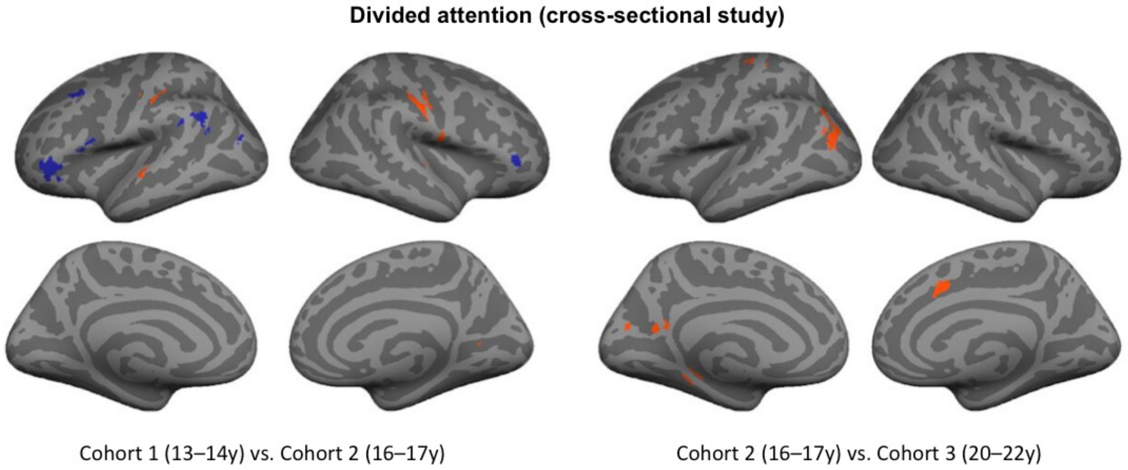

Figure 6: Significant changes of activation in the divided attention task in the cross-sectional study. Areas that increased activity with age are colored red, and areas of decreased activity are marked with blue. Voxel-wise height threshold t = 1, cluster size > 50 vox, uncorr. p<.01.

In the **divided attention** task which is displayed in Figure 6, mostly decreases in activation with age were found when comparing cohorts 1 and 2. The decreases were focused on prefrontal (orbitofrontal, inferior and middle frontal gyri), temporal (middle and superior temporal gyri), and inferior parietal areas, predominantly in the left hemisphere. Activation increased slightly with age in the right precentral gyrus. When comparing cohorts 2 and 3, no decreases were observed. Increases occurred mostly in the left temporal and occipital lobe junction (middle occipital gyrus). Cohorts 1 and 3 were not compared because there was no longitudinal equivalent for the comparison, as the 13–14–year-old participants of the longitudinal study had not yet been measured in their early twenties.

Longitudinal results

The coordinates and sizes of main clusters (p<.01, uncorrected) found in the longitudinal comparison are reported in Table 1. When comparing activity related to the **selective attention** task (Figure 7) between the two measurement points for Cohort 1 (at age 13–14 and 15–16), activation was found to decrease in the prefrontal cortex bilaterally (medial surface of the superior frontal gyrus, anterior cingulate) and on the anterior middle temporal gyrus and left angular gyrus. Small increases with age were found in the left parietal lobule and right precuneus. With cohort 2, decreased activity was found in the caudate nucleus and prefrontal cortex from age 16–17 to age 18–19. Activity increased with age in the left parietal motor areas (supplementary motor area, motor cortex), and left precuneus.

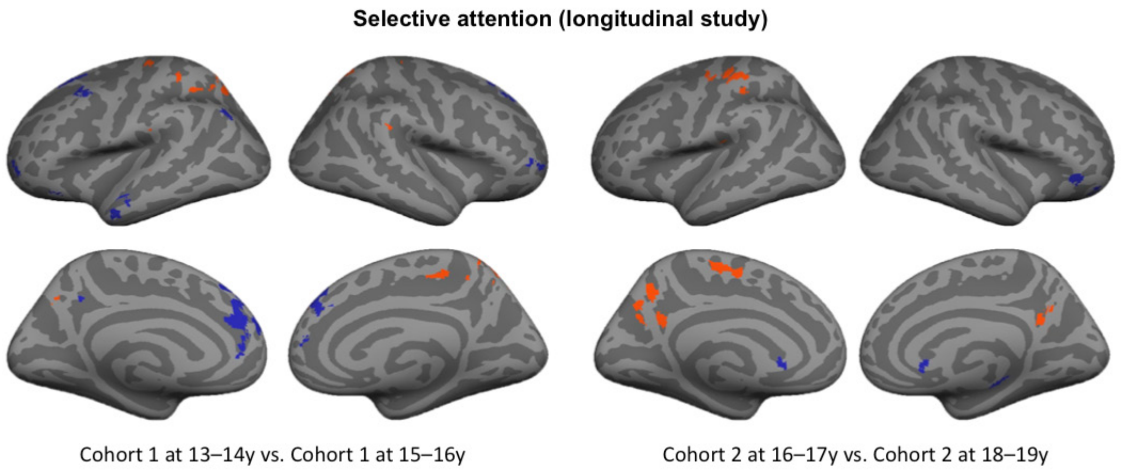

Figure 7: Significant changes of activation in the selective attention task in the longitudinal study. Areas that increased activity with age are colored red, and areas of decreased activity are marked with blue. Voxel-wise height threshold t = 1, cluster size >50 vox, uncorr. p<.01

In the **divided attention task** (Figure 8) with Cohort 1, decreases in activation from age 13–14 to age 15–16 were also focused on the prefrontal cortex (predominantly left MFG and IFG) but more laterally than in the selective task. A similar decrease in the middle temporal gyrus was also found. A small increase in activation with age was located in the left precuneus. With Cohort 2, no decreases in activation were found in the longitudinal design. Activity increases were focused on the left supplementary motor area and left precuneus.

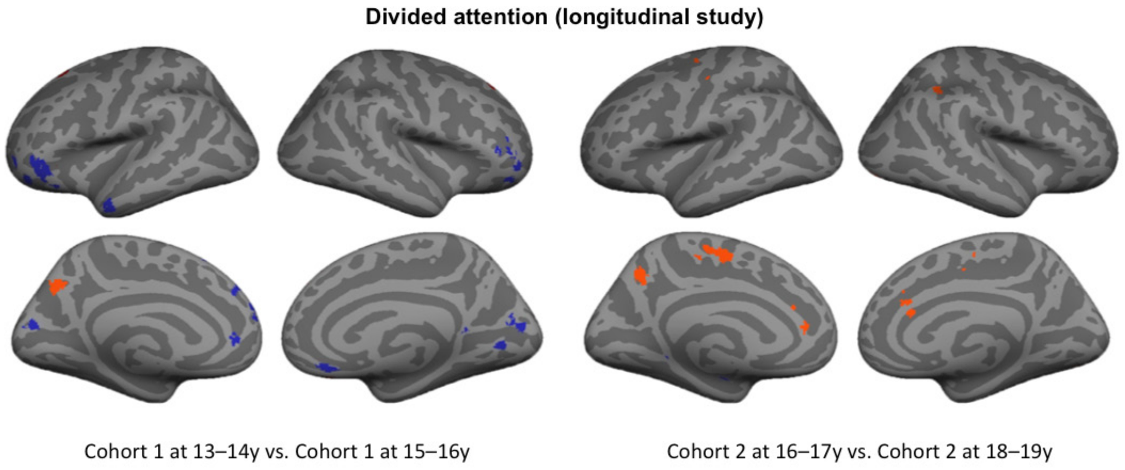

Figure 8: Significant changes of activation in the divided attention task in the longitudinal study. Areas that increased activity with age are colored red, and areas of decreased activity are marked with blue. Voxel-wise height threshold t = 1, cluster size >50 vox, uncorr. p<.01.

	Region of peak	Brodmann area	Cluster size	Peak x, y, z	Peak T-value
LONGITUDINAL					
Selective attention 13–14y vs 15–16y					
increased activity	Inferior parietal lobule L	BA40	345 vox	−30, −48, 44	4,55
	Precuneus R	BA5	265 vox	10, −58, 68	3,46
decreased activity	Angular gyrus L	BA39	180 vox	−42, −78, 34	4,58
	Medial superior frontal gyrus L	BA8	798 vox	−6, 38, 52	4,23
	Medial superior frontal gyrus L	BA10	186 vox	−10, 58, 26	4,02
Selective attention 16–17y vs 18–19y					
increased activity	Postcentral gyrus L	BA3	290 vox	−32, −30, 52	5
	Precuneus L	BA23/7	200 vox	−10, −54, 22	4,1
decreased activity	Caudate R	BA25	244 vox	8 , 24, 0	5,28
Divided attention 13–14y vs 15–16y					
increased activity	(no clusters under p<.01)				
decreased activity	Inferior frontal gyrus (orbital) L	BA47	350 vox	−44, 36, −8	4,1
	Inferior frontal gyrus (pars triangularis)	BA45	380 vox	48, 38, 6	3,64
	Calcarine R	BA17	378 vox	6, −80, 12	3,38
Divided attention 16–17y vs 18–19y					
increased activity	Supplementary motor area L	BA4/6	226 vox	−10, −22, 58	3,97
decreased activity	(no clusters under p<.01)				
CROSS-SECTIONAL					
Selective attention 13–14y vs 16–17y					
increased activity	Paracentral lobule R	BA5/4	223 vox	6, −40, 78	4,15
	Superior temporal gurys L	BA48	380 vox	−64, −28, 22	3,62
	Supramarginal gyrus R	BA48	212 vox	44, −34, 32	3,32
decreased activity	(no clusters under p<.01)				
Selective attention 16–17y vs 20–22y					
increased activity	Postcentral gyrus L	BA3	241 vox	−32, −30, 52	4,6
decreased activity	(no clusters under p<.01)				
Divided attention 13–14y vs 16–17y					
increased activity	(no clusters under p<.01)				
decreased activity	Middle temporal gyrus L	BA39	478 vox	−54, −60, 24	4,45
	Inferior frontal gyrus (orbital) L	BA47	313 vox	−46, 34, −2	4,04
Divided attention 16–17y vs 20–22					
increased activity	Middle occipital gyrus L	BA19	405 vox	−36, −75, 38	3,86
decreased activity	(no clusters under p<.01)				

Table 1: Location and size of main clusters (p<.01, uncorrected) of increased and decreased activity in the selective and divided attention tasks. Coordinates of BOLD response peaks within the cluster are reported according to MNI space along with the peak T-value. L=left hemisphere, R=right hemisphere, BA=Brodmann's area.

4. Discussion

This study examined the normal development of brain networks related to selective and divided attention in adolescence using functional magnetic resonance imaging. To study the behavioral development of selective and divided attention, the participants performed variations of a sentence congruence judgment task during fMRI. Both cross-sectional and longitudinal study designs were used, in order to assess possible differences in the results they produce. The first hypothesis was that behavioral performance would improve in both tasks, as the processing becomes more efficient with neural development. The second hypothesis was that brain activity would become less frontal with age and more concentrated in posterior task-relevant areas. Thirdly, the longitudinal study was expected to reveal similar changes as the cross-sectional results but in larger areas.

In general, there were several differences in cross-sectional and longitudinal results. Behaviorally, the longitudinal results did not reveal age-related changes in performance, while the cross-sectional results implied development. Although the task performance did not improve, there were some changes in brain activity with age. The longitudinal fMRI results showed changes in different brain areas than the cross-sectional comparisons. However, the effects were very subtle and did not survive correction, so larger samples would be required to detect age-effects more clearly. When interpreting the results, selective and divided attention cannot be completely separated from other contributing executive functions, as the tasks demanded both sustaining the task instructions in working memory and inhibiting the unattended stimuli. (Jennifer Adrienne Johnson & Zatorre, 2006)

4.1 Development of selective attention

The behavioral results of the selective attention task performance corroborated Hypothesis 1 in the cross-sectional study, and were against Hypothesis 1 in the longitudinal study. The cross-sectional results in Figure 2 implied that Cohort 2 (16–17 years) and Cohort 3 (20–22 years) performed better in the task than Cohort 1 (13–14 years), but Cohort 3 did not differ from Cohort 2. This would imply that the development of selective attention in this particular task type would continue until adolescence, but behavioral development would cease before adulthood. However, the longitudinal results (Figure 3) did not imply development in task performance from age 13–14 to 15–16 in Cohort 1, or from age 16–17 to 18–19 in Cohort 2. These longitudinal results put the differences found in the cross-sectional study to question. The results are in contradiction with the view from previous studies that the effect of interference on performance decreases with age, which has been attributed to better inhibitory skills and top-down control of attention (Konrad et al., 2005; Plude et al., 1994; Takio et al., 2009). It also has to be noted that the studies proposing this have all been cross-sectional.

Some explanation for the lack of developmental differences might be found in the participants' age-span: the compared age groups were quite close together, and the longitudinal measurements were performed at a relatively small interval of 1.5 years. Differences might be clearer with longer measurement intervals, but more longitudinal research is needed to confirm this. As the participants performed the same task twice in the longitudinal study, there is a possibility of a practice effect which could have leveled out individual differences in task performance. It could also be the case that the ability to control selective attention matures before age 13. Looking at previous research, this is quite unlikely, as the inhibitory mechanisms has been found to develop well into adolescence (Luna et al., 2010), and a filtering task like the one used in this study should require inhibition of the distractor.

In a dichotic listening study by Takio and colleagues (2009), top-down control of attention began to emerge already in 10–11-year-olds, and was fully matured in the adult group (19–32-year-olds). Some development could be expected to occur between these age groups from age 12 to 18, which is roughly the age-span examined in the present study. The selected age groups might still have missed some transitional step from childhood to adulthood, as the development of executive functions is not necessarily linear (Best & Miller, 2010). The sentence task used in this study was a bit more complex than the Go/No-go or visual search tasks that are often used in inhibition and attention studies, because it also required semantic comprehension. The task probably tapped other functions besides attention, which is a common challenge in executive functions research as the functions are interrelated (Best & Miller, 2010). Behavioral development in different tasks and functions can also vary, which could explain some of the present results.

Contrary to the behavioral results, the brain imaging results from the selective attention tasks did reveal age-related changes in activation patterns. The longitudinal results were in accordance with Hypothesis 2, that activation decreases in the prefrontal cortex and increases in other task-relevant areas. The largest changes occurred in early adolescence. Interestingly, the recruited areas differed substantially between the designs, which was against the Hypothesis 3. In the cross-sectional study, activation increases found between Cohort 1 and Cohort 2 focused mainly around temporal areas (Figure 4), but in the longitudinal study activation increased with age in the parietal lobe (inferior parietal lobule, IPL) instead (Figure 6). Increased parietal activation with age has also been found in the study by Adleman and colleagues (2002) using a Stroop-task which demands inhibition and selective attention. Activation in parietal regions has been connected with maintaining and reorienting attention (Konrad et al., 2005) and shifting attention between modalities (Shomstein & Yantis, 2004).

The longitudinal study also revealed decreases of activation from age 13–14 to 15–16 in dorsolateral and dorsomedial prefrontal cortex (e.g. middle and superior frontal gyri, Figure 6), that were barely detectable in the cross-sectional comparison. Greater dorsolateral prefrontal activity in children compared to adolescents and young adults is in accordance with some previous executive function studies by Durston and colleagues (2006) as well as Tamm and colleagues (2002). Dorsolateral prefrontal cortex (DLPFC) has been connected with e.g. working memory and cognitive control, so Tamm and colleagues concluded that children recruited more of this area because of inefficient strategies, leading to larger processing demands on the DLPFC.

In addition to inefficient strategies, other explanations have been suggested for the decreased PFC activity. If the prefrontal cortex is seen as the modulator of activity in other brain regions (e.g. (Miller & Cohen, 2001), the late maturation of PFC and its connectivity could cause children to require more effort in processing than adults. Luna and colleagues (2010) suggest that children and adolescents rely heavily on PFC activation to reach adult levels in task performance, because the connections to other brain regions and ability to use this network efficiently is still immature. This theory could explain the changes in brain function combined with the limited change in task performance that were found in this study.

According to our longitudinal results in Figure 6, from age 16–17 to 18–19 activity around the supplementary motor area (SMA) and the precuneus (PrC) increased with age, combined with small decreases in the prefrontal cortex and caudate nucleus. Similar but more restricted increases in motor regions could be seen in the cross-sectional results. The SMA is thought to be involved in the implementation of motor inhibition as well as performance monitoring (Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004). The caudate nucleus, a part of the basal ganglia, is also connected to the implementation of inhibition (Casey et al., 2001). Greater basal ganglia recruitment in adolescents compared to adults could be caused by their larger susceptibility to interference and increased inhibitory demands. The precuneus has been previously linked with executive functions e.g. conflict adaptation (Egner & Hirsch, 2005), dual tasking (Szameitat et al., 2002), and selective attention and inhibition (Booth et al., 2003). These changes occurring after age 16 could be interpreted as fine-tuning of cognitive control, inhibition and performance monitoring, and a shift to more efficient use of task-relevant areas outside the PFC.

The results indicate that activation related to selective attention becomes less focused on the prefrontal cortex and increases in parietal areas relevant to the task from early adolescence to adulthood. More efficient recruitment of task-related regions with age has been previously suggested in studies of other executive functions (Durston et al., 2006; Luna et al., 2010; Tamm et al., 2002). If the adolescent brain becomes less reliant on prefrontal processing and is able to recruit more posterior areas, the recruited network starts to resemble an adult fronto-parietal network that has been associated with top-down cognitive control (Luna et al., 2010). According to (Fair et al., 2007) the fronto-parietal network (including e.g. DLPFC, IPL, PrC) strengthens its connections in adolescence and becomes more distinct from other circuitries. According to them, this integration could underlie the maturation of cognitive control. In our study, functional changes seemed to continue from adolescence to early adulthood in selective attention, but the changes were probably too subtle to be translated to the behavioral task, or the task did not completely tap the desired functions. Luna and colleagues (2010) also point out that adolescents may perform equally well to adults in executive function tasks, but adolescent brain activation resembles adult activation during a difficult task. This could also be the case in the current study.

4.2 Development of divided attention

Development of task performance in the divided attention task gave support to Hypothesis 1 in the cross-sectional study, but the results were against Hypothesis 1 in the longitudinal study similarly to selective attention. Although the longitudinal results did not indicate statistically significant development in task performance between the measurement points ($p<.0.55$), a nonsignificant trend could be seen in the divided attention task between the two measurement points in both age cohorts (Figure 3). A clearer improvement was found in the cross-sectional study between Cohort 1 and Cohort 2 (Figure 2). As in the case of selective attention, Cohort 3 did not differ from Cohort 2 in task performance. In conclusion, it seems that dual tasking performance might still develop between ages 13 and 16, but this needs to be confirmed with further longitudinal studies. Previously it has been found that age affects the extent of the dual tasking cost only in complex or difficult task conditions (Saxena et al., 2017), suggesting that the sentence task used in the current study was not quite challenging enough to produce clear differences. The high performance on the single task (undistracted attention task) reinforces this conclusion.

This was the first study to investigate the brain network of divided attention from a developmental perspective, so the hypotheses had to be drawn from studies regarding other executive functions. The results did corroborate Hypothesis 2, as dividing attention seemed to recruit prefrontal areas less with age, and posterior task-relevant areas more. Both in longitudinal and cross-sectional results, the dorsolateral prefrontal cortex (MFG/IFG) activation decreased from age 13–14 to around 16 and the changes were lateralized more to the left side (Figures 5 and 7).

Dorsolateral prefrontal activation has been reported in previous studies of divided attention, and it has been connected to manipulation of information in working memory (e.g. Johnson & Zatorre, 2006) as well as coordination of interfering task processing (Szameitat et al., 2002). Both interpretations could be plausible in the current study, as the participants had to process the semantic meaning of one sentence and keep the other sentence active in working memory at the same time, as well as to coordinate processing between the two sentences. In the study by Johnson and Zatorre (2006), they found that participants with poor divided attention performance recruited the sensory cortices less and the DLPFC more, and opposite results were found with good performers. Their conclusion was that the inability to properly recruit sensory cortices is compensated with increased prefrontal recruitment during divided attention.

This explanation could also be applied to development: greater DLPFC activation in younger participants could be caused by more effortful working memory processing in order to improve divided attention performance. In addition to the decreased activation in the DLPFC, there was a small increase in precuneus activation from age 13–14 to 16–17 in the longitudinal study, which was not evident in the cross-sectional comparison. As in the selective attention condition, the increased precuneus activity with age could be interpreted as improved ability to recruit areas related to cognitive control outside the PFC, as the integration between these areas matures.

From age 16–17 to 18–19 the longitudinal study showed increased activity related to divided attention in the SMA and precuneus regions, but no significant activation decreases (Figure 7). The pattern of activation was very similar to the longitudinal results in the selective attention task (Figure 6). In conclusion, posterior areas (PrC, SMA) related to divided attention, inhibition and executive control (Booth et al., 2003; Szameitat et al., 2002) are recruited more efficiently in adulthood than in adolescence. These results were, however, quite different to the ones found in the cross-sectional study of divided attention, where activity was found to increase mostly occipitally. This difference in the affected areas was against our original Hypothesis 3.

Taken together, results suggest that divided attention seems to develop behaviorally until age 13 and possibly up to age 16, while the brain activity pattern becomes less frontal and more parietal quite similarly to selective attention. The stronger reliance on prefrontal cortex in younger adolescents could reflect an immature (fronto-parietal) network that is compensated by increased prefrontal cortex recruitment (Jennifer Adrienne Johnson & Zatorre, 2006; Luna et al., 2010).

4.3 Selective vs. divided attention

In overall task performance, dividing attention between the tasks was more difficult compared to selective attention in all age groups. The percentage of correct answers was in general quite high: even the youngest participants performed at 70% in the divided attention task. No significant differences were observed in the adolescent development of selective and divided attention task performance. A wider age-range and more measurement points would likely be required to track differences in their behavioral development. It also has to be noted that previous studies have not found conclusive behavioral evidence that dual tasking affects children's performance more than adults' (Saxena et al., 2017). More research is still needed to assess whether the behavioral developmental pattern of divided attention differs from selective attention.

In terms of brain function, no direct statistical comparison was made between the selective and divided attention conditions, but some similarities and differences in their results can be discussed. The main focus here is on the longitudinal study, as it is a more reliable way to examine development (e.g. Casey et al., 2005). From age 13–14 to 15–16, a prefrontal activity decrease in the left hemisphere was found in both task types, but the activity was more medial during selective attention, reaching the anterior cingulate. The role of anterior cingulate in cognitive control is thought to be in conflict detection (Braver, Barch, & Gray, 2001) and error-related processing (Rubia, Smith, Taylor, & Brammer, 2007). In addition to cognitive control, the conflict detection related activity could also be caused by the sentence congruence judgement task that was used. Interestingly there did not seem to be large differences in the magnitude of the frontal changes, although divided attention has been found to activate frontal cortex more than selective attention in adults (Moisala et al., 2015).

The similar decreased activity around DLPFC in both tasks might suggest that top-down cognitive control would become less effortful with age as PFC and its connections develop. This interpretation would have to be confirmed by performing the task with equated task difficulty for age. Only dividing attention caused increased precuneus activity in the younger age group, which could be related to the task being more demanding in coordination than the selective attention task. In turn, selective attention caused a distributed posterior parietal increase in the left hemisphere from age 13–14 to 15–16, and in motor areas from age 16–17 to 18–19. Parietal areas e.g. the superior parietal lobule has been previously connected with modulation of attention (Pessoa et al., 2003). The slightly larger increased activation in motor areas during selective attention could reflect a greater demand for inhibiting the distractor.

The overlapping results could mean that selective and divided might share a similar system of top-down executive control. Similar parietal and frontal recruitment in areas involved in executive control (e.g. IPS, MFG, PrC) can also be seen in some previous studies of selective and divided attention (Moisala et al., 2015; Szameitat et al., 2002). Selective and divided attention could be, like other executive functions, separable while still sharing some mechanisms. More neuroimaging studies are still needed to confirm these similarities.

The activity increases from age 16–17 to 18–19 were very much alike in selective and divided attention in the longitudinal study. Changes were focused around left precuneus and SMA regions in both tasks, but the affected areas were larger in selective attention. The longitudinal results suggest that brain activity related to divided attention could have a different, possibly longer developmental trajectory than selective attention. More longitudinal fMRI studies are needed to better understand the changes in brain function occurring from adolescence to adulthood.

4.4 Longitudinal vs. cross-sectional designs

All the longitudinal and cross-sectional analyses were calculated separately and were not statistically compared, but surprisingly clear distinctions could be seen in the results the designs produced. If the study question would have been examined only cross-sectionally, the conclusions drawn from the results would have been completely different. The behavioral cross-sectional results strongly indicated a difference in performance between the youngest two age groups, which was not evident when the development was tracked within individuals. The longitudinal measurement interval was slightly shorter than the age difference between the cross-sectional cohorts, which might have affected the results.

Although the changes in activation were quite small in general, the fMRI results also differed substantially between the designs. This was against our original Hypothesis 3, according to which the changes would have been in similar areas. The only similarity between the designs was the decreased left IFG activity in the divided attention task. The affected area did seem to be larger in the longitudinal study, although this would have to be confirmed with further statistical comparisons.

The developmental study by Durston and colleagues (2006), that used both longitudinal and cross-sectional designs, also found that their longitudinal study revealed additional reduction of activation compared to the cross-sectional results. This was seen as evidence that longitudinal studies are more sensitive to subtle changes in brain activity than studies comparing different age-groups. The extent of change in brain activity could also be distorted in cross-sectional studies due to e.g. inter-individual variance (Gogtay et al., 2004). In the current study, it seems possible that the cross-sectional comparison exaggerated the magnitude of change in task performance, given that the sample size per cohort group was relatively small.

4.5 Conclusions and future directions

The present results give support to the notion that development of attention continues from adolescence to early adulthood at least in terms of brain function. Most changes were witnessed in early adolescence (from 13 to 16 years). Results on behavioral development were inconclusive: the cross-sectional results implied development but the longitudinal comparison did not. Some potential differences in the neural development of divided and selective attention were found. The prefrontal decreases from age 13–14 to 15–16 seemed to be more lateral in divided attention than selective attention, and parietal increases were more prominent in selective attention. In future research, it would be interesting to study the developmental trajectory of divided attention further with longitudinal fMRI studies, as this was the first study to examine the development of divided attention with fMRI. Diffusion tensor imaging (DTI) could also be useful in revealing the development of neural connections between the prefrontal cortex and other brain regions.

The fMRI results of the current study on the development of attention are mostly parallel to previous findings that executive functioning becomes less reliant on the PFC with age and other task-relevant areas are recruited more efficiently (e.g. Luna et al., 2010; Tamm et al., 2002). This developmental pattern could indicate that the need to compensate poor performance with increased PFC effort (i.e. top-down control) decreases with age, as the PFC and its integration with other areas develops (e.g. Johnson & Zatorre, 2006) or the performance strategies become more efficient with age (Tamm et al., 2002). On a more abstract level, the results would also fit Miller and Cohen's (2001) integrative theory that goals and the means to achieve them are represented in the PFC, which exerts top-down bias signals to other parts of the brain to perform the task.

This study was one of the first to simultaneously use both longitudinal and cross-sectional designs to examine the development of executive functions. The results of the two designs were surprisingly different both in terms of task performance and brain function, which emphasizes the importance of conducting longitudinal developmental studies. Although the study designs were not directly statistically compared, this study gives some indication on the possible distortions that cross-sectional studies can create. Study design should be carefully considered in future developmental research, as nearly all previous studies on the topic have been cross-sectional. It would be interesting to examine the developmental pattern also from childhood to adolescence by using longitudinal studies with larger age-spans.

The current study had some methodological limitations. Sample size per cohort was relatively small, and the longitudinal study was conducted with only two measurement points that were quite close together. These factors made it impossible to directly compare the longitudinal and cross-sectional results, and might have affected the magnitude of the fMRI and behavioral results negatively. Larger samples should also be used in future studies, as the varied maturation rates of individual adolescents can be accentuated in small samples. The inter-individual variation of brain structure can also distort especially cross-sectional results. The current results were possibly also affected by the task not being demanding enough to show clear development, as well as the fact that the participants performed the task at the same difficulty level twice in the longitudinal study. This makes it challenging to differentiate the effect of age from performance differences. Task difficulty and measurement intervals should be taken into account in future studies.

This study provided new information on the adolescent development of selective and divided attention both behaviorally and in terms of brain function. It also demonstrated the importance of studying development with longitudinal designs. Examining the normal development of executive functions and the role of adolescence in this process is important, as it helps to better understand the behavior and capabilities of adolescents.

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