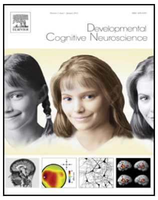
Developmental Cognitive Neuroscience 5 (2013) 63–70

Contents lists available at SciVerse ScienceDirect

Developmental Cognitive Neuroscience

journal homepage: http://www.elsevier.com/locate/dcn



Changes in neural mechanisms of cognitive control during the transition from late adolescence to young adulthood

Kim Veroude[a,*], Jelle Jolles[a], Gerda Croiset[b], Lydia Krabbendam[a]

[a] Department of Educational Neuroscience, Faculty of Psychology and Education & LEARN! Institute, VU University Amsterdam, The Netherlands
[b] Institute for Research and Education, VU University Medical Center Amsterdam, The Netherlands

ARTICLE INFO

Article history:
Received 5 September 2012
Received in revised form
27 November 2012
Accepted 18 December 2012

Keywords:
Brain
Development
Sex
Stroop
Interference resolution
Emotion

ABSTRACT

The transition from late adolescence to young adulthood is marked by anatomical maturation of various brain regions. In parallel, defining life changes take place, such as entrance into college. Up till now research has not focused on functional brain differences during this particular developmental stage. The current cross-sectional fMRI study investigates age differences in cognitive control by comparing late adolescents, 18–19 years old, with young adults, 23–25 years old. Seventy-four male and female medical students carried out a combined cognitive and emotional Stroop task. Overall, lateral frontoparietal and medial parietal activation was observed during cognitive interference resolution. Young adults showed stronger activation in the dorsomedial prefrontal cortex, left inferior frontal gyrus, left middle temporal gyrus and middle cingulate, compared to late adolescents. During emotional interference resolution, the left precentral and postcentral gyrus were involved across age and sex. The dorsomedial prefrontal cortex and precuneus were activated more in young adults than in late adolescents. No sex-related differences were found in this homogeneous sample. The results suggest that the neural bases of cognitive control continue to change between late adolescence and young adulthood.

1. Introduction

The life period between the ages 18 and 25 is a time in which important changes take place, such as obtaining a college degree, leaving home, establishing new social relations and reaching financial independence. This phase has been referred to as emerging adulthood (Arnett, 2000) and is characteristic for industrialized societies, where young people have prolonged educational tracks to qualify for highly technical jobs. During this period, structural maturation of the brain and cortical networks is ongoing (Lebel and Beaulieu, 2011; Tamnes et al., 2010), which has been linked to environmental transitions (Bennett and Baird, 2006). Particularly areas within the prefrontal cortex that are important for cognitive control, the ability to direct behavior towards a goal, continue to develop until the early 20s (Giedd and Rapoport, 2010; Toga et al., 2006). These high-order association areas, including the lateral and medial prefrontal cortex as well as the cingulate cortex, reach their peak in cortical thickness last (Shaw et al., 2008). Another region that matures late, as indicated by gray matter loss, is the lateral temporal lobe (Gogtay et al., 2004). Anatomical trajectories are likely linked to functional development of cognitive processes in the adolescent brain (Blakemore and Choudhury, 2006; Casey et al., 2005; Crone and Ridderinkhof, 2011; Steinberg, 2005). It has been shown that neural correlates of control mature at least until age 18 (Bunge and Wright, 2007; Luna et al., 2010; Rubia et al., 2006; Velanova et al., 2009). However, little is known about changes in brain mechanisms underlying cognitive control during the transition from late

---

[*] Corresponding author at: Department of Educational Neuroscience, Faculty of Psychology and Education & LEARN! Institute, VU University Amsterdam, Van der Boechorststraat 1, 1081 BT Amsterdam, The Netherlands. Tel.: +31 20 598 3455.
E-mail address: k.veroude@vu.nl (K. Veroude).

1878-9293/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.dcn.2012.12.002

adolescence to young adulthood, around the ages of 18 until 25.

An important aspect of cognitive control is interference resolution, inhibition of an automatic response in favor of a voluntary response, and can be measured using the Stroop task (MacLeod, 1991; Nee et al., 2007). There is some evidence from functional magnetic resonance imaging (fMRI) studies that the neural underpinnings of the Stroop task develop further after age 18. In 7–22 year olds, there was a positive correlation between age and activation during interference in the left lateral and medial prefrontal cortex as well as left lateral and medial parietal cortex (Adleman et al., 2002). According to this research, the functional role of the parietal lobe develops until age 12 while frontal involvement changes until age 18 or beyond. On another Stroop paradigm activation of the left lateral prefrontal cortex seemed to increase from age 14 until around age 21 and slightly decrease from age 21 until age 25 (Andrews-Hanna et al., 2011). Increased activation of the right lateral prefrontal cortex with age and with performance was found in participants 7–57 years old (Marsh et al., 2006). Although these studies use a wide age range, the findings indicate that maturation of neural processes related to interference resolution on the Stroop task might extend into adulthood.

Differences in brain activation between adolescents and adults have also been observed during cognitive control over interfering emotional stimuli (Crone, 2009; Monk et al., 2003; Passarotti et al., 2009; Wang et al., 2008). Cognitive and emotional interference resolution engaged similar prefrontal control regions in adolescents aged 16 and 17 performing a variant of the counting Stroop task (Mincic, 2010). No information is available with respect to developmental patterns, as the adolescents were not compared to adults and no other neuroimaging studies have examined development using an emotional Stroop paradigm. During adolescence, cognitive control is particularly difficult in the context of emotional stimuli (Casey et al., 2011), therefore it can be expected that age-related differences are especially pronounced on an emotional variant of the Stroop task.

The lack of knowledge concerning functional brain maturation during the transition from late adolescence to young adulthood has motivated the current fMRI study. Here, differences between 18–19 year olds and 23–25 year olds are investigated on a combined cognitive and emotional Stroop task. The 18–19 year olds are Freshman and Sophomore students in Medical College while the 23–25 year olds are medical students at the Junior or Master level. A homogeneous sample of medical students was chosen to control for possible variation due to differences in intelligence, life experiences and daily activities. Compared to the students in the first years, the students in the final years have already completed courses and practical classes and are involved in clinical training. Students 18–19 years old and students 23–25 years old are termed late adolescents and young adults respectively since it is proposed that between these ages, development towards a complete adult-like pattern of brain functioning occurs. This notion contrasts with the common assumption that people of 18 and older are adults. Instead, we focus on changes within this age range, which can be considered a separate developmental stage. We predict stronger activation in young adults compared to late adolescents, particularly in the prefrontal cortex, during interference resolution. The effect is assumed to be larger during emotional compared to cognitive interference resolution.

An additional question pertains to possible differences between male and female students. It has been demonstrated that the neural bases of cognitive tasks might differ for males and females (Bell et al., 2006). An interaction effect between age and sex was found in 13–38 year olds performing a motor Stroop task (Christakou et al., 2009). In this study, increased activation with age in medial prefrontal areas was shown for females, while for males a positive correlation between age and activation of temporal regions was observed. Additionally, brain activation related to emotional interference can vary between males and females (Koch et al., 2007). To further explore sex-related activation differences on the combined cognitive and emotional Stroop task, in addition to age differences, we include male as well as female late adolescents and young adults.

2. Methods

2.1. Participants and procedure

A total of 74 healthy right-handed volunteers were included in this study. Participants consisted of 21 female late adolescents (range = 18.39–19.98 years, mean = 19.11, SD = 0.44), 17 male late adolescents (range = 18.36–19.91 years, mean = 18.92, SD = 0.53), 18 female young adults (range = 23.24–24.95 years, mean = 24.07, SD = 0.46) and 18 male young adults (range = 23.05–25.95 years, mean = 24.03, SD = 0.89). They were recruited from Medical College at VU University Amsterdam and the University of Amsterdam. Written informed consent was obtained prior to the study and participants received monetary compensation. The study was approved by the Medical Ethics Committee of VU Medical Centre.

All volunteers were right-handed, had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. Mean estimation of receptive vocabulary, an aspect of verbal IQ, was 110.3 (SD = 6.71) on the Peabody Picture Vocabulary Test-III-NL, within the normal range for adults holding a university degree (mean = 112.0, SD = 9.00; Schlichting, 2005). There was no significant difference between scores of the four groups: female late adolescents, male late adolescents, female young adults and male young adults ($F = 1.02$, $p = 0.39$).

The volunteers completed a behavioral session of 1.5 h and an fMRI session of 1 h. During the behavioral session which took place 1 or 2 days before the fMRI session, the fMRI tasks were practiced. In addition, a neuropsychological test battery was administered. During the fMRI session, participants performed a combined cognitive and emotional Stroop task. A social appraisal task and a Go/NoGo paradigm were also performed and will be described elsewhere.

2.2. Experimental paradigm

A combined cognitive and emotional Stroop task was carried out in the fMRI scanner (see Fig. 1; Evers et al., 2006). Words printed in four different colors were presented on a back-projection screen that could be seen through a tilted mirror attached to the head coil. Participants indicated the color of the ink by button press with the left middle finger used for blue, left index finger for red, the right index finger for green and right middle finger for yellow. In the behavioral session and in the fMRI session, participants practiced the task to learn the correspondence between stimuli and responses. In case they forgot which buttons to use, they could look at the bottom of the screen where the order of colors was written in white letters.

The task consisted of two runs, each containing 40 congruent color words (e.g. the word red printed in red ink), 40 incongruent color words (e.g. the word blue printed in red), 24 positive emotional words (e.g. friend), 24 negative emotional words (e.g. boring) and 24 neutral words (e.g. house). At the beginning of the task, an instruction screen was presented for 6 s. The participants were instructed to respond accurate and as fast as possible to the color of the ink. Incongruent words were expected to induce cognitive interference while the congruent words were expected to result in facilitation (MacLeod, 1991; MacLeod and MacDonald, 2000). The negative emotional words were included to induce emotional interference (Frings et al., 2010). Positive words should result in less emotional interference, because of the absence of threat (McKenna and Sharma, 1995). The neutral words formed the baseline condition.

Words were presented in a semi-randomized order with never the same color three times in a row and each color equally often in every condition. Every 2 s a word was shown on a black screen. The word stayed on the screen until a response was given with a maximum duration of 2 s. After a response, a blank black screen was shown until the next word appeared. Two runs of the task were counterbalanced across participants. These were preceded by a practice run of 40 neutral words. In the training session 1 or 2 days earlier, two Stroop blocks were performed with 40 congruent words, 40 incongruent words and 72 neutral words. The goal of the practice procedure was to familiarize the participants with the task and the color-button correspondence.

2.3. Data acquisition

Images were acquired on a General Electric 3 T head-only MRI scanner in ascending order. A T2*-weighted echo planar imaging (EPI) sequence was used with the following parameters: time to repetition (TR) = 2000 ms, time to echo (TE) = 35 ms, flip angle (FA) = 80°, field of view (FOV) = 22 cm × 22 cm, number of slices = 35, voxel size = 3.5 mm × 3.5 mm × 3 mm. A T1-weighted anatomical scan was acquired to aid with spatial normalization (TR = 7.876 ms, TE = 3.06 ms, FA = 12°, FOV = 22 cm × 22 cm, number of slices = 166, voxel size = 1 mm × 1 mm × 1 mm).

2.4. Behavioral data analysis

Reaction times and response errors were recorded. To compare reaction times of the conditions Congruent, Incongruent, Positive and Negative to the baseline condition Neutral, four paired samples *t*-tests were performed ($p < 0.01$, Bonferroni corrected for multiple comparisons). Cognitive interference time was assessed for each participant by calculating the difference in reaction time between the condition Incongruent and the condition Neutral. Emotional interference time was calculated by subtracting the reaction time of the condition Neutral from the reaction time of the condition Negative. The effects of Age and Sex on cognitive interference time (Incongruent–Neutral) and emotional interference time (Negative–Neutral) were examined using independent samples *t*-tests ($p < 0.01$, Bonferroni corrected for multiple comparisons).

For error percentages, paired samples *t*-tests were conducted ($p < 0.01$, Bonferroni corrected for multiple comparisons) to compare the conditions Congruent, Incongruent, Positive and Negative to the baseline condition Neutral. Cognitive interference error rate was defined for each participant as the difference in error percentage between the condition Incongruent and the condition Neutral. The difference in error percentage between the condition Negative and the condition Neutral constitutes the emotional interference error rate. Independent samples *t*-tests ($p < 0.01$, Bonferroni corrected for multiple comparisons) were employed to determine effects of Age and Sex on cognitive interference error rate (Incongruent–Neutral) and emotional interference error rate (Negative–Neutral).

2.5. fMRI data analysis

Statistical Parametric Mapping (SPM8, www.fil.ion.ucl.ac.uk/spm) was used to analyze the fMRI data. Preprocessing steps included realignment of the images with a six-parameter rigid body transformation to correct for head movement. Next, functional images of each participant were coregistered to the structural image and normalized to the MNI template. Spatial smoothing was performed with a 7-mm full width at half maximum (FWHM) isotropic Gaussian kernel.

At the first level, a General Linear Model (GLM) was specified with the onsets of every condition. The events with a fixed duration of 0 were convolved with a hemodynamic response function. High-pass filtering was used to remove low-frequency noise and motion parameters were included as regressors of no interest. For each participant, the conditions Congruent, Incongruent, Positive and Negative were contrasted with the baseline condition Neutral. Individual contrast images were entered into second-level analyses.

To confirm previous findings on brain activation during the Stroop task, simple effects of the conditions Congruent, Incongruent, Positive and Negative were calculated. These simple effect analyses were conducted on the entire sample of 74 participants, thus including all four groups. Results were thresholded at $p < 0.05$, Family Wise Error (FWE) rate corrected. *t*-Tests were conducted for the

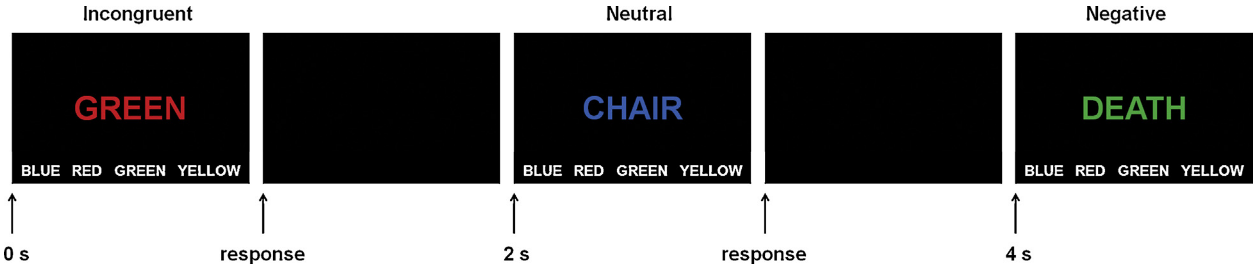


Figure 1. The combined cognitive and emotional Stroop task. Colored words were presented on the screen with a fixed interval of 2 s. The task of the participant was to press a button corresponding to the color of the ink. A black screen was shown after a response. In this example, an incongruent color word, neutral word and negative emotional word are illustrated. Congruent color words and positive emotional words were also included.

conditions Incongruent and Negative (versus the baseline Neutral) to test for the effect of Age (late adolescent, young adult) and the effect of Sex (male, female) during cognitive and emotional interference resolution. A threshold of $p < 0.005$ uncorrected for height was applied and corrected for magnitude with a cluster size $k = 58$ derived from a Monte–Carlo simulation (3dClustSim in AFNI, http://afni.nimh.nih.gov/afni), equivalent to a threshold of $p < 0.05$, FWE corrected.

3. Results

3.1. Behavioral results

Mean reaction times and error rates for all conditions are shown in Table 1. Reaction times in the condition Congruent were shorter than in the condition Neutral ($t(73) = -6.39$, $p < 0.001$), indicative of facilitation. The reaction times in the condition Positive were not significantly different from reaction times in the condition Neutral ($t(73) = 0.41$, $p = 0.68$). Cognitive and emotional interference occurred on this Stroop task, as demonstrated by longer reaction times in the condition Incongruent as well as the condition Negative compared to the condition Neutral ($t(73) = 12.87$, $p < 0.001$ and $t(73) = 5.63$, $p < 0.001$, respectively). There were no effects of sex on cognitive interference time ($t(72) = 0.72$, $p = 0.48$) or emotional interference time ($t(72) = 0.01$, $p = 0.99$). There was no effect of age on cognitive interference time ($t(72) = 0.20$, $p = 0.85$) and a trend towards larger emotional interference times in late adolescents compared to young adults ($t(72) = 2.23$, $p = 0.03$).

A trend was detected towards a smaller error percentage in the condition Congruent compared to the condition Neutral ($t(73) = -2.12$, $p = 0.04$). Error percentages in the conditions Positive and Neutral did not significantly differ from each other ($t(73) = 0.27$, $p = 0.79$). The error percentages in the conditions Incongruent and Negative were larger than in the condition Neutral ($t(73) = 5.40$, $p < 0.001$ and $t(73) = 7.55$, $p < 0.001$, respectively). No effects of age ($t(72) = 0.03$, $p = 0.98$) and sex ($t(72) = -0.66$, $p = 0.51$) on cognitive interference error rate were present. There were also no effects of age ($t(72) = 0.42$, $p = 0.67$) and sex ($t(72) = 0.06$, $p = 0.95$) on emotional interference error rate.

Table 1
Mean reaction times (ms) and error rates (%), including standard deviations.

	Reaction times	Error rates
Incongruent	759.48 (152.58)	12.64 (11.83)
Congruent	627.41 (98.36)	4.90 (4.52)
Negative	679.09 (115.91)	11.82 (6.43)
Positive	657.71 (107.80)	6.64 (6.50)
Neutral	656.44 (109.06)	6.42 (6.02)
Cognitive interference (Incongruent–Neutral)	103.04 (68.86)	6.22 (9.91)
Emotional interference (Negative–Neutral)	22.65 (34.60)	5.40 (6.16)

3.2. fMRI results

3.2.1. Condition effects

To determine which brain areas were involved in performing the Stroop task, simple effects of the conditions Congruent, Incongruent, Positive and Negative were tested across age and sex, thus grouping all participants together. No significant results were found for the conditions Congruent and Positive (compared to the baseline Neutral). During cognitive interference resolution (Incongruent–Neutral), activation was observed in the left inferior parietal gyrus extending into the precuneus, the left inferior frontal gyrus extending into the left precentral gyrus, right inferior parietal gyrus, right precentral gyrus as well as right inferior frontal gyrus and right middle frontal gyrus. Additional small clusters were shown in the left supplementary motor area and bilateral insula. During emotional interference resolution (Negative–Neutral), activation was found in the left precentral gyrus extending into left postcentral gyrus, the cerebellum and a small cluster in left supplementary motor area (see Table 2).

3.2.2. Age effects

There was no effect of sex during cognitive and emotional interference resolution. In both conditions, an effect of age was shown with young adults displaying more activation than late adolescents, as illustrated in Fig. 2. During the condition Incongruent (versus the baseline Neutral), young adults activated the following regions more than late adolescents: the dorsomedial prefrontal cortex (MNI = −14 28 42, $Z = 4.14$), the left middle temporal gyrus (MNI = −63 −39 −6, $Z = 3.71$), the left inferior frontal gyrus (MNI = −39 18 −15, $Z = 3.59$) and middle cingulate (MNI = −4 −21 48, $Z = 3.41$). Thus, involvement

Table 2
Areas in which condition effects were observed ($p < 0.05$, FWE-corrected).

	MNI coordinates				
Peak of activation	*x*	*y*	*z*	*Z*-value	Cluster size
Cognitive interference (Incongruent–Neutral)					
Left inferior parietal gyrus	−28	−70	42	7.80	607
Left inferior parietal gyrus	−35	−53	42	7.48	Part of the same cluster
Precuneus	−7	−74	48	6.83	Part of the same cluster
Left inferior frontal gyrus	−42	25	30	6.86	274
Left precentral gyrus	−53	11	39	6.14	Part of the same cluster
Left precentral gyrus	−42	−4	60	4.82	8
Left precentral gyrus	−32	−4	69	4.59	Part of the same cluster
Left precentral gyrus	−35	−18	69	4.76	5
Right inferior parietal gyrus	35	−56	45	6.21	122
Right inferior parietal gyrus	32	−67	42	5.79	Part of the same cluster
Right precentral gyrus	42	7	30	5.70	170
Right inferior frontal gyrus	46	25	30	5.45	Part of the same cluster
Right middle frontal gyrus	46	32	39	5.45	Part of the same cluster
Right middle frontal gyrus	39	4	57	4.66	6
Left supplementary motor area	−4	11	57	5.09	13
Right insula	32	25	3	4.93	11
Left insula	−35	18	0	4.84	9
Emotional interference (Negative–Neutral)					
Left precentral gyrus	−39	−21	66	9.33	325
Left postcentral gyrus	−35	−25	54	8.96	Part of the same cluster
Cerebellum	21	−56	−27	5.61	37
Cerebellum	7	−67	−24	4.57	Part of the same cluster
Left supplementary motor area	−7	−14	57	5.31	13

of these regions during cognitive interference resolution increases with age. During the condition Negative (versus the baseline Neutral), young adults demonstrated more activation than late adolescents in the dorsomedial prefrontal cortex (MNI = −18 28 42, $Z = 3.71$) and the precuneus (MNI = −18 −60 24, $Z = 3.53$). Engagement of these areas during emotional interference resolution is thus stronger in 23–25 year olds than in 18–19 year olds.

4. Discussion

The current study revealed differences in brain activation between late adolescents (18–19 years old) and young adults (23–25 years old) during cognitive control. Our results indicate protracted functional development of the cortex into the 20s. This is in accordance with findings on anatomical maturation of the brain (Yurgelun-Todd, 2007) and environmental changes that take place during this transitional period (Casey et al., 2010). Although similar behavioral performance on the Stroop task is observed in participants aged 18 and older, underlying neural correlates differ. This was shown here by stronger engagement of several brain regions in young adults compared to late adolescents for cognitive as well as emotional interference resolution.

Across all participants, bilateral and medial parietal cortex as well as bilateral frontal cortex, including the precentral gyrus and the left supplementary motor area, was activated during cognitive interference resolution. This is consistent with previous research demonstrating fronto-parietal engagement on the Stroop task (Compton et al., 2003; Egner and Hirsch, 2005). During emotional interference resolution, activation of the left precentral and left postcentral gyrus, the cerebellum and left supplementary motor area was observed. Engagement of the left postcentral gyrus was reported earlier with the same paradigm (Evers et al., 2006). We did not observe activation of the anterior cingulate cortex, which has been found on the cognitive (Carter et al., 2000; Laird et al., 2005; Mayer et al., 2012; Nee et al., 2007) and emotional Stroop task (Etkin

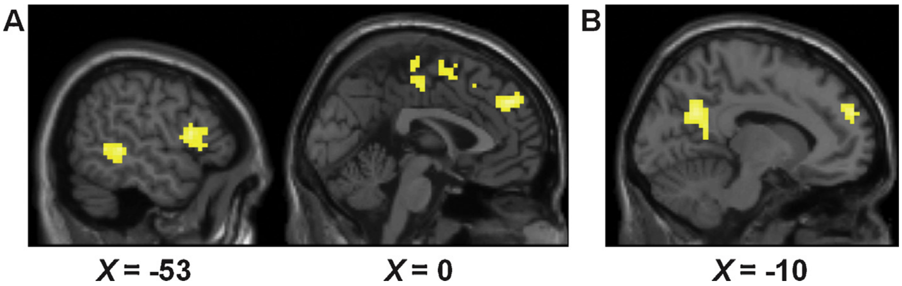


Fig. 2. Brain regions that were activated more in young adults compared to late adolescents. (A) During cognitive interference, an effect of age was found in the dorsomedial prefrontal cortex, left inferior frontal gyrus, the left middle temporal gyrus and middle cingulate. (B) Age-related differences for emotional interference were found in the dorsomedial prefrontal cortex and precuneus.

et al., 2006; Haas et al., 2006). However, lesion studies suggest that this region is not necessary for cognitive control (Fellows and Farah, 2005; Mansouri et al., 2009).

Age differences were shown in left lateral and medial prefrontal cortex during cognitive interference resolution, extending the findings of Adleman et al. (2002) in 7–22 year olds. Another study implied a pattern of increasing left prefrontal activation until age 21 and decreasing activation thereafter (Andrews-Hanna et al., 2011). This was revealed in post hoc tests while the main analyses compared adolescents aged 14–17 with adults aged 18–25. The current results indicate that when focusing on the narrow age range from 18–25, prefrontal activation appears to increase with age. The 23–25 year olds also engaged the middle cingulate and left middle temporal gyrus more than 18–19 year olds did. For emotional interference resolution, an effect of age was found in the dorsomedial prefrontal cortex and in the precuneus. Previous research has demonstrated that the dorsomedial prefrontal cortex plays a role in processing negative emotional words on the Stroop task (Compton et al., 2003). Involvement of the cuneus, a region posterior to the precuneus, has also been reported (Mincic, 2010). It has been proposed that during adolescence, cognitive control is particularly difficult for emotional stimuli (Casey et al., 2011; Steinberg, 2005). Nonetheless, we observed differences between late adolescents and young adults during emotional as well as cognitive interference resolution, yet in different regions of the brain. It therefore seems that cognitive control over both types of stimuli develops further after the age of 18.

From late adolescence to young adulthood, increased activation in prefrontal cortex and other areas was found. A recent review reported age-related increases as well as decreases in prefrontal activation during cognitive control (Crone and Dahl, 2012). These authors concluded that the variability in prefrontal recruitment demonstrates flexibility of this brain region in adolescence, which is related to the context, such as motivation for a certain task. Unfortunately, it is difficult to relate the current findings to task-related behavior, since differences in brain activation were not accompanied by differences in reaction times or accuracy. There was a trend visible towards less emotional interference in 23–25 year olds than in 18–19 year olds, suggesting improved performance in young adults. In this age range, developmental effects might be too small to reach significance at the behavioral level, although the effects can still be observed at the neural level.

The differences between late adolescents and young adults are probably due to an interaction between biological effects of age and environmental influences. Our sample consists of 18–19 year old Freshman and Sophomore students and 23–25 year old Junior and Master students in Medical College. The 23–25 year olds are in the final years of the curriculum and have had more experience with situations in which cognitive control is required compared to the 18–19 year olds. During the college years, students may improve their cognitive control skills which are needed for planning, avoiding distractions and focusing on exams. Changes over time may thus be related to the educational setting rather than being solely age-specific. In order to distinguish between environmental and biological factors, future studies might benefit from concurrently investigating functional and structural development in this age range.

We used a homogeneous group consisting of students in Medical College only to exclude possible confounding factors, such as differences in IQ, habits and lifestyle. Medical students have an intensive curriculum which requires them to spend much time in class or doing practical work. This makes their daily routines similar to one another and different from those of other students who have more freedom in planning their study behavior. Additionally, medical students share characteristics with respect to learning motivation, intellectual capacity and past education involving beta-disciplines. Including a homogeneous sample increases the possibility of finding age effects, which are small compared to the overall task effects. Age-related differences were indeed detected in the participants of this study. At this moment, our results are only valid for the population of medical students. The conclusions are limited to a group of intelligent young people who are known to have a specific trajectory of cortical maturation (Shaw et al., 2006). Future research could provide more insight into development during the transition from late adolescence to young adulthood by testing participants between 18 and 25 years old who are pursuing a different degree or have a full-time job. Another suggestion would be to follow people longitudinally in order to reduce between-subject variation.

With respect to possible sex-related activation differences, none were observed for cognitive and emotional interference resolution. This is a relevant finding as previously, differences between males and females were found on a Go/NoGo task (Garavan et al., 2006), a Stop-signal task (Li et al., 2009) and a motor Stroop task (Christakou et al., 2009). These studies, however, did not control for confounding variables in the same way as was done here. The reported sex differences may be due to the fact that the participant groups had a more heterogeneous composition and males and females differed on several aspects, such as education. Alternatively, the presence or absence of sex differences might depend on the specific paradigm used (Bell et al., 2006). The current fMRI results indicate that in 18–25 year old medical students, there is an effect of age on a combined cognitive and emotional Stroop task, independent of sex. This implies that from late adolescence to young adulthood, concurrent with biological maturation and social transitions, functional changes in the brain are ongoing.

Conflict of interest

The authors have no conflicts of interest.

Acknowledgements

This work was supported by The Netherlands Organisation for Scientific Research [VICI grant 453 11 005 to L.K.]. We would like to thank Lisbeth Evers for providing the Stroop task and Martina Knežević, Imke Jansen, Dirk Heslenfeld and Ton Schweigmann for help with data collection.

References

Adleman, N.E., Menon, V., Blasey, C.M., White, C.D., Warsofsky, I.S., Glover, G.H., Reiss, A.L., 2002. A developmental fMRI study of the Stroop color-word task. Neuroimage 16 (1), 61–75, http://dx.doi.org/10.1006/nimg.2001.1046.

Andrews-Hanna, J.R., Mackiewicz Seghete, K.L., Claus, E.D., Burgess, G.C., Ruzic, L., Banich, M.T., 2011. Cognitive control in adolescence: neural underpinnings and relation to self-report behaviors. PLoS ONE 6 (6), e21598, http://dx.doi.org/10.1371/journal.pone.0021598.

Arnett, J.J., 2000. Emerging adulthood: a theory of development from the late teens through the twenties. American Psychologist 55 (5), 469–480, http://dx.doi.org/10.1037//0003-066X.55.5.469.

Bell, E.C., Willson, M.C., Wilman, A.H., Dave, S., Silverstone, P.H., 2006. Males and females differ in brain activation during cognitive tasks. Neuroimage 30 (2), 529–538, http://dx.doi.org/10.1016/j.neuroimage.2005.09.049.

Bennett, C.M., Baird, A.A., 2006. Anatomical changes in the emerging adult brain: a voxel-based morphometry study. Human Brain Mapping 27 (9), 766–777, http://dx.doi.org/10.1002/hbm.20218.

Blakemore, S.J., Choudhury, S., 2006. Development of the adolescent brain: implications for executive function and social cognition. Journal of Child Psychology and Psychiatry 47 (3–4), 296–312, http://dx.doi.org/10.1111/j.1469-7610.2006.01611.x.

Bunge, S.A., Wright, S.B., 2007. Neurodevelopmental changes in working memory and cognitive control. Current Opinion in Neurobiology 17 (2), 243–250, http://dx.doi.org/10.1016/j.conb.2007.02.005.

Carter, C.S., Macdonald, A.M., Botvinick, M., Ross, L.L., Stenger, V.A., Noll, D., Cohen, J.D., 2000. Parsing executive processes: strategic vs. evaluative functions of the anterior cingulate cortex. Proceedings of the National Academy of Sciences of the United States of America 97 (4), 1944–1948, http://dx.doi.org/10.1073/pnas.97.4.1944.

Casey, B.J., Duhoux, S., Malter Cohen, M., 2010. Adolescence: what do transmission, transition, and translation have to do with it? Neuron 67 (5), 749–760, http://dx.doi.org/10.1016/j.neuron.2010.08.033.

Casey, B.J., Jones, R.M., Somerville, L.H., 2011. Braking and accelerating of the adolescent brain. Journal of Research on Adolescence 21 (1), 21–33, http://dx.doi.org/10.1111/j.1532-7795.2010.00712.x.

Casey, B.J., Tottenham, N., Liston, C., Durston, S., 2005. Imaging the developing brain: what have we learned about cognitive development? Trends in Cognitive Sciences 9 (3), 104–110, http://dx.doi.org/10.1016/j.tics.2005.01.011.

Christakou, A., Halari, R., Smith, A.B., Ifkovits, E., Brammer, M., Rubia, K., 2009. Sex-dependent age modulation of frontostriatal and temporoparietal activation during cognitive control. Neuroimage 48 (1), 223–236, http://dx.doi.org/10.1016/j.neuroimage.2009.06.070.

Compton, R.J., Banich, M.T., Mohanty, A., Milham, M.P., Herrington, J., Miller, G.A., Heller, W., 2003. Paying attention to emotion: an fMRI investigation of cognitive and emotional Stroop tasks. Cognitive, Affective & Behavioral Neuroscience 3 (2), 81–96, http://dx.doi.org/10.3758/CABN.3.2.81.

Crone, E.A., 2009. Executive functions in adolescence: inferences from brain and behavior. Developmental Science 12 (6), 825–830, http://dx.doi.org/10.1111/j.1467-7687.2009.00918.x.

Crone, E.A., Ridderinkhof, K.R., 2011. The developing brain: from theory to neuroimaging and back. Developmental Cognitive Neuroscience 1 (2), 101–109, http://dx.doi.org/10.1016/j.dcn.2010.12.001.

Crone, E.A., Dahl, R.E., 2012. Understanding adolescence as a period of social-affective engagement and goal flexibility. Nature Reviews Neuroscience 13, 636–650, http://dx.doi.org/10.1038/nrn3313.

Egner, T., Hirsch, J., 2005. The neural correlates and functional integration of cognitive control in a Stroop task. Neuroimage 24 (2), 539–547, http://dx.doi.org/10.1016/j.neuroimage.2004.09.007.

Etkin, A., Egner, T., Peraza, D.M., Kandel, E.R., Hirsch, J., 2006. Resolving emotional conflict: a role for the rostral anterior cingulate cortex in modulating activity in the amygdala. Neuron 51 (6), 871–882, http://dx.doi.org/10.1016/j.neuron.2006.07.029.

Evers, E.A., van der Veen, F.M., Jolles, J., Deutz, N.E., Schmitt, J.A., 2006. Acute tryptophan depletion improves performance and modulates the BOLD response during a Stroop task in healthy females. Neuroimage 32 (1), 248–255, http://dx.doi.org/10.1016/j.neuroimage.2006.03.026.

Fellows, L.K., Farah, M.J., 2005. Is anterior cingulate cortex necessary for cognitive control? Brain 128, 788–796, http://dx.doi.org/10.1093/brain/awh405.

Frings, C., Englert, J., Wentura, D., Bermeitinger, C., 2010. Decomposing the emotional Stroop effect. The Quarterly Journal of Experimental Psychology 63 (1), 42–49, http://dx.doi.org/10.1080/17470210903156594.

Garavan, H., Hester, R., Murphy, K., Fassbender, C., Kelly, C., 2006. Individual differences in the functional neuroanatomy of inhibitory control. Brain Research 1105 (1), 130–142, http://dx.doi.org/10.1016/j.brainres.2006.03.029.

Giedd, J.N., Rapoport, J.L., 2010. Structural MRI of pediatric brain development: what have we learned and where are we going? Neuron 67 (5,), 728–734, http://dx.doi.org/10.1016/j.neuron.2010.08.040.

Gogtay, N., Giedd, J.N., Lusk, L., Hayashi, K.M., Greenstein, D., Vaituzis, A.C., Thompson, P.M., 2004. Dynamic mapping of human cortical development during childhood through early adulthood. Proceedings of the National Academy of Sciences of the United States of America 101 (21), 8174–8179, http://dx.doi.org/10.1073/pnas.0402680101.

Haas, B.W., Omura, K., Constable, R.T., Canli, T., 2006. Interference produced by emotional conflict associated with anterior cingulate activation. Cognitive, Affective, & Behavioral Neuroscience 6 (2), 152–156, http://dx.doi.org/10.3758/CABN.6.2.152.

Koch, K., Pauly, K., Kellermann, T., Seiferth, N.Y., Reske, M., Backes, V., Habel, U., 2007. Gender differences in the cognitive control of emotion: an fMRI study. Neuropsychologia 45 (12), 2744–2754, http://dx.doi.org/10.1016/j.neuropsychologia.2007.04.012.

Laird, A.R., McMillan, K.M., Lancaster, J.L., Kochunov, P., Turkeltaub, P.E., Pardo, J.V., Fox, P.T., 2005. A comparison of label-based review and ALE meta-analysis in the Stroop task. Human Brain Mapping 25 (1), 6–21, http://dx.doi.org/10.1002/hbm.20129.

Lebel, C., Beaulieu, C., 2011. Longitudinal development of human brain wiring continues from childhood into adulthood. The Journal of Neuroscience 31 (30), 10937–10947, http://dx.doi.org/10.1523/JNEUROSCI. 5302-10.2011.

Li, C.S., Zhang, S., Duann, J.R., Yan, P., Sinha, R., Mazure, C.M., 2009. Gender differences in cognitive control: an extended investigation of the Stop signal task. Brain Imaging and Behavior 3 (3), 262–276, http://dx.doi.org/10.1007/s11682-009-9068-1.

Luna, B., Padmanabhan, A., O'Hearn, K., 2010. What has fMRI told us about the development of cognitive control through adolescence? Brain and Cognition 72, 101–113, http://dx.doi.org/10.1016/j.bandc.2009.08.005.

MacLeod, C.M., 1991. Half a century of research on the Stroop effect: an integrative review. Psychological Bulletin 109 (2), 163–203, http://dx.doi.org/10.1037/0033-2909.109.2.163.

MacLeod, C.M., MacDonald, P.A., 2000. Interdimensional interference in the Stroop effect: uncovering the cognitive and neural anatomy of attention. Trends in Cognitive Sciences 4 (10), 383–391, http://dx.doi.org/10.1016/S1364-6613(00)01530-8.

Mansouri, F.A., Tanaka, K., Buckley, M.J., 2009. Conflict-induced behavioural adjustment: a clue to the executive functions of the prefrontal cortex. Nature Reviews Neuroscience 10 (2), 141–152, http://dx.doi.org/10.1038/nrn2538.

Marsh, R., Zhu, H., Schultz, R.T., Quackenbush, G., Royal, J., Skudlarski, P., Peterson, B.S., 2006. A developmental fMRI study of self-regulatory control. Human Brain Mapping 27 (11), 848–863, http://dx.doi.org/10.1002/hbm.20225.

Mayer, A.R., Teshiba, T.M., Franco, A.R., Ling, J., Shane, M.S., Stephen, J.M., Jung, R.E., 2012. Modeling conflict and error in the medial frontal cortex. Human Brain Mapping 33 (12), 2843–2855, http://dx.doi.org/10.1002/hbm.21405.

McKenna, F.P., Sharma, D., 1995. Intrusive cognitions: an investigation of the emotional Stroop task. Journal of Experimental Psychology 21 (6), 1595–1607, http://dx.doi.org/10.1037/0278-7393.21.6.1595.

Mincic, A.M., 2010. Neural substrate of the cognitive and emotional interference processing in healthy adolescents. Acta Neurobiologiae Experimentalis 70 (4), 406–422, Retrieved from http://www.ane.pl/

Monk, C.S., McClure, E.B., Nelson, E.E., Zarahn, E., Bilder, R.M., Leibenluft, E., Pine, D.S., 2003. Adolescent immaturity in attention-related brain engagement to emotional facial expressions. NeuroImage 20 (1), 420–428, http://dx.doi.org/10.1016/S1053-8119(03)00355-0.

Nee, D.E., Wager, T.D., Jonides, J., 2007. Interference resolution: insights from a meta-analysis of neuroimaging tasks. Cognitive, Affective, and Behavioral Neuroscience 7 (1), 1–17, http://dx.doi.org/10.3758/CABN.7.1.1.

Passarotti, A.M., Sweeney, J.A., Pavuluri, M.N., 2009. Neural correlates of incidental and directed facial emotion processing in adolescents and adults. Social Cognitive and Affective Neuroscience 4 (4), 387–398, http://dx.doi.org/10.1093/scan/nsp029.

Rubia, K., Smith, A.B., Woolley, J., Nosarti, C., Heyman, I., Taylor, E., Brammer, M., 2006. Progressive increase of frontostriatal brain activation from childhood to adulthood during event-related tasks of cognitive control. Human Brain Mapping 27 (12), 973–993, http://dx.doi.org/10.1002/hbm.20237.

Shaw, P., Greenstein, D., Lerch, J.P., Clasen, R., Lenroot, R., Gogtay, N., Giedd, J., 2006. Intellectual ability and cortical development in children and adolescents. Nature 440 (30), 676–679, http://dx.doi.org/10.1038/nature04513.

Shaw, P., Kabani, N.J., Lerch, J.P., Eckstrand, K., Lenroot, R., Gogtay, N., Wise, S.P., 2008. Neurodevelopmental trajectories of the human cerebral cortex. The Journal of Neuroscience 28 (14), 3586–3594, http://dx.doi.org/10.1523/JNEUROSCI. 5309-07.2008.

Schlichting, L., 2005. Peabody Picture Vocabulary Test-III-NL. Harcourt Test Publisher, Amsterdam.

Steinberg, L., 2005. Cognitive and affective development in adolescence. Trends in Cognitive Sciences 9 (2), 69–74, http://dx.doi.org/10.1016/j.tics.2004.12.005.

Tamnes, C.K., Ostby, Y., Fjell, A.M., Westlye, L.T., Due-Tonnessen, P., Walhovd, K.B., 2010. Brain maturation in adolescence and young adulthood: regional age-related changes in cortical thickness and white matter volume and microstructure. Cerebral Cortex 20 (3), 534–548, http://dx.doi.org/10.1093/cercor/bhp118.

Toga, A.W., Thompson, P.M., Sowell, E.R., 2006. Mapping brain maturation. Trends in Neurosciences 29 (3), 148–159, http://dx.doi.org/10.1016/j.tins.2006.01.007.

Velanova, K., Wheeler, M.E., Luna, B., 2009. The maturation of task set-related activation supports late developmental improvements in inhibitory control. The Journal of Neuroscience 29 (40), 12558–12567, http://dx.doi.org/10.1523/JNEUROSCI. 1579-09.2009.

Wang, L., Huettel, S., De Bellis, M.D., 2008. Neural substrates for processing task-irrelevant sad images in adolescents. Developmental Science 11 (1), 23–32, http://dx.doi.org/10.1111/j.1467-7687.2007.00661.x.

Yurgelun-Todd, D., 2007. Emotional and cognitive changes during adolescence. Current Opinion in Neurobiology 17 (2), 251–257, http://dx.doi.org/10.1016/j.conb.2007.03.009.