MIND, BRAIN, AND EDUCATION

Neural Correlates of Performance Monitoring During the Transition to Young Adulthood

Martina Knežević[1,2], Kim Veroude[1], Jelle Jolles[1], and Lydia Krabbendam[1]

ABSTRACT— Cognitive challenges during transition to adulthood are generally high and require particular skills, such as self-control, performance evaluation, and behavioral adjustment for success in everyday living. However, age and sex differences in timing and efficiency of brain maturational processes in the early twenties are not well known. We used a go/no-go paradigm and fMRI to focus on the neural processes underlying response inhibition and performance monitoring during the transition from late adolescence (aged 18–19) to young adulthood (aged 23–25). During performance monitoring, late adolescents showed more activation in right inferior frontal gyrus than young adults, while males showed more activation in left inferior parietal lobe than females. No effects of age and sex were found for response inhibition. Our findings suggest that age and sex-related differences in neural basis of performance monitoring continue to change between late adolescence and young adulthood.

The transition from late adolescence to young adulthood is a period of profound changes, during which young people achieve legal adulthood, complete education, and enter the labor market full-time, perhaps marry, and/or become parents for the first time (Billari & Liefbroer, 2010). It is marked by constantly changing real-life situations, which require sophisticated higher cognitive skills. For instance, unanticipated events or dynamic changes in the immediate environment necessitate a high level of self-control for success in school and work situations, as well as in everyday living. One of the most important self-control functions crucial for mature adult behavior is response inhibition—the ability to withdraw or suppress inappropriate responses (Dillon & Pizzagalli, 2007; Swick, Ashley, & Turken, 2011). For making an optimized decision, one must be able to continuously assess on going actions and their outcomes in order to implement appropriate behavioral adjustments. This process of evaluating outcomes and detecting performance errors or conflicting responses is known as performance monitoring (Huster et al., 2011; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004). Both of these cognitive skills, response inhibition and performance monitoring, develop progressively from childhood to adulthood. They are susceptible to impairments as found in neurodevelopmental disorders such as attention deficit hyperactivity disorder, obsessive-compulsive disorder, and antisocial personality disorder (de Mathis et al., 2011). The brain functional networks underlying response inhibition and performance monitoring include a number of frontal regions such as the anterior cingulate cortex and the ventrolateral and dorsolateral prefrontal cortex, as well as the bilateral parietal cortex (see Aron, 2011 for review). The aim of this study was to investigate brain activation during the transition from late adolescence to young adulthood, using a go/no-go task to focus on the neural processes underlying response inhibition and performance monitoring.

Postmortem research has demonstrated significant changes during puberty and adolescence in the prefrontal cortex (Petanjek et al., 2011; Rakic, Bourgeois, & Goldman-Rakic, 1994) reporting that synaptic proliferation and pruning continue throughout adolescence and into early adulthood. Studies using magnetic resonance imaging (MRI)

[1]Department of Educational Neuroscience, VU University Amsterdam
[2]Psychology Department, Centre for Croatian Studies, University of Zagreb

Address correspondence to Martina Knežević, Psychology Department, Centre for Croatian Studies, University of Zagreb Borongajska 83d, 10000 Zagreb, Croatia. e-mail: martina.knezevich@gmail.com

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provided further evidence of structural brain maturation after adolescence (Fjell et al., 2012; Tamnes et al., 2011; Westlye et al., 2010). Maturation of the prefrontal cortex shows a linear increase from childhood to adulthood in white matter volume (Fjell et al., 2012; Westlye et al., 2010), whereas gray matter volume appears to follow an inverted U-shaped pattern, peaking around mid adolescence (Tamnes et al., 2010, 2011). This pattern of development is thought to reflect ongoing neuronal events, such as synaptic proliferation, pruning, and axonal myelination, which are believed to be essential for the remaining synaptic circuits to become more efficient (see Crone & Ridderinkhof, 2011 for review). Neuroimaging studies suggest that cognitive development is supported by changes in brain activation, showing both increases and decreases in prefrontal cortical activity (Crone & Ridderinkhof, 2011). For example, one study found progressive age-related changes in prefrontal regions associated with improvements in response inhibition, accompanied by increased brain activation in right inferior prefrontal cortex in adults (20–42 years) compared to adolescents (10–17 years) (Rubia, Smith, Taylor, & Brammer, 2007). Another study found decreased activity in left medial prefrontal cortex during successful response inhibition in adults (25–30 years) compared to adolescents (9–19 years) (Cohen et al., 2010). One fMRI study that explored qualitative changes in brain activation during positive or negative feedback on performance adjustment comparing children (8–9 years), adolescents (11–13 years), and young adults (18–25 years) revealed separable developmental trajectories for involvement of dorsolateral prefrontal and parietal cortex (van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008). Dorsolateral prefrontal and parietal cortices were more activated in young adults during negative feedback, but during positive feedback in children. It appears that young adults adjust their behavior considering negative feedback and conflict signals, whereas children are more focused toward valuing positive feedback while adjusting their performance. In terms of feedback processing, adolescence appears to be a transition period.

Sex-related differences in timing and efficiency of maturational processes have also been noted (Bramen et al., 2012; Liu, Zubieta, & Heitzeg, 2012). Females show earlier maturational peaks in gray matter reduction and white matter increase in frontal, temporal, and striatal brain regions compared to males (Bramen et al., 2012; see Lenroot & Giedd, 2010 for review). Evidence from neuropsychological studies have shown that impulsiveness ratings are generally higher in males than females (Liu et al., 2012; Rubia, Hyde, Halari, Giampietro, & Smith, 2010) and many neurodevelopmental disorders characterized by impaired impulse control are more common in males than females (Ibanez, Blanco, Moreryra, & Saiz-Ruiz, 2003; Liu et al., 2012). Impulsiveness has consistently been correlated with poor performance in tasks of response inhibition (Aron, 2011; Fjell et al., 2012; Liu et al., 2012). However, relatively few studies have explored sex differences in response inhibition, revealing different patterns of brain activation in males and females. For example, using a Stop task, Rubia et al. (2013) found increased activation in left inferior and superior frontal and striatal regions in females, while males showed increased activation in right inferior and superior parietal areas. Another study used a go/no-go task and found increased activation in females in left middle temporal gyrus and increased activation in males in anterior cingulate cortex (Liu et al., 2012).

In summary, robust age and sex differences were noted in the prefrontal cortex during childhood and adolescence. Despite the late developmental improvements in the ability to monitor, stop, or withdraw the on going response and its importance in fulfilling everyday tasks, research on systems supporting inhibitory changes during progression to adulthood is scarce. In order to examine whether and how the experience of adult transitions and the protracted development of prefrontal cortex foster response inhibition and performance monitoring, this study focused on a narrow age range (18–25), comparing late adolescents (age 18–19) and young adults (age 23–25). Given the evidence from previous developmental imaging studies that used response inhibition tasks (Huster et al., 2011; Rubia et al., 2013; Velanova, Wheeler, & Luna, 2009), we expect that late adolescents will show more activation than young adults in brain regions responsible for successful inhibition and performance monitoring, namely medial prefrontal cortex and lateral inferior prefrontal cortex (Tamnes et al., 2010; Velanova et al., 2009). Given that males and females show different brain regional activity during response inhibition and performance monitoring (Garavan, Hester, Murphy, Fassbender, & Kelly, 2006; Liu et al., 2012; Rubia et al., 2013), we expect that females will show increased activation in frontal brain regions compared to males, whereas males will show increased activation in parietal regions compared to females.

MATERIAL AND METHODS

Participants

A total of 71 healthy right-handed volunteers from the Medical School of VU University Amsterdam and the University of Amsterdam were included in this study, and divided into four groups: late adolescents aged 18–19 with 20 females (age range = 18.9–19.1 years, $M = 18.9$, $SD = 0.2$) and 16 males (age range = 18.7–19.1 years, $M = 18.9$, $SD = 0.34$), and young adults aged 23–25 with 18 females (age range = 23.9–24.6 years, $M = 24.3$, $SD = 0.8$) and 17 males (age range = 23.7–24.6 years, $M = 24.1$, $SD = 0.9$). The students were recruited by personal letters and advertisements on campus. They were not suffering from

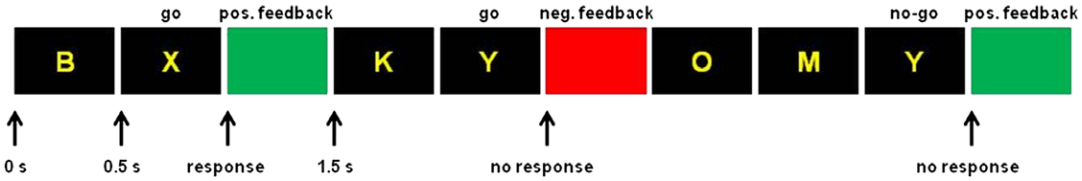

Fig. 1. The go/no-go task. The letters X and Y were presented serially mixed with other letters (fillers). The task of the participants was to press a button on alternating presentations of X and Y (go trials) and to refrain from responding by repetitions of X or Y (no-go or inhibition trials). Correct responses were followed by a green square (positive feedback), and incorrect responses were followed by a red square (negative feedback).

significant past or present neurological or psychiatric problems, and were screened for MRI contraindications. The study was approved by the VU Medical Centre Medical Ethics Committee and was conducted according to the principles of the Declaration of Helsinki and in accordance with the Medical Research Involving Human Subjects Act (WMO). All participants gave written informed consent before their inclusion in the study and were paid 25 euro. Data of a subsample have been reported previously (Veroude, Jolles, Knežević et al., 2013).

Procedure

The go/no-go motor inhibition task was used (Figure 1), as described by Evers et al. (2006), programmed in E-prime V2.0 (Psychology Software Tools, http://www.psynet.com/). A stream of letters (yellow on a black background) was presented, showing one letter every 500 ms with a 0-ms interstimulus interval. The letters X and Y were presented serially mixed with other letters (fillers). The participants' task was to press a button on alternating presentations of X and Y (go trials), and to refrain from responding by repetitions of X or Y (no-go or inhibition trials). No responses were required on the filler trials. Correct responses on the go trials and correct inhibition of responses on the no-go trials were followed by a green square (positive feedback). No positive feedback was provided after correctly omitted filler trials. A red square (negative feedback) was presented after responses to no-go trials, responses to letters other than X and Y, omission of a response on go trials, and to responses after the offset of the stimulus. In total, 1,000 stimuli were presented, of which 24 were no-go and 150 were go trials, divided into two runs each lasting about five minutes. During the experimental task, both response time (RT) and response accuracy were measured on each trial. Two different versions were counterbalanced across participants. Participants were trained one or two days before the actual testing. The training started with 400 stimuli including 120 go trials and no no-go trials, and participants responded on X and Y independent of the previous trial. During the second part of the training, 350 stimuli were presented of which 55 were go trials and 7 were no-go trials. Participants also performed a Stroop task and a social appraisal task, which are described elsewhere (Veroude, Jolles, Croiset, & Krabbendam, 2013a, 2013b).

MRI Scanning

The participants were scanned using a General Electric 3 Tesla head-only scanner at the VU Medical Centre in Amsterdam. Head fixation was accomplished by using foam padding. Earplugs dampened scanner noise. The experimenter communicated with participants via a built-in intercom system. An LCD projector projected stimuli onto a screen at the head of the scanner bore, viewable via a mirror attached to the head coil. Structural images were acquired using a T1-weighted sequence (TR = 7.876 ms, TE = 3.06 ms, flip angle = 12°, field of view = 22 × 22 cm, number of slices = 166, voxel size = 1 × 1 × 1 mm). Functional images were acquired using an echo-planar sequence sensitive to BOLD contrast (T2*) (TR = 2,000, TE = 35, flip angle = 80°, field of view = 22 × 22 cm, number of slices = 35, voxel size = 3.5 × 3.5 × 3 mm). Participants performed two functional runs (each lasting about 5 min). During each run, 195 images for all slices were collected resulting in a total of 390 images. The first three images in each run, acquired while the instruction was on the screen, were discarded to allow stabilization of longitudinal magnetization.

Performance Data Analysis

The percentages of correctly executed go trials and inhibited no-go trials, and the reaction time (RT) after a correct response on go trials were analyzed using analysis of variance (ANOVA; SPSS version 19 for Windows, IBM Corporation, Armonk, NY) with age and sex as a between-subjects factors. The rejection criterion was set at $p < .05$.

Image Analysis

Preprocessing

The imaging data were analyzed using Statistical Parametric Mapping (SPM8; http://www.fil.ion.ucl.ac.uk/spm/) and MarsBaR (http://marsbar.sourceforge.net) region-of-interest toolbox for SPM8. Preprocessing procedures

Table 1
Performance Data for the Go/No-Go Task

Sex		Age		
		Late adolescents	*Young adults*	*Total*
Female	Correct go (%)	91.9 ± 4.5	90.2 ± 8.7	91.1 ± 6.8
	Error go (%)	8.1 ± 4.5	9.8 ± 8.7	8.9 ± 6.8
	Correct no-go (%)	77.8 ± 18.1	83.9 ± 9.4	80.7 ± 14.8
	Error no-go (%)	22.2 ± 18.1	16.3 ± 9.4	19.6 ± 14.8
	Go RT (ms)	388.1 ± 17.6	398.6 ± 15.9	393.1 ± 17.4
Male	Correct go (%)	90.0 ± 5.2	93.9 ± 3.7	92.0 ± 4.8
	Error go (%)	10.0 ± 5.2	6.1 ± 3.7	8.0 ± 4.8
	Correct no-go (%)	74.8 ± 19.1	78.2 ± 12.5	76.6 ± 15.9
	Error no-go (%)	25.2 ± 19.1	21.8 ± 12.5	23.5 ± 15.9
	Go RT (ms)	389.6 ± 19.5	384.0 ± 21.8	386.7 ± 20.6
Total	Correct go (%)	91.1 ± 4.9	92.0 ± 6.9	91.5 ± 5.9
	Error go (%)	8.9 ± 4.9	8.0 ± 6.9	8.5 ± 5.9
	Correct no-go (%)	76.5 ± 18.4	81.2 ± 11.2	78.8 ± 15.3
	Error no-go (%)	23.7 ± 18.4	19.0 ± 11.2	21.4 ± 15.3
	Go RT (ms)	388.8 ± 18.2	391.5 ± 20.1	390.1 ± 19.1

Notes. Behavioral measures presented are the mean percentages ± standard deviations of correct and error go and no-go responses and mean reaction times in milliseconds ± standard deviations to correct go responses. RT = response time.

included within-subject realignment to correct for head movement. Images were then coregistered to the anatomical image and thereafter spatially normalized to the standard Montreal Neurological Institute (MNI) structural template. Finally, the images were spatially smoothed using a Gaussian (7 mm full width at half maximum) kernel.

Whole Brain Analysis

At the first level, a general linear model (GLM) was specified for each participant with the onsets of correct go trials, correct no-go trials, and errors (incorrect go and incorrect no-go trials together). A canonical hemodynamic response function (HRF) was convolved with the events of interest. High-pass filtering was used to remove low-frequency noise and motion parameters were included as regressors of no interest. The following task-related contrasts were calculated for each subject individually. To assess brain activation associated with *response inhibition*, correct no-go trials were compared with correct go trials (no-go vs. go, contrast 1). To assess brain activation related to *performance monitoring*, error trials (incorrect go and incorrect no-go trials together) were compared to correct trials (correct go and correct no-go trials together, errors vs. corrects, contrast 2).

Individual contrasts were then taken to a second level analysis, where the whole brain activation associated with response inhibition and performance monitoring was calculated for all subjects. Results were thresholded at $p < .05$, family wise error (FWE) rate corrected.

Regions of Interest Analysis

Thereafter, these data showing response inhibition and performance monitoring-related increases in activity were used to identify regions of interest (ROI) and test for age (late adolescents, young adults) and sex (male, female) differences.

In order to limit multiple comparisons, ROIs were obtained by selecting the four largest significant clusters of the whole brain analysis that have also been consistently found in other studies (Christakou et al., 2009; Cohen et al., 2010; Huster et al., 2011; Swick, Ashley, & Turken, 2008), using a threshold of $p < .05$, FWE corrected. We believe this to be a strong approach for detecting small effects, with the limitation that it is not possible to look at the effects of age and sex in the whole brain analysis, because this analysis would not be independent from the ROI selection. Accordingly, the regions used for the ROI analyses (with corresponding MNI coordinates of peak voxels within the activation clusters) were (1) *for response inhibition* (contrast 1): left and right dorsolateral prefrontal cortex (MNI = −53 18 36; 53 14 33), left and right inferior parietal lobe (MNI = −35 −56 45; 35 −53 45), (2) *for performance monitoring* (contrast 2): left and right inferior frontal gyrus (MNI = −49 14 3; 53 14 9), left and right inferior parietal lobe (MNI = −53 -46 51; 53 −46 42). Ten millimeter spheres were built around the center coordinates in MarsBaR and ROI activity was extracted as an average of all voxels within the ROI. A threshold of $p < .05$ was applied for the ROI analyses.

RESULTS

Performance Data

We tested age and sex differences in performance and RT between late adolescents (aged 18–19) and young adults (aged 23–25), and possible interactions of age, sex, and the

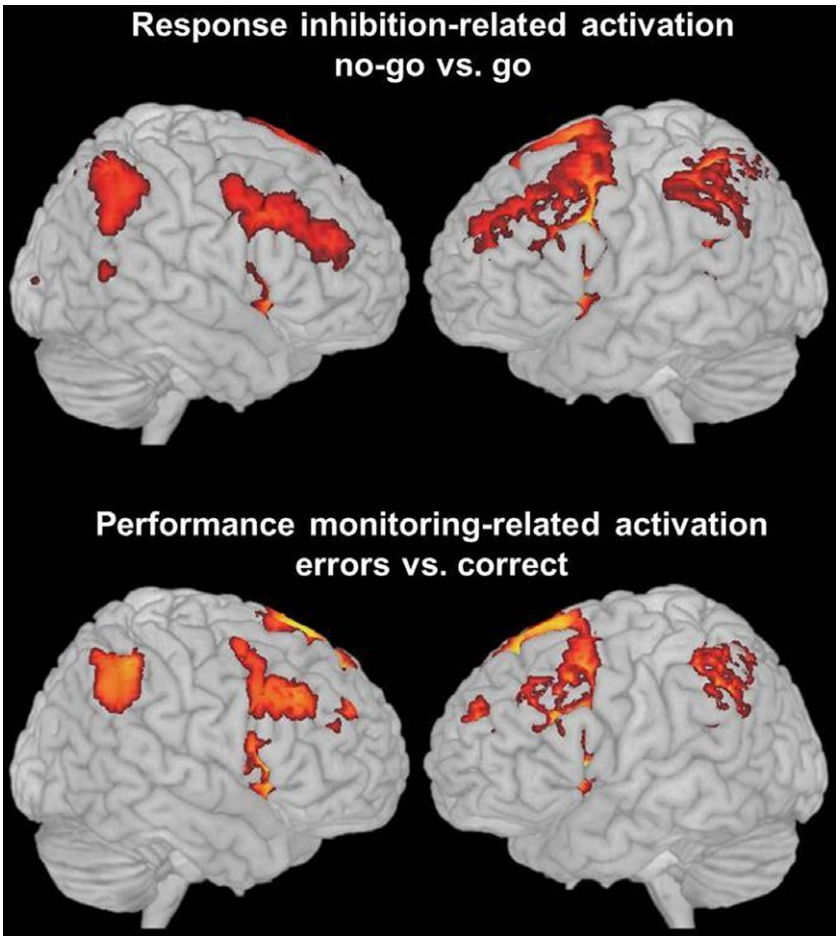

Fig. 2. Results from the whole brain analysis. Brain regions that showed significant, $p < .05$, family wise error (FWE)–corrected, response inhibition (no-go vs. go) and performance monitoring-related (errors vs. corrects) activation across all participants include large activation clusters in frontal, parietal, and temporal lobes for response inhibition, and in frontal, parietal, and temporal lobes for performance monitoring. Montreal Neurological Institute (MNI) coordinates are reported in Tables 1 and 2, Supporting Information.

performance on the go/no-go task. Table 1 summarizes the accuracy data and RTs.

The participants made 18 (±9) errors on average (incorrect go and incorrect no-go trials together). The only significant difference in performance was found in interaction between age and sex on the percentage of the correct go presses, $F(1, 67) = 4.2$, $p = .04$, where males improved their performance with age (90% vs. 94%), whereas females showed the opposite effect, that is, better performance in late adolescence than in young adulthood (92% vs. 90%).

No other significant differences were found. More specifically, there were no age differences in the percentage of correct go presses, $F(1, 67) = 0.6$, $p = .4$, correct no-go withholds, $F(1, 67) = 1.7$, $p = .2$, or the RTs corresponding to correct go responses, $F(1, 67) = 0.3$, $p = .6$. Also, there were no sex differences in the percentage of correct go presses, $F(1, 67) = 0.4$, $p = .5$, correct no-go withholds, $F(1, 67) = 1.4$, $p = .2$, or the RTs corresponding to correct go responses, $F(1, 67) = 2.1$, $p = .1$. No other interactions were found: correct no-go withholds, $F(1, 67) = 0.1$, $p = .7$, or age, sex and RTs to correct go responses, $F(1, 67) = 3.3$, $p = .1$.

Imaging

Whole Brain Analysis

Brain activation related to response inhibition (no-go vs. go, contrast 1) and performance monitoring (errors vs. corrects, contrast 2) is shown in Figure 2, and the MNI coordinates are reported in Tables 1 and 2, Supporting Information.

Response inhibition. Across all participants, brain activation related to response inhibition (no-go vs. go, contrast 1) was observed in a large clusters in frontal (right inferior frontal gyrus (BA45), bilateral dorsolateral prefrontal cortex (BA9), left middle frontal gyrus (BA10), left precentral gyrus (BA4)), parietal (bilateral inferior parietal lobe (BA40), left superior parietal lobe (BA40)) and temporal

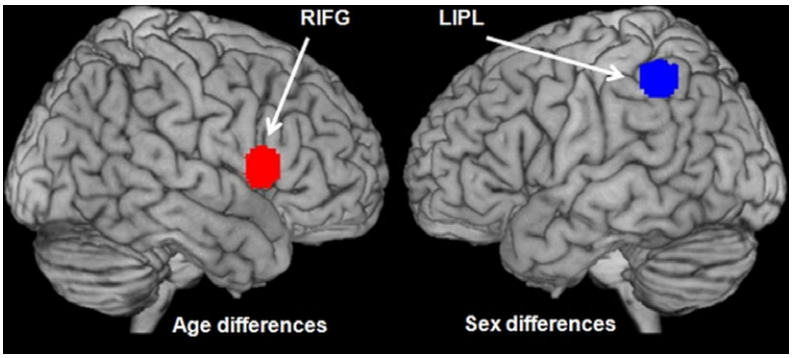

Fig. 3. Age and sex activation differences observed in regions of interests (ROIs). During performance monitoring, right inferior frontal gyrus (RIFG) was activated more in late adolescents compared to young adults, and left inferior parietal lobe (LIPL) was activated more in males compared to females.

(left middle temporal gyrus (BA10), right superior temporal gyrus (BA22), left fusiform gyrus (BA37)) lobes, as well as in bilateral insula (BA13), bilateral ventral tegmental area, bilateral posterior cingulate gyrus (BA23), right thalamus, left occipital gyrus (BA18), and right palidum (see Figure 2).

Performance monitoring. Across all participants, large activation clusters related to performance monitoring (errors vs. corrects, contrast 2) were found in frontal (right dorsomedial prefrontal cortex (BA9), right inferior frontal gyrus (BA45), right supplementary motor area (BA6)), parietal (bilateral inferior and left superior parietal lobe (BA40)), and temporal lobe (right middle temporal gyrus (BA21)), as well as left insula, bilateral ventral tegmental area, bilateral caudate nucleus, and left thalamus (see Figure 2).

ROI Analysis

Age and sex differences in brain activation. We performed ROI analyses using spheres around peak coordinates of the four largest clusters: bilateral dorsolateral prefrontal cortex and bilateral inferior parietal lobe for response inhibition, and bilateral inferior frontal gyrus and bilateral inferior parietal lobe for performance monitoring, based on their activation patterns in the whole-brain analysis and based on the literature (Garavan et al., 2006; Rubia et al., 2007, 2013; van Duijvenvoorde et al., 2008).

During response inhibition (contrast 1, no-go vs. go), we found no age or sex differences in underlying neural activation in right dorsolateral prefrontal cortex ($t = 0.1$, $p = .5$; $t = 1.5$, $p = .9$), right inferior parietal lobe ($t = 0.9$, $p = .2$; $t = 0.7$, $p = .8$), left dorsolateral prefrontal cortex ($t = 0.8$, $p = .2$; $t = 0.4$, $p = .8$), or left inferior parietal lobe ($t = 0.7$, $p = .3$; $t = 0.5$, $p = .3$).

During the performance monitoring (contrast 2, errors vs. correct) late adolescents showed stronger activity in right inferior frontal gyrus than young adults ($t = 1.7$, $p = .04$), and males showed stronger activity in left inferior parietal lobe than females ($t = 2.0$, $p = .03$, see Figure 3). No effects of age or sex were found in the other ROIs: right inferior frontal gyrus ($t = 1.1$, $p = .9$), left inferior parietal lobe ($t = 0.7$, $p = .2$), left inferior frontal gyrus ($t = 1.4$, $p = .1$; $t = 1.6$, $p = .9$), or right inferior parietal lobe ($t = 1.2$, $p = .1$; $t = 0.3$, $p = .6$).

DISCUSSION

The goal of this study was to investigate brain activation during the transition from late adolescence to young adulthood, using a go/no-go task to focus on the neural processes underlying response inhibition and performance monitoring. Our main findings highlight specific regions showing activation differences during performance monitoring, particularly more activation in right inferior frontal gyrus for late adolescents compared to young adults, and more activation in left inferior parietal lobe for males compared to females. In addition, young adult males performed better than late adolescent males (90% vs. 94%), while among females, late adolescents performed better than young adults (92% vs. 90%). These behavioral differences were only found for accuracy on go trials, showing a marginally significant interaction effect between age and sex. However, we found no main effects of age or sex on accuracy and RTs. We thus believe that the effects of age and sex on brain activation cannot be explained by performance differences.

Performance Monitoring

Performance monitoring activates several brain regions in healthy adults, including ventral and dorsal anterior cingulate cortex, posterior medial frontal cortex, bilateral inferior

frontal gyrus, bilateral parietal cortex, motor and premotor cortex, and insula (Fitzgerald et al., 2010; Mueller, Brass, Waszak, & Prinz, 2007; Ridderinkhof et al., 2004). Our study is consistent with these findings, showing large activation clusters related to performance monitoring in dorsomedial prefrontal cortex, supplementary motor area, inferior frontal gyrus, inferior and left superior parietal lobe, middle temporal gyrus, ventral tegmental area, insula, caudate nucleus, and left thalamus.

Age Differences

Age differences were shown in right inferior frontal gyrus, which late adolescents recruited more than young adults during performance monitoring. Performance monitoring includes evaluating outcomes and detecting performance errors, and this ability to detect errors and monitor performance is crucial to successful behavioral control (Luna, Padmanabhan, & O'Hearn, 2010). Furthermore, functional imaging (Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010; Menon, Adleman, White, Glover, & Reiss, 2001) and lesion studies (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Picton et al., 2007) demonstrated that inferior frontal gyrus is critical for successful performance, and a possible center for control mechanism that suppresses irrelevant responses. Studies that previously compared the neural basis of cognition in children, adolescents, and adults show inconsistent results (Cohen et al., 2010; Hwang, Velanova, & Luna, 2010; Rubia et al., 2013; Velanova et al., 2009). Some studies report increased prefrontal activation with age while other studies show decreased activation with age (see Crone & Dahl, 2012 for review). It has been suggested that this inconsistency in findings reveals a more flexible system for recruiting cognitive control skills in adolescence and is possibly influenced by motivational factors, such as task instructions or motivation and the benefit of high task performance (Crone & Dahl, 2012). One possibility is that to achieve similar performance as young adults, late adolescents in our study needed additional activation of regions crucial for performance monitoring, such as right inferior frontal gyrus.

Even though it has not yet been established how differences in brain activation relate to structural and functional development, some possibilities have been proposed. Studies have shown that regions where brain activity correlates with task performance become more focal with age, and this shift in cortical patterns of activity is likely related to maturational processes (e.g., synaptic pruning or axonal myelination) in the developing human brain even in the early twenties (Crone & Ridderinkhof, 2011). This shift to more focal activation may represent attenuation of activation which may be reflected either in the number of regions activated or in the extent of activated tissue. The remaining neural networks become more functionally specialized, causing higher signal-to-noise ratio and possibly improved performance with age (Fjell et al., 2012; Hwang, Velanova, & Luna, 2010). Considering that we did not find age effects in brain activation during response inhibition, it could be that the neural system underlying performance monitoring matures more slowly than the neural system underlying response inhibition. However, this notion will have to await further research.

Sex Differences

In our study, males had more activation in left inferior parietal lobe compared to females during performance monitoring. As explained above, performance monitoring enables flexible adjustment of goal-directed behaviors (Dillon & Pizzagalli, 2007). While evaluating outcomes and detecting performance errors, an individual is able to evaluate the adequacy and success of his or her performance (Fitzgerald et al., 2010). It is possible that this left inferior parietal lobe activation in males compared to females in our study represents activation related to increased motor preparedness for response execution. Left inferior parietal lobe participates in motor attention as part of a posterior attention network that assists the anterior attention network in improving performance (Fitzgerald et al., 2010; Posner & Dehaene, 1994; Posner & Rothbart, 1990; Rushworth, Krams, & Passingham, 2001).

The increased brain activation in cognitive tasks might reflect greater effort, less neural efficiency, or an appropriate distributing of resources. As the brain–behavior relationship is not straightforward, the functional significance of this activation difference between males and females in the parietal lobe may only be interpreted as an indirect index of one of these processes.

We hypothesized that females will show activation increases in the frontal region compared to males, because this was found in previous studies (Christakou et al., 2009; Rubia et al., 2010). Comparing our results with previous studies, it appears that sex differences in the inferior frontal regions for motor response inhibition during development may be stronger in childhood and the adolescent years and then even out in early adulthood.

Response Inhibition

Neuroimaging studies (Chikazoe, 2010; Garavan et al., 2006; Levy & Wagner, 2011; Swick et al., 2008) suggest that response inhibition is accomplished by a distributed cortical network, including presupplementary motor area and dorsolateral and ventrolateral prefrontal cortex (the posterior part of the inferior frontal gyrus, inferior frontal junction, and inferior frontal gyrus/insula), as well as various subregions of the anterior cingulate, occipital, temporal, and parietal lobes (Aron, 2011). In line with these studies, this study showed that different brain regions in dorsolateral and

ventrolateral prefrontal cortex, as well as parietal, temporal, and subcortical lobe are involved in response inhibition. Most of the prefrontal activation in our study was located within right inferior frontal gyrus, right dorsolateral prefrontal cortex, and right insula. Large activation clusters were also found in right inferior parietal lobe and right superior temporal gyrus. This right hemispheric dominance during inhibitory control was found previously (Aron, 2011; Garavan et al., 2006), including the middle and inferior frontal gyrus, frontal limbic area, anterior insula, and inferior parietal lobe. Also, these brain areas have been implicated in inhibition across various cognitive paradigms, such as response inhibition in the Stop Signal Task (Hampshire et al., 2010), set shifting on the Wisconsin Card Sorting Task (Swick et al., 2011), or cognitive interference inhibition in the Simon task (Rubia et al., 2006).

In contrast to our expectations, no age or sex differences were found in brain activation during response inhibition. It is possible that inhibition of the motor response on the go/no-go task was relatively easy, because our participants were students in higher education (medical students) and they performed with a high level of accuracy (79% no-go, 92% go), and this is why there were no age or sex differences in response inhibition. In a previous study, we administered a more difficult Stroop task to the same sample and did find an effect of age on brain activation during cognitive inhibition (Veroude et al., 2013a).

We used a homogeneous sample of medical students to control for possible variation due to differences in intelligence or daily activities. Including a homogeneous sample increases the possibility of finding age effects, which were indeed found among the participants of this study. Future research should include late adolescents and young adults who are pursuing a different degree or a professional career, in order to provide more insight into development between 18 and 25 years. As our data come from a cross-sectional sample, replication in a longitudinal study would help to reduce between-subject variation and to establish sequences of events.

CONCLUSION

Comparing a sample of late adolescent and young adult females and males on a motor inhibition task, we found age differences in right inferior frontal gyrus activity and sex differences in left inferior parietal lobe activity during performance monitoring. Our findings suggest age and sex-related differences in the neural basis of performance monitoring between late adolescence and young adulthood, and point to the importance of using narrow age ranges when investigating developmental differences at this transitional stage.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Table S1. Response Inhibition–Related Activation (No-Go vs. Go).

Table S2. Performance Monitoring–Related Activation (Errors vs. Correct).

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