DEVELOPMENT OF COGNITIVE FLEXIBILITY IN LATE ADOLESCENCE: INVESTIGATING BEHAVIORAL PERFORMANCE AND NEURAL ACTIVATION IN A TASK-SWITCHING PARADIGM

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Sair K. Lazzaro

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This thesis was presented

by

Sair K. Lazzaro

It was defended on

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and approved by

Jamie Hanson, PhD, Assistant Professor, University of Pittsburgh Department of Psychology

Melissa Libertus, PhD, Assistant Professor, University of Pittsburgh Department of Psychology

Jennifer Roth, PhD, Associate Professor, Carlow University Department of Psychology

Thesis Director: Beatriz Luna, PhD, Professor, University of Pittsburgh Department of

Psychiatry

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Successful cognitive control relies on both the ability to instantiate higher-order cognitive functions and the ability to flexibly switch between them in service of changing task demands, i.e. cognitive flexibility. While a wealth of important work on the development of cognitive control in adolescence has focused on the development of executive functions, there has been a relative lack of work on the development of cognitive flexibility. Here we address this limitation by investigating the development of cognitive flexibility using a task-switching paradigm in a large sample of adolescents and young adults (ages 14-32, n = 82). For a subset of subjects that had usable fMRI data (n=56), we assessed task-switching performance and analyzed fMRI data collected in-scanner while they performed the task-switching paradigm. We observed that successful task-switching was associated with widespread activation of frontoparietal and visual processing brain areas. A component of this larger task-switching system, the left inferior parietal cortex, showed age-related reductions in neural activation specifically during task-switching into trials that taxed inhibitory control. These neural findings occurred in parallel with age-related improvements in successful task-switching performance in the same context. This pattern of results suggests that task-switching into the most cognitively demanding contexts follows a protracted development that extends through adolescence and young adulthood. Further, the age-related reduction in parietal cortex activation suggests that adolescents have greater reliance on the frontoparietal system, which has been implicated in transient aspects of cognitive control, to achieve adult-like performance. Taken together, our results suggest that a key aspect of cognitive maturation in adulthood is the ability to flexibly switch between cognitive tasks with limited cost to performance and a decreasing reliance on frontoparietal regions across adolescence.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PREFACE

       I would like to thank my thesis director, Dr. Beatriz Luna, for the opportunity to research, write, and defend this thesis with her guidance. Special thanks to Dr. Bart Larsen for his dedicated tutelage and mentorship during the research and writing of this thesis, and without whom this project would not have been possible. There are not enough words in the world to express my gratitude. Additional thanks to all committee members, whose time and advice is much appreciated, and to everyone in the Laboratory of Neurocognitive Development for their support during my work here. Lastly, my sincerest appreciation for Kristie Budihardjo, Jennifer Crook, Renata Mitchell, and Alina Quach for their invaluable encouragement and faith in this thesis and in me throughout our shared time in undergraduate studies.

1.0   INTRODUCTION

1.1   COGNITIVE CONTROL AND ADOLESCENCE

Cognitive control is the ability to coordinate internal goals and external behavior in the face of complex and potentially distracting environments. Successful cognitive control relies on the ability to consistently instantiate higher-order cognitive functions, such as working memory, response selection and inhibition, task-set switching, and performance monitoring, as well as the ability to flexibly engage and disengage these processes according to task demands (Badre 2011; Lenartowicz et al. 2010; Sabb et al. 2008). As such, cognitive control may be broken down into two facets: 1) executive function, i.e. the ability to successfully engage higher-order cognitive processes, and 2) cognitive flexibility, the ability to successfully switch between these executive functions (Luna et al. 2015).

The ability to successfully use cognitive control has been linked to the function of distributed set of brain systems, including the frontoparietal, dorsal attention, and cingulo-opercular networks. The frontoparietal system, consisting of areas of prefrontal and posterior parietal cortices, has been functionally linked to transient aspects of cognitive control, such as rule-updating, task-switching, and performance monitoring, and is thus thought to be central to adjusting control in response to task feedback or changing task demands (Cole et al., 2013; Dosenbach et al., 2007; Larsen et al., 2017). This is in contrast to the dorsal attention and

cingulo-opercular systems (consisting of the intraparietal sulcus and frontal eye field, and the medial frontal cortex, insula, and frontal operculum respectively) which are thought to be involved in more sustained aspects of cognitive control, such as goal-directed sustained attention and across-trial rule-set maintenance (Fox et al. 2006; Vossel, Geng, & Fink, 2014).

Cognitive control continues to develop throughout childhood, adolescence, and early adulthood. Importantly, children and adolescents can execute cognitive control at a given instance, but are less consistently successful over time when performance is compared to that of adults (Luna et al. 2015). Adolescence, in particular, is marked by a reduction in the variability of cognitive control performance and increasing consistency in successful execution with age; in this way, adolescence may be conceptualized as a period of refinement of cognitive control, which manifests as decreasing error rates in tasks with high demands on cognitive function (Luna, Padmanabhan, & O'Hearn, 2010). Understanding the transition into adult-like cognitive control is particularly important because adolescence is the age of emergence of a variety of psychopathology including schizophrenia, mood disorders, substance abuse disorders that are characterized, at least in part, by impairments in cognitive control (Giedd, Keshavan, & Paus, 2009; Luna & Sweeney, 2004). Thus, understanding the normative development of cognitive control may provide insight into the development of abnormalities in cognitive control.

1.2   COGNITIVE FLEXIBILITY

Prior work on the development of cognitive control in adolescence has been primarily focused on development of executive functions, and less is known about the development of cognitive flexibility. Studies have shown that executive functions such as inhibitory control

(Luna & Sweeney, 2004; Thomas, 2013; Williams et al. 1999), working memory (Crone et al. 2006; Luciana et al. 2005), and performance monitoring (Rubia et al., 2006; Wiersema, van der Meere, & Roeyers, 2007) continue to show improvement through late adolescence both in terms of correct response rates and response times. Studies involving the development of cognitive flexibility are scarce, but work in adult task-switching and cognitive flexibility has found evidence for the differential recruitment of frontoparietal regions associated with transient cognitive control (Braver, Reynolds, & Donaldson, 2003). Some prior work in this area has confirmed that adolescents lack the consistency that adults demonstrate in task-switching conditions and exhibit higher variability in successful performance in task-switching (Cepeda, Kramer, & Gonzalez de Sather, 2001; Reimers & Maylor, 2005); however, cognitive flexibility is still largely unexplored in a developmental context.

To add to the body of knowledge on the development of cognitive flexibility in adolescence, here we investigate the neural underpinnings of cognitive flexibility and their development during adolescence. Specifically, we employ a task-switching paradigm that engages flexible switching between executive functions, including working memory and inhibitory control, in service of changing task demands, and administer it to a developmental sample of adolescents and young-adults while they undergo fMRI. We hypothesize that cognitive flexibility (the ability to successfully switch between executive functions) will improve with age, with adults showing greater rates of correct responses than adolescents during task switching. Further, considering the role of the frontoparietal system in transient aspects of cognitive control, such as task switching and rule-updating, we hypothesize that these age-related improvements in cognitive flexibility will be related to the development of components of the frontoparietal system over the course of adolescence.

3

2.0   METHODS

2.1   SAMPLE

Eighty-two adolescents and young adults participated in this study (ages 14-32; $M = 21.93$, $SD = 5.05$; 43 Female). Six of these participants did not complete an MR visit. Subjects were excluded from all analyses if they had high omission rate (omission $> 20\%$; n = 4) due to concerns with compliance with experiment instructions. Exclusions from MR analysis included participants with less than 25 correct trials in the pure condition (n = 4) and those with incomplete MR data (n = 12); the final sample for MR analyses was comprised of 56 subjects. Participant demographics are reported in Table 1. Study inclusion criteria included childhood (age 10) IQ scores greater than 80, no self-reported history of psychiatric or neurological disorder, no current use of psychiatric medication, no history of head injury with loss of consciousness, and no MRI contraindications, including pregnancy, claustrophobia, and non-removable metal in the body. The Institutional Review Board at the University of Pittsburgh approved this study.

Table 1. Participant Demographics.

Variable	Behavioral Sample Range (*M*, *SD*)	fMRI Sample Range (*M*, *SD*)	Exclusions Range (*M*, *SD*)
n	82	56	26
Age	14-32 (21.93, 5.05)	14-30 (22.45, 5.14)	14-32 (20.35, 4.27)
Sex (F)	43	26	17
IQ	85-125 (105.86, 9.64)	85-122 (107.32, 9.29)	85-125 (102, 9.71)
Income	4-8.5 (5.84, 1.05)	4-8.5 (5.93, 1.01)	4-8 (5.59, 1.16)
Father Education	3-7 (5.75, 1.25)	3-7 (5.74, 1.26)	4-7 (5.76, 1.25)
Mother Education	2-7 (5.85, 1.12)	2-7 (5.89, 1.19)	4-7 (5.75, 0.85)

Note: Education levels are: 1 = less than 7th grade, 2 = junior high school, 3 = partial high school, 4 = completed high school or equivalent, 5 = some college, 6 = completed college, 7 = completed postgraduate training. Income levels are: 4 = less than $25,000; 5 = $25,001-50,000; 6 = $50,001-75,000; 7 = $75,001-100,000; 8 = $100,001-250,000; 9 = greater than $250,001. Two participants did not indicate mother's education, 8 participants did not indicate father's education, and 4 participants did not report income.

2.2   TASK DESIGN

Participants performed a modified multi-source interference task (see Figure 1) that was designed to tax two different aspects of cognitive control: inhibitory control and working memory, as well as a visuomotor control condition. Each trial consisted of a cue stimulus that indicated the upcoming task type, followed by a series of three digits, and was terminated with a button push. At the start of each trial, participants were presented with a cue, represented by the color of a fixation cross that indicated the rule-set for the upcoming trial. Trials were either congruent (green), interference (red), or working memory (blue). Following the cue, sets of three digits (0, 1, 2, and/or 3) were presented. Three-digit sets consisted of one unique digit (target) and two matching digits (distractors). Participants were asked to indicate the position of the target digit by making a button press with the corresponding fingers (Bush et al. 2003). Subjects were provided a button glove with keys corresponding to the digits one, two, and three from left to right and told to use the index, middle, and ring fingers of the right hand for responses.
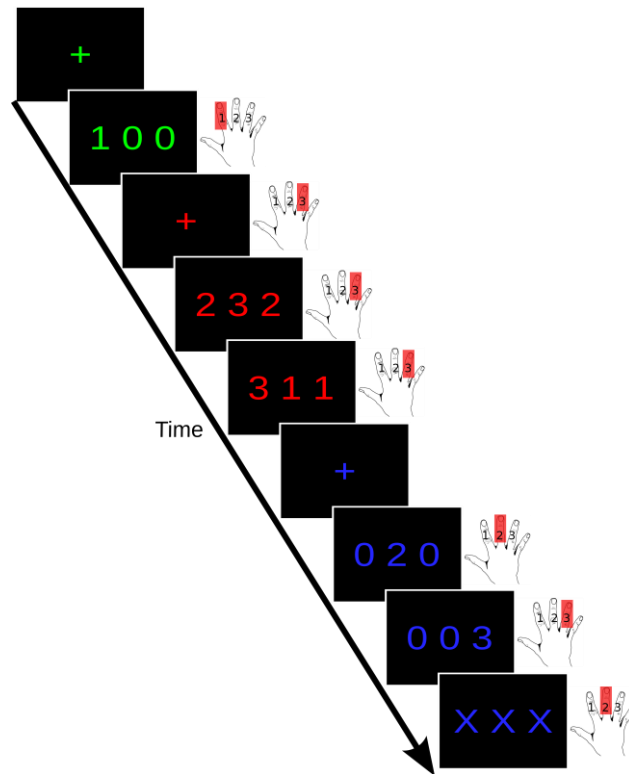
Figure 1. Modified multi-source interference task.
Each trial starts with a colored fixation cross that acts as a cue (green represents visuomotor "congruent", red represents inhibitory control "interference", and blue represents working memory "n-back"). "XXX" trials are n-back probes. The above example is from a "mixed" block in which subjects are required to switch between conditions. In "pure" blocks subjects see consecutive trials of one trial type only.

Visuomotor response trials (Congruent) featured the target number in a corresponding position to the physical location of the response digit, while inhibitory control trials (Interference) introduced a mismatch in target position and location of correct button (Bush et al. 2003). The working memory (N-back) trial type functioned as a two-back n-back task (Kirchner, 1958; Owen, McMillan, Laird, & Bullmore, 2005). Participants had to maintain the sequence of target identities in working memory and were occasionally presented with probe trials (XXX) to signal the participant to recall the correct response from two trials back in the sequence. Three "pure" blocks comprised of 35 sequential trials of one type were included in order to estimate the hemodynamic response for each trial type (Ollinger, Shulman, & Corbetta, 2001). Six "mixed"

blocks of 60 trials each interleaved all three trial types at random to provide a task-switching condition. Within switch blocks, 11 trials were switches, and switch trials could occur a minimum of two trials after the previous switch (2-8 trials, $M = 4.87$, $SD = 1.89$). The order of the blocks was counterbalanced across participants. Each trial consisted of a fixation cues lasting 0.5 s, followed by the three-digit stimulus presentation that remained on screen until a response was made or the trial timed out (1.0, 1.3, and 1.5 s for Congruent, Interference, and N-back respectively). Each trial was followed by a variable inter-trial interval lasted an average of 1.77 seconds and followed an exponential distribution. Participants performed this task once during a lab visit outside the MR scanner, then a second time inside the scanner while acquiring fMRI. Considering the different setup of N-back blocks and the resulting direct measure of performance for working memory switch trials, for the purpose of this study, we limited trial types to Interference and Congruent.

2.3   ANALYSIS

2.3.1   Behavioral

For statistical analyses, Task Type was defined as rule-set for the current trial (Congruent, Interference, Working Memory). Switch Type was defined as either "pure" (trial from the pure block), "switch" (a switch trial from the mix block), or non-switch (a non-switch trial from the mix block). The final categorical variable, Switch From, is the trial type of the immediately preceding trial. Reaction time was calculated as the mean reaction time of correct trials of that task condition, and accuracy as the total number of correct trials divided by the total number of

trials. Switch Cost was calculated as the accuracy of non-switch trials subtracted from the switch trial accuracy.

Primary behavioral analysis was performed with linear mixed and mixed-effects models to examine main effects and interactions between task conditions and age measures and were implemented in MATLAB R2016a (The Mathworks, Inc.; fitlm and fitlme) using default settings. Trials with omission errors were excluded from the analysis. All statistical analyses carried out on behavioral data were also performed on behavioral data collected in-scanner.

2.3.2 Functional MRI

2.3.2.1 Data Acquisition

Stimuli were presented onto a screen behind the scanner using EPrime software (Psychology Software Tools, Inc., Pittsburgh, PA) and were visible to the subject through a mirror mounted to the head coil. Reaction time was recorded as the interval in milliseconds from the three digit stimulus to response (button press on MRI safe button box). Trials were marked correct if the button response (Pointer Finger, Middle Finger, or Ring Finger, right hand glove) correctly indicated the identity of the target number. If no response was given after a specified period specific to the trial type (1000, 1300, and 1500ms for Congruence, Interference, and N-back respectively), the trial was "timed-out" and marked as an omission error.

Imaging data were collected using a 3.0-T Siemens Magnetom TIM Trio (Erlangen, Germany) at the Magnetic Resonance Research Center at the University of Pittsburgh. Structural images were collected using a magnetization prepared rapid acquisition gradient-echo (MP-rage) pulse sequence with 192 slices (1 mm slice thickness; 1 mm isotropic voxels). Functional data were collected using an echo-planar imaging (EPI) sequence with the following parameters: TR

= 1.0s (4x multiband acceleration), TE = 30 ms, Flip Angle = 55°, and 96 x 96 acquisition matrix with a field of view of 220 mm. Sixty slices were collected in the axial plane with an isotropic voxel size of 2.3 mm.

Standard techniques were used to preprocess the functional data and used the same pipeline as previous work from our group (Paulsen et al. 2015). This included wavelet de-spiking, slice timing correction, motion correction (Jenkinson et al. 2002), brain extraction, non-linear registration of functional data to a standardized anatomical brain (MNI-152 template), spatial smoothing with FWHM of 4.25 mm (SUSAN; Smith & Brady, 1997), high pass filtering at 0.008 Hz, and rescaling to a 10,000-unit global median.

2.3.2.2 Statistical Analysis

All imaging analysis was performed with Analysis and Visualization of Functional Neuroimages (AFNI, Bethesda, MD) software (Cox, 1996). To estimate the average hemodynamic response function (HRF) for the task events, trial time courses for correct trials were modeled using TENT basis functions spanning 25s with 26 time steps. Six rigid-body head motion parameters and their derivatives, as well as run-wise 0 through 3rd order polynomials, were used as nuisance regressors. The current and preceding TR were censored if the Euclidean norm head motion distance surpassed 0.9mm. This choice of censoring threshold was guided by work examining motion outliers in task-based fMRI (Siegel et al., 2014). Notably in this sample, motion was not significantly correlated with age ($r = -0.126$, $p = 0.32$).

Based on visual inspection of the HRF, we limited between-subject analyses to peak trial evoked response window by averaging the hemodynamic response between TRs 5 and 7 (5-7 seconds) after the onset of the trial to account for hemodynamic lag. In order to detect potential subtle differences in the shape of the HRF as a function of condition, omnibus group effects were

examined on correct trial time courses and entered into a voxel-wise multivariate model (3dMVM; Chen et al. 2015). To accurately compare differences in activation at peak response to trial onset, models using either TR (18 time points) or peak (mean of activation for TR 5-8, at estimated peak of response) were run. Peak or TR (if applicable), Task Type (Congruence and Interference), and Switch Type (Switch, Non-Switch, and Pure) were entered as within-subject effects and age measures (Age at MR scan) were entered as between-subject effects. As age was best modeled as an inverse function in behavioral data analyses, age was also modeled as an inverse function in fMRI analyses. Post-hoc GLTs were added to test for specific conditions and comparisons, as well as timepoints (if applicable). An interaction term between condition and trial type was used to identify voxels whose correct, trial-wise HRF significantly varied as a function of age or inverse age. Voxelwise testing was masked to only include voxels with a 50% or greater probability of being grey matter in the MNI-152 template and at least 98% EPI coverage in all subjects across all runs. Results were corrected for multiple comparisons using family-wise error correction based on cluster size within the voxelwise space as defined above. Cluster size thresholds were determined through a Monte Carlo simulation using AFNI's 3dClustSim program with mean spatial autocorrelation parameters estimated from residuals from TENT deconvolution. This analysis specified that 8 or more contiguous (faces touching) voxels with a single voxel threshold of $p = 0.005$ ($q < 0.05$) for age at scan were required to achieve corrected, cluster-level alphas of less than 0.05. Timecourses for conditions were extracted and HRFs plotted for visualization.

3.0   RESULTS

3.1   BEHAVIORAL

3.1.1   Task Performance

We observed main effects of Task Type (Interference, Congruent) for both accuracy (see Table 2**Table 2** for parameter estimates, and standard errors, and p values) and reaction time such that participants were faster and more accurate on Congruent trials (Figure 2). Effects of Switch Type (Switch, Non-Switch) were also observed, with participants performing slower and less accurately for switch trials. Interaction between task type and switch type for both accuracy and reaction time was observed, such that the greatest cost of performance occurred on switch trials of the Interference trial type.
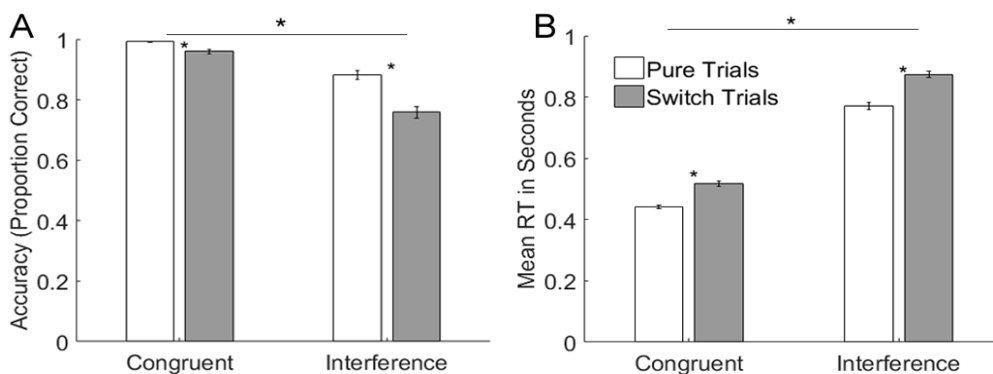

Figure 2. Comparative performance for out-of-scanner visit split by task type and switch type. Figure 2A depicts accuracy in proportion correct for Interference and Congruent task types with switch and pure performance within these conditions. Figure 2B illustrates these same conditions for reaction time in seconds.

11

Table 2. Task Performance Linear Models for out of-scanner participant visit.

Linear Model	df	Coefficient	SE	p
Accuracy ~ TaskType	778	-0.152	0.007	$< 10^{-73}$****
Accuracy ~ SwitchType	777	-0.0744	0.0125	$< 10^{-8}$****
Accuracy ~ TaskType*SwitchType	774			
TaskType:Interference		-0.108	0.0156	$< 10^{-11}$****
SwitchType:Non-Switch		-0.0075	0.0135	0.578
SwitchType:Switch		-0.0312	0.0135	**0.0211***
TaskType*SwitchType:Non-Switch		-0.0249	0.0191	0.194
TaskType*SwitchType:Switch		-0.0863	0.0191	$< 10^{-5}$****
RT ~ TaskType	778	0.329	0.00475	$< 10^{-75}$****
RT ~ SwitchType	777	0.0879	0.0184	$< 10^{-7}$****
RT ~ TaskType*SwitchType	774			
TaskType:Interference		0.329	0.00858	$< 10^{-180}$****
SwitchType:Non-Switch		0.0425	0.00743	$< 10^{-7}$****
SwitchType:Switch		0.0746	0.00743	$< 10^{-21}$****
TaskType*SwitchType:Non-Switch		-0.0258	0.0105	**0.0143***
TaskType*SwitchType:Switch		0.026	0.0105	**0.0111***

Note: Note: *p < 0.05, **p < 0.01, ****p < 0.0001

3.1.2 Development of Task Performance

We observed a significant age by Task Type interaction for both accuracy (Parameter Estimate = 0.0033, *SE* = 0.0015, *p* = 0.024*) and reaction time (Parameter Estimate = -0.0019, *SE* = 0.00094, *p* = 0.043*), an effect that was driven by age-related improvement in reaction time and accuracy in interference trials. Age by Switch Type interactions were not significant for either accuracy (Parameter Estimate = 0.004, *SE* = 0.0025, *p* = 0.109) or reaction time (Parameter

Estimate = 0.00035, *SE* = 0.0037, *p* = 0.924). Three-way interactions between age, Switch Type, and Task Type were significant for accuracy only (Parameter Estimate = 0.0076, *SE* = 0.0038, *p* = 0.043*), with greatest cost to performance occurring in Interference switch trials, but improving with increasing age. To visualize this three-way interaction, we calculated switch cost as the difference in performance in switch and pure conditions, and plotted switch cost as a function of age separately for both Interference and Congruent trials. Switch cost increased with age, as depicted in Figure 3.
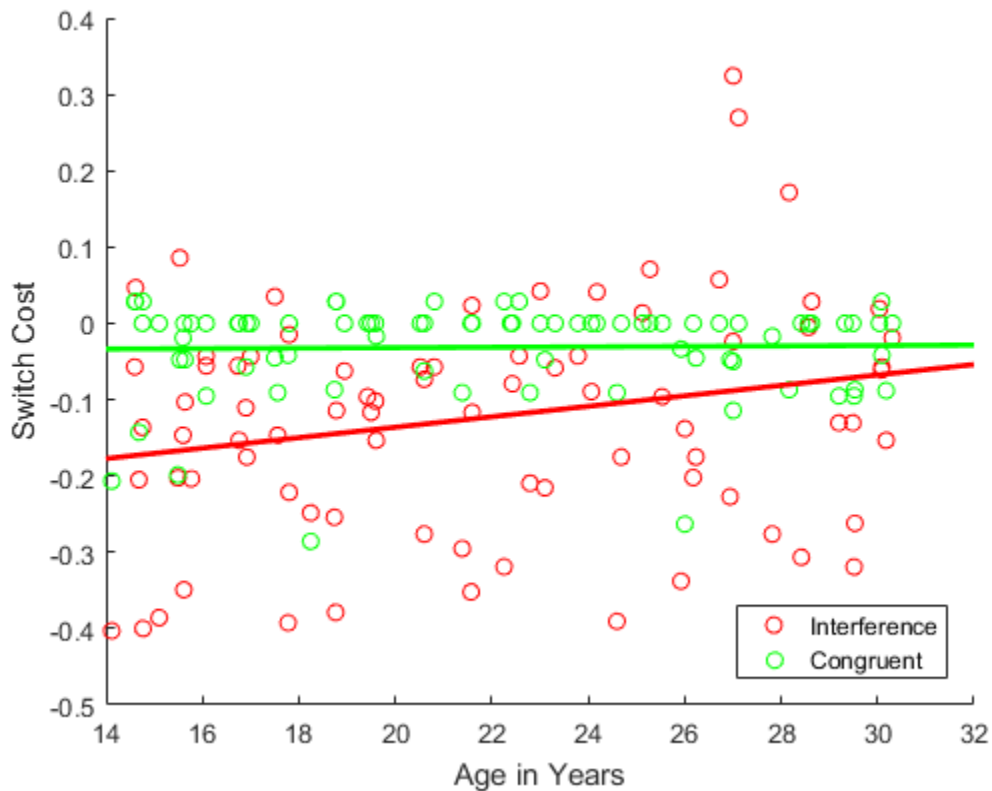

Figure 3. Switch cost plotted as a function of age for Interference and Congruent task types. Switch cost calculated as the difference in performance between switch and pure conditions, then plotted using least squares line.

3.1.3   In-Scanner Performance

In-scanner performance was similar to out-of-scanner measures in directionality of effects. Task performance followed the same pattern of results as the behavioral visit. Developmental effects were no longer significant for reaction time by age and task type (Parameter Estimate = -0.00018, $SE = 0.0033$, $p = 0.96$). In-scanner performance did not show a three-way interaction between age, task type, and switch type for accuracy (Parameter Estimate = 0.0025, $SE = 0.0025$, $p = 0.3$).

3.2   BRAIN ACTIVITY

3.2.1   Task Effects

We observed main effects of task type (Interference, Congruent) in frontal and parietal cortices, such that participants showed greater activation in Interference trials (Figure 4). Main effects of switch type were also observed, with participants showing greater occipital cortex activation in switch conditions compared to non-switch and pure trials (Figure 5). Interaction between task type and switch type was observed, such that the greatest activation patterns occurred in fronto-parietal cortex for Interference Switch conditions, as shown in Figure 6.
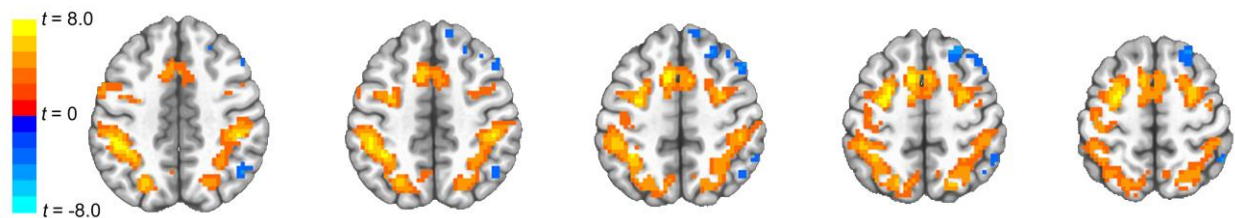

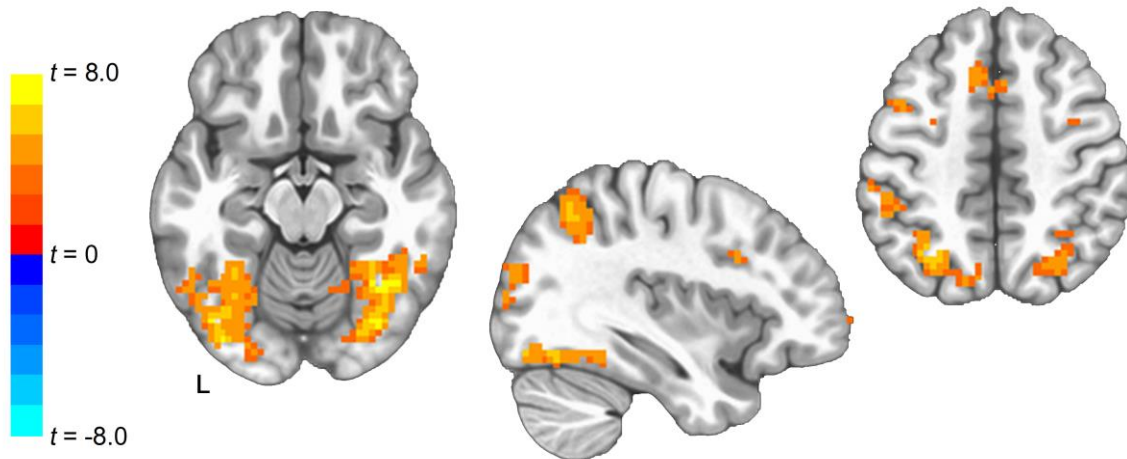**Figure 4.** Brain Activation main effects for Task Type (Interference – Congruent contrast).

14

Figure 5. Brain Activation main effects for Switch Type (Switch – Non-Switch contrast).
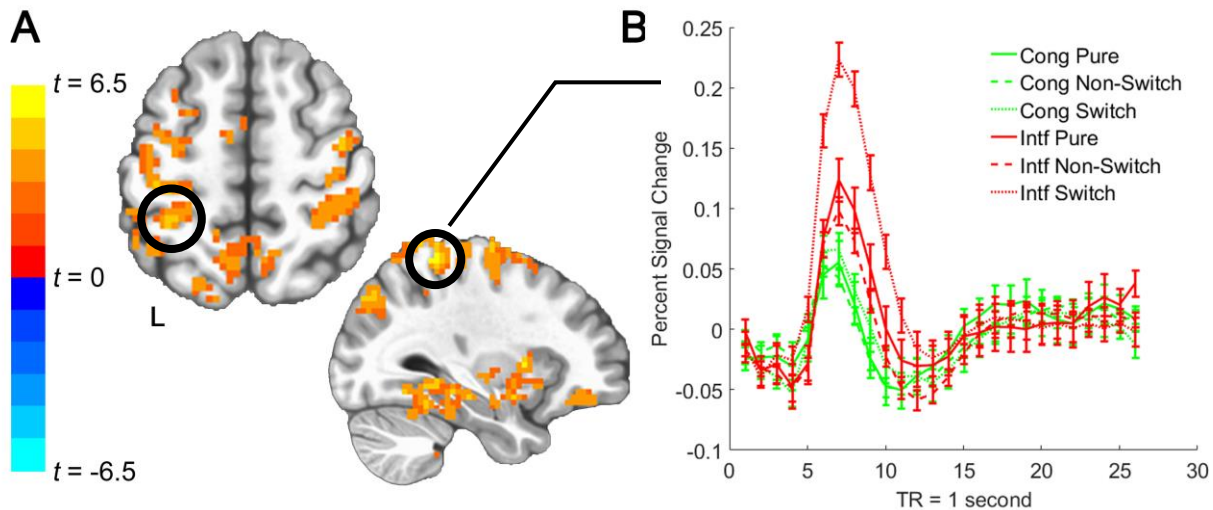

Figure 6. Neural activation for TaskType x SwitchType interaction with associated HRF.
Figure 6A depicts neural activation for task type and switch type interaction, with figure 6B providing HRF plotted for selected ROI (indicated by circle; subcomponent of greater frontoparietal supercluster). 6A axial image z-coordinate = 59.0; cluster MNI coordinates x = 34, y = 40, z = 59 (RAI).

3.2.2 Developmental Effects

Switch type (switch, pure contrasts) activated left frontal cortices differentially across the developmental span such that activation on switches decreased with increasing age regardless of

the task type condition (Figure 7). No significant task type by age interactions were observed in the fMRI data.
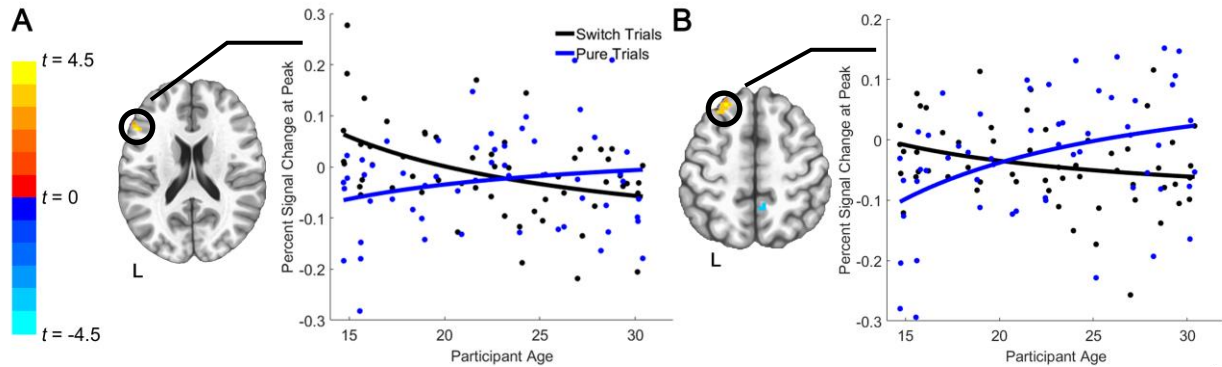

Figure 7. Age by Switch Type neural activation patterns for frontal cortex ROIs.
7A axial image z-coordinate = 19.0; cluster MNI coordinates x = 53, y = -26, z = 20 (RAI). 7B axial image z-coordinate = 55.0; cluster MNI coordinates x = 23, y = -32, z = 56 (RAI).

We did not observe a three-way interaction between age, Task Type, and Switch type; follow up posthoc analyses revealed an age by Switch Type interaction for Interference trials only in left inferior parietal cortex. The ROI appeared to be more active in Interference switch conditions for younger participants, and decreased in relative signal change across the developmental span (Figure 8).
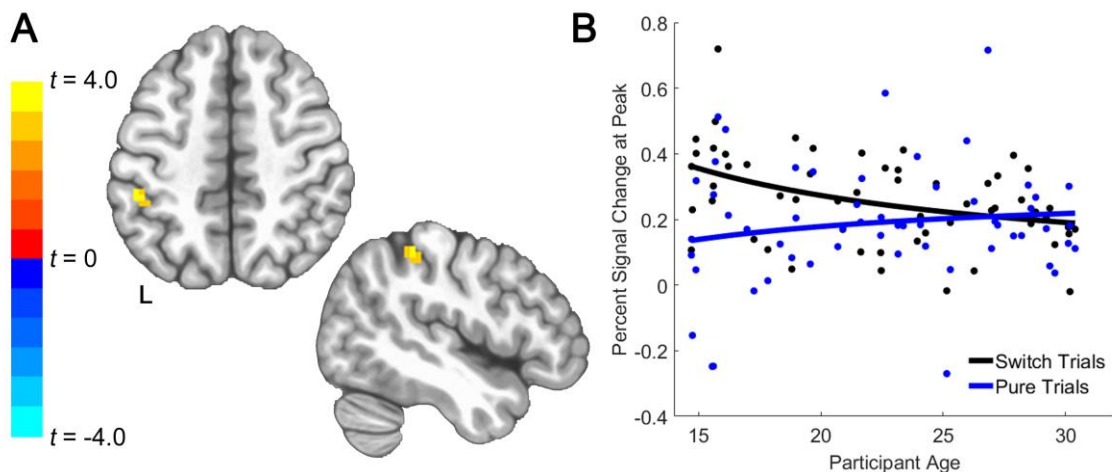

Figure 8. Age by Switch Type interaction for Interference task type only.
Figure 8A depicts neural activation for inferior parietal ROI, with 8B showing age effects for switch, nonswitch in interference condition. Axial image z-coordinate = 49.0, sagittal image z-coordinate = 47.0. Cluster MNI coordinates x = 47, y = 38, z = 50 (RAI).

16

4.0   DISCUSSION

Adolescence may be conceptualized as a period of refinement of cognitive control, which we hypothesize may be driven by continued development of cognitive flexibility. Prior work in cognitive control has studied the development of executive functioning without much focus on the element of flexibility, which we investigate here using a task-switching paradigm. This study design investigates the neural underpinnings of cognitive flexibility by engaging higher-order cognitive processes and changing task demands in order to assess flexibility. Of particular interest in our brain analyses were regions implicated with cognitive attentional networks and linked to multi-source interference tasks, such as the frontoparietal attention system, the cingulo-opercular network, and the dorsal attention stream.

4.1   TASK-SWITCHING

Strong primary effects of task-switching were evident in behavioral and neural measures. Performance, as measured by accuracy and reaction time, was significantly affected by more cognitively demanding conditions such as inhibitory control task types and switch trials meant to tax executive function when compared to less complex visuomotor tasks. Common attentional systems were activated by cognitively demanding conditions, with task-switching leading to greater activation of visual and parietal cortices than congruent tasks and non-switch trials, thus

supporting prior work that indicates continued development of aspects of the frontoparietal system as critical for transient aspects of cognitive control and performance monitoring (Bush & Shin, 2006; Rubia et al., 2006). Interestingly, we also observed robust activation of occipital regions following the visual processing stream, indicating the importance of the visual cue for rule-set information in switch conditions (as opposed to non-switch or pure trials, where the cue information has little value). Differential activation for switch conditions highlights both the task-monitoring and top-down components of attention as well as the incorporation of context-specific cues in successful performance on cognitively demanding trials.

4.2   DEVELOPMENT

Simple task-switching (i.e. between less cognitively demanding tasks) behavior appears adult-like in our youngest subjects, but more complex switches come with greater costs for accuracy and reaction time in younger subjects. Complex task-switching that engages the highest level of cognitive resources appears to show protracted development: we observed a decreasing switch cost from adolescence to adulthood, with adults showing greater accuracy over adolescents while switching into the inhibitory control task. This finding replicates prior studies in development of cognitive control in adolescence, where decreasing switch costs across the developmental span were also observed (Reimers & Maylor, 2005). The results suggest that a key aspect of cognitive maturation in adulthood is the ability to flexibly switch between cognitive tasks with limited cost to performance or speed. These findings were paired with an observation that switch cost for less cognitively demanding conditions showed no developmental effects, suggesting that this ability is already mature by adolescence, a finding supported by developmental research in cognitive

control (Crone & Dahl, 2012; Luna et al., 2010; Magar, Phillips, & Hosie, 2010). Future work seeking to investigate the development of these cognitive processes would require a sample with younger adolescents, and may indeed find age-related changes in less cognitively demanding conditions as well as more robust developmental effects aligning with our findings.

No effect of task type (inhibitory control vs. visuomotor processing) was observed across the developmental span, but switch trials showed greater recruitment of both frontoparietal and ventral stream brain networks when compared to pure and non-switch trials. This effect was such that adolescents showed greater activation in these regions than adults, implying that adolescents must have greater activation in this region to successfully switch between conditions and achieve adult-like performance. Though to a lesser degree than adolescents, adults continued to recruit these areas on correct trials, indicating that the transient frontoparietal task-attentional and cue-context visual ventral stream networks are critical for task success regardless of developmental stage.

Effects of age and task-switching on performance were mirrored by the recruitment of brain regions associated with transient aspects of cognitive control. Specifically, recruitment of the left inferior parietal cortex during switches into interference trials was greater for adolescents than adults and decreased with age across the developmental span, suggesting that these trial conditions require a more effortful cognitive process for adolescents; reliance on this region may decrease as synaptic pruning occurs or as complementary brain systems become sufficient to successfully meet task demands. Developmentally-sensitive activation observed in the inferior parietal lobule is congruent with findings from other work in adolescent task-switching, that found task-switching recruited parietal cortex and that recruitment decreased with increasing age (Rubia et al., 2006). Interestingly, these changes may be occurring in parallel to the recruitment

19

of brain regions involved in more sustained elements of cognitive control as adolescents develop, such as more inferior aspects of parietal cortex (Velanova, Wheeler, & Luna, 2009), though we did not observe age-related changes in brain regions thought to be associated with aspects of cognitive control.

Many conditions, particularly those with low cognitive demand, showed no developmental effects across our sample, suggesting that these functions have reached developmental maturity prior to the age-range included in our sample (i.e. <14 years old). It is important to emphasize that our sample focuses on late adolescence and early adulthood, increasing the likelihood that certain systems have finished development by the ages represented in the sample. The lack of developmental maturity in task-switching to a visuomotor task highlights and lends specificity to our finding that task switches to the inhibitory control task showed the greatest age-related improvement, with both switch cost to performance and neural activation of the left inferior parietal lobule decreasing across the developmental span. In adults this area still shows activation, suggesting that recruitment of the region is essential for successful task switching but that switches into conditions with high cognitive demand have the most protracted developmental timecourse.

This study suffers from certain limitations which stem from the task-switching paradigm and particularly involve the less cognitively demanding task conditions. Participants successfully completed non-switch trials at high accuracy rates regardless of developmental stage, resulting in ceiling effects for statistical conclusions. In a broader context, the paradigm chosen taxes a narrow range of cognitive functions related to task-switching and cognitive flexibility. Tasks were chosen such that visuomotor response components were common to all task types, with the primary difference between trials lying in cognitive manipulation required for success.

Therefore, this aspect of task-switching tested a limited number of cognitive functions and did not engage broader characteristics of cognitive flexibility such as reward or emotional motivation, which may have different timescales of development during the adolescent period.

While the brain and behavioral findings of this study occur in parallel, it is yet unknown what effect performance has on neural activation. Future work could address this through an analysis of the effects of performance on brain activation, such that strength of the measured response changing with age may also vary according to speed of response or rate of accurate responses. Building on our findings in parietal cortex and visual processing streams, a connectivity analysis exploring the age-related changes in top-down modulation of visual attention would provide further insight into the results of this study as well as linking the observed neural activation to the broader context of brain systems changing with age.

This study has found that cognitive flexibility continues to improve with age, particularly when task demands are high. These age-related improvements in cognitive flexibility occur in parallel with age-related changes in brain areas known to be involved in attentional processing and cognitive control. Successful engagement of cognitive flexibility in high-demand task-switching contexts continues to develop even over a late adolescent period. These components of cognitive flexibility showing protracted development may be critical to the refinement of cognitive control abilities that occurs before adulthood, and therefore integral to the understanding of emerging psychopathology in this period.

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