INTERACTIONS BETWEEN COGNITIVE CONTROL AND DEFAULT MODE NETWORKS IN HEALTHY ADOLESCENTS: SEX DIFFERENCES AND IMPLICATIONS FOR MAJOR DEPRESSIVE DISORDER

By

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ABBREVIATIONS

ANOVA – Analysis of Variance
BOLD – Blood-Oxygen-Level Dependent
CDI – Children’s Depression Inventory
CON – Congruent
CRQ – Co-Rumination Questionnaire
DLPFC – Dorsolateral Prefrontal Cortex
DMN – Default Mode Network
FD – Frame-to-Frame Displacement
FMRI – Functional Magnetic Resonance Imaging
FOV – Field of View
FPN – Fronto-Parietal Network
GLM – General Linear Model
INCON – Incongruent
IPL – Inferior Parietal Lobule
IQ – Intelligence Quotient
ISP – Index of Social Position
L – Left
MCQ-A – Meta-Cognitions Questionnaire for Adolescents
MDD – Major Depressive Disorder
MFG – Middle Frontal Gyrus
MPFC – Medial Prefrontal Cortex
MRI – Magnetic Resonance Imaging
MTG – Middle Temporal Gyrus
OHSU – Oregon Health & Science University
PCC – Posterior Cingulate Cortex
PCG – Postcentral Gyrus
PL – Paracentral Lobule
PTM – Prosocial Tendencies Measure
R – Right
ROI – Region of Interest
RSFC – Resting State Functional Connectivity
RT – Reaction Time
SES – Socioeconomic Status
SFG – Superior Frontal Gyrus
SMS – Sexual Maturation Scale
SPL – Superior Parietal Lobule
SPP-A – Self-Perception Profile for Adolescents
SRP – Self-Referential Processing
STAI – State-Trait Anxiety Inventory
TE – Echo Time
TI – Inversion Time
TOSCA-A – Test of Self-Conscious Affect for Adolescents
TR – Repetition Time
WASI – Wechsler Abbreviated Scale of Intelligence

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ABSTRACT

Risk for major depressive disorder (MDD) increases dramatically during adolescence and disproportionately affects girls. The mechanisms mediating sex differences in the risk for MDD are not fully understood; however, interactions between social, cognitive and neurodevelopmental factors likely explain some of this risk. Adolescent girls are more prosocial and experience more interpersonal stress than boys, which may contribute to the gender discrepancy in MDD onset. Moreover, given their prosocial nature, girls may more readily integrate social feedback from peers into their own identity via self-referential processing (SRP) that engages cortical midline structures (i.e. medial prefrontal and posterior cingulate cortices). These brain regions overlap with the default mode network (DMN), which displays aberrant activation and functional connectivity during SRP and rumination. Importantly, functional connectivity between DMN and the fronto-parietal network (FPN; i.e. dorsolateral prefrontal cortex and inferior parietal lobule) may also be disrupted in MDD, particularly during cognitive control, indicating that the interaction between DMN and FPN warrants investigation.

State (i.e. task-induced) and trait (i.e. resting state) functional connectivity were assessed in healthy adolescents (15 – 18 years) to determine sex differences in connectivity between DMN and FPN using functional magnetic resonance imaging (fMRI). An affective SRP induction was implemented to elicit activation of the DMN. Immediately following SRP trials, participants engaged in a cognitive control task (i.e. Flanker task) that typically recruits the FPN. State functional connectivity was measured by regressing out task activation signal and correlating the residual blood-oxygen-level dependent (BOLD) signal of bilateral DMN and FPN seed regions with every other voxel in the brain. A 2x2 analysis of variance (ANOVA) was conducted for each seed region comparing functional connectivity between girls and boys and between Flanker trials that followed SRP (Post-SRP Flanker) and Control (Post-Control Flanker) trials. Functional connectivity of bilateral DMN and FPN seed regions with 1) regions of interest (ROI) determined by the state functional connectivity analyses and 2) the whole brain was assessed using resting state fMRI data and compared by sex with two-sample *t*-tests for each seed region.

Girls reported more co-rumination, which involves the frequent discussion of problems with a same-sex peer, and worse cognitive control performance, particularly during Post-SRP Flanker trials, as reflected by more errors of omission. In fact, co-rumination mediated the sex difference in errors of omission. Girls also showed stronger state functional connectivity between DMN and FPN during Post-SRP Flanker trials. Trait functional connectivity analyses indicated that girls have stronger coupling between DMN-FPN, albeit between different brain regions identified in the state functional connectivity analyses. Moreover, DMN-FPN trait functional connectivity mediated sex differences in co-rumination. Together, these findings indicate that trait functional connectivity between DMN and FPN may explain sex differences in cognitive control in an affective context via co-rumination. These patterns of state and trait functional connectivity reflect those observed in MDD; therefore, future studies should examine this mechanism longitudinally in youth at risk for MDD to confirm its relevance as a sex-specific risk factor.

CHAPTER 1: INTRODUCTION

1.1 Sex Differences in Adolescent Major Depression

Following perinatal organization, substantial and dynamic physiological, social and neural change occurs during adolescence, marking this developmental period as a second wave of plasticity (Spear, 2013). In addition to promoting necessary and healthy milestones of adolescent neurodevelopment, this extended brain plasticity also heightens vulnerability for biological and/or psychological insult (Lee et al., 2014). The majority of adolescents thrive; however, a subset develops a range of problematic behaviors that may evolve into mental illness. Recent estimates from the Substance Abuse and Mental Health Services Administration indicate that over 11% of adolescents between the ages of 12 and 17 years have had at least one major depressive episode in the past year. This percentage of adolescents is primarily comprised of girls, with approximately three times as many girls reporting a depressive episode, compared to boys (Hedden et al., 2015). Other estimates indicate that by the age of 15, girls are 50% more likely than boys to have experienced a major depressive episode (Hankin et al., 1998). What is more, this elevated risk in females, which ranges from 1.7:1 to 2.4:1, persists across the lifespan (Kessler et al., 1994; Kessler et al., 1993; Weissman et al., 1991).

The rise in depression observed in females coincides with the onset of puberty, and in fact, pubertal status has a greater influence on rates of depression than age (Angold et al., 1998). Moreover, the transition from pre-puberty to post-puberty is linked with increased negative affect in females, which interacts with estrogen levels to account for a large proportion of depressive symptoms (Brooks-Gunn and Warren, 1989). Indeed, some research suggests that pubertal maturation serves to sensitize females to the depressogenic effects of negative life events. For instance, the association between puberty and depression is mediated by heightened peer stress in girls, but not boys (Conley et al., 2012). In addition, a link between early pubertal maturation and internalizing symptoms has been reported and may be partially attributed to girls' heightened sensitivity to interpersonal stress (Ge et al., 1994; Natsuaki et al., 2009). Social changes that accompany pubertal development may have more negative psychological effects in girls relative to boys (Patton et al., 2008). For instance, adolescent girls report deterioration in attachments within family and school contexts to a larger degree than boys, such that family conflict and bullying predict symptoms of depression in girls (Patton et al., 2008). Indeed, among a sample of adolescents with remitted depression, girls retrospectively report a higher incidence of negative life events during the 6 months prior to depression onset (Cyranowski et al., 2000). This heightened sensitivity to interpersonal stress easily lends itself to negative cognitive styles and ruminative tendencies in girls. For instance, greater exposure to interpersonal stress and a ruminative response style in girls predicts sex differences in depressive symptoms (Abela and Hankin, 2008; Hamilton et al., 2015). Thus, certain aspects of adolescent social development may place a subset of girls at risk for major depressive disorder (MDD). However, most adolescent girls do not develop depressive symptoms, indicating that other developmental sex differences may be at play.

MDD is characterized not only by depressive symptoms, but also by executive functioning deficits (Snyder, 2013). Currently, it has not been established whether deficits in executive functions precede or follow diagnoses of depression. Some research suggests that executive functioning may be taxed when negative emotions are engaged

(Gladwin and Figner, 2014). In adolescent patients with depression, it has been observed that inhibitory control suffers when youth are primed by a negative emotional stimulus (Colich et al., 2016). Negative stimuli effectively serve to amplify negative emotions present in depression, such as sadness, which are ordinarily regulated during successful inhibitory control (Luciana, 2016). Outside of an emotional context, poor working memory prospectively predicts depressive symptoms, while better working memory predicts engagement of coping strategies that modify emotional reactions and attention regulation in youth (Evans et al., 2016). Executive functioning, or cognitive control, develops across adolescence and the ability to implement cognitive control depends on the magnitude of executive load, which is determined by changing internal and external demands, as well as the integrity of underlying neural structures designed to support cognitive control functions (Luciana and Collins, 2012). Due to the relative delay in maturation of cognitive control-related brain regions (e.g. dorsolateral prefrontal and inferior parietal cortices) relative to subcortical regions supporting motivation and affective processing (e.g. reward and limbic structures) (Casey, 2015; Ernst, 2014; Galvan et al., 2006; Somerville et al., 2010; Steinberg, 2010), adolescents may not effectively regulate sub-cortically driven impulses in situations of heightened executive load, such as in socio-emotional contexts (Luciana and Collins, 2012; Smith et al., 2013). A higher propensity for elevated executive load may explain why adolescents generally do not display fully mature cognitive control processing (Luciana, 2016; Luna et al., 2010). Moreover, high executive load may interfere with self-regulatory capacity that may render some individuals vulnerable to psychopathology.

Subsequent sections of this chapter will explore sex differences in social development that my place adolescent girls at greater risk for the depressogenic effects of negative life events, as well as examine the brain regions important for social development and sex differences therein (**1.2 Adolescent Sex Differences in Social Development**). An emphasis will be placed on self-referential processing (SRP), a construct that intersects social development, cognitive control and rumination (**1.3 Self-Referential Processing (SRP) and Underlying Neural Networks**). Sex differences in the development of cognitive control will also be detailed *(***1.4 Sex Differences in Development of Cognitive Control**) in order to understand how affective self-referential processing may function to increase executive load and negatively impact cognitive control (**1.5 Interactions between Default Mode and Cognitive Control Networks**). After a brief summary (**1.6 Summary**), the aims and hypotheses of this dissertation will be detailed (**1.7 Dissertation Aims and Hypotheses**), followed by a brief conclusion (**1.7 Conclusions**).

1.2 Adolescent Sex Differences in Social Development

The transition from childhood to adulthood is typified by a shift in orientation from parents and family to peers and romantic partners (Larson and Richards, 1994; Steinberg and Morris, 2001). As adolescents assert more autonomy and disengage from parental control, peer groups play a more critical role in shaping social behavior (Berzonsky and Adams, 2003). Moreover, development of one's identity in relation to the social world undergoes extensive maturation during the adolescent period (Coleman & Hendry, 1990). Indeed, adolescents' self-identity, particularly in social contexts, is readily defined by the perceived opinions of their peers (Cole, 1991; Cole et al., 1997;

Harter, 1999; Harter et al., 1998; Pfeifer et al., 2009). The perceived opinions of others about oneself are believed to be incorporated into direct self-evaluations, or what one thinks of oneself, as perspective taking becomes more automatic and internalized (Baldwin, 1895; Cooley, 1902; Mead, 1934). This theory was tested using functional magnetic resonance imaging (fMRI) to measure brain activation during social self-evaluation in adults and adolescents (Pfeifer et al., 2009). While adults recruit regions of the brain previously implicated in direct self-evaluation (i.e. medial prefrontal cortex and medial posterior cingulate cortex) (Pfeifer et al., 2007), adolescents additionally recruit brain regions relevant for social perception and perspective taking (temporal-parietal junction), even when they are not prompted to do so. A longitudinal assessment of social self-evaluations indicates that recruitment of the medial prefrontal cortex increases across early adolescence (Pfeifer et al., 2013); thus, medial prefrontal cortical activation is also relevant for social self-processing during adolescence. Subsequent research has shown that adolescents also activate the striatum, a region of the brain important for processing salient and reinforcing stimuli (Schultz et al., 1997), during reflected (i.e. perceived opinions of others) social self-evaluation, and that this activation was positively correlated with age and pubertal stage (Jankowski et al., 2014). Importantly, these findings were specific to social self-evaluation and not academic or physical self-evaluation, indicating that perceived social appraisal is particularly salient and perhaps reinforcing in adolescence. There is also some evidence to support a reinforcing effect of peer evaluation. Using a social evaluation task, Guyer and colleagues demonstrated that adolescents report higher positive well-being when receiving positive feedback from more desirable peers (Guyer et al., 2014; Guyer et al., 2012). Peer acceptance also elicited activation of the striatum regardless of peer desirability (Guyer et al., 2012). What is more, during anticipation of social feedback from high-interest peers, girls activate the striatum to a larger extent with increasing age, while boys show no age-related change (Guyer et al., 2009). Thus, adolescents demonstrate an orientation to peer groups that is supported, in part, by regions of the brain underlying reward processing and social cognition (Nelson et al., 2005). Self-identity is informed by increasingly relevant social feedback; however, given gender differences in social development and sex differences in brain maturation (see **1.4 Sex Differences in Neurodevelopment of Cognitive Control**), the process of integrating social feedback into one’s identity may differ by sex during adolescence.

Sex differences in neural responsiveness to social feedback are likely a reflection of sex differences in peer relationship processes and how they inform behavioral and social-cognitive styles, social stress and relationship provisions (i.e. emotional benefits derived from a friendship, such as feelings of closeness) (Rose and Rudolph, 2006). For instance, observational studies (Hops et al., 1997; Strough and Berg, 2000) and reports by peers (Bukowski, 1994; Lempers and Clark-Lempers, 1993) suggest that adolescent girls are more prosocial than boys. Adolescent girls place more value on social goals (Ford, 1982) and having dyadic relationships (Markovits et al., 2001). They also endorse goals for intimacy and nurturance (Jarvinen and Nicholls, 1996) and report stronger same-sex peer attachments than boys (Gorrese and Ruggieri, 2012). Indeed, compared to boys, girls engage in more self-disclosure in friendships (Buhrmester and Furman, 1987; Camarena et al., 1990; Crockett et al., 1984; Lempers and Clark-Lempers, 1993; Rose, 2002) and have more positive expectations about the outcomes of self-disclosure, such as expecting that talking about problems will make them feel cared for, understood and like their feelings are no longer bottled up (Rose et al., 2012). In fact, sex differences in such expectations partially explain sex differences in self-disclosure (Rose et al., 2012). Perhaps due to social orientation, girls also report higher levels of friendship stress (e.g. having a friend stop talking to them; having a friend tell their secret, etc.) (Forteza et al., 1996; Rudolph, 2002; Rudolph and Conley, 2005). Thus, the peer relationship process characteristically observed in girls is accompanied by benefits and drawbacks. Benefits include emotional support from friends, greater intimacy with friends and increased self-esteem; however, drawbacks include increased sensitivity to others' distress and to the status of peer relationships and friends, as well as higher exposure to social stressors. Given this, female-linked relationship processes have the potential to promote intimate relationships and inhibit antisocial behavior, but also to enhance vulnerability for emotional difficulties (Rose and Rudolph, 2006). Boys also experience benefits and costs for their adopted peer relationship processes. Larger peer groups (Parker and Seal, 1996) and more competitive play (Gabriel and Gardner, 1999) are some benefits, while drawbacks include greater exposure to direct physical and verbal peer victimization (Rudolph, 2002; Storch et al., 2003) and fewer emotional provisions from friends (Rose et al., 2007). These male-linked processes may serve to hinder the development of intimate relationships and contribute to behavioral problems, but may also promote group-based relationships and protect against emotional problems (Rose and Rudolph, 2006). Thus, neither sex-linked peer relationship process is adaptive or maladaptive – both contain costs and benefits that serve distinct functions.

For the majority of adolescents, social development proceeds unremarkably, but for others, some of the drawbacks associated with certain peer relationship processes may lead to dysfunction or psychopathology. In the case of female-linked peer relationship processes, increased sensitivity to the distress of others and the status of peer relationships, as well as the greater likelihood to experience social stressors and ruminate in response to stress may lead to a range of emotional difficulties, among them major depressive disorder. Indeed, the increased salience of social stimuli observed in adolescence is accompanied by increased self-consciousness and concern with the opinions of others, particularly peers (Steinberg, 2005). Across adolescence, girls generally report more self-consciousness (Allgood-Merten et al., 1990; Davis and Franzoi, 1986; Rankin, 2004) and lower self-esteem (Allgood-Merten et al., 1990; McClure et al., 2010; Moksnes and Espnes, 2013) than boys. Higher self-consciousness has been linked with internalizing symptoms (Bowker and Rubin, 2009; Nie et al., 2014), while lower self-esteem relates to state depression, particularly in girls (Moksnes and Espnes, 2012). Moreover, positive friendship quality, which is more highly valued by girls, can also augment internalizing problems (Bowker & Rubin, 2009). This counterintuitive finding may be explained by the higher incidence of co-rumination in girls, compared to boys (Rose, 2002). That is, in response to stress, girls will co-ruminate with a friend, typically a same-sex peer, which may lead to both closer friendships and more depression and anxiety symptoms (Hankin et al., 2010; Rose, 2002). Co-rumination is characterized by frequent discussion of problems, mutual encouragement of discussing problems, revisiting the same problem repeatedly, speculating about causes and consequences of problems, and focusing on negative feelings (Rose, 2002; Rose and

Rudolph, 2006). Several studies have found a positive association between internalizing symptoms and co-rumination in adolescence (Bastin et al., 2015; Criss et al., 2016; Guarneri-White et al., 2015; Guassi Moreira et al., 2016; Hruska et al., 2015; Nicolai et al., 2013; Rose, 2002; Rose et al., 2014; Schwartz-Mette and Rose, 2012; Stone and Gibb, 2015; Stone et al., 2011; Tompkins et al., 2011; White and Shih, 2012). Many studies also report that adolescent girls endorse more co-rumination than boys (Bastin et al., 2015; Guarneri-White et al., 2015; Guassi Moreira et al., 2016; Hankin et al., 2010; Murdock et al., 2015; Rose, 2002; Rose et al., 2007; Rose et al., 2014; Rose et al., 2012; Stone et al., 2011; Stone et al., 2013; Tompkins et al., 2011; White and Shih, 2012), although not all (Criss et al., 2016; Hruska et al., 2015; Stone et al., 2010), and co-rumination has been shown predict internalizing symptoms, particularly when facing interpersonal stress (Bastin et al., 2015; Nicolai et al., 2013; Rose et al., 2007; Stone and Gibb, 2015). Co-rumination was also reported to mediate sex differences in depression onset and predict episode severity and duration (Rose, 2002). However, more recent studies indicate that youth who co-ruminate, regardless of gender, are at heightened risk for depression (Hankin et al., 2010; Stone et al., 2011). Youth with a current diagnosis of major depressive disorder report higher co-rumination (Waller et al., 2014), while current co-rumination may also predict a previous diagnosis of major depression (Stone et al., 2010). Rumination, which is defined as a persistent, self-reflective and uncontrollable focus on depressed mood and its causes and consequences (Nolen-Hoeksema, 1991), may be a potential mechanism through which co-rumination leads to depression. Indeed, the creator of the Co-Rumination Questionnaire for adolescents hypothesized that co-rumination cultivates risk for emotional distress by reinforcing ruminative tendencies about one’s own problems (Rose, 2002). Evidence for this hypothesis was provided by a prospective study that reported co-rumination indirectly increased depressive symptoms by increasing rumination tendencies (Stone and Gibb, 2015). Compared to males, adult women (Johnson and Whisman, 2013) and girls (Rood et al., 2009) from non-clinical and clinical samples report more rumination. Interpersonal stress, which is more common in adolescent girls (Forteza et al., 1996; Rudolph, 2002; Rudolph and Conley, 2005), predicts rumination (Hamilton et al., 2015; Stange et al., 2014) and accounts for sex differences in rumination in healthy adolescents. Thus, as adolescents’ self-identity is increasingly being shaped by peers, sex differences in friendship processes also inform adaptive and maladaptive behaviors that emerge in response to interpersonal stress.

1.3 Self-Referential Processing (SRP) and Underlying Neural Networks

Rumination is an unhealthy type of SRP that elicits more activation of medial prefrontal and anterior cingulate cortices in patients with major depression relative to healthy controls (Nejad et al., 2013). In fact, patients with depression display robust activation of posterior cingulate cortex outside of a ruminative context (Drevets et al., 2002; Hamilton et al., 2011), raising the possibility that the basic processes underlying self-reflection may be disrupted in major depression. Given that adolescence is characterized by heightened self-consciousness and concern with the opinions of peers (Steinberg, 2005), studying SRP in healthy adolescents may provide insight into potential mechanisms of risk for major depression. Sex differences in peer relationship processes, interpersonal stress and concern with social feedback inform self-identity and may explain sex differences in the onset of depression during adolescence; however, the mechanisms through which healthy self-reflection evolves into unhealthy rumination have not been studied. SRP and the network of brain regions that support its function may constitute one such mechanism.

In healthy individuals, SRP has been associated with activation of the insula, temporal pole, hippocampus and amygdala (Fossati et al., 2003; Gusnard et al., 2001; Johnson et al., 2006; Kelley et al., 2002; Ochsner and Gross, 2005; Phan et al., 2004; Schmitz and Johnson, 2006; van der Meer et al., 2010); however, the most commonly activated regions are located in dorsal and ventral medial prefrontal and anterior cingulate cortices, as well as posterior cingulate cortex and precuneus (Northoff et al., 2006), also referred to as cortical midline structures (Northoff and Bermpohl, 2004). These commonly activated regions of the SRP network overlap with regions of the default mode network (DMN), specifically ventral medial prefrontal and posterior cingulate cortices (Davey et al., 2016; Qin and Northoff, 2011; Raichle et al., 2001; Spreng and Grady, 2010). Other regions of the DMN include lateral temporal cortex and hippocampus (Buckner et al., 2008). The DMN is an intrinsic functional network that has been detected with resting state functional connectivity (RSFC) magnetic resonance imaging (Raichle et al., 2001) and is deactivated during cognitive control tasks (Anticevic et al., 2010; Li et al., 2007). RSFC measures the correlations over time of fluctuating BOLD signals when someone is at rest. Regions of the brain that are correlated over time are thought to be functionally connected, and regions that are commonly functionally coupled are thought to comprise an intrinsic network, with the DMN being one of the most studied. At rest, the brain is thought to engage in mind-wandering, mentalizing, or SRP (Gusnard et al., 2001), which is reflected by DMN activation. Not surprisingly, rumination in healthy individuals is associated with activation of cortical midline structures (Kross et al., 2009).

In patients with depression, hyper-activation of cortical midline structures is observed (Renner et al., 2015; Sarsam et al., 2013; Sheline et al., 2010) and is associated with degree of rumination (Freton et al., 2014; Lemogne et al., 2012; Nejad et al., 2013). In addition, RSFC studies show aberrant patterns of connectivity in patients with depression (Berman et al., 2011; Northoff et al., 2011). Specifically, nodes of the DMN appear to be hyper-connected to each other (Greicius et al., 2007; Kaiser et al., 2015), particularly anterior brain regions, such as medial prefrontal cortex (Zhu et al., 2012). Moreover, stronger within-network connectivity of the DMN is positively related to rumination in patients with MDD (Berman et al., 2011; Hamilton et al., 2011; Whitfield-Gabrieli and Ford, 2012), as well as in healthy controls (Berman et al., 2011; Luo et al., 2016). It is not surprising that cortical midline structures are active during rumination or that hyper-connectivity of DMN is linked to rumination since rumination is a type of SRP; however, this provides an opportunity to study a potential neural mechanism underlying risk for depression in adolescent girls. Examining the impact of affective SRP on cognitive control in a sample of healthy adolescents may provide insight about the potential for heightened executive load – due to an affective SRP induction – to impair cognitive control performance in a sex-specific fashion.

1.4 Sex Differences in Neurodevelopment of Cognitive Control

The adolescent brain undergoes vast maturational change in many of the brain regions important for cognitive control (Sowell et al., 2001; Vrticka et al., 2014), including dorsolateral prefrontal cortex, inferior frontal cortex, anterior insular cortex, dorsal premotor cortex, anterior cingulate cortex/pre-supplementary motor area and posterior parietal cortex. This set of regions forms a fronto-parietal network (FPN) that implements cognitive control in a variety of task contexts (Cole and Schneider, 2007; Dosenbach et al., 2008). Cortical gray matter volume and thickness decrease over the course of adolescence and young adulthood (Gogtay et al., 2004), which is thought to reflect synaptic pruning (Jernigan et al., 1991; Selemon, 2013). Importantly, parietal and frontal lobes display the most protracted rates of development (Gogtay et al., 2004). Maturation of gray matter in frontal and parietal cortices, as well as the development of white matter connecting these regions, are accompanied by superior cognitive control performance (Darki and Klingberg, 2014). Moreover, white matter connectivity across various tracts is actively developing during adolescence in a sex-specific fashion, and maturation of one such tract, the cingulum (where girls mature earlier than boys), is related to inhibitory control performance (Simmonds et al., 2014). The cingulum connects hippocampus to the cingulate and dorsolateral prefrontal cortices, which are components of the FPN (Cole and Schneider, 2007; Dosenbach et al., 2008) that support cognitive control (Luna et al., 2010). Sex differences in FPN gray matter maturation have not been reported by more recent longitudinal studies (Ducharme et al., 2016; Vijayakumar et al., 2016); however, sex differences in functional activation and connectivity of FPN brain regions have been consistently reported in adolescence (Alarcon et al., 2014; Christakou et al., 2009; Clements-Stephens et al., 2009; Cservenka et al., 2015; Hjelmervik et al., 2014; Li et al., 2010; Rubia et al., 2010; Rubia et al., 2013; Schweinsburg et al., 2005; Weiss et al., 2003; White et al., 2014). Though the majority of these studies do not report sex differences in performance, most report differences in prefrontal cortex activation or connectivity patterns (Alarcon et al., 2014; Christakou et al., 2009; Cservenka et al., 2015; Hjelmervik et al., 2014; Li et al., 2010; Rubia et al., 2010; Rubia et al., 2013; Schweinsburg et al., 2005; Weiss et al., 2003; White et al., 2014), which is perhaps due to the protracted development of the prefrontal cortex and potential sex differences therein; though, this remains to be confirmed experimentally.

1.5 Interactions between Default Mode and Cognitive Control Networks

According to a recent meta-analysis of functional brain activation in adolescent major depression, regions of the FPN are hypoactive, while regions of the DMN are hyperactive during various tasks (Miller et al., 2015). As detailed above, this pattern of underactive FPN and overactive DMN may be linked to rumination (Davey et al., 2012; Hamilton et al., 2011; Kelley et al., 2002; Marchetti et al., 2012; Ray et al., 2005; Sheline et al., 2010; Vanderhasselt et al., 2011; Wagner et al., 2015). Moreover, depressed individuals show robust functional connectivity between anterior DMN nodes and the FPN during conditions of rest (Davey et al., 2012; Lemogne et al., 2009; Sheline et al., 2010). The DMN and FPN are generally functionally distinct networks in healthy individuals (De Luca et al., 2006; Fox et al., 2005; Fransson, 2005; Greicius et al., 2003); therefore, heightened connectivity between these networks may be a neurobiological marker of depression. Over-activation of the DMN and/or hyper-connectivity between DMN and FPN during tasks that require cognitive effort may also lead to worse cognitive control performance. Indeed, some studies indicate that optimal performance on a cognitive control task requires deactivation of the DMN (Anticevic et al., 2010; Li et al., 2007) or a functional dissociation of DMN and FPN (Hampson et al., 2010; Keller et al., 2015; Kelly et al., 2008). Patients with MDD demonstrate deficient deactivation of the DMN during cognitive control tasks that is correlated with worse performance (Wagner et al., 2015; Wagner et al., 2006); this effect may be more robust in adolescents (Bartova et al., 2015). Thus, the intrinsic functional architecture of the DMN and its interactions with the FPN are disrupted in depression and may underlie behavioral and cognitive symptoms of depression. In fact, these findings lend support to the cognitive theory of depression, which posits that patients with MDD allocate more attention to negative stimuli and display errors in the cognitive appraisal of their experiences (Clark and Beck, 1999). For instance, hyper-connectivity between DMN and the FPN may reflect ineffective regulation of negative self-focus (Davey et al., 2012; Hamilton et al., 2011; Kelley et al., 2002; Marchetti et al., 2012; Ray et al., 2005; Sheline et al., 2010; Vanderhasselt et al., 2011; Wagner et al., 2015), which may manifest in poorer cognitive control performance (Bartova et al., 2015; Jacobs et al., 2014; Wagner et al., 2015; Wagner et al., 2006).

Sex differences in RSFC between DMN and FPN have been examined in late adolescence/early adulthood (mean age 22 years); however, there is some discordance in the findings. One study reported higher regional homogeneity (a measure of local functional connectivity) of both DMN and FPN in females compared to males (Xu et al., 2015), while another study reported higher regional homogeneity of DMN in females and FPN in males (Wang et al., 2012). A third study reported that females showed higher functional connectivity of the FPN compared to males (Hjelmervik et al., 2014), while yet another study reported higher functional connectivity of the FPN in males relative to females (Smith et al., 2014b). Only two studies have examined sex differences in RSFC of DMN and FPN across adolescence; however, one reported no sex differences (Sole-Padulles et al., 2016) and the second study reported higher regional efficiency of the DMN in girls, compared to boys (Wu et al., 2013). Studies measuring functional connectivity associated with social behavior have reported sex differences. For instance, during an action-observation paradigm, adolescent boys recruit a socioemotional network that includes temporal parietal junction, temporal pole, and superior temporal sulcus, among other regions, rather than recruiting an action observation network during angry conditions, whereas girls do not show differential connectivity patterns (Shaw et al., 2011). A study in late adolescence (mean age 21 years) reported that females score higher on empathizing, while males score higher on systemizing, which is the drive to analyze systems. Higher empathizing scores were positively correlated with stronger within-DMN RSFC, while systemizing was positively correlated with stronger within-FPN RSFC in males only (Takeuchi et al., 2014). Thus, adolescent sex differences in DMN-FPN functional connectivity may not emerge as readily as sex differences in within-network connectivity or functional connectivity between DMN and socio-emotional processing brain regions, particularly in socio-emotional contexts.

1.6 Summary

In sum, a fine balance between activation of FPN and deactivation of DMN during cognitive control is necessary for optimal performance (Anticevic et al., 2010; Li et al., 2007), and this balance is disrupted in depression (Bartova et al., 2015; Wagner et al., 2015; Wagner et al., 2006). Functional coupling between FPN and DMN and decreased performance during a cognitive control task that followed a negative SRP induction has been reported previously in healthy adults (Wagner et al., 2013). Depression symptoms were correlated with activation of DMN during negative SRP conditions; thus, the presentation of negative self-relevant stimuli effectively heightened executive load and negatively affected subsequent performance on an inhibitory control task (Wagner et al., 2013). A later study in adults with depression demonstrated that FPN brain regions were more weakly activated during the same inhibitory control task that was preceded by a negative SRP induction, resulting in performance deficits; activation of DMN during negative SRP was again correlated to depression symptoms (Wagner et al., 2015). Together, these studies suggest that the functional interaction of DMN and FPN during cognitive control conditions of heightened executive load may serve as a risk factor for depression. The interaction of these networks under these conditions has not been studied in adolescence, nor have sex differences been explored in this context. Given the rise in the incidence of depression during adolescence, it is critical to examine risk for depression during this developmental period, particularly in girls, who constitute the larger proportion of diagnosed cases. Social development of adolescent girls may uniquely position them to experience social stressors and integrate social feedback into their self-identity (Allgood-Merten et al., 1990; Conley et al., 2012; Davis and Franzoi, 1986; Moksnes and Espnes, 2012; Natsuaki et al., 2009; Pfeifer et al., 2009; Rankin, 2004); thus, providing a mechanism for heightened executive load to interfere with cognitive control, as reflected by inappropriate functional coupling between FPN and DMN.

1.7 Dissertation Aims and Hypotheses

1.7.1 Specific Aim I

In order to examine sex differences in the interaction of affective SRP and cognitive control in healthy adolescents, I measured transient functional connectivity patterns between DMN and FPN, as well as cognitive control performance during an inhibitory control task that followed an affective SRP induction. Transient functional connectivity is defined as state-induced coupling of brain regions or networks, which may not correspond to more persistent, trait functional connectivity that is measured during rest. Previous work has demonstrated an influence of affective SRP on cognitive control performance and brain activation in healthy adults (Wagner et al., 2013), but this effect may be larger in adolescents because of their biased awareness of self, which is informed largely by peers (Steinberg, 2005). Given their heightened social orientation (Rose and Rudolph, 2006), girls may display an even larger effect than boys, perhaps due to higher executive load precipitated by affective self-relevant statements. Thus, I predicted 1) BOLD response in medial prefrontal cortex and posterior cingulate cortex (i.e. DMN) precipitated by an affective SRP induction would interact with BOLD response in the FPN, specifically dorsolateral prefrontal and inferior parietal cortices, as reflected by increased functional connectivity between these networks during cognitive control trials that followed the affective SRP induction, and 2) this SRP-induced transient, or *state*, functional connectivity between DMN and FPN would be greater in girls compared to boys, indicating a more sustained influence of affective SRP on cognitive control processing. I hypothesized 3) a negative correlation between cognitive control performance in the scanner and DMN-FPN functional connectivity that would be larger in girls, compared to boys. As such, I also predicted that relative to boys, 4) girls would report increased social orientation, as measured by questionnaires of social skills and friendship quality, which would also positively correlate with functional coupling between FPN and DMN.

1.7.2 Specific Aim II

To confirm that the sustained influence of affective SRP on cognitive control is indeed a transient, *state* effect, RSFC of DMN and FPN was examined as a measure of *trait* functional connectivity. Analyses of sex differences in DMN and FPN within- and between-network RSFC were pursued. Correlations with inhibitory control task performance were conducted to measure associations between trait functional connectivity and cognitive control. Under such conditions of rest, I hypothesized 1) minimal between-network functional connectivity between DMN and FPN, as these networks are functionally distinct in the absence of a task (De Luca et al., 2006; Fox et al., 2005; Fransson, 2005; Greicius et al., 2003). However, if present, I predicted higher DMN-FPN trait functional connectivity would be negatively correlated with inhibitory control performance, based on studies showing that higher functional RSFC between DMN and FPN is correlated with poorer cognitive control performance (Hampson et al., 2010; Keller et al., 2015; Kelly et al., 2008). Lastly, based on research reporting a correlation between rumination and within-DMN RSFC in healthy controls (Berman et al., 2011; Luo et al., 2016), as well as a correlation between within-DMN RSFC and empathizing (Takeuchi et al., 2014), I hypothesized that individuals with higher social orientations (i.e. girls) would have stronger within-DMN trait functional connectivity.

1.8 Conclusions

During adolescence, the concept of self evolves in the context of increasingly valued peer influence, which varies by sex. Heightened social orientation can be accompanied by negative consequences, such as self-consciousness, interpersonal stress and maladaptive coping behaviors. Thus, understanding how affective SRP impacts other adaptive neural processes, like cognitive control, and how, in certain instances, aberrations in these functions can develop into psychopathology is particularly relevant during adolescence. Sex differences in adolescent neurodevelopment are common and likely share bidirectional influences with social, SRP and cognitive control functions. Exploring sex differences in the neural correlates of affective SRP and its interactions with cognitive control function during healthy adolescence may provide insight into the sex-specific processes that confer risk for major depression.

CHAPTER 2: MATERIALS AND METHODS

2.1 Participants

A sample of healthy adolescents from the greater Portland Metro Area was recruited through fliers, advertisements and mailings distributed in the community. Many of the youth in this sample were already participating in an ongoing neurodevelopmental study (R01 AA017664). As the primary aims of this dissertation involved the examination of sex differences, matching males and females based on age and pubertal stage was paramount. Only youth between the ages of 15 and 18 years were targeted, as they were more likely to have reached late puberty (Tanner Stages 4 or 5). Youth who had not reached late puberty were excluded from the sample (Tanner Stage ≤ 3). Importantly, any youth who were home-schooled or not enrolled in school were excluded, due to the potential for vast differences in peers groups and socialization. An effort was made to recruit youth from diverse communities to ensure a racially and ethnically representative sample of participants from the Portland Metro Area.

2.2 Procedure

All procedures were approved by the OHSU Institutional Review Board. Following a 15-minute pre-screen telephone conversation with the youth and a parent (conducted separately), initial eligibility was determined. Youth assent and parent consent forms (for minors) were mailed to the families and reviewed over the phone. Youth who were 18 years old signed their own consent forms. A more comprehensive structured telephone interview was scheduled for youth and their parent separately, if they consented to participate. During that interview, the Diagnostic Interview for Children Predictive Scales was administered to youth and parents to exclude for the presence of current psychiatric disorder in youth based on Diagnostic Statistical Manual-IV criteria (Lucas et al., 2001). The Customary Drug Use and Drinking Record was also administered to youth to determine self-reported alcohol and drug use (Brown et al., 1998). Youth who reported ≥ 3 lifetime alcohol binge occasions (defined as ≥ 4 drinks per occasion for females and ≥ 5 drinks per occasion for males), any alcohol binge occasion in the past 6 months, ≥ 20 lifetime uses of marijuana, any marijuana use in the past 6 months, smoking > 4 cigarettes per day, or any other drug use were excluded from the study. Additional exclusionary criteria included DSM-IV Axis I psychotic disorder in either biological parent (e.g. bipolar I or schizophrenia); parent-reported prenatal exposure to alcohol or drugs; serious medical condition(s), including significant head trauma (loss of consciousness ≥ 2 minutes); learning disability; inability of parent to provide family history information; current use of psychotropic medications; premature birth (< 36 weeks); uncorrected vision problems; magnetic resonance imaging (MRI) contraindications (e.g. braces or claustrophobia); left-handedness (Oldfield, 1971); and pregnancy. Youth and parents were compensated $10 each for completing the comprehensive structured interviews.

Once enrolled in the study, youth completed two sessions, a neuropsychological testing session and an MRI session, at Oregon Health & Science University (OHSU). Moreover, these sessions occurred within three months of the youth and parent telephone interviews. In cases where youth were unavailable for visits within the three-month time frame, screening was repeated to confirm eligibility before scheduling sessions. Sessions could be scheduled on the same day or separate days, but within 7 days of each other. In addition, girls' MRI sessions were scheduled during the follicular phase (within 10 days of menstruation onset) of their menstrual cycle to account for variation in cognitive performance and brain response across the menstrual cycle, which has been reported previously (Andreano and Cahill, 2010; Bayer et al., 2013; Diekhof, 2015; Dreher et al., 2007; Ossewaarde et al., 2011; Schoning et al., 2007; Smith et al., 2014a). Youth and parents were compensated $100 and $50, respectively, for completing the neuropsychological and MRI testing sessions.

2.2.1 Neuropsychological Testing Session

A battery of neuropsychological tests and behavioral measures were administered (Cservenka et al., 2012; Cservenka et al., 2015; Herting et al., 2010; Seghete et al., 2013); however, for the purposes of this study, only the following measures will be detailed: the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999), the Children's Depression Inventory (Kovacs, 1985), the Test of Self-Conscious Affect for Adolescents (Tangney, 1989), the Prosocial Tendencies Measure (Carlo, 2003), the Meta-Cognitions Questionnaire for Adolescents (Cartwright-Hatton et al., 2004), the Self-Perception Profile for Adolescents (Harter et al., 1998), and the Co-Rumination Questionnaire (Rose, 2002) (see **2.3 Assessments and Questionnaires**).

2.2.2 MRI Testing Session

At the beginning of the MRI scan session, youth completed the Tanner Sexual Maturation Scale (Taylor et al., 2001) and state anxiety component of the Spielberger State-Trait Anxiety Inventory for Children (Spielberger, 1983). Parents completed the Hollingshead Index of Social Position (Hollingshead, 1975) (see **2.3 Assessments and Questionnaires**). Parents also completed an MRI safety questionnaire on behalf of their child and all questions were reviewed with the youth prior to scanning. Participants older than 18 years old completed their own MRI safety questionnaires. All girls were asked confidentially to confirm there was a very minimal chance of pregnancy at the time of their scan. Prior to scanning, youth practiced the Affective SRP-Flanker task (see **2.4 Affective Self-Referential Processing (SRP)-Flanker Task**) on a laptop computer and were explained the MRI procedure by a trained research assistant and the scan operator (G.A.). In preparation for the scan, youth were provided with earplugs and MRI compatible, sound-attenuating headphones. Participants laid in a supine position on the MRI scan bed, and pillows were placed around their heads to limit head movement. A mirror mounted on the head coil permitted the participants to view the task projected on a screen at the back of the bore. Lastly, youth were provided with a four-button MRI compatible button box to record responses during the task.

At the completion of the scan, participants completed an exit questionnaire to assess whether the task induced any type of distress and to confirm understanding of the task. The questionnaire also assessed participants' motivation and interest in the task (see **Appendix A** for exit questionnaire).

2.3 Assessments and Questionnaires

2.3.1 Wechsler Abbreviated Scale of Intelligence (WASI)

As an estimate of general cognitive ability, the 2-subtest version of the WASI was administered to all youth. The 2-subtest version includes Vocabulary and Matrix Reasoning sections. From these measures, an estimated Full Scale IQ score was calculated for every participant; higher scores indicate greater estimated intellectual ability. IQ was examined in this sample as it has been linked to inhibitory control in adolescents (Yucel et al., 2012).

2.3.2 Tanner's Sexual Maturation Scale (SMS)

An estimate of pubertal development was included in this study, because it is a common confounding variable when studying adolescent sex differences. The Tanner's SMS describes the onset and progression of pubertal changes using a 5-point scale with Stage 1 corresponding to pre-pubertal and Stage 5 corresponding to adult-like sexual maturity. Modified line drawings of Tanner's SMS were used to collect self-reported sexual maturation. Boys rated their pubertal maturation based on their genital development and pubic hair growth, while girls rated their breast development and pubic hair growth. In an attempt to mitigate confounds created by sex differences in pubertal development, only adolescents in Tanner Stages 4 or 5 were included in the study.

2.3.3 Hollingshead Index of Social Position (ISP)

Many studies have reported an association between socioeconomic status (SES) and executive functioning in children and adolescents (Boelema et al., 2014; Bradley and Corwyn, 2002; Farah et al., 2006; Spielberg et al., 2015). As such, this study measured SES using the Hollingshead ISP, a questionnaire administered to a parent to determine education and occupational levels of both parents. Scores range from 1 to 7, with 1 indicating attainment of a professional degree or professional occupation and 7 indicating less than seven years of education or unskilled work. Occupation scores are multiplied by 7 and education scores are multiplied by 4 and the sum of these products indicate the social position of the head of the household, the parent who earns a higher income. Total scores range from 11 to 77, reflecting upper to lower class categories. If a participant does not live with both parents, the head of the household may be defined as 1) the parent who the participant spends most of her time with or 2) the parent with the higher income when time is split equally between two parents.

2.3.4 Children's Depression Inventory (CDI)

Although major depression was an exclusionary criterion for this study, there are a range of sub-threshold depressive symptoms reported by healthy adolescents (Kovacs, 1985; Smucker et al., 1986) that meaningfully predict long-term interpersonal problems (Allen et al., 2014b). Importantly, this study aimed to inform potential mechanisms of sex differences in depression; thus, incorporating a measure of depressive symptoms was critical for this work. The CDI is a 27-item questionnaire that is comprised of five sub-scales: Negative Mood, Negative Self-Esteem, Anhedonia, Ineffectiveness and Interpersonal Problems. Participants marked one of three statements that best described how they felt in the past two weeks, and a trained research assistant assigned a score of 0, 1 or 2 for each item marked. Raw scores on each sub-scale and the raw total score were converted to T-scores. T-scores ranging from 45 – 55 are considered average, while T-scores exceeding 65 represent clinically relevant elevations in depressive symptoms (much above average (66 – 70) or very much above average (>70)).

2.3.5 Spielberger State-Trait Anxiety Inventory (STAI) for Children

Youth completed the state anxiety scale of the STAI to assess situational anxiety prior to MRI scanning. This questionnaire was administered to estimate anxiety prior to scanning, as well as to examine sex differences in state anxiety, which tend to co-occur with depressive symptoms. The state anxiety scale of the STAI contains 20 items that ask youth how they feel in that particular moment. Items emphasize subjective, consciously perceived feelings of apprehension, tension and worry. Responses were made on a 4-point scale, with 1 corresponding to ‘Not at all’ and 4 corresponding to ‘Very much so’. Raw scores were converted to T-scores and range from 20 to 80, with higher scores indicating higher state anxiety.

2.3.6 Test of Self-Conscious Affect for Adolescents (TOSCA-A)

The TOSCA-A is a self-report measure that contains 10 negative and 5 positive scenarios yielding indices of Shame-proneness, Guilt-proneness, Externalization (of cause of blame), Detachment/Unconcern, Alpha Pride (pride in the entire self) and Beta Pride (pride stemming from evaluation of a specific behavior). Shame-proneness and Guilt-proneness are both negative self-conscious emotions that are generally positively correlated with each other. Shame is considered a counterproductive emotion, as it emphasizes global and stable unworthiness of the self, which tends to foster avoidance behavior. On the other hand, guilt is considered a more productive emotion, as it focuses on the wrongness of a particular, controllable action, thus promoting reparative behaviors (Lewis, 1971; Tangney et al., 1992). Shame-proneness has been shown to be positively related to Externalization and also negatively associated with Alpha Pride, while Guilt-proneness and Beta Pride are negatively associated (Tangney et al., 1992). For each scenario in the measure, participants rated whether a series of reactions corresponding to an index of the measure described how they would feel on a visual analog scale (ranging from ‘Not at all likely’ to ‘Very likely’). The Shame-proneness sub-scale is negatively related to interpersonal functioning, while the Guilt-proneness sub-scale relates to other-oriented empathy (Tangney et al., 1995). Thus, these particular variables provide information about participants’ social orientations and self-consciousness levels.

2.3.7 Prosocial Tendencies Measure (PTM)

The PTM was used as a measure of prosocial behavior. Participants were instructed to rate how much 23 different statements described them on 5-point scale, where 1 corresponded to ‘Does not describe me at all’ and 5 corresponded to ‘Describes me greatly’. In addition to a global prosocial behavior score, the PTM provides sub-scores on Altruistic, Compliant, Emotional, Dire, Anonymous, and Public prosocial behaviors. Females generally score higher on measures of Altruistic, Anonymous, Compliant and Emotional prosocial behaviors, indicating that internalized, empathic motives likely promote prosocial actions. In contrast, males tend to rate higher on Public prosocial behaviors, suggesting that they are more likely to engage in prosocial action when an audience is present (Carlo, 2003).

2.3.8 Meta-Cognitions Questionnaire for Adolescents (MCQ-A)

Meta-cognition refers to the processes involved in control, modification and interpretation of thinking itself (Wells and Cartwright-Hatton, 2004) and it is involved in the development and maintenance of psychological disorders, including depression (Callesen et al., 2014; Papageorgiou and Wells, 2001; Wells et al., 2012; Yilmaz et al., 2011). Research shows that patients with depression hold both negative (e.g. ‘When I start worrying I cannot stop’) and positive (e.g. ‘Worrying helps me cope’) metacognitive beliefs about rumination (Papageorgiou and Wells, 2001), indicating that rumination is not only symptomatic of depression, but may also function as a coping strategy. The MCQ-A is a 30-item instrument comprised of 5 scales: Cognitive Confidence, Positive Beliefs, Cognitive Self-Consciousness, Uncontrollability and Danger, and Need to

Control Thoughts. Youth indicated how much they agreed with every statement on a scale of 1 (‘Do not agree’) to 4 (‘Agree very much’).

2.3.9 Self-Perception Profile for Adolescents (SPP-A)

The Social Competence, Close Friendships and Global Self-Worth domains of the SPP-A were used to asses social success and self-esteem. This measure employs a structured alternative format (Harter, 1982), which involves the participant deciding what type of teenager he/she is using a two-choice response format (e.g. Like Me – Unlike Me), then specifying the *degree* to which a statement describes him/her (i.e. ‘Really True for me’ or ‘Sort of True for me’). This format legitimizes either choice (‘type’ of adolescent) - discouraging responses based on social desirability - and broadens the range of choices over the typical two-choice format. Every subscale contains 5 questions scored from 1 to 4, with higher values indicating most adequate self-judgment.

2.3.10 Co-Rumination Questionnaire (CRQ)

The CRQ was created to explain the discrepancy in risk for MDD in girls compared to boys, despite girls reporting closer friendships, which generally protect against emotional difficulties. Co-rumination is both social (unlike rumination) and maladaptive (unlike self-disclosure) due to the negative focus of conversation between same-sex friends. The CRQ is comprised of 27 items in 9 content areas: 1) frequency of discussing problems, 2) discussing problems instead of engaging in other activities, 3) encouragement by the focal child of the friend’s discussing problems, 4) encouragement by the friend of the focal child’s discussing problems, 5) discussing the same problem repeatedly, 6) speculation about the causes of problems, 7) speculation about consequences of problems, 8) speculation about parts of the problem that are not understood, and 9) focusing on negative feelings. Items were rated on a 5-point scale based on the degree to which the item described the participants, with 1 corresponding to ‘Not at all true’ and 5 corresponding to ‘Really true.’ The mean of all 27 items represented the co-rumination score.

2.4 Affective Self-Referential Processing (SRP)-Flanker Task

The Affective SRP-Flanker task was developed with a mixed block/event-related design and combines elements of a previously published self-referential task (Jankowski et al., 2014) and a version of the Eriksen flanker task (Eriksen and Eriksen, 1974) that utilizes arrows (Bunge et al., 2002; Casey et al., 2000; Fan et al., 2002; Kelly et al., 2008). Two types of blocks were presented that either consisted of 1) SRP trials immediately followed by Flanker trials or 2) Control trials immediately followed by Flanker trials. Blocks contained six SRP or Control trials (4 s each), which were immediately followed by presentation of five Flanker trials (0.8 s each; Figure 1). Blocks (4 SRP and 4 Control) were presented for approximately 38 s and separated by 12 s of fixation. Presentation of SRP and Control blocks alternated and half of the participants were randomly assigned a version of the task where SRP blocks were presented first, while the remaining participants completed a version of the task where Control blocks were presented first. The onset of SRP, Control and Flanker trials was preceded by a 2 s cue: ‘DOES THIS DESCRIBE YOU?’, ‘CAN THIS CHANGE?’, and ‘CENTER ARROW,’ respectively. The task was presented with E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) and responses were recorded for all trials. Prior to scanning, youth were provided with a brief demonstration of the task and allowed to practice.

SRP and Control blocks contained the same stimuli, but participants were instructed to respond differently based on the condition. Participants viewed positively- and negatively-valenced trait phrases representing academic, physical and social domains (see **Appendix B** for list of phrases). During SRP trials, participants were instructed to respond based on whether a given phrase described them (yes or no response option). In contrast, in the Control trials, participants were instructed to make evaluations based on the malleability of the same traits with respect to people in general (yes or no response option; see **Appendix C** for task instructions). Stimuli were presented in a randomized order, regardless of valence and domain, and each stimulus was presented once per condition. In the scanner, participants were presented with a stimulus in the center of the screen for 1.5 s then the words 'YES' and 'NO' were presented below the stimulus phrase for 2.5 s during which participants made a button-box response based on the task condition. 'YES' was always presented in the bottom left corner of the screen and 'NO' was always presented in the bottom right corner of the screen. Presentation of SRP and Control trials was jittered (mean = 2.5 s); participants viewed a fixation cross at the center of the screen in between trials.

During Flanker trials, participants viewed a row of 5 arrows pointing right or left. The four flanking arrows all pointed the same direction; however, the center arrow pointed in a congruent direction (40%) or incongruent direction (60%). Flanker trials were jittered (mean = 2.5 s) with fixation presented between trials. Congruent and incongruent trials were presented pseudo-randomly within blocks. Participants were instructed to make a button-box response to indicate whether the center arrow was pointing left or right, regardless of where the other arrows were pointing (see **Appendix**

B for task instructions). They were asked to respond as quickly and as accurately as possible during the 0.8 s display of the arrows. Flanker trials were presented rapidly in order to increase attentional demands and decrease the likelihood of self-referential thoughts during these trials.

2.5 Image Data Acquisition

Imaging data were acquired on a 3T Siemens Magnetom Tim Trio system (Siemens Medical Solutions, Erlangen, Germany) using a twelve-channel head coil. Data were collected in the axial plane oblique to the anterior-posterior commissure using a high-angular resolution T2*-weighted echo-planar BOLD sequence. During the Affective SRP-Flanker Task, functional images were collected in one run using the following parameters: TR = 2000 ms, TE = 30 ms, matrix = 240 x 176, FOV = 256 mm, flip angle = 90°, 33 contiguous slices, resolution = 3.8 mm^3, 282 repetitions, 9:30 min. During rest, functional images were collected in two runs with the following parameters: TR = 2500 ms, TE = 30 ms, matrix = 240 x 176, FOV = 256 mm, flip angle = 90°, 36 contiguous slices, resolution = 3.75 x 3.75 x 3.8 mm, 124 repetitions, 5:17 min/run. Participants were instructed to stay still and fixate on a white cross in the center of a black screen while thinking about nothing in particular; youth confirmed wakefulness once they completed the scan. A whole-brain, high-resolution T1-weighted MPRAGE scanning sequence was collected in the sagittal plane (TR = 2300 ms, TE = 3.58 ms, TI = 900 ms, matrix = 240 x 126, FOV = 240 mm, flip angle = 10°, 160 contiguous slices, resolution 1 x 1 x 1.1 mm, 176 repetitions, 9:14 min) for co-registration to functional data. Resting state scans were always completed before the Affective SRP-Flanker Task scan.

2.6 Specific Aim I

2.6.1 Image Preprocessing and Single-Subject Analysis

Data were preprocessed using in-house software that implements 4dfp tools developed at Washington University and have been previously published (Alarcon et al., 2015; Fair et al., 2012). Functional data preprocessing steps included slice-time correction, image debanding, volume registration, including a 6-parameter rigid body motion alignment and re-alignment, normalization to a mode value of 1000, co-registration to the anatomical file, transformation to Talairach standard space and resampling to a 3 mm^3 resolution. The first four frames of functional data were excluded to allow BOLD signal to reach steady-state, and the remaining data were modeled in participant native space. A general linear model (GLM) using a mixed block/event-related design was implemented to analyze the functional task data. SRP and Control blocks were modeled with boxcar functions, while SRP, Control and Flanker events were modeled without an assumed response shape. Flanker congruent and incongruent trials were modeled separately, as were errors trials, task instruction trials and start cues for SRP and Control blocks.

2.6.2 Task-Regression and Additional Image Processing

A growing number of studies suggest that baseline or spontaneous neural activity continues during tasks and that task-related activation represents a combination of spontaneous activity and responses to task stimuli (Arfanakis et al., 2000; Fair et al., 2007; Fox et al., 2006; Gavrilescu et al., 2008; Kucukboyaci et al., 2013; Zhang and Li, 2010; Zhang and Li, 2012c). Thus, by regressing task signal from a time course, the spontaneous activity remains. However, the resulting functional connectivity patterns of task-regressed and resting state time courses are not identical, which may reflect “contamination” of task-regressed signal by task processes (Arfanakis et al., 2000), or nonlinear effects of a task that are not removed with linear regression (Fair et al., 2007). Alternatively, it is possible that task engagement acutely alters functional connectivity (Fair et al., 2007; Fransson, 2006; Hampson et al., 2004; Lowe et al., 2000), which is what will be measured in the current study. Residual files were created from the GLM by removing all modeled effects, including linear trends and the baseline. Residual files underwent additional processing, including image detrending, multiple regression of whole-brain signal, white matter signal, cerebrospinal fluid signal and their derivatives, as well 24 motion-related regressors ($R\ R^2\ R_{t-1}R_{t-1}^2$, where R = [X, Y, Z pitch yaw roll], t = current timepoint and t – 1 = preceding timepoint) (Friston et al., 1996), and band-pass filtering (0.009 to 0.08 Hz) (Alarcon et al., 2015).

2.6.3 Defining Task-Regressed Time Courses

Two vectors each representing frames of data during Post-SRP Flanker and Post-Control Flanker trials were created per subject. A different, motion censoring vector representing usable frames of data, based on a strict motion criterion of frame-to-frame displacement (FD), were also created per subject. The FD method indexes head movement relative to adjacent volumes and is based on the following scalar formula: $FD_i = |\Delta dix| + |\Delta diy| + |\Delta diz| + |\Delta\alpha i| + |\Delta\beta i| + |\Delta\gamma i|)$, where $\Delta dix = d(i - 1)x – dix$ (Power et al., 2012). Frames were excluded from analysis if they exceeded a threshold of 0.5 mm, and uncensored segments of data with fewer than 5 contiguous frames were subsequently censored as well. This threshold was determined based on research showing that motion scrubbing thresholds for task fMRI data are most effective within the range 0.5 – 1.1 mm

(Siegel et al., 2014); to err on the conservative side, a 0.5 mm threshold was selected. The motion censoring vector was multiplied by the Post-SRP Flanker vector and the Post-Control Flanker vector. The product of these vectors included 1) frames of data with minimal motion from Post-SRP Flanker trials and 2) frames of data with minimal motion from Post-Control Flanker trials. An FD remaining mean variable was calculated for every individual, representing the degree of micro-movement (in the range of millimeters) of this remaining motion-censored data.

2.6.4 Selecting Regions of Interest (ROIs)

Bilateral dorsolateral prefrontal and inferior parietal cortices are key nodes of the fronto-parietal network (Cole and Schneider, 2007), while medial prefrontal and posterior cingulate cortices represent hubs of the default mode (and SRP) network. A list of potential coordinates was created using a functionally-defined set of ROIs based on several meta-analyses of task fMRI data and functional connectivity mapping (Cohen et al., 2008; Power et al., 2012; Power et al., 2010). ROIs are modeled as 10 mm diameter spheres centered upon ROI coordinates (Power et al., 2011). FPN and DMN coordinates that most closely matched those reported in FPN (Cole and Schneider, 2007) and DMN in the context of self-referential processing (Northoff et al., 2006) were selected and their functional associations were confirmed on neurosynth.org. Refer to Table 1 for final selection of seed regions.

2.6.5 Creating Functional Connectivity Maps

Time courses from every seed region per condition (Post-SRP Flanker and Post-Control Flanker) were extracted and correlated with every voxel in the brain, generating correlation coefficients that underwent a Fischer’s z transformation to improve data normality. Limiting the time series by task condition (Post-SRP Flanker and Post-Control Flanker) greatly reduced the number of usable frames for functional connectivity analysis; thus, prior to starting group analyses, the number of remaining frames per condition and per subject was determined, and the quality of functional connectivity maps was assessed via visual inspection. Image processing details can be seen in Figure 2.

2.6.6 Data Analysis

2.6.6.1 Participant Characterization

Sex differences in demographic variables were examined with independent samples *t*-tests, with the exception of Tanner Stage, which was determined with a Chi-square analysis. Sex differences in FD remaining mean were assessed with an independent samples *t*-test and correlations between FD remaining mean and age were determined with Pearson's correlation. Reaction time (RT), errors of omission and accuracy on Flanker trials were analyzed with repeated measures analysis of variance (ANOVA). Due to a priori hypotheses about sex differences in Flanker performance, post-hoc sex differences were examined in the case of statistically significant main effects of sex, as well as interactions between sex and task condition. Correlations between personality measures, Flanker performance (RT, accuracy and omission errors) and significant functional connectivity findings were conducted with Spearman correlations. To reduce the number of correlations and the likelihood of Type II error, only significant functional connectivity findings from Post-SRP Flanker conditions and Flanker performance from Incongruent Flanker trials were analyzed. In addition, multiple comparisons correction was employed using the Benjamini-Hochberg procedure (Benjamini and Hochberg, 1995).

All statistical analyses were carried out with IBM SPSS Statistics 20 (Armonk, NY: IBM Corp) and bar graphs and plots were created with GraphPad Prism version 7 for Windows (GraphPad Software, La Jolla, California, USA, www.graphpad.com).

2.6.6.2 Task-Regressed Functional Connectivity Analysis

Task-regressed functional connectivity group analyses were conducted with Analysis of Functional NeuroImages (Cox, 1996) using a 2 x 2 ANOVA (within-group: Post-SRP Flanker and Post-Control Flanker functional connectivity maps; between-group: girls and boys). Congruent and Incongruent trials of the Flanker task were collapsed to preserve detection power. A voxel-wise threshold of $p < 0.01$ and a cluster-wise threshold of $p < 0.05$ was implemented using Monte Carlo simulation (minimum cluster size ≥ 46 voxels), bringing the voxel-wise threshold to $p < 0.0004$, corrected. Average Z values from significant clusters were extracted and plotted for visualization. Given that group differences in functional connectivity may be due to differences in positive connectivity, negative connectivity, or a combination of both, one-sample *t*-tests were conducted for every seed region and each condition and sex for aid in interpretation of sex differences results.

2.7 Specific Aim II

2.7.1 Image Preprocessing and Single-Subject Analysis

The initial resting state data preprocessing steps were identical to those of the task activation data (see *2.6.1 Image Preprocessing and Single-Subject Analysis)*: slice-time correction, image debanding, volume registration, normalization to a mode value of 1000, anatomical co-registration, Talairach standardization and resampling to a 3 mm^3 resolution. Subsequent image processing was conducted on concatenated resting state runs and included image detrending, multiple regression, including whole-brain signal, white matter signal, cerebrospinal fluid signal and their derivatives, as well 24 motion-related regressors ($R\ R^2\ R_{t-1}R_{t-1}{}^2$, where R=[X Y Z pitch yaw roll], t=current time point and t-1=preceding time point) (Friston et al., 1996), and lastly, band-pass filtering (0.009 to 0.08 Hz). Frames of data were excluded from analysis if they exceeded an FD threshold of 0.3 mm, as previously published (Alarcon et al., 2015; Costa Dias et al., 2015; Graham et al., 2016; Graham et al., 2015) and uncensored segments of data with fewer than 5 contiguous frames were subsequently censored as well. An FD remaining mean variable was calculated for every individual. Motion-scrubbed time courses from every seed region were correlated with every voxel in the brain, generating functional connectivity maps, comprised of correlation coefficients that underwent a Fischer's z transformation to improve data normality. Image processing details can be seen in Figure 2.

2.7.2 Resting State Functional Connectivity (RSFC) Analysis

In order to determine whether task-regressed functional connectivity results were indeed *state* effects and did not reflect *trait* functional connectivity patterns that differentiated male and female adolescents, RSFC analyses were first restricted to regions where significant effects were found in the task-regressed functional connectivity analyses (see *2.6.6.2 Task-Regressed Functional Connectivity Analysis)*. To accomplish this, RSFC maps were masked with ROIs created from task-regressed functional connectivity results; activity of DMN and FPN seed regions was then correlated with voxels restricted to these ROIs. Independent samples *t*-tests compared RSFC of males and females. A voxel-wise threshold of $p < 0.05$ and a cluster-wise threshold of $p < 0.05$ was implemented using Monte Carlo simulation (minimum cluster size ≥ 5), bringing the voxel-wise threshold to $p < 0.005$, corrected. Average Z values from significant clusters were extracted and plotted for visualization. Next, whole-brain, voxel-wise analyses with FPN and DMN seed regions were conducted to examine other potential *trait* functional connectivity patterns that differentiated male and female adolescents using independent samples *t*-tests. A voxel-wise threshold of $p < 0.05$ and a cluster-wise threshold of $p < 0.05$ was implemented using Monte Carlo simulation (minimum cluster size ≥ 81), bringing the voxel-wise threshold to $p < 0.00007$, corrected. Average Z values from significant clusters were extracted and plotted for visualization. Finally, one-sample *t*-tests of whole-brain, voxel-wise functional connectivity of DMN and FPN seed regions were conducted for males and females separately to interpret group differences.

2.7.3 State versus Trait Functional Connectivity

State and trait functional connectivity were directly compared to determine if sex differences in state functional connectivity (determined in 2.6.6.2 Task-Regressed Functional Connectivity Analysis) were statistically different from sex differences in trait functional connectivity (determined in *2.7.2 Resting State Functional Connectivity (RSFC) Analysis*). ROIs were functionally defined using masks of clusters that indicated 1) significant main effects of sex or interactions between sex and task condition from the task-regressed functional connectivity analyses and 2) significant sex differences from the resting state functional connectivity analyses. Two-way ANOVAs were conducted with sex as the between-subject factor (girls versus boys) and functional connectivity type as the within subject factor: Task (SRP-Control) versus Rest. For each ANOVA, a voxel-wise threshold of $p < 0.05$ and a cluster-wise threshold of $p < 0.05$ was implemented using Monte Carlo simulation (minimum cluster size ≥ 7), bringing the voxel-wise threshold to $p < 0.009$, corrected. To correct for the number of analyses, a Benjamini-Hochberg correction will be utilized. Average Z values from significant clusters were extracted and plotted for visualization.

2.8 Analytic Strategy

As detailed in **1.6 Dissertation Aims and Hypotheses**, the first aim of this dissertation was to measure sex differences in state functional connectivity of default mode and fronto-parietal networks, as well as performance during an inhibitory control task that followed an affective SRP induction. Armed with the knowledge that adolescent girls in this sample rated themselves higher on co-rumination compared to boys, further analysis of sex differences in cognitive control function was warranted. The results of this analysis will be detailed in Chapter 3. To compare to the results of Aim I, trait RSFC of the same networks and correlations with inhibitory control performance were investigated in Aim II and also detailed in Chapter 3.

Table 1. Functional Connectivity Analysis Seed Regions

	Talairach Coordinates (X, Y, Z)
Dorsolateral Prefrontal Cortex	
Left	-41, 33, 24
Right	37, 13, 42
Inferior Parietal Lobule	
Left	-41, -56, 41
Right	41, -55, 45
Medial Prefrontal Cortex	
Left	-8, 42, 27
Right	8, 48, 9
Posterior Cingulate Cortex	
Left	-11, -57, 14
Right	7, -50, 29

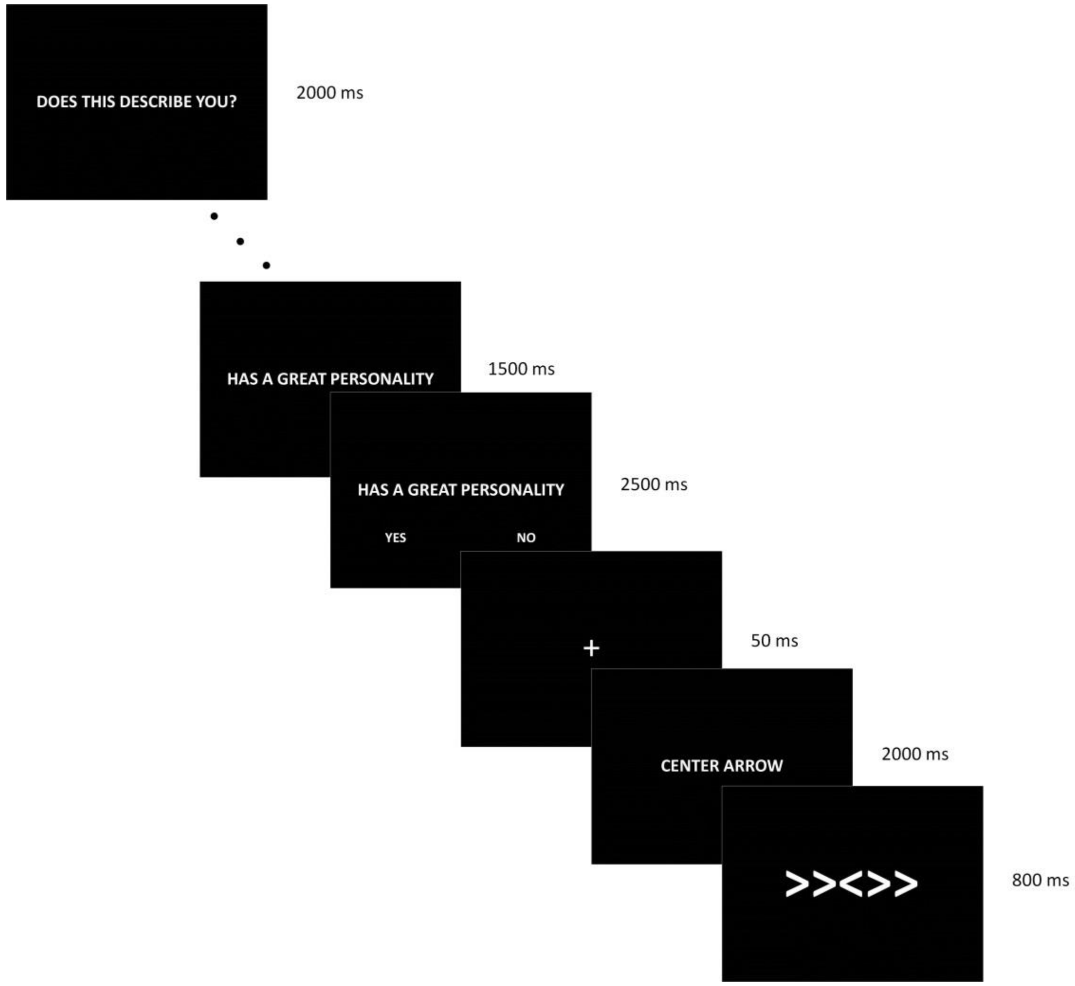

Figure 1. Example of an SRP Block Condition. Following a 2 s cue, six jittered SRP trials were presented. Immediately after the last SRP trial, another 2 s cue indicated the beginning of five jittered Flanker trials. The last SRP and first Flanker trials are depicted here.

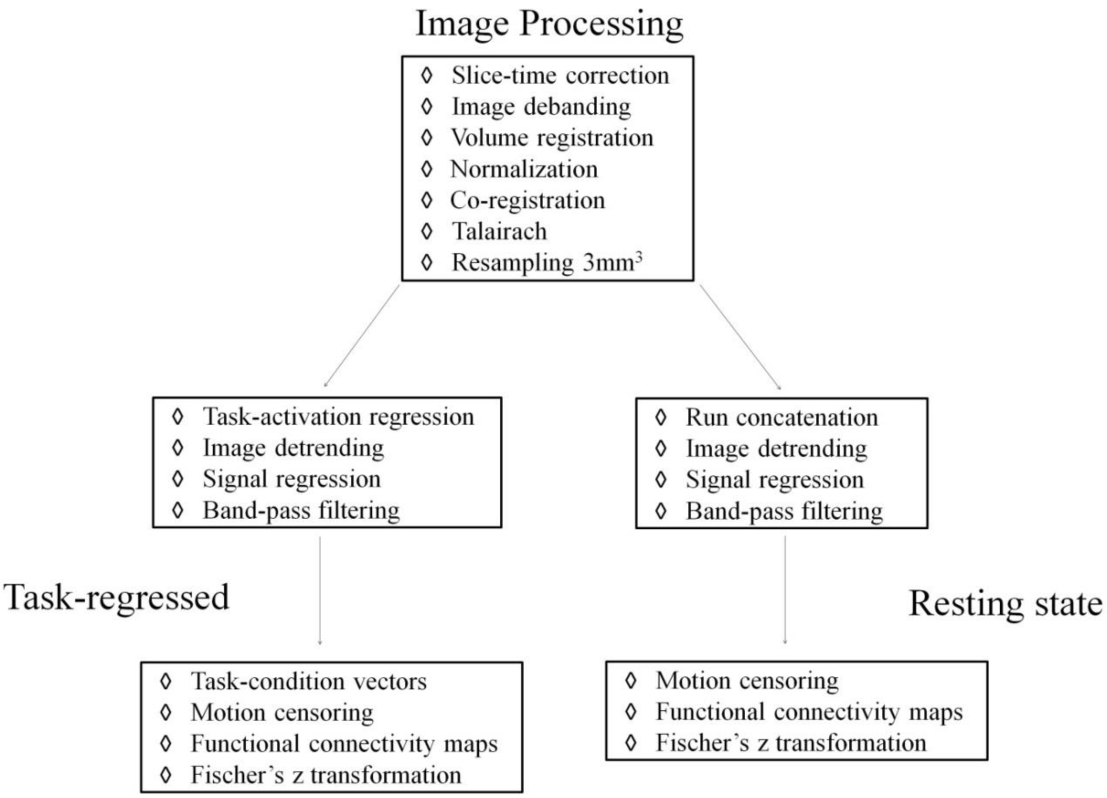

Figure 2. Flow chart of task-regressed and resting state functional connectivity processing steps.

CHAPTER 3: RESULTS

3.1 Full-Sample Participant Characterization and Task Performance

Demographic data were collected on 49 adolescents (girls = 25). Girls and boys were matched on age, pubertal stage, IQ, SES and racial distribution. All participants were within the age range of 15 and 18 years and in Tanner stages 4 or 5 (Table 1). Participants in Tanner Stage 5 were statistically older than youth in Tanner Stage 4 (t_{47} = -2.34, *p* = 0.02). The majority of youth fell within normal ranges of depressive and state anxiety symptoms; however, two girls and 1 boy had slightly above average CDI Total T-Scores (57 – 62) and 1 girl had a very much above average T-Score (71). Girls and boys were statistically matched on depressive and state anxiety symptoms (Table 2). Responding on the PTM, MCQ-A, and SPP-A was statistically similar between boys and girls; however, girls reported higher scores on the CRQ and Alpha Pride sub-scale of the TOSCA-A compared to boys (Table 3). Age was negatively correlated with the PTM mean score (ρ = -0.34, *p* = 0.02). When examined by sex, this correlation was significant for girls (ρ = -0.43, *p* = 0.03), but not boys (ρ = -0.16, *p* = 0.45). SPP-A Global Self-Worth was significantly lower for youth in Tanner Stage 5 versus Stage 4 (U = 125.00, *p* = 0.02). When examined by sex, this effect was significant in girls (U = 22.00, *p* = 0.01), but not boys (U = 36.00, *p* = 0.45).

Behavioral data from SRP and Control trials were missing from one (female) individual due to a technical problem. For SRP trials, there was a significant main effect of domain (*F*(3.77, 173.51) = 24.03, *p* < 0.001, Greenhouse-Geisser correction), but no significant main effect of sex (*F*(1, 46) = 0.37, *p* = 0.36) or interaction of domain and sex (*F*(3.77, 173.51) = 1.48, *p* = 0.21, Greenhouse-Geisser correction). Post-hoc analysis of simple effects indicated that youth believed Positive Academic traits described them more than Negative Academic, Negative Social, Positive Physical and Negative Physical traits (all $p < 0.05$, Tukey's), but not Positive Social traits ($p > 0.05$, Tukey's). Further, youth agreed that Positive Social traits described them more than Negative Academic, Negative Social and Negative Physical traits (all $p < 0.05$, Tukey's), but not Positive Physical ($p > 0.05$, Tukey's). Finally, Positive Physical traits were endorsed more than Negative Academic, Negative Social and Negative Physical (all $p < 0.05$, Tukey's) traits. Thus, overall youth agreed that positive traits described them more than negative traits.

Similarly, a repeated measures ANOVA indicated a main effect of domain in the Control condition ($F(5, 230) = 14.38$, $p < 0.001$). A main effect of sex ($F(1, 46) = 0.01$, $p = 0.91$) and the interaction of domain and sex ($F(5, 230) = 1.26$, $p = 0.28$) were not statistically significant. Post-hoc comparisons showed that the main effect of domain was driven by an overall difference in Positive Academic traits, such that youth believed Positive Academic traits were the least malleable, compared to all other traits (all $p < 0.05$, Tukey's).

Reaction time (RT) on the Flanker trials was examined with repeated measures ANOVA, and results indicated a significant main effect of trial type ($F(3, 141) = 55.60$, $p < 0.001$), as well as a significant main effect of sex ($F(1, 47) = 4.41$, $p = 0.04$). However, the interaction between trial type and sex was not statistically significant ($F(3, 141) = 0.22$, $p = 0.88$). Post-hoc analysis indicated that participants were slower to respond during Post-SRP and Post-Control Incongruent Flanker trials compared to both Post-SRP and Post-Control Congruent Flanker trials (all $p < 0.05$, Tukey's). Post-SRP and Post-Control Congruent Flanker trials did not differ based on RT ($p > 0.05$, Tukey's), nor did

Post-SRP and Post-Control Incongruent Flanker trials ($p > 0.05$, Tukey's). Post-hoc sex comparisons were not significantly different (all $p > 0.05$, Sidak); however, girls were slower to respond overall (Figure 1).

Accuracy significantly differed based on trial type ($F(2.06, 96.68) = 9.33$, $p < 0.001$, Greenhouse-Geisser correction); however the main effect of sex ($F(1, 47) = 0.91$, $p = 0.35$) and interaction between trial type and sex ($F(2.06, 96.68) = 0.58$, $p = 0.57$, Greenhouse-Geisser correction) were not statistically significant. The effect of trial type was such that more errors were committed during Post-Control Incongruent compared to Post-SRP ($p < 0.05$, Tukey's) and Post-Control ($p < 0.05$, Tukey's) Congruent Flanker trials. Accuracy did not differ between Post-SRP Incongruent and Post-SRP or Post-Control Congruent Flanker trials (all $p > 0.05$, Tukey's). Post-SRP and Post-Control Congruent Flanker accuracy did not differ, nor did Post-SRP and Post-Control Incongruent Flanker accuracy (all $p > 0.05$, Tukey's) (Figure 1).

A statistically significant main effect of trial type was observed for errors of omission ($F(3, 141) = 6.56$, $p = 0.001$), as was a main effect of sex ($F(1, 47) = 7.10$, $p = 0.01$). The interaction between trial type and sex was not statistically significant ($F(3, 141) = 1.00$, $p = 0.39$). More errors of omission were committed during Post-SRP Incongruent relative Post-SRP Congruent ($p < 0.05$, Tukey's) and Post-Control Congruent ($p < 0.05$, Tukey's) Flanker trials. Errors of omission differed between Post-Control Incongruent and Post-SRP ($p < 0.05$, Tukey's) and Post-Control ($p < 0.05$, Tukey's) Congruent Flanker trials. Post-SRP and Post-Control Congruent Flanker trials did not differ in terms of errors of omission ($p < 0.05$, Tukey's), nor did Post-SRP and Post-Control Incongruent Flanker trials ($p < 0.05$, Tukey's). The post-hoc analysis of sex indicated that girls made more errors of omission during Post-SRP Incongruent Flanker trials than boys ($p < 0.05$, Sidak) (Figure 1).

To follow up with the significant sex difference in Post-SRP Incongruent Flanker errors of omission, a mediation analysis was conducted to test whether co-rumination explained this effect. Mediation was performed with the PROCESS macro (Hayes, 2013) in SPSS with sex as the independent measure, errors of omission as the dependent measure and co-rumination as a mediator. Bias corrected bootstrapped 95% confidence intervals were determined with 1000 bootstrapped samples. The direct effect of sex on errors of omission became statistically insignificant once co-rumination was included in the model, indicating that co-rumination fully mediated the effect of sex on errors of omission during Post-SRP Incongruent Flanker trials (Figure 2).

Responding on the exit questionnaire indicated that boys and girls identified with the statements in the task to a similar degree (U = 295.00, $p = 0.92$). The sexes did not differ on how the task made them feel (U = 273.00, $p = 0.57$), level of interest in the task (U = 242.60, $p = 0.19$) or how important it was to do well on the task (U = 287.50, $p = 0.78$).

3.2 Specific Aim I

Based on the strict motion censoring criteria employed in the current study, 9 of 49 participants had zero frames of data and could not be included in imaging analyses; subsequent results will be based on data from the remaining 40 individuals (20 girls). The number of frames of data used in the imaging analysis were not statistically different by sex for either the SRP ($t_{38} = 0.82$, $p = 0.42$) or Control ($t_{38} = 0.80$, $p = 0.43$) conditions.

On average, the same number of frames were analyzed in SRP versus Control conditions per subject ($t_{39} = 0.04$, $p = 0.97$). Boys and girls did not differ statistically on mean FD of the remaining frames for SRP ($t_{38} = 0.52$, $p = 0.61$) or Control ($t_{38} = 1.66$, $p = 0.11$) conditions. Age was negatively correlated with FD remaining mean of the Control condition ($r^2 = -0.37$, $p = 0.02$), but not the SRP condition ($r^2 = -0.23$, $p = 0.16$).

3.2.1 Participant Characterization

Boys and girls did not differ statistically based on age, pubertal stage, IQ, SES or race distribution (Table 4). CDI Total T-Score and subscale T-Scores were not statistically different by sex; however, girls reported more state anxiety than boys at a statistical trend level (Table 5). Male and female responses on the MCQ-A, PTM, TOSCA-A and SPP-A were statistically similar; however, girls reported higher CRQ mean scores (Table 6). Similar to the full sample, age was negatively correlated with the PTM mean score ($\rho = -0.34$, $p = 0.03$). When examined by sex, this correlation was not significant in girls ($\rho = -0.32$, $p = 0.17$) or boys ($\rho = -0.34$, $p = 0.14$). SPP-A Global Self-Worth was significant lower for youth in Tanner Stage 5 versus Stage 4 ($U = 61.00$, $p = 0.01$). When examined by sex, this effect was observed in girls ($U = 4.00$, $p = 0.002$), but not boys ($U = 23.00$, $p = 0.44$). Thus, the only differences from the full sample were the lack of sex difference in TOSCA-A Alpha Pride scores and the nonsignificant correlation between PTM and age in girls when examined separately from boys.

3.2.2 Behavioral Responding during SRP and Control Trials

Behavioral responding during SRP trials was nearly identical to the full sample, with a significant main effect of domain ($F(3.78, 140.00) = 20.53$, $p < 0.001$, Greenhouse-Geisser correction), but no significant main effect of sex ($F(1, 37) = 0.58$, p

= 0.45) or interaction of domain and sex (*F*(3.78, 140.00) = 0.68, *p* = 0.60, Greenhouse-Geisser correction). Post-hoc analysis of simple effects indicated that youth believed Positive Academic traits described them more than Negative Academic, Negative Social, Positive Physical and Negative Physical traits (all $p < 0.05$, Tukey's), but not Positive Social traits ($p > 0.05$, Tukey's). Further, youth agreed that Positive Social traits described them more than Negative Academic, Negative Social and Negative Physical traits (all $p < 0.05$, Tukey's), but not Positive Physical traits ($p > 0.05$, Tukey's). Lastly, Positive Physical traits were endorsed more than Negative Academic and Negative Physical traits (all $p < 0.05$, Tukey's).

Similar to the full sample, a repeated measures ANOVA indicated a main effect of domain in the Control condition (*F*(5, 185) = 11.56, $p < 0.001$), while the main effect of sex (*F*(1, 37) = 0.10, *p* = 0.76) and the interaction of domain and sex (*F*(5, 185) = 0.84, *p* = 0.53) were not statistically significant. Post-hoc comparisons showed that the main effect of domain was driven by an overall difference in Positive Academic traits, such that youth believed Positive Academic traits were the least malleable, compared to all other traits (all $p < 0.05$, Tukey's).

3.2.3 Behavioral Responding during Flanker Trials

3.2.3.1 Reaction Time

Reaction time (RT) on the Flanker trials was examined with repeated measures ANOVA, and results indicated a significant main effect of trial type (*F*(2.31, 87.81) = 49.33, $p < 0.001$, Greenhouse-Geisser correction), as well as a significant main effect of sex (*F*(1, 38) = 4.20, $p < 0.05$). However, the interaction between trial type and sex was not statistically significant (*F*(2.31, 87.81) = 0.52, $p = 0.62$, Greenhouse-Geisser correction). Post-hoc analysis showed that youth responded more slowly during Post-SRP Incongruent Flanker trials than Post-SRP and Post-Control Congruent Flanker trials (all $p < 0.05$, Tukey's). Post-Control Incongruent Flanker trial responding was slower than responding during Post-SRP and Post-Control Congruent Flanker trials (all $p < 0.05$, Tukey's). However, RT did not differ between Post-SRP and Post-Control Congruent Flanker trials ($p > 0.05$, Tukey's) nor Post-SRP and Post-Control Incongruent Flanker trials ($p > 0.05$, Tukey's). Post-hoc sex comparisons were not significantly different (all $p > 0.05$, Sidak); however, girls were slower to respond overall. RT during Flanker trials was nearly identical to what was reported in the full sample. RT during Post-SRP and Post-Control Incongruent Flanker trials was not significantly correlated with CRQ mean scores across the sample or by sex (all $\rho > 0.05$, corrected).

3.2.3.2 Accuracy

Accuracy significantly differed based on trial type (*F*(2.03, 77.18) = 4.88, $p = 0.01$, Greenhouse-Geisser correction); however the main effect of sex (*F*(1, 38) = 0.52, $p = 0.48$) and interaction between trial type and sex (*F*(2.31, 87.81) = 1.42, $p = 0.25$, Greenhouse-Geisser correction) were not statistically significant. The effect of trial type was such that more errors were committed during Post-Control Incongruent compared to Post-SRP Congruent Flanker trials ($p < 0.05$, Tukey's). However, accuracy did not differ between 1) Post-SRP and Post-Control Incongruent, 2) Post-SRP and Post-Control Congruent, 3) Post-SRP Incongruent and Post-SRP Congruent or 4) Post-SRP Incongruent and Post-Control Congruent Flanker trials (all $p > 0.05$, Tukey's). Accuracy on Flanker trials was nearly identical to what was reported in the full sample. Accuracy during Post-SRP and Post-Control Incongruent Flanker trials was not correlated with CRQ mean scores across the sample or by sex (all $p > 0.05$, corrected).

3.2.3.3 Errors of Omission

A statistically significant main effect of trial type was observed for errors of omission ($F(3, 114) = 4.71$, $p = 0.004$), as was a main effect of sex ($F(1, 38) = 6.32$, $p = 0.02$). The interaction between trial type and sex was not statistically significant ($F(3, 114) = 0.70$, $p = 0.56$). More errors of omission were committed during Post-SRP Incongruent relative to Post-SRP Congruent Flanker trials ($p < 0.05$, Tukey's). However, errors of omission did not differ between 1) Post-SRP Incongruent and Post-Control Congruent, 2) Post-Control Incongruent and Post-SRP Congruent, 3) Post-Control Incongruent and Post-Control Congruent, 4) Post-SRP and Post-Control Congruent or 5) Post-SRP and Post-Control Incongruent Flanker trials (all $p > 0.05$, Tukey's). The post-hoc simple effects of sex were not statistically significant (all $p > 0.05$, Sidak); however, girls committed more errors of omission in general.

Omission errors on Flanker trials were similar to what was reported in the full sample; however, one notable difference was the lack of a statistically significant post-hoc effect explaining the main effect of sex on errors of omission in the smaller sample. By comparison, the full sample results indicated that this effect was driven by girls committing more errors of omission during Post-SRP Incongruent Flanker trials. Errors of omission during Post-SRP Incongruent Flanker trials were not significantly correlated with CRQ mean scores across the sample or by sex (all $p > 0.05$, corrected). However, co-rumination was positively correlated with errors of omission during Post-SRP

Incongruent Flanker trials across the sample ($\rho = 0.54$, $p = 0.008$, corrected) and in boys ($\rho = 0.56$, $p = 0.02$, corrected), but not girls ($\rho = 0.43$, $p = 0.03$, corrected).

3.2.4 Exit Questionnaire Responses

Similar to the full sample, responding on the exit questionnaire indicated that boys and girls did not differ based on identification with the statements in the task, interest in the task or their belief that it was important to do well on the task (all $U \leq 154.00$, $p \geq 0.22$).

3.2.5 State (Task-Regressed) Functional Connectivity Analyses

Analysis of dorsolateral prefrontal cortex (DLPFC) state functional connectivity yielded significant effects with the left DLPFC seed region only. Specifically, a significant interaction between sex and condition emerged in left ventral/dorsal striatum and right precuneus, such that girls showed stronger functional coupling between these regions and the left DLPFC during SRP relative to boys. Post-hoc analysis revealed that girls had stronger functional coupling between left DLPFC and both striatum and precuneus during Post-SRP Flanker trials compared to boys ($p < 0.05$, Sidak; Figure 3). Results of the right inferior parietal lobule (IPL) seed region analysis indicated a significant main effect of sex, such that girls had stronger functional coupling between IPL and left mPFC and cuneus compared to boys. A significant interaction between condition and sex also emerged in left middle frontal gyrus (MFG) connectivity, such that girls had stronger coupling between right IPL and left MFG during Post-SRP Flanker trials relative to boys ($p < 0.05$, Sidak; Figure 4). There were no significant effects in the left IPL seed region analysis (Table 7).

A significant main effect of sex emerged in the functional connectivity between left mPFC and right posterior cerebellum, with girls showing stronger functional coupling. Moreover, in the right mPFC seed analysis, a significant interaction between sex and condition was found with right MFG functional connectivity. Girls had stronger functional coupling between mPFC and MFG during the Post-SRP Flanker condition compared to boys ($p < 0.05$, Sidak; Figure 5). PCC seed analyses did not yield any significant results (Table 7).

CRQ mean scores were not significantly correlated to state functional connectivity across the sample or by sex (all $p > 0.05$, corrected). Likewise, Flanker performance was not significantly correlated with state functional connectivity (all $p > 0.05$, corrected).

Examination of one-sample *t*-test functional connectivity maps by sex indicated that both sexes had similar patterns of functional connectivity for all seed regions (see Figures 6 - 9 for left hemisphere seed results); thus, results from the two-way ANOVAs can be interpreted to mean that girls showed stronger positive functional coupling of seed regions compared to boys.

3.3 Specific Aim II

Of the forty participants included in the task-regressed functional connectivity analysis, 2 (male) participants could not be included in the resting state functional connectivity analysis due to excessive head motion (FD > 0.3 mm). Of the remaining 38 participants, frames of data used in the resting state functional connectivity analysis were not statistically different by sex ($t_{36} = 0.53$, $p = 0.60$). Boys and girls did not differ statistically on mean FD of the remaining frames ($t_{36} = 0.001$, $p = 1.00$). Age was not correlated with FD remaining mean ($r^2 = 0.11$, $p = 0.52$).

3.3.1 Participant Characterization

Sex differences in demographic information and questionnaire responding were assessed with this smaller subset of participants. Boys and girls did not differ statistically based on age ($t_{36} = 0.87$, $p = 0.39$), pubertal stage ($\chi^2 = 0.40$, $p = 0.53$), IQ ($t_{36} = 1.49$, $p = 0.15$), SES ($t_{36} = 0.38$, $p = 0.71$) or racial distribution ($\chi^2 = 0.93$, $p = 0.63$). CDI Total T-Score and subscale T-Scores were not statistically different by sex (all $t_{20.26} \leq 1.07$, $p \geq 0.30$); STAI state anxiety scores also did not differ by sex ($t_{36} = 1.68$, $p = 0.10$). Similar to the task-regressed functional connectivity sample, girls reported higher CRQ scores ($U = 75.0$, $p = 0.002$). Responses on the remaining questionnaires (MCQ-A, PTM, TOSCA-A and SPP-A) were not statistically different by sex (all $U \geq 123.5$, $p \geq 0.10$).

Age was negatively correlated with PTM mean scores ($\rho = -0.33$, $p = 0.04$), although not when examined by sex for either girls ($\rho = -0.32$, $p = 0.17$) or boys ($\rho = -0.33$, $p = 0.18$). SPP-A Global Self-Worth was significantly lower for youth in Tanner Stage 5 versus Stage 4 ($U = 46.5$, $p = 0.007$), while SPP-A Close Friendships was significantly lower for youth in Tanner Stage 5 versus 4 at a trend level ($U = 68.0$, $p = 0.06$). When examined by sex, SPP-A Global Self Worth was lower in Tanner Stage 5 versus Stage 4 girls ($U = 4.0$, $p = 0.002$), but not boys ($U = 15.0$, $p = 0.43$), and SPP-A Close Friendships did not differ by Tanner Stage for either sex (all $U \geq 22.0$, $p \geq 0.20$).

3.3.2 Trait (Resting State) Functional Connectivity ROI Analyses

Seed-based resting state functional connectivity analyses were conducted with voxels contained within masked regions determined from the task-regressed functional connectivity results (see Table 8). For instance, resting state functional connectivity between left DLPFC and left ventral/dorsal striatum, as well as right precuneus were tested. Functional connectivity between left DLPFC and right precuneus (Figure 10), but not left ventral/dorsal striatum, was significantly higher in girls compared to boys. All other remaining ROI analyses did not show significant sex differences in resting state functional connectivity.

3.3.3 Trait (Resting State) Functional Connectivity Whole-Brain Analyses

Connectivity between left DLPFC and right postcentral gyrus (PCG) was significantly stronger in girls, compared to boys. Likewise, coupling between right DLPFC and 1) left middle temporal gyrus (MTG) and 2) paracentral lobule (PL) and 3) left PCC was significantly stronger in girls, compared to boys. In contrast, boys showed stronger coupling between right DLPFC and right MFG, relative to girls (Table 5; Figure 11). Resting state functional connectivity of bilateral IPL was not significantly different by sex.

Left mPFC was more functionally connected at rest with left superior parietal lobule (SPL) and right PCC in girls, relative to boys. Similarly, right mPFC was more strongly functionally coupled with left SPL in girls, compared to boys. Although sex differences in resting state functional connectivity of left PCC were not observed, girls showed stronger functional coupling between right PCC and 1) left MTG, 2) left PCC, 3) left SPL and 4) right superior frontal gyrus (SFG) (Table 8; Figure 12).

Across the sample, CRQ mean scores were significantly and positively correlated with functional connectivity between 1) left DLPFC and PCG ($\rho = 0.42$, $p = 0.02$, corrected), 2) right DLPFC and MTG ($\rho = 0.57$, $p = 0.008$, corrected), 3) right DLPFC and PL ($\rho = 0.57$, $p = 0.01$, corrected), 4) right DLPFC and PCC ($\rho = 0.51$, $p = 0.02$, corrected), 5) left mPFC and SPL ($\rho = 0.49$, $p = 0.03$, corrected), 7) right mPFC and SPL ($\rho = 0.39$, $p = 0.03$, corrected), 8) right PCC and MTG ($\rho = 0.60$, $p = 0.004$, corrected), 9) right PCC and PCC ($\rho = 0.44$, $p = 0.03$, corrected), 10) right PCC and SPL($\rho = 0.55$, $p = 0.02$, corrected), and 11) right PCC and SFG ($\rho = 0.35$, $p = 0.04$, corrected) (Figure 13). Correlations between CRQ and trait functional connectivity were not statistically significant when examined by sex (all $p > 0.05$, corrected). Due to the significance of these correlations, as well as the significant sex differences in co-rumination and trait functional connectivity, mediation analyses were pursued to determine if trait functional connectivity mediated the effect of sex on co-rumination. Only right DLPFC – left MTG (FPN-DMN) trait functional connectivity significantly mediated the effect of sex on co-rumination (Figure 14).

RT, accuracy (i.e. incorrect responding) and errors of omission during Post-SRP Flanker Incongruent trials were not significantly correlated with trait resting state functional connectivity across the sample (all $p > 0.05$, corrected). However, incorrect responding during Post-SRP Flanker Incongruent trials was positively correlated with trait resting state functional connectivity between right mPFC and SPL ($\rho = 0.70$, $p = 0.008$, corrected) and right PCC and SPL ($\rho = 0.61$, $p = 0.004$, corrected) in girls (Figure 15), but not boys (both $p > 0.05$, corrected). When examined by sex, RT and errors of omission during Post-SRP Incongruent Flanker trials were not significantly correlated with trait functional connectivity (all $p > 0.05$, corrected). Post-Control Incongruent Flanker trial RT, accuracy and errors of omission were not significantly related to trait functional connectivity across the sample and by sex (all $p > 0.05$, corrected).

Examination of one-sample *t*-test resting state functional connectivity maps by sex indicated that both sexes has similar patterns of functional connectivity for all seed regions (see Figures 16 – 19); thus, results from the two-way ANOVAs can be interpreted to mean that girls showed stronger positive functional coupling of seed regions compared to boys.

3.3.4 State versus Trait Functional Connectivity

Based on results from state (*3.2.5 State (Task-Regressed) Functional Connectivity Analyses*) and trait (*3.3.3 Trait (Resting State) Functional Connectivity Whole-Brain Analyses*) functional connectivity, ROI analyses were conducted for 1) left DLPFC (using masks of right precuneus, left striatum and left PCG); 2) right DLPFC (using masks of left MTG, right PL, left PCC and right MFG); 3) right IPL (using masks of left cuneus, left mPFC and right MFG); 4) left mPFC (using masks of left posterior cerebellum, left SPL and right PCC); 5) right mPFC (using masks of right MFG and left SPL); and 6) right PCC (using masks of left MTG, left PCC, left SPL and right SFG). Due to the large number of analyses (n=19), results were corrected for multiple comparisons using a Benjamini-Hochberg procedure.

Analyses of left DLPFC functional connectivity indicated there was a significant main effect of sex with precuneus and striatum connectivity, such that girls had stronger functional connectivity overall, compared to boys. Moreover, significant interactions between functional connectivity and sex emerged, with girls showing more task functional connectivity than boys, but similar connectivity during rest, between left DLPFC and both precuneus and striatum. Main effects of functional connectivity type were not statistically significant. Functional connectivity between right DLPFC and PCG, as well as PCC, reflected significant main effects of sex, with girls showing stronger functional connectivity overall, as compared to boys. A significant interaction between functional connectivity type and sex emerged in the right DLPFC – MFG connection, such that girls showed stronger task functional connectivity, while boys showed stronger resting state functional connectivity. There were no other significant main effects or interactions between right DLPFC and these regions or MTG.

Analyses of right IPL indicated no significant effects with cuneus or mPFC functional connectivity. However, a significant main effect of sex with MFG emerged, with girls showing stronger functional connectivity overall than boys. A significant main effect of functional connectivity type also emerged between right IPL and MFG, such that trait was stronger than state functional connectivity, regardless of sex. Finally, a significant interaction between sex and functional connectivity type with this region indicated that boys and girls had comparable trait functional connectivity, but girls had stronger task functional connectivity than boys.

A significant main effect of sex was observed between left mPFC and SPL functional connectivity, such that girls showed stronger connectivity overall than boys. All other main effects and interactions between left mPFC and SPL, as well as posterior cerebellum, were not statistically significant. Additional significant main effects of sex were observed between right mPFC and PCC, MFG and SPL, with girls showing stronger functional connectivity overall. A main effect of functional connectivity type with PCC indicated that trait functional connectivity was stronger than state connectivity. Finally, a significant interaction emerged with MFG, such that girls showed stronger task functional connectivity than boys, but similar trait functional connectivity. All other main effects and interactions with right mPFC were not statistically significant.

Main effects of sex were observed between right PCC and MTG, PCC, SPL and SFG, such that girls showed stronger functional connectivity overall, compared to boys. Main effects of functional connectivity type also emerged between the same regions and right PCC, indicating that trait functional connectivity was stronger than state functional connectivity, regardless of sex. Interactions between sex and functional connectivity type were not statistically significant.

Table 1. Full Sample Participant Characteristics

	Girls (n=25)	**Boys (n=24)**	**All**	***p*-value**
Age (years)	16.3 (0.9)	16.7 (0.9)	16.5 (0.9)	0.13
Tanner Stage (4/5)	7/18	5/19	12/37	0.40
IQ[a]	111.3 (9.7)	113.9 (10.1)	112.6 (9.9)	0.36
SES[b]	27.2 (14.5)	25.6 (12.8)	26.4 (13.6)	0.69
White (%)	88	92	90	0.65

[a] Wechsler Abbreviated Scale of Intelligence (2-subtest version)

[b] Hollingshead Index of Social Position; lower values indicate higher socioeconomic status (SES); means for girls and boys correspond to upper middle class

Table 2. Full Sample Depression and Anxiety Symptoms

	Girls (n=25)	**Boys (n=24)**	**All**	***p*-value**
CDI Total[a]	45.2 (9.6)	43.3 (6.1)	44.2 (8.1)	0.43
Negative Mood[b]	44.7 (11.4)	45.4 (6.3)	45.0 (9.2)	0.80
Interpersonal Problems[a]	49.0 (10.3)	45.7 (2.9)	47.5 (7.7)	0.17
Ineffectiveness[a]	44.7 (8.5)	44.8 (6.9)	44.8 (7.7)	0.99
Anhedonia[a]	46.3 (9.3)	44.5 (7.6)	45.4 (8.5)	0.49
Negative Self-Esteem[a]	46.4 (8.0)	43.1 (5.5)	44.8 (7.0)	0.12
STAI State Anxiety[c]	41.3 (4.8)	39.4 (5.7)	40.3 (5.3)	0.21

[a] Children's Depression Inventory T-Score; statistics were based on square-root transformed values from 45 participants (girls = 23)
[b] Children's Depression Inventory T-Score; statistics were based on data from 45 participants (girls = 23)
[c] Spielberger State-Trait Anxiety Inventory for Children

Table 3. Full Sample Personality Questionnaires

	Girls (n=25)	**Boys (n=24)**	**All**	***p*-value**
Test of Self-Conscious Affect for Adolescents				
Shame	2.8 (0.5)	2.6 (0.5)	2.7 (0.5)	0.08
Guilt	3.9 (0.4)	3.7 (0.6)	3.8 (0.5)	0.43
Externalization	2.2 (0.5)	2.1 (0.6)	2.2 (0.6)	0.40
Detached	3.0 (0.4)	2.8 (0.7)	2.9 (0.6)	0.08
Alpha Pride	3.6 (0.6)	3.3 (0.6)	3.5 (0.6)	0.03*
Beta Pride	3.9 (0.5)	3.8 (0.4)	3.8 (0.4)	0.35
Co-Rumination Questionnaire				
Mean Score	3.0 (0.8)	2.1 (0.8)	2.6 (0.9)	< 0.001***
Meta-Cognitions Questionnaire for Adolescents				
Mean Score	1.9 (0.4)	1.9 (0.3)	1.9 (0.3)	0.60
Cognitive Confidence	1.6 (0.4)	1.9 (0.6)	1.7 (0.5)	0.06
Positive Beliefs	1.7 (0.6)	1.4 (0.5)	1.6 (0.6)	0.09
Cognitive Self-Consciousness	2.6 (0.6)	2.6 (0.6)	2.6 (0.6)	0.83
Uncontrollability and Danger	1.8 (0.5)	1.6 (0.6)	1.7 (0.5)	0.05
Need to Control Thoughts	1.7 (0.5)	2.0 (0.5)	1.9 (0.5)	0.06
Prosocial Tendencies Measure				
Mean Score	3.2 (0.4)	3.0 (0.3)	3.1 (0.4)	0.09
Public	1.8 (0.7)	1.9 (0.7)	1.8 (0.7)	0.32
Emotional	3.4 (1.0)	3.0 (0.9)	3.2 (1.0)	0.12
Altruistic	4.4 (0.5)	4.1 (0.7)	4.2 (0.6)	0.10
Dire	3.7 (0.7)	3.3 (0.7)	3.5 (0.8)	0.06
Compliant	3.9 (0.8)	3.7 (0.8)	3.8 (0.8)	0.49
Anonymous	2.4 (0.9)	2.5 (0.8)	2.5 (0.8)	0.51
Self-Perception Profile for Adolescents				

Social Competence	3.0 (0.5)	3.0 (0.6)	3.0 (0.6)	0.63
Close Friendships	3.4 (0.4)	3.4 (0.7)	3.4 (0.6)	0.65
Global Self-Worth	3.1 (0.7)	3.2 (0.7)	3.1 (0.7)	0.80

Mann-Whitney U statistical significance at *$p < 0.05$, ***$p < 0.001$

Table 4. Task-Regressed Functional Connectivity Participant Characteristics

	Girls (n=20)	**Boys (n=20)**	**All**	***p*-value**
Age (years)	16.4 (0.9)	16.6 (0.9)	16.5 (0.9)	0.55
Tanner Stage (4/5)	5/15	4/16	9/31	0.50
IQ[a]	110.6 (9.0)	115.3 (9.2)	112.9 (9.3)	0.11
SES[b]	26.0 (13.1)	26.0 (14.0)	26.0 (13.4)	0.99
White (%)	85	90	88	0.65

[a] Wechsler Abbreviated Scale of Intelligence (2-subtest version)

[b] Hollingshead Index of Social Position; lower values indicate higher socioeconomic status (SES); means for girls and boys correspond to upper middle class

Table 5. Task-Regressed Functional Connectivity Participant Depression and Anxiety Symptoms

	Girls (n=18)	**Boys (n=18)**	**All**	***p*-value**
CDI Total[a]	45.2 (9.6)	43.3 (6.1)	44.2 (8.2)	0.68
Negative Mood	44.7 (12.2)	45.2 (6.0)	44.9 (9.5)	0.88
Interpersonal Problems[a]	49.4 (11.3)	46.0 (2.9)	47.7 (8.3)	0.25
Ineffectiveness[a]	43.8 (6.0)	44.9 (7.0)	44.4 (6.4)	0.63
Anhedonia [a]	46.1 (9.3)	44.9 (8.0)	45.5 (8.6)	0.71
Negative Self-Esteem[a]	45.9 (8.6)	43.6 (5.9)	44.8 (7.4)	0.37
STAI State Anxiety[b]	41.8 (5.0)	38.4 (5.7)	40.1 (5.5)	0.06

[a] Children’s Depression Inventory T-Score; statistics were based on square-root transformed values

[b] Spielberger State-Trait Anxiety Inventory for Children T-Score; statistics based on a sample of 20 girls and 20 boys

Table 6. Task-Regressed Functional Connectivity Personality Questionnaires

	Girls (n=20)	**Boys (n=20)**	**All**	***p*-value**
Test of Self-Conscious Affect for Adolescents				
Shame	2.8 (0.6)	2.6 (0.5)	2.7 (0.6)	0.11
Guilt	3.8 (0.4)	3.6 (0.6)	3.7 (0.5)	0.42
Externalization	2.3 (0.5)	2.1 (0.6)	2.2 (0.6)	0.21
Detached	3.0 (0.4)	2.8 (0.7)	2.9 (0.6)	0.06
Alpha Pride	3.6 (0.6)	3.4 (0.6)	3.5 (0.6)	0.13
Beta Pride	3.8 (0.4)	3.8 (0.4)	3.8 (0.4)	0.62
Co-Rumination Questionnaire				
Mean Score	3.0 (0.8)	2.1 (0.8)	2.5 (0.9)	0.001**
Meta-Cognitions Questionnaire for Adolescents				
Mean Score	1.9 (0.4)	1.9 (0.4)	1.9 (0.4)	0.72
Cognitive Confidence	1.6 (0.4)	1.9 (0.7)	1.8 (0.6)	0.09
Positive Beliefs	1.7 (0.6)	1.5 (0.5)	1.6 (0.6)	0.14
Cognitive Self-Consciousness	2.6 (0.7)	2.6 (0.6)	2.6 (0.6)	0.74
Uncontrollability and Danger	1.8 (0.5)	1.6 (0.6)	1.7 (0.6)	0.11
Need to Control Thoughts	1.7 (0.5)	2.0 (0.5)	1.9 (0.6)	0.06
Prosocial Tendencies Measure				
Mean Score	3.2 (0.5)	3.0 (0.3)	3.1 (0.4)	0.20
Public	1.8 (0.8)	1.9 (0.8)	1.9 (0.7)	0.67
Emotional	3.3 (1.1)	2.9 (1.0)	3.1 (1.0)	0.29
Altruistic	4.3 (0.5)	4.1 (0.7)	4.2 (0.6)	0.39
Dire	3.7 (0.8)	3.4 (0.7)	3.5 (0.8)	0.17
Compliant	3.8 (0.8)	3.6 (0.9)	3.7 (0.8)	0.56
Anonymous	2.4 (0.9)	2.5 (0.7)	2.5 (0.8)	0.69

Self-Perception Profile for Adolescents				
Social Competence	3.0 (0.5)	3.0 (0.6)	3.0 (0.5)	0.81
Close Friendships	3.4 (0.4)	3.3 (0.7)	3.4 (0.6)	0.90
Global Self-Worth	3.1 (0.6)	3.0 (0.7)	3.1 (0.7)	0.72

Mann-Whitney U statistical significance at $^{**}p < 0.01$

Table 7. Task-Regressed Functional Connectivity Results

Seed Region	Functionally Coupled Region	BA	Voxels (mm^3)	Peak Talairach Coordinates (X, Y, Z)	Cohen's d[a]
Main Effect of Sex					
R Inferior Parietal Lobule	L Medial Prefrontal Cortex	10	109	-14, 48, 9	0.53
	L Cuneus	18	48	-4, -102, 0	0.49
L Medial Prefrontal Cortex	L Posterior Cerebellum		65	32, -84, -27	0.48
Condition-by-Sex Interaction					
L Dorsolateral Prefrontal Cortex	L Ventral/Dorsal Striatum		49	-10, 9, -6	0.39
	R Precuneus	7	46	8, -75, 39	0.40
R Inferior Parietal Lobule	L Middle Frontal Gyrus	46/10	68	-34, 42, 6	0.39
R Medial Prefrontal Cortex	R Middle Frontal Gyrus	9/10	70	38, 36, 18	0.38

[a] Cohen's d effect sizes range from small (d = 0.2), medium (d = 0.5) and large (d = 0.8); BA = Brodmann Area; L = left; R = right

Table 8. Resting State Functional Connectivity Results

Seed Region	Functional Coupled Region	BA	Voxels (mm^3)	Peak Talairach Coordinates (X, Y, Z)	Cohen's d[a]
Region of Interest Analysis: Girls > Boys					
L Dorsolateral Prefrontal Cortex	R Precuneus	19	5	4, -81, 45	0.05
Whole-Brain Analysis: Girls > Boys					
L Dorsolateral Prefrontal Cortex	R Postcentral Gyrus	5	220	40, -42, 60	0.10
R Dorsolateral Prefrontal Cortex	L Middle Temporal Gyrus	21	156	-53, -24, -9	0.08
	R Paracentral Lobule	6	113	10, -24, 75	0.07
	L Posterior Cingulate Cortex	31	100	-5, -57, 27	0.09
L Medial Prefrontal Cortex	L Superior Parietal Lobule	7	352	-38, -66, 51	0.11
	R Posterior Cingulate Cortex	30	102	1, -48, 18	0.09
R Medial Prefrontal Cortex	L Superior Parietal Lobule	7	90	-35, -66, 48	0.11
R Posterior Cingulate Cortex	L Middle Temporal Gyrus	21	120	-56, -12, -9	0.09
	L Posterior Cingulate Cortex	30	102	-2, -48, 18	0.12
	L Superior Parietal Lobule	7	92	-32, -66, 54	0.12

	R/L Superior Frontal Gyrus	9/10	90	1, 54, 30	0.10
Whole-Brain Analysis: Boys>Girls					
R Dorsolateral Prefrontal Cortex	R Middle Frontal Gyrus	46	110	43, 27, 24	0.10

[a]Cohen's d effect sizes range from small (d = 0.2), medium (d = 0.5) and large (d = 0.8); BA = Brodmann Area; L = left; R = right

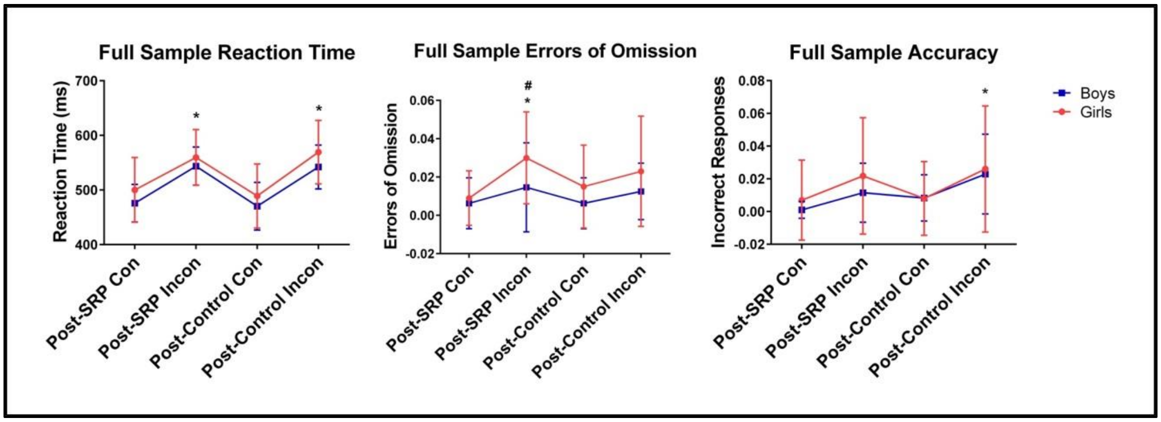

Figure 1. Full-Sample Flanker Performance (n = 49). A main effect of condition was present for reaction time (left), errors of omission (middle) and accuracy (right). A main effect of sex was present for reaction time (left) and errors of omission (middle), but not accuracy (right). *$p < 0.05$, Tukey's multiple comparisons correction, compared to Post-SRP Con and Post-Control Con trials. $^{\#}p < 0.05$, Sidak multiple comparisons correction, compared to boys. SRP = self-referential processing; Con = Congruent; Incon = Incongruent.

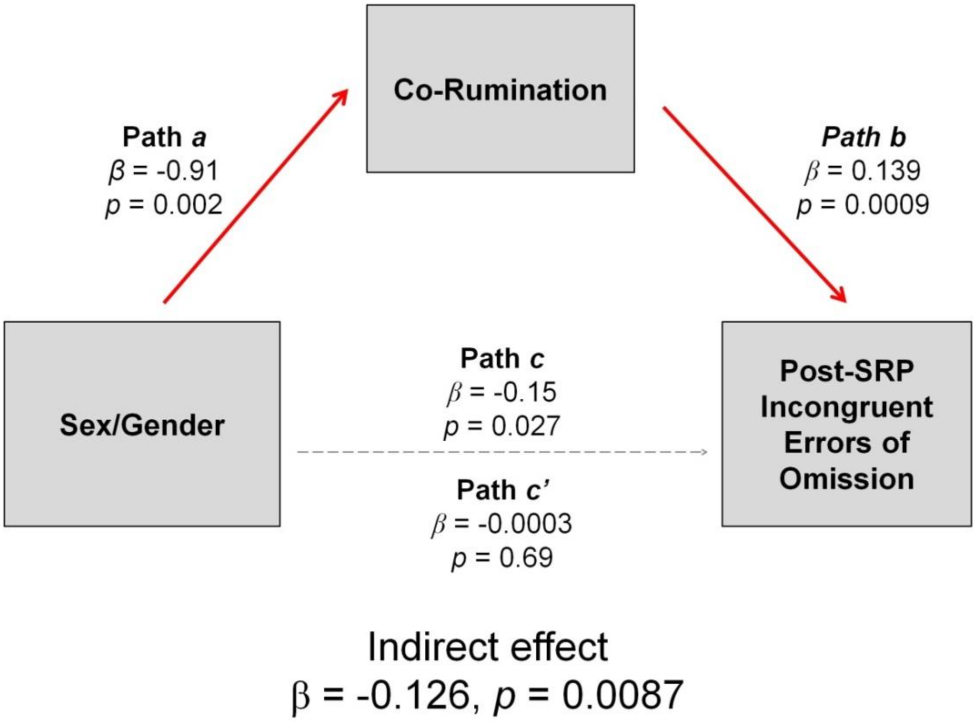

Figure 2. Co-rumination mediated the effect of sex on Post-SRP Incongruent Flanker errors of omission (n = 49). The direct effect of sex on Post-SRP Incongruent Flanker errors of omission (β = -0.15, *p* = 0.027) became non-significant (β = -0.003, *p* = 0.69) when co-rumination was introduced in the model as a mediator. The indirect effect of co-rumination on Post-SRP Incongruent Flanker errors of omission was statistically significant (β = -0.126, *p* = 0.0087), indicating that co-rumination fully mediated the effect of sex on Post-SRP Incongruent Flanker errors of omission.

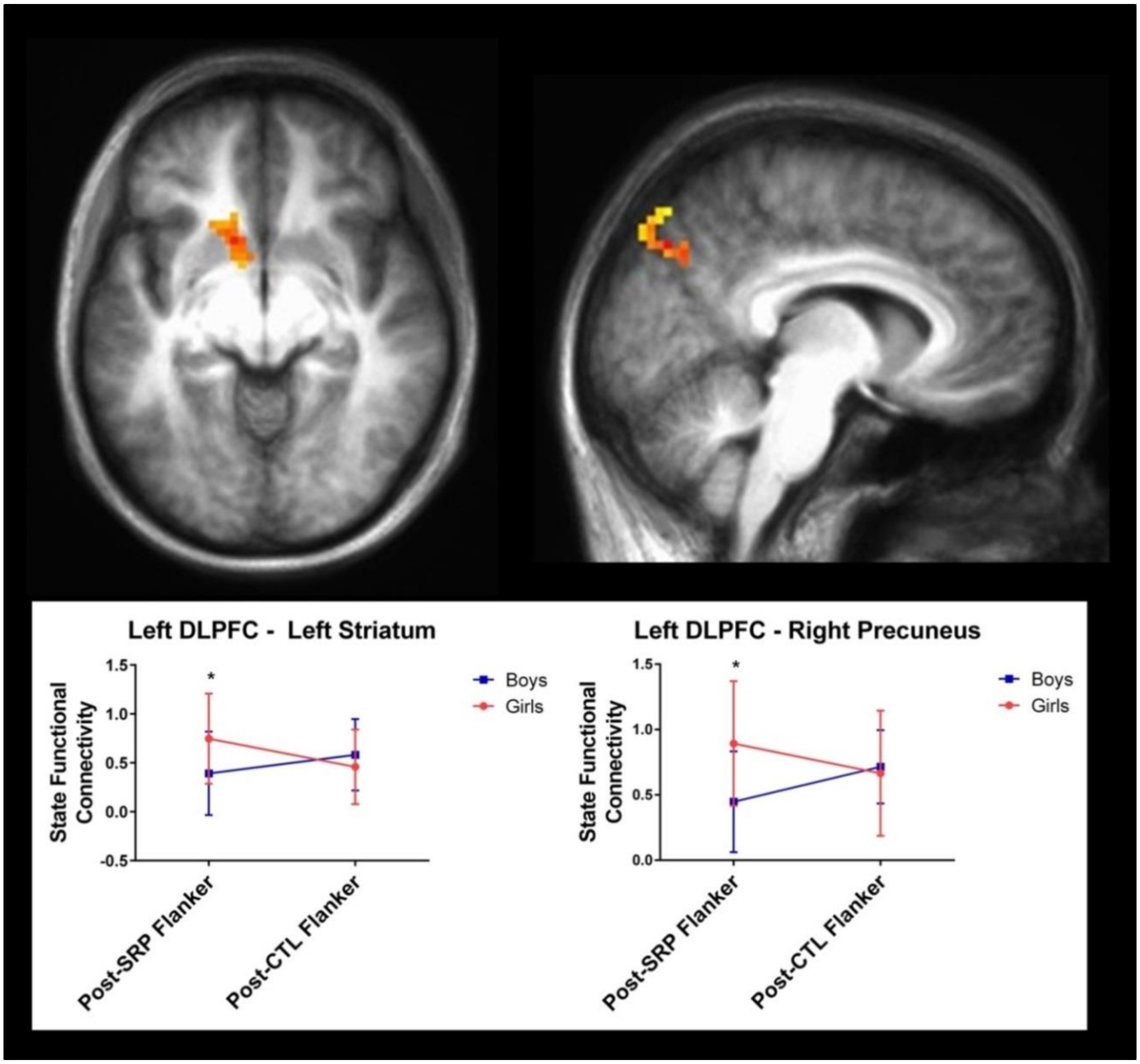

Figure 3. Girls display stronger dorsolateral prefrontal cortex (DLPFC) state functional connectivity during Post-SRP Flanker conditions (n = 40). A two-way ANOVA of left DLPFC functional connectivity resulted in two regions where a significant condition-by-sex interaction was found: the left striatum (including caudate nucleus and nucleus accumbens; left) and left precuneus (right). The interactions were such that girls had stronger functional coupling of these regions with the left DLPFC during Post-SRP Flanker trials, compared to boys. *$p < 0.05$, Sidak multiple comparisons correction.

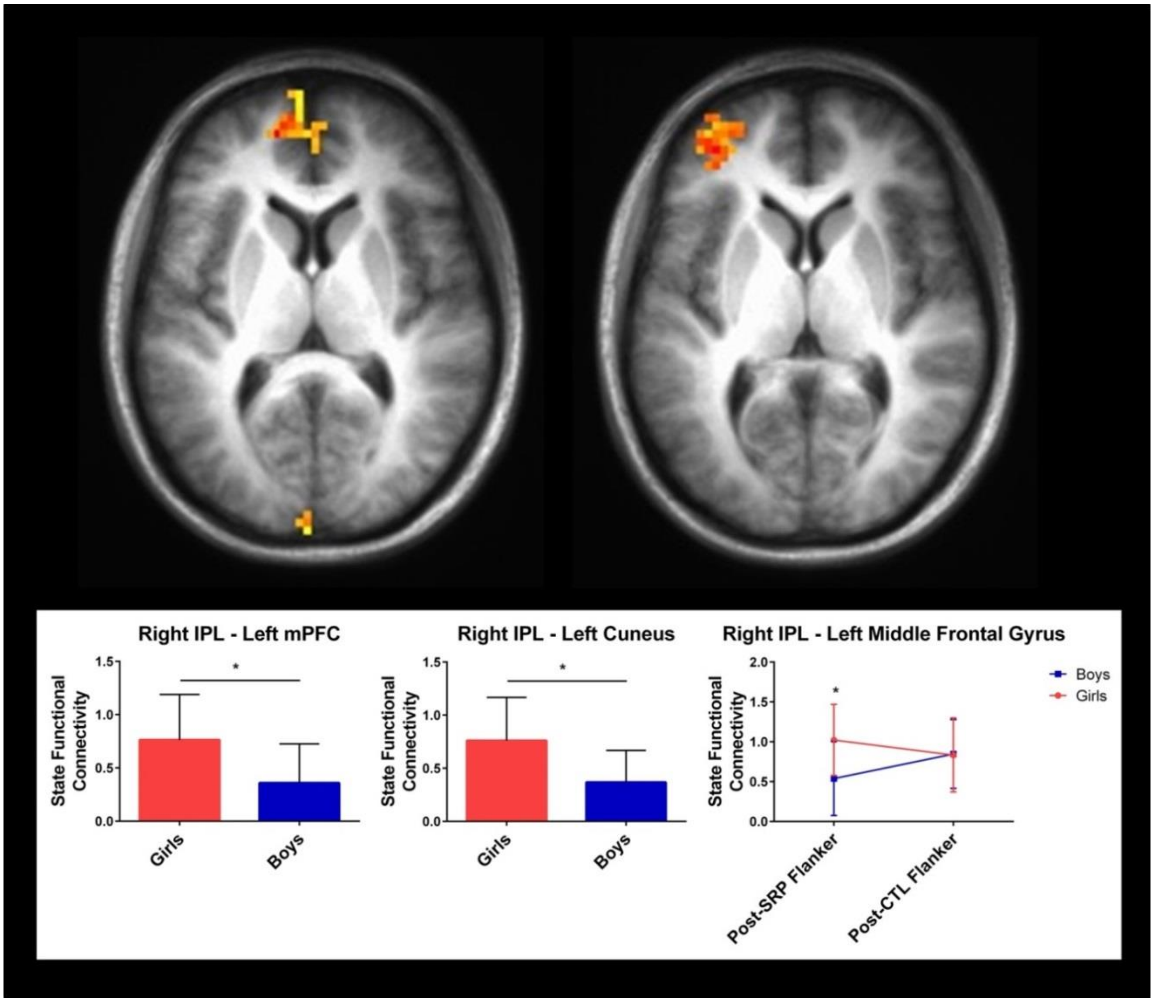

Figure 4. Girls display stronger inferior parietal lobule (IPL) state functional connectivity during Post-SRP Flanker conditions (n = 40). A two-way ANOVA of right IPL functional connectivity resulted in two regions where a main effect of sex was present: left medial prefrontal cortex and cuneus (left). In both cases, girls showed stronger functional coupling with right IPL. A significant condition-by-sex interaction was found with left middle frontal gyrus (right), such that girls had stronger functional coupling of this region with the right IPL during Post-SRP Flanker conditions, compared to boys. **p* < 0.05, Sidak multiple comparisons correction.

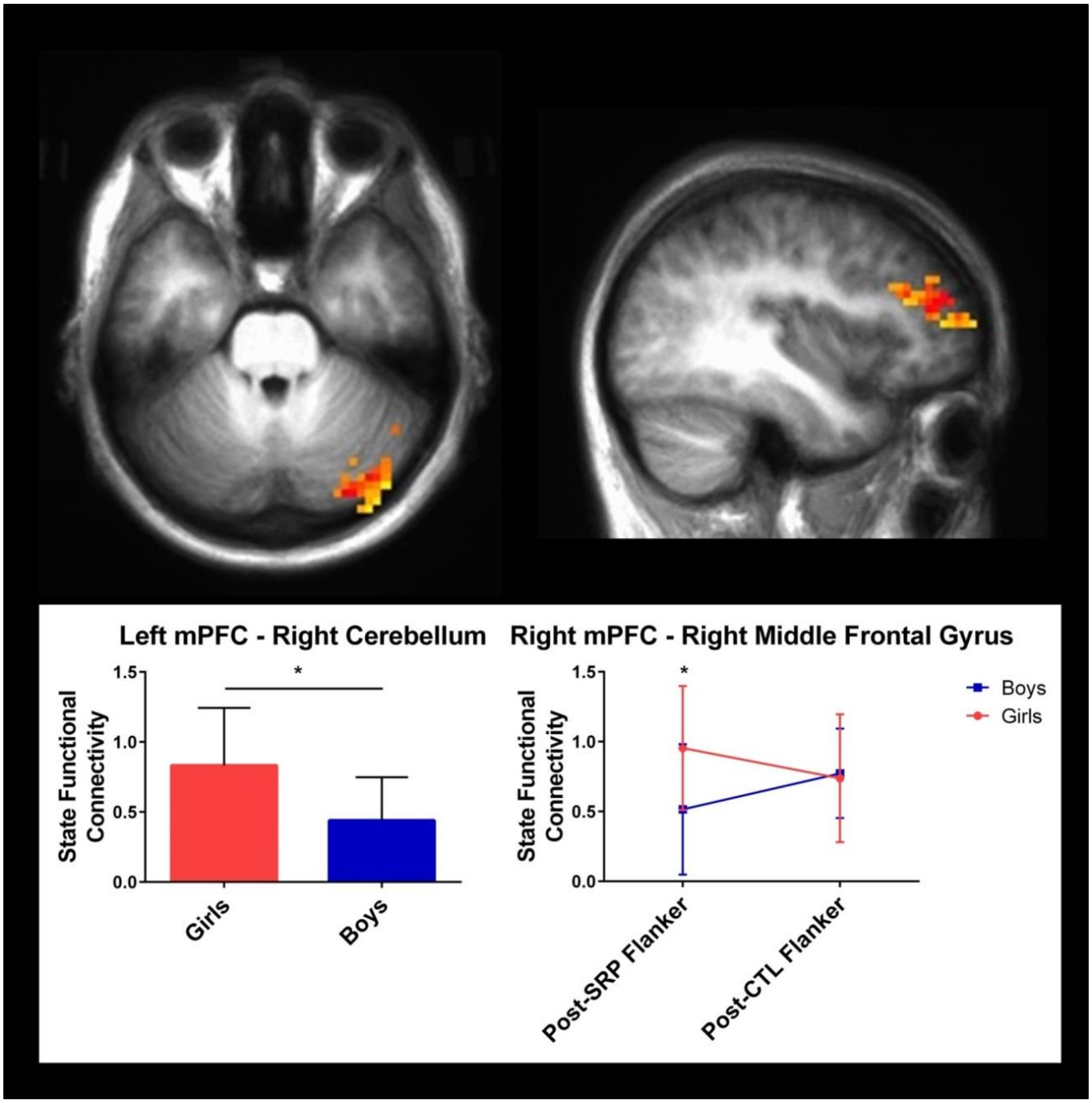

Figure 5. Girls display stronger medial prefrontal cortex (mPFC) state functional connectivity during Post-SRP Flanker conditions (n = 40). A two-way ANOVA of left mPFC functional connectivity resulted in one region where a main effect of sex was present – right posterior cerebellum (left) – such that girls showed stronger functional coupling with left mPFC. A significant condition-by-sex interaction also emerged with right middle frontal gyrus (right), such that girls had stronger functional coupling of this

region with the right mPFC during Post-SRP Flanker conditions, compared to boys. $^*p < 0.05$, Sidak multiple comparisons correction.

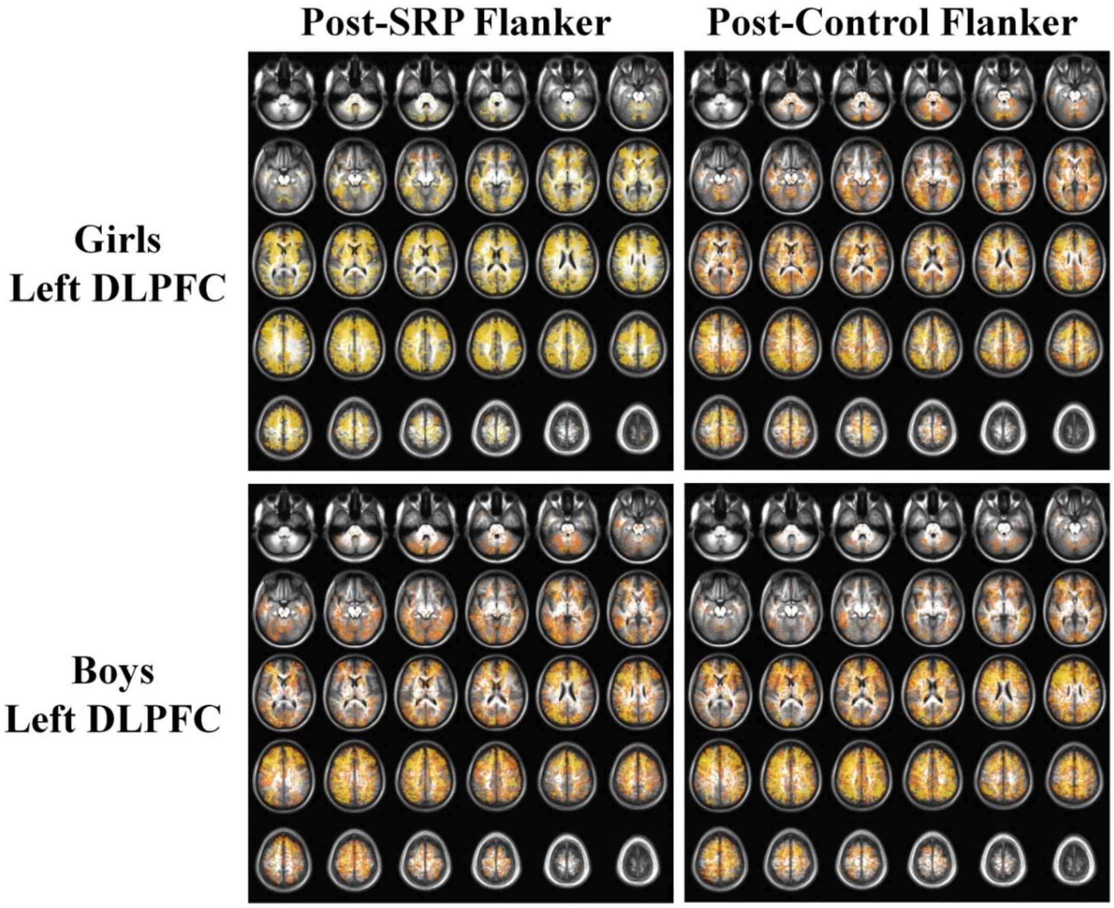

Figure 6. One-sample *t*-tests of left dorsolateral prefrontal cortex (DLPFC) task-regressed functional connectivity maps for each condition and sex (T ≥ 7.10).

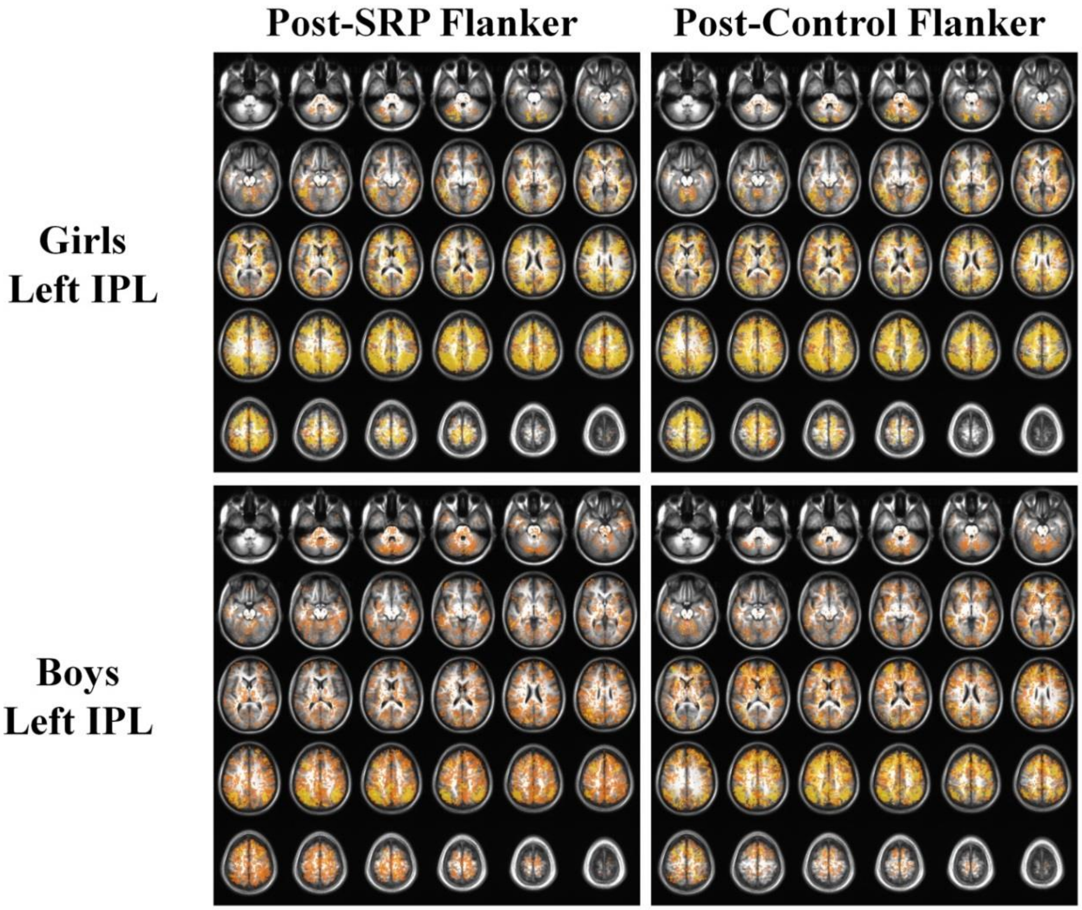

Figure 7. One-sample *t*-tests of left inferior parietal lobule (IPL) task-regressed functional connectivity maps for each condition and sex ($T \geq 7.10$).

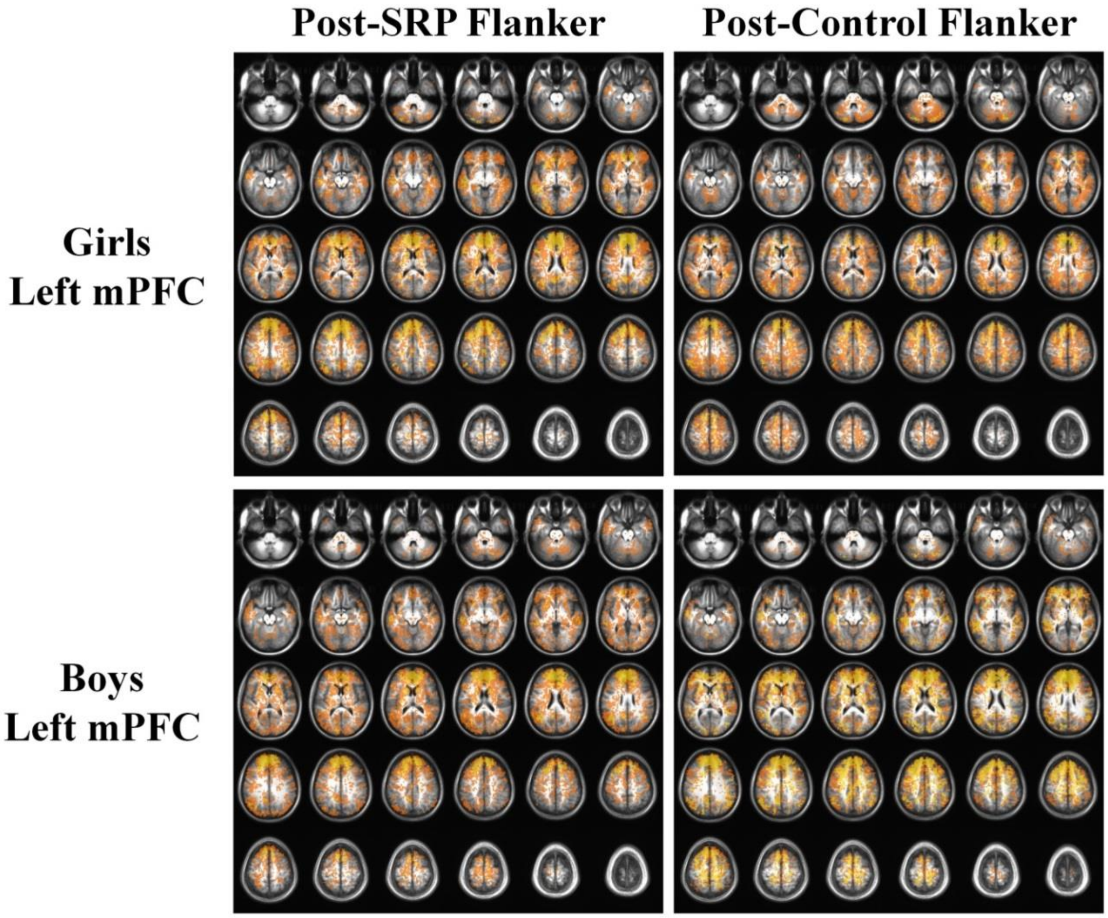

Figure 8. One-sample *t*-tests of left medial prefrontal cortex (mPFC) task-regressed functional connectivity maps for each condition and sex ($T \geq 7.10$).

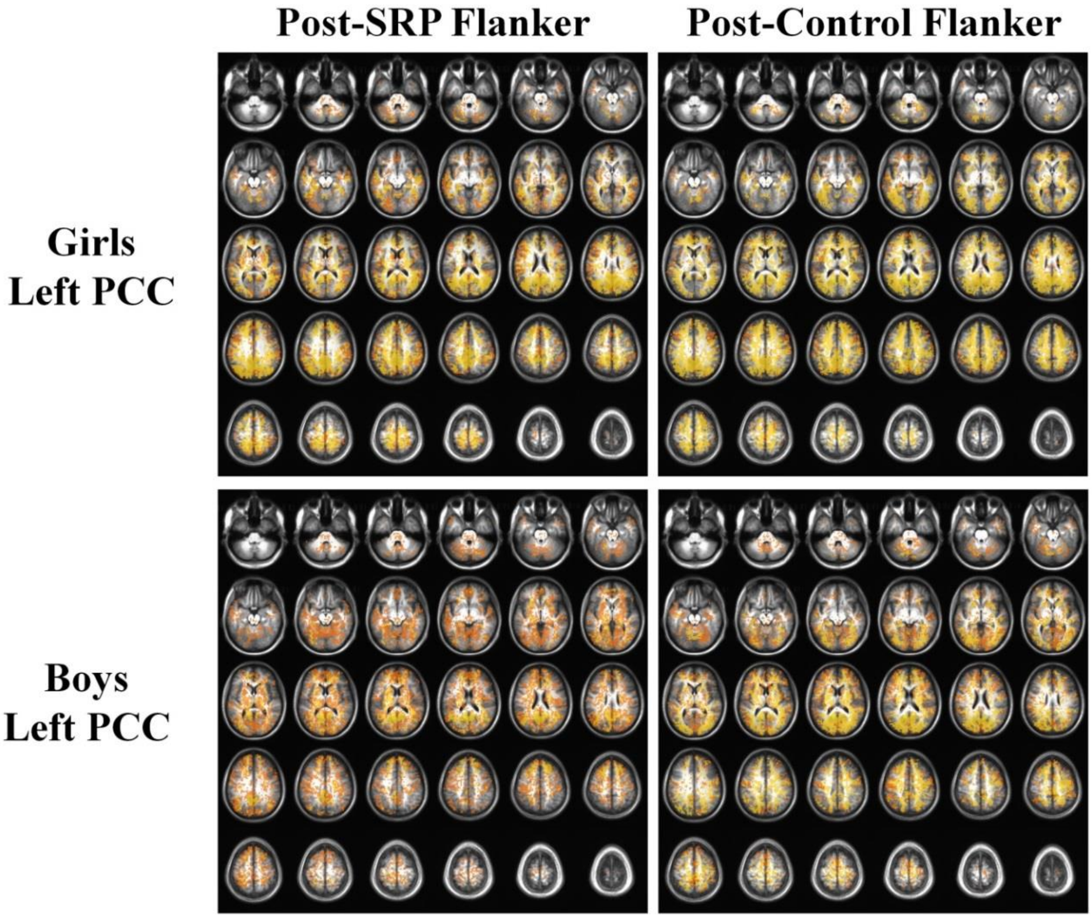

Figure 9. One-sample *t*-tests of left posterior cingulate cortex (PCC) task-regressed functional connectivity maps for each condition and sex ($T \geq 7.10$).

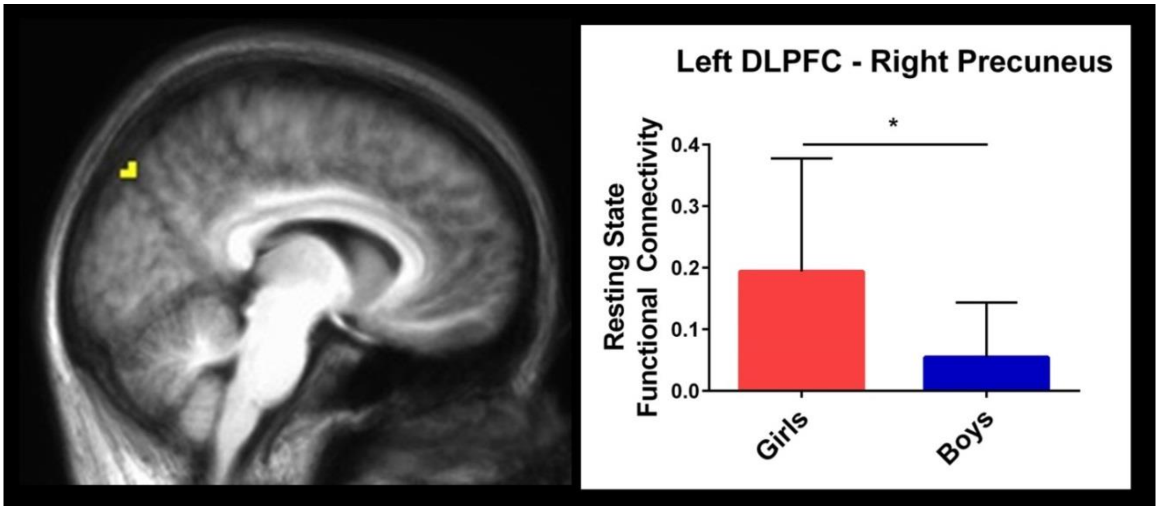

Figure 10. Trait functional connectivity sex differences explain state functional connectivity between dorsolateral prefrontal cortex (DLPFC) and precuneus (n = 38). The left DLPFC – right precuneus resting state functional connectivity region of interest analysis indicated that girls show stronger coupling between these regions compared to boys. Asterisk indicates voxel-wise correction of $p < 0.05$ and Monte Carlo multiple comparisons cluster-wise correction of $p < 0.05$ (minimum cluster size ≥ 5 voxels), or a corrected voxel-wise threshold of $p < 0.005$.

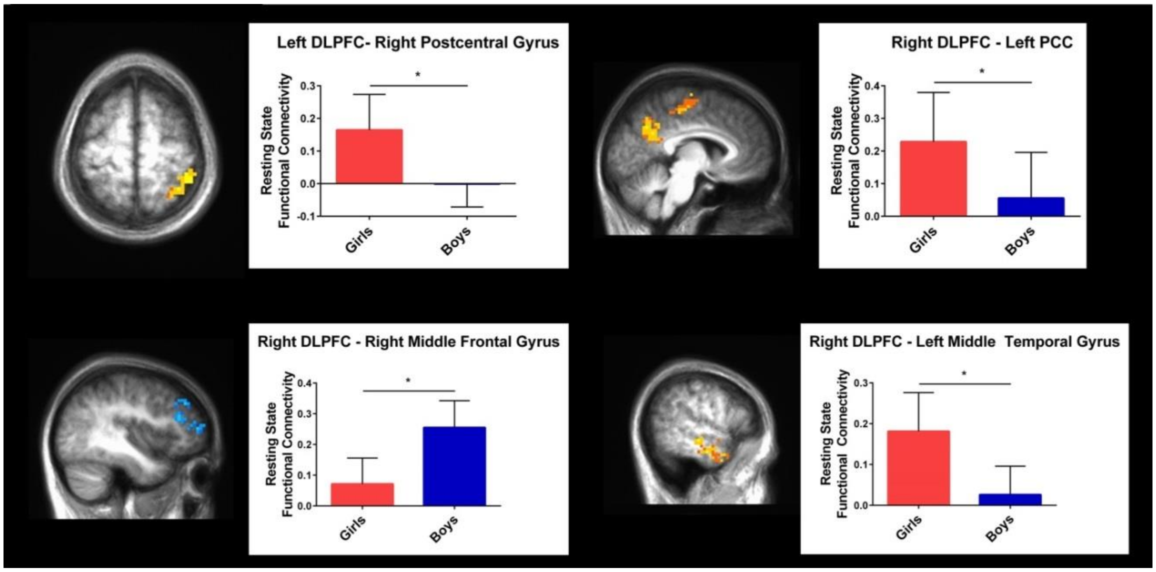

Figure 11. Sex differences in dorsolateral prefrontal cortex (DLPFC) trait functional connectivity (n = 38). The left DLPFC whole-brain resting state functional connectivity analysis indicated that girls show stronger coupling between this region and right postcentral gyrus (top left). Right DLPFC whole-brain resting state functional connectivity analysis indicated that boys show stronger coupling between this region and right middle frontal gyrus (bottom left), while girls shower stronger coupling between right DLPFC and left posterior cingulate cortex (top right) and middle temporal gyrus (bottom right). Asterisk indicates voxel-wise correction of $p < 0.05$ and Monte Carlo multiple comparisons cluster-wise correction of $p < 0.05$ (minimum cluster size ≥ 81 voxels), or a corrected voxel-wise threshold of $p < 0.00007$.

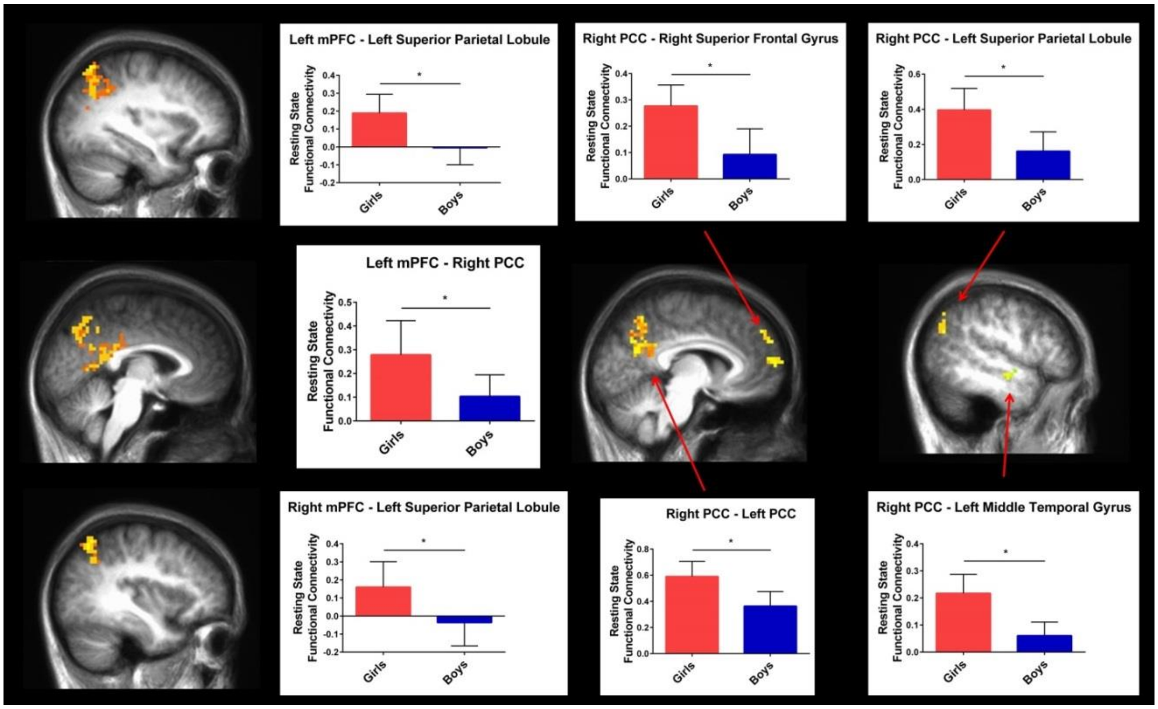

Figure 12. Sex differences in default mode network trait functional connectivity (n = 38). Left medial prefrontal cortex (mPFC) whole-brain resting state functional connectivity analysis indicated that girls showed stronger coupling between this region and left superior parietal lobule (top left) and right posterior cingulate cortex (middle left). Right mPFC whole-brain resting state functional connectivity analysis indicated that girls had stronger coupling between this region and left superior parietal lobule (bottom left). Right posterior cingulate cortex (PCC) whole-brain resting state functional connectivity analysis indicated that girls showed stronger coupling between this region and right superior frontal gyrus (middle top), left PCC (middle bottom), left superior parietal lobule (right top) and left middle temporal gyrus (right bottom). Asterisk indicates voxel-wise correction of $p < 0.05$ and Monte Carlo multiple comparisons cluster-wise correction of $p < 0.05$ (minimum cluster size ≥ 81 voxels), or a corrected voxel-wise threshold of $p < 0.00007$.

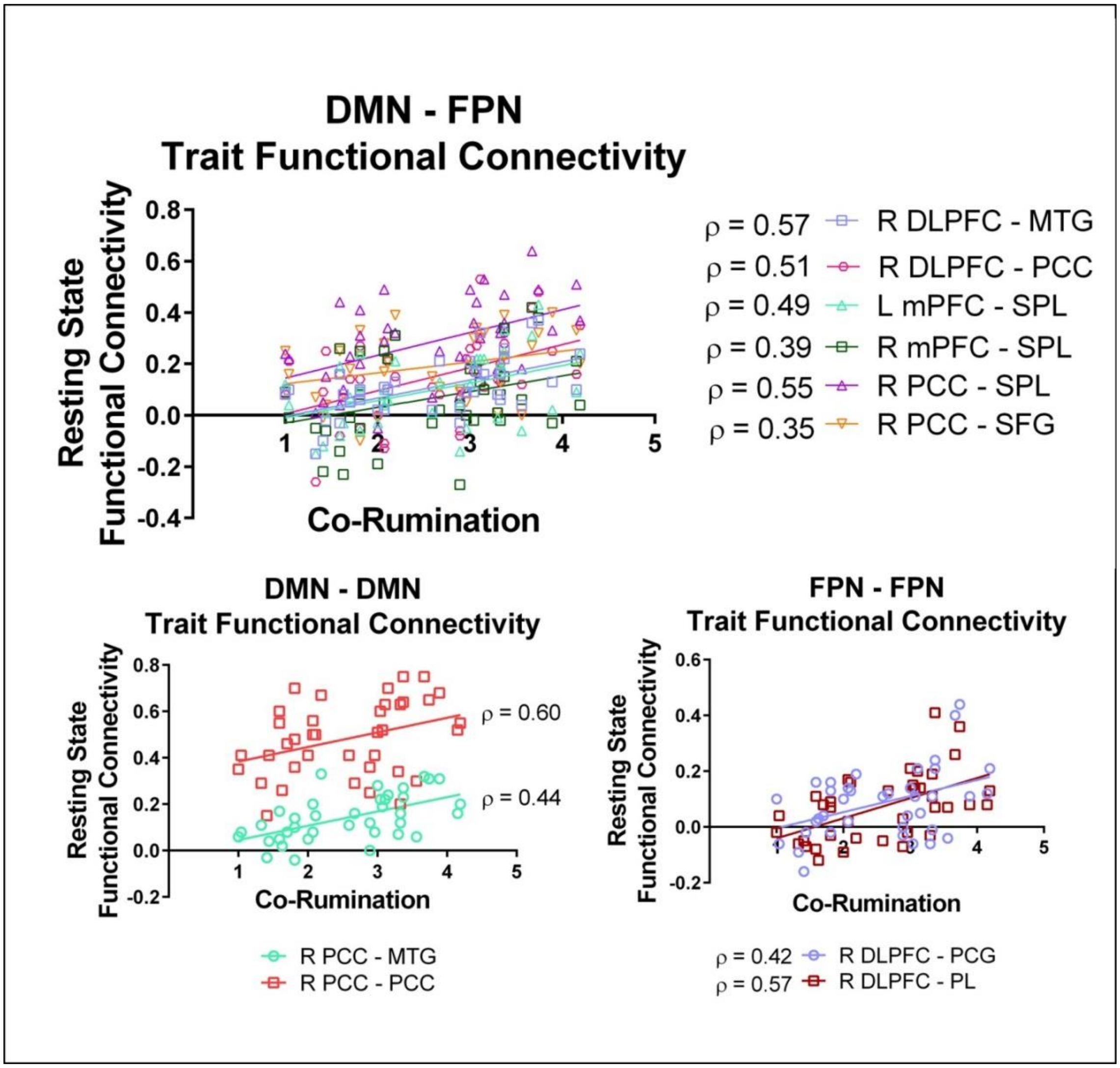

Figure 13. Trait functional connectivity correlates with co-rumination (n = 38). Resting state functional connectivity between default mode network (DMN) and fronto-parietal network (FPN) was positively correlated with co-rumination (top). Within-DMN (bottom left) and within-FPN (bottom right) resting state functional connectivity was also positively correlated with co-rumination. R = right; L = left; DLPFC = dorsolateral prefrontal cortex; MTG = middle temporal gyrus; PCC = posterior cingulate cortex; mPFC = medial prefrontal cortex; SPL = superior parietal lobule; SFG = superior frontal

gyrus; PCG = postcentral gyrus; PL = paracentral lobule. All results were significant at $p < 0.05$ with Benjamini-Hochberg correction.

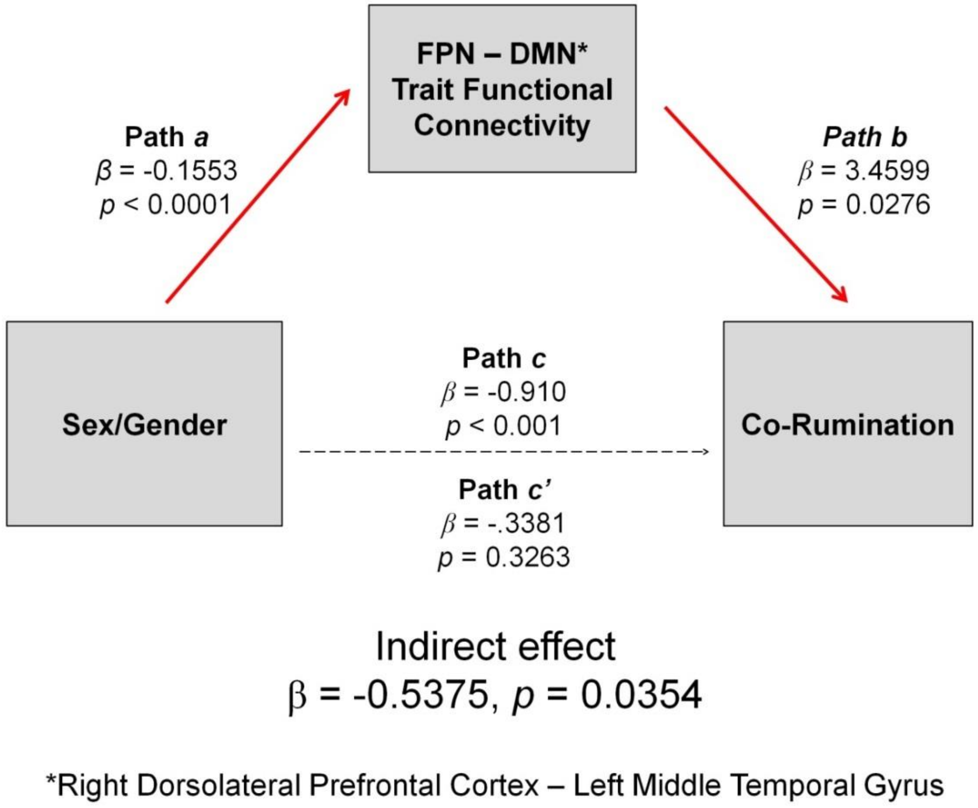

Figure 14. Fronto-parietal network (FPN) - Default mode network (DMN) trait functional connectivity mediated the effect of sex on co-rumination (n = 38). The direct effect of sex on co-rumination (β = -0.910, *p* < 0.001) became non-significant (β = -0.3381, *p* = 0.3263) when FPN-DMN, specifically right dorsolateral prefrontal cortex – left middle temporal gyrus, trait functional connectivity was included in the model as a mediator. The indirect effect of trait functional connectivity on co-rumination was statistically significant (β = -0.5375, *p* = 0.0354), indicating that FPN-DMN trait functional connectivity fully mediated the effect of sex on co-rumination.

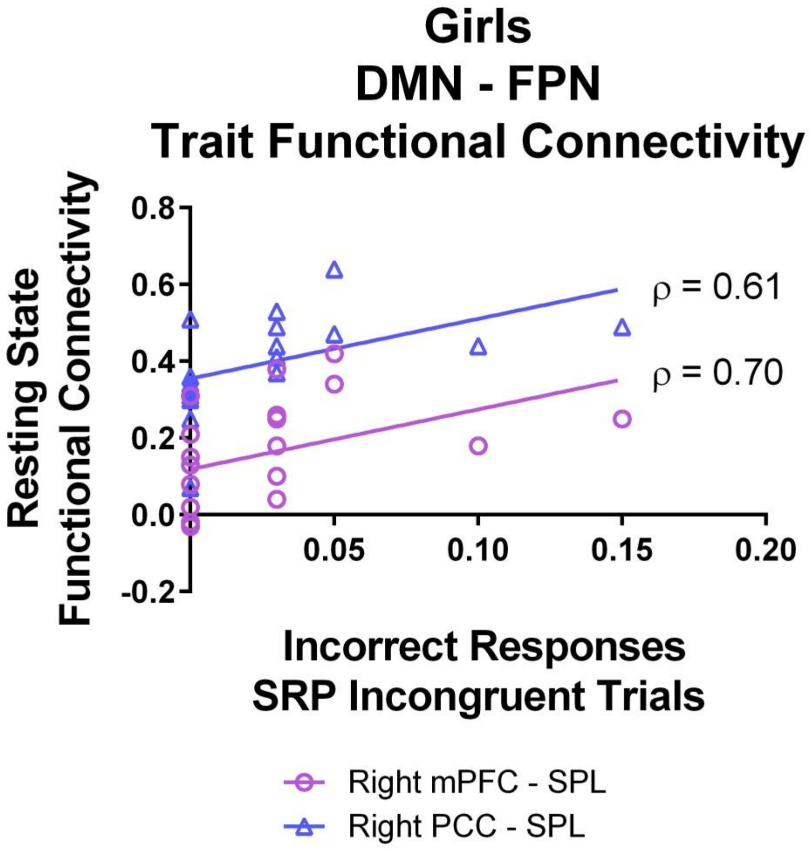

Figure 15. Default mode network (DMN) – fronto-parietal network (FPN) trait functional connectivity is negatively related to cognitive control performance in girls (n = 38). Incorrect responding during Post-SRP Incongruent Flanker trials was positively correlated with trait functional connectivity between right medial prefrontal cortex (mPFC) and superior parietal lobule (SPL), as well as right posterior cingulate cortex (PCC) and SPL in girls. All results were significant at $p < 0.05$ with Benjamini-Hochberg correction.

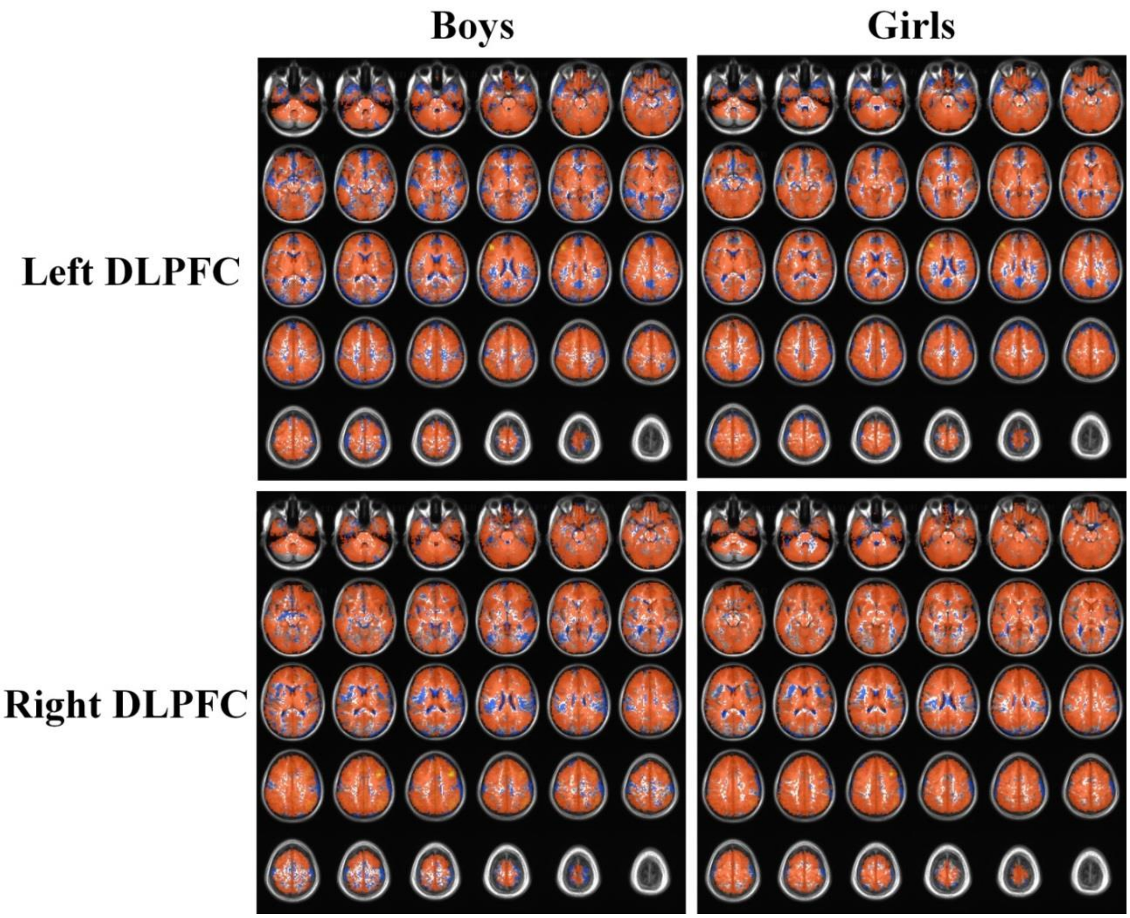

Figure 16. One-sample *t*-tests of bilateral dorsolateral prefrontal cortex (DLPFC) resting state functional connectivity maps for each sex (T ≥ 2.10).

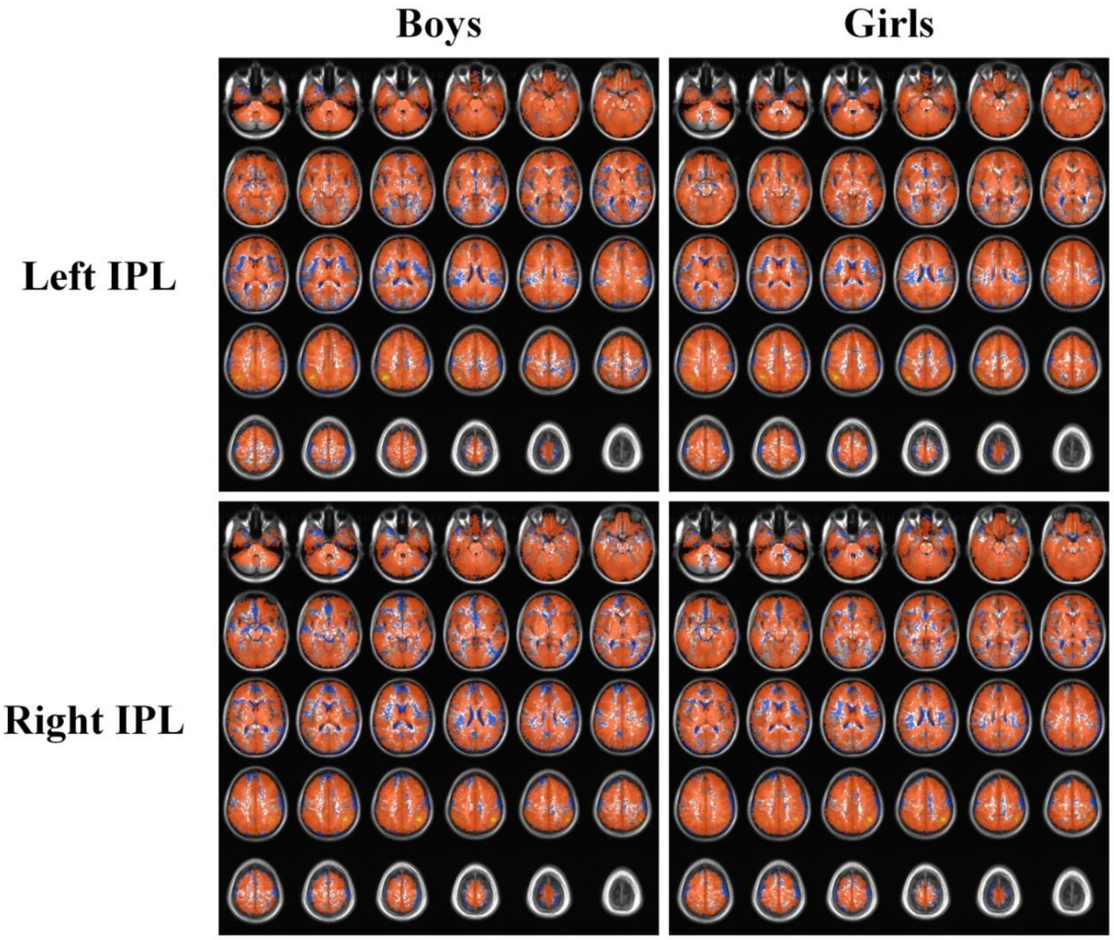

Figure 17. One-sample *t*-tests of bilateral inferior parietal lobule (IPL) resting state functional connectivity maps for each sex (T ≥ 2.10).

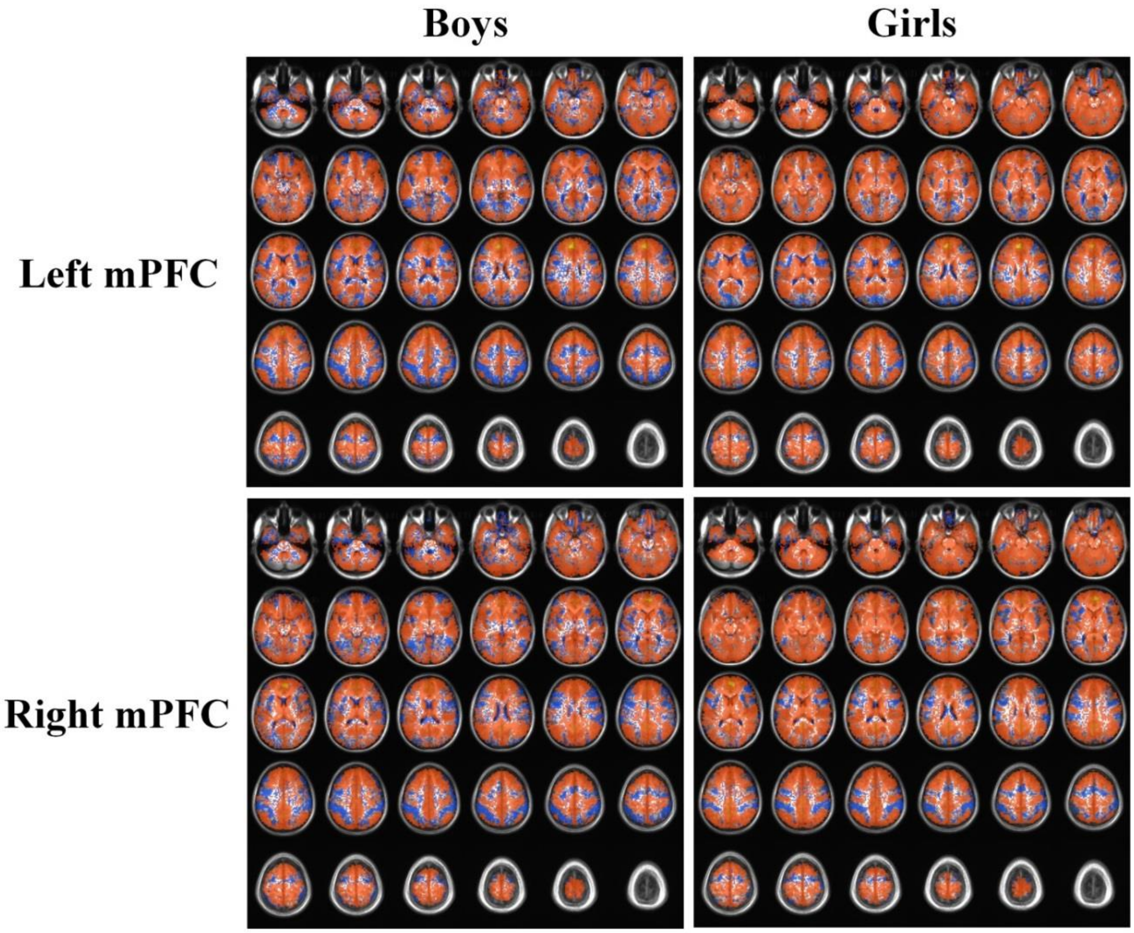

Figure 18. One-sample *t*-tests of bilateral medial prefrontal cortex (mPFC) resting state functional connectivity maps for each sex ($T \geq 2.10$).

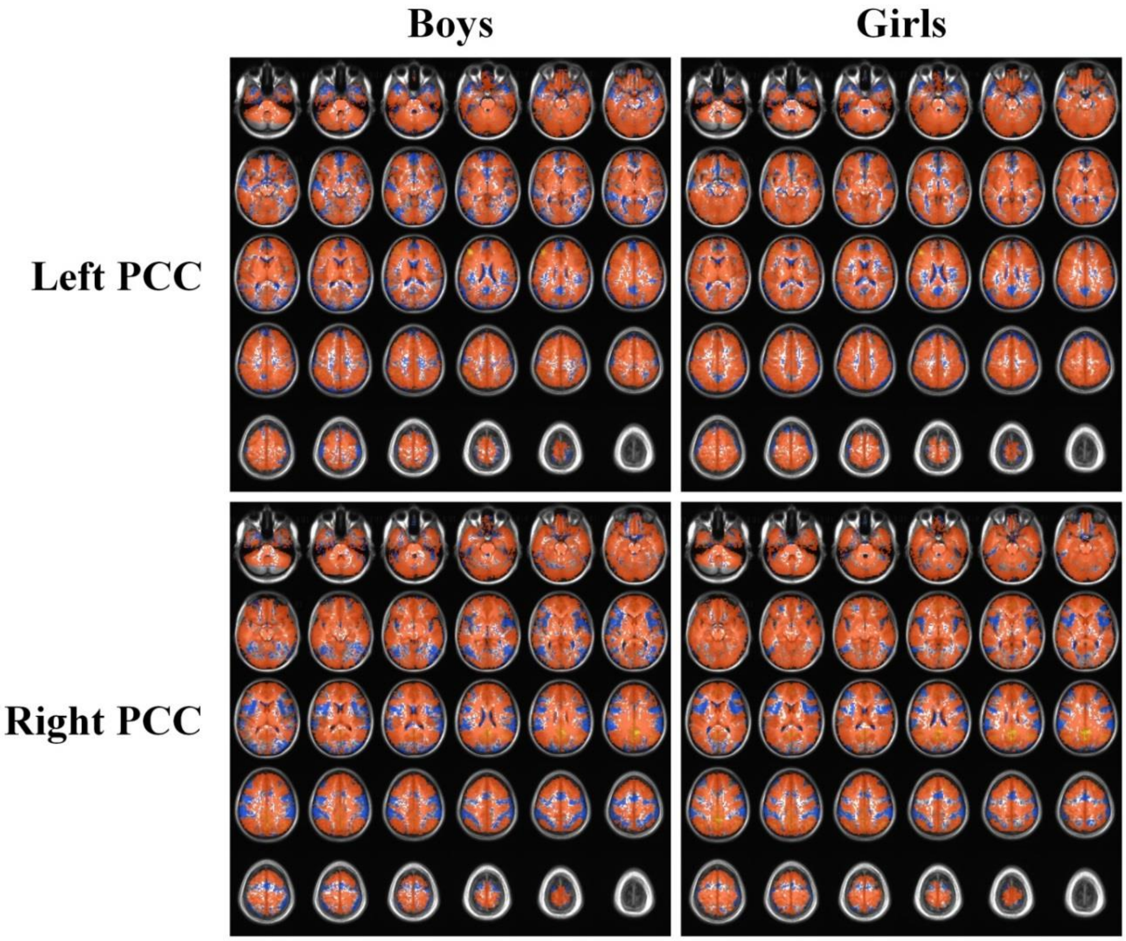

Figure 19. One-sample *t*-tests of bilateral posterior cingulate cortex (PCC) resting state functional connectivity maps for each sex ($T \geq 2.10$).

CHAPTER 4: DISCUSSION

The primary aims of this dissertation were to examine sex differences in the interaction between affective self-referential processing (SRP) and cognitive control using task-regressed functional connectivity (i.e. state functional connectivity) and resting state functional connectivity (RSFC; i.e. trait functional connectivity) measured with functional magnetic resonance imaging (fMRI). I hypothesized girls would show a stronger effect of SRP on cognitive control, as indicated by deficits in performance in Post-SRP Flanker trials and altered state functional connectivity patterns. Specifically, I predicted that girls would demonstrate stronger state functional connectivity between the default mode network (DMN) and the fronto-parietal network (FPN) during Post-SRP Flanker conditions, as this pattern of connectivity has been shown to correspond with lapses in attention and a general worsening of performance during cognitive control tasks (Hampson et al., 2010; Keller et al., 2015; Kelly et al., 2008). Moreover, I hypothesized that girls would show stronger within-DMN trait functional connectivity, which would correspond with a more prosocial orientation. Previous work has shown that individuals who rate higher on empathizing also show stronger within-DMN RSFC (Takeuchi et al., 2014). Finally, I predicted that stronger DMN-FPN trait functional connectivity would correspond with worse cognitive control performance, as demonstrated previously (Hampson et al., 2010; Keller et al., 2015; Kelly et al., 2008).

In accordance with the hypotheses of this study, healthy adolescent girls demonstrated stronger state functional connectivity between DMN and FPN during cognitive control trials that were preceded by SRP trials, as compared to boys. Moreover, girls showed stronger within-network connectivity of the FPN, indicating a potential compensatory mechanism specific to SRP conditions, such that, in girls, stronger within-FPN connectivity counterbalances DMN-FPN connectivity. These findings were supported by Flanker task performance in the full sample, but not the smaller state functional connectivity sample, in that girls demonstrated more errors of omission on Post-SRP Incongruent Flanker trials compared to boys, perhaps due heightened executive load during Post-SRP conditions. Girls also reported more co-rumination than boys, reflecting a more negative cognitive style in social contexts, which mediated the effect of sex on Post-SRP Incongruent Flanker errors of omission. Thus, the negative influence of the affective SRP context on cognitive control performance may be specific to girls precisely because they co-ruminate more than boys

RSFC analyses indicated that state functional connectivity sex differences were indeed transient, as RSFC region of interest (ROI) analyses did not yield any statistically significant sex differences. One exception was the functional connection between left DLPFC and right precuneus, which was significantly higher in girls compared to boys at rest, suggesting that this particular functional connection is stronger in girls regardless of cognitive context. Indeed, direct comparison of task (SRP-Control) and resting state functional connectivity indicated that girls had stronger functional connectivity than boys, regardless of task condition. Examination of whole-brain trait functional connectivity indicated that both sexes demonstrated functional coupling between FPN and DMN; however, girls had stronger DMN-FPN RSFC. Moreover, girls showed stronger within-DMN trait functional connectivity, as hypothesized. Although co-rumination was not correlated with state functional connectivity, it was positively correlated with nearly all RSFC findings, including within-DMN, within-FPN and DMN-

FPN connections. In fact, DMN-FPN trait functional connectivity mediated the effect of sex on co-rumination, suggesting that co-rumination is shaped by trait functional connectivity and goes on to explain state differences in Post-SRP Flanker performance. Trait functional connectivity of DMN-FPN was also positively associated with incorrect responses during Post-SRP Incongruent Flanker trials in girls, but not boys. Thus, these findings indicate that sex differences in co-rumination may be due to differences in DMN-FPN trait functional connectivity between the sexes, and that stronger DMN-FPN trait functional connectivity negatively impacts cognitive control performance during an affective SRP context in girls only.

Subsequent sections of this chapter will explore the implications of the findings detailed in this dissertation. First, I will discuss the characterization of the current sample and their performance on SRP and Flanker trials (**4.1 Participant Characterization and Task Performance**). Next, I will interpret results of task-regressed and resting state functional connectivity analyses independently and in relation to each other, as well as in relation to co-rumination and performance on Flanker trials (**4.2 Functional Connectivity**). Then, I will provide alternate interpretations and discuss limitations of this research (**4.3 Strengths, Limitations and Alternative Interpretations**). Future directions and broader implications of this work, particularly in relation to adolescent risk factors for MDD will be discussed (**4.4 Future Directions and Implications for Major Depressive Disorder (MDD)**), followed by final conclusions *(***4.5 Conclusions***).*

4.1 Participant Characterization and Task Performance

Due to the thorough characterization of the study sample, males and females were matched on several demographic variables, such as SES, IQ and race, as well as developmental factors, like age and pubertal stage. Indeed, the careful screening of participants may explain the lack of sex differences in depressive symptoms, which are sometimes reported in healthy adolescents (Rose, 2002; Schraedley et al., 1999). Alternatively, the adolescents in this study may exhibit fewer risk factors than the typical teenager in the general population. For instance, common risk factors for developing MDD – poor academic achievement and low SES (O'Connell et al., 2009) – were well above average in the current sample. Other risk factors such as early substance use, diagnosis of another psychiatric disorder (e.g. anxiety, conduct disorder) and head injury (O'Connell et al., 2009) were exclusionary criteria for this study, minimizing the likelihood that these risk factors typically present in the average adolescent would be present in the current sample. However, other potential MDD risk factors were not accounted for in this study (e.g. childhood trauma, family dysfunction); therefore, the degree of MDD risk and representativeness to the general population cannot be conclusively determined for the youth in this study.

Contrary to my hypothesis, compared to boys, girls did not report 1) more negative self-perceptions, as measured with the Self-Perception Profile for Adolescents (SPP-A), 2) more negative meta-cognitions, as measured with the Meta-Cognitions Questionnaire for Adolescents (MCQ-A), or 3) more self-conscious affect, as measured with the Test of Self-Conscious Affect for Adolescents (TOSCA-A). Although girls did not report more prosocial behaviors, as measured with the Prosocial Tendencies Measure (PTM), they reported higher co-rumination scores, as measured with the Co-Rumination Questionnaire (CRQ), indicating that girls engage in more ruminative self-disclosure with friends, which is a prosocial behavior that occurs in a negative emotional context (Rose, 2002). Interestingly, girls in the current study did not endorse closer friendships relative to boys, as other studies have reported (Camarena et al., 1990; Rose, 2002; Rose and Asher, 1999), nor was co-rumination related to close friendships; thus, co-rumination may not be fostering better friendship quality among girls, as has been reported previously (Rose, 2002). However, co-rumination was positively correlated with mean scores on the PTM, particularly in girls, supporting the interpretation that co-rumination shares features with prosocial behavior.

In contrast to previous research showing that adolescent girls have lower self-esteem than boys (Allgood-Merten et al., 1990; McClure et al., 2010; Moksnes and Espnes, 2013), girls and boys in the current sample reported similar global self-worth. In fact, in the full sample, girls scored higher on Alpha Pride on the TOSCA-A, reflecting more pride in oneself, which may indicate that girls had higher self-esteem. This conclusion must be interpreted with caution, however, given that the Alpha Pride sub-scale of the TOSCA-A has low internal consistency (Tangney, 1989), and self-esteem was not measured directly in the current study. Interestingly, youth who reported more advanced pubertal development had lower global self-worth compared to youth in an earlier pubertal stage; this effect was only found in girls when the sexes were examined separately. Physical changes that occur over the course of puberty are generally perceived as more negative for girls and more positive for boys (Petersen and Crockett, 1985; Simmons et al., 1983; Taga et al., 2006; Tobin-Richards et al., 1983). Indeed, one study conducted in adolescent girls found that body mass predicted physical self-worth a year later (Knowles et al., 2009). Moreover, boys report greater self-esteem than girls in the following domains of physical self-esteem: physical strength, physical condition and physical self-worth (Altintas and Asci, 2008). Thus, self-esteem and self-worth may be more strongly tied to pubertal development, rather than gender per se.

4.2 Behavioral Responding during SRP and Control Trials

Responding during SRP conditions indicated that adolescents were more likely to endorse positive than negative qualities about themselves. Specifically, youth believed positive academic and social traits described them more than other traits, while negative social traits were endorsed the least. Many studies have reported a self-positivity bias, such that individuals are faster respond to and endorse positive rather than negative self-relevant information (Chen et al., 2014; Watson et al., 2007; Yang et al., 2014; Zhang et al., 2013); moreover, self-positivity is positively correlated with self-esteem in late adolescence/early adulthood (Zhang et al., 2013). Sex differences in responding were not observed during SRP conditions, indicating that boys and girls did not differ in their self-perceptions about emotionally-salient traits across domains of life that are generally relevant to adolescents (i.e. academic, social and physical). This conclusion is supported by the lack of sex differences in self-perception as measured by the SPP-A Social Competence and Global Self-Worth sub-scales. With regards to the Control condition, youth believed traits from all domains were malleable; however, positive academic traits were the least malleable. Boys and girls did not differ in their perceptions about the malleability of any traits, strongly indicating that the Control condition was perceived similarly by sex, and thus functioned as an adequate experimental control.

4.3 Behavioral Responding during Flanker Trials

Performance on the Flanker trials reflected that of previous studies, where participants were slower to respond during incongruent relative to congruent trials

(Bunge et al., 2002; Casey et al., 2000; Fan et al., 2002; Kelly et al., 2008; Mennes et al., 2011; Wager et al., 2005). This pattern was observed within both SRP and Control conditions. Across conditions, Post-SRP Incongruent and Post-Control Incongruent Flanker trails were the most difficult, as reflected by slower RT, than the corresponding congruent trials and congruent trials from the opposite condition. However, there were no differences in difficulty between the two types of incongruent trials, nor the two types of congruent trials, indicating that, for the most part, the SRP conditions did not increase the difficulty of the task. Similar patterns were observed with accuracy, which also reflects task difficulty, and errors of omission, which more closely represent lapses in attention (Matthews et al., 2000). Across all conditions, girls responded more slowly and committed more errors of omission than boys, perhaps because they perceived the entire task as more difficult, or perhaps because they were more deliberate in their responding. The design of this study does not provide a means to differentiate between response strategies; thus, future studies may consider parametric modulation of task difficulty or retrospective self-report as ways to address this question.

Importantly, post-hoc analysis of significant main effects revealed a condition-specific sex difference in performance, as indexed by errors of omission, such that girls made more errors than boys during Post-SRP Incongruent Flanker trials. Therefore, there is some evidence that the higher rates of omission errors in girls are due to SRP interfering with performance of the most difficult type of Flanker trial (i.e. Incongruent), perhaps by increasing executive load (Luciana, 2016). It is also possible that the effect of SRP on cognitive control performance was more pervasive for girls and persisted across conditions, contributing to their slower reaction times and higher rates of omission errors overall. The design of this study permitted a temporal dissociation of SRP and Control conditions of approximately one minute; however, that may not have been sufficient time for the influence of SRP to dissipate, particularly for girls. Examination of the functional connectivity of networks supporting SRP and cognitive control may provide further insight, as detailed below.

4.2 Functional Connectivity

4.2.1 State Functional Connectivity

Despite the lack of significant interactions between sex and task conditions in behavior, these interactions were present in functional connectivity results. Consistent with my hypothesis, girls displayed stronger DMN-FPN functional connectivity during Post-SRP Flanker trials. Post-hoc examination of these interactions indicated that functional connectivity differed by sex in Post-SRP, but not Post-Control Flanker conditions. It is notable that sex-by-condition interactions occurred between both local (right mPFC – MFG) and long-range (left DLPFC – right precuneus) connections, suggesting that affective SRP may limit the ability of DMN to decouple from FPN more broadly. Connectivity with the posterior cingulate cortex (PCC), the posterior DMN seed region, was not significantly related to sex, task condition or the interaction of sex and condition; however, the precuneus is also considered a posterior node of the DMN (Buckner et al., 2008; Fransson and Marrelec, 2008), which was identified with left DLPFC seed region analysis. In addition to stronger DMN-FPN connectivity, girls displayed more robust within-FPN functional connectivity (right IPL –MFG) and stronger fronto-striatal connectivity (left DLPFC – dorsal/ventral striatum) during Post-SRP Flanker trials, perhaps as a means to compensate for the ineffective decoupling of

DMN and FPN nodes. Indeed, the DLPFC – striatal circuit, in particular, is crucial for intact executive functioning (Alexander et al., 1990; Hampshire et al., 2012). The stronger within-FPN state functional connectivity observed in girls was not hypothesized; however, previous research has shown that the degree of functional coupling within FPN is positively related to successful inhibitory control in adults (Reineberg et al., 2015; Xu et al., 2014; Zhang and Li, 2012b). As much of the extant literature suggests, the normative pattern of connectivity during cognitive control is reflected by DMN-FPN anti-correlations (De Luca et al., 2006; Fox et al., 2005; Fransson, 2005; Greicius et al., 2003); thus, stronger within-FPN connectivity in girls may reflect an attempt to compensate – albeit insufficiently, given the larger number of omission errors committed during Post-SRP Incongruent Flanker trials – for ineffective decoupling of DMN-FPN during cognitive control. Notably, performance on Post-SRP and Post-Control Incongruent Flanker trials did not correlate with state functional connectivity; therefore, sex differences in state functional connectivity may represent distinct neural mechanisms in boys and girls to lead to similar performance (i.e. convergent sex differences) (Becker et al., 2016).

Several main effects of sex in state functional connectivity also emerged in this study. For instance, nodes of the FPN and DMN were more functionally correlated in girls compared to boys, regardless of task condition. This may suggest that girls demonstrated stronger coupling between DMN-FPN at a trait level, such that coupling between these networks is stronger in girls regardless of task context, which is confirmed through comparison with functional connectivity during a task-free state (see *4.3 Trait Functional Connectivity)*. In addition, compared to boys, girls showed stronger state functional coupling between left mPFC and the right posterior cerebellum. This particular region of the cerebellum has been repeatedly implicated in theory of mind and higher-order social cognition (Carrington and Bailey, 2009; Spunt and Adolphs, 2014; Van Overwalle et al., 2014), suggesting that its connectivity with mPFC, a key region for SRP, may support integration of social information with self-identity – a mechanism that may be more streamlined in girls compared to boys.

Finally, girls demonstrated stronger state functional connectivity between right IPL and left cuneus, a brain region supporting visuospatial selective attention (Hahn et al., 2006). Errors of omission were not correlated with functional connectivity between IPL and the cuneus; therefore, the higher rate of omission errors in girls may not reflect lapses in attention per se, but rather interference by SRP on behavioral responding. Participant responses to the task were not recorded following the 800 ms presentation of a Flanker stimulus; thus, it is not possible to determine whether youth eventually made a response to the stimulus 800 ms after its presentation. In order to understand the sex difference in errors of omission, the standard deviations of RT for all Flanker trials were compared by sex. Despite longer RT in girls, most responding on the Flanker trials occurred within 700 ms; however, girls showed significantly more variability in RT during all trial types ($F(1,47) = 9.780$, $p = 0.003$), indicating a range of SRP effects on inhibitory control performance, such that perhaps only a subset of girls experience interference from SRP trials.

4.2.2 Trait Functional Connectivity

Region of interest (ROI) RSFC analyses were conducted using results from the state functional connectivity analyses as masks; time courses from these ROIs were correlated with time courses from the DMN and FPN seed regions. These analyses were conducted to confirm that state functional connectivity did not reflect trait sex differences in functional coupling. Results from the ROI RSFC analyses demonstrated that only functional connectivity between DLPFC and precuneus was stronger in girls compared to boys, indicating that functional connectivity did change in a sex-specific fashion based on the task conditions (i.e. state functional connectivity). However, girls displayed stronger trait functional connectivity between a number of *other* DMN and FPN nodes in the whole-brain analyses. Girls showed stronger trait functional connectivity between 1) right DLPFC and middle temporal gyrus (MTG) 2) right DLPFC and left PCC, 3) bilateral mPFC and left superior parietal lobule (SPL) and 4) right PCC and left SPL, while there were no DMN-FPN functional connections that were more robust in boys. The MTG is part of the DMN (Buckner et al., 2008), while the left SPL has been identified as a node of the FPN (Scolari et al., 2015) and dorsal attention network (Corbetta et al., 2008), sometimes referred to as the dorsal fronto-parietal attention network (Szczepanski et al., 2013). Critically, DMN-FPN trait functional connectivity was positively associated with the number of incorrect responses on Post-SRP Incongruent Flanker trials in girls. Thus, overall, higher DMN-FPN trait functional connectivity predicted worse cognitive control performance in an affective SRP context, specifically in girls.

One potential mechanism through which DMN-FPN trait functional connectivity may influence cognitive control performance during an emotionally salient context is through co-rumination. Indeed, DMN-FPN RSFC significantly mediated the effect of sex on co-rumination, which, in turn, explained the sex differences in Post-SRP Incongruent Flanker errors of omission in the full sample. Co-rumination has not been studied in relation to cognitive control performance, nor have its underlying neural correlates been examined. However, given that it shares features with rumination (Rose, 2002), one might anticipate that higher co-rumination would predict worse cognitive control performance during an affective SRP context. Other studies have shown that higher rumination is positively linked with difficulty inhibiting negative information during an affective Go/No-Go task in adolescents (Hilt et al., 2014). Similarly, a study in healthy young adults showed that cognitive control impairments were observed when negative task stimuli were personally relevant to the individual; these cognitive control impairments were also positively related to rumination (Beckwe et al., 2014). Thus, co-rumination and rumination may be operating through similar mechanisms (i.e. stronger DMN-FPN trait functional connectivity) to disturb cognitive control performance in emotionally salient and personally relevant contexts.

In contrast, a lot of evidence indicates that within-DMN RSFC is a primary mechanism supporting rumination in individuals diagnosed with MDD (Berman et al., 2011; Hamilton et al., 2011; Whitfield-Gabrieli and Ford, 2012; Zhu et al., 2012) and even healthy controls (Berman et al., 2011; Luo et al., 2016). Likewise, in the current study, within-DMN trait functional connectivity was stronger in girls compared to boys and was positively correlated with co-rumination, as hypothesized. Thus, DMN-FPN trait functional connectivity may explain the link between higher co-rumination and worse cognitive control performance in an affective SRP context, while within-DMN trait functional connectivity may relate to co-rumination more directly. Importantly, these mechanisms appear to be represented in girls more so than boys, calling into question which factors shape DMN-FPN trait functional connectivity.

4.2.3 State versus Trait Functional Connectivity

Direct comparisons of state and trait functional connectivity in the nodes identified in both task-regressed and resting state functional connectivity indicated that girls had stronger FPN-DMN functional connectivity during the task state, as compared to the resting state. Notably, the sexes did not differ in functional connectivity during rest, except in the case of an FPN-FPN connection (right DLPFC – MFG), where boys showed stronger functional connectivity than girls, who had stronger task-based functional connectivity than boys. Importantly, trait functional connectivity was generally more robust than state functional connectivity, similar to previous studies showing smaller correlation coefficients in task-regressed versus resting state functional connectivity analyses (Fair et al., 2007; Zhang and Li, 2012a; Zhang and Li, 2012c), purportedly due to attenuation of BOLD fluctuations during task engagement (Fransson, 2006). Indeed, more robust trait functional connectivity may explain why co-rumination and task behavior were only associated with resting, but not task-regressed, functional connectivity. It is noteworthy that despite robust trait functional connectivity, effect sizes were generally larger for state functional connectivity. This discrepancy may be explained by results showing that compared to boys, girls had stronger state functional connectivity, as well as stronger functional connectivity overall. Thus, effect sizes of state functional connectivity analyses may be capturing these sex differences, which were not as readily observed in trait functional connectivity.

4.4 Strengths, Limitations and Alternative Interpretations

Strengths of this study include a well-characterized sample, an experimental design that permitted the comparison of state and trait functional connectivity and rigorous data processing that included motion scrubbing. Girls and boys were very well-matched on various demographic and developmental variables, which served to eliminate potential confounds that could explain the current findings. However, one limitation of this work was the relatively small sample size, which was especially relevant given that task-regressed functional connectivity analyses only includes frames of data from Flanker trials that did not exceed the motion threshold. This analytical approach greatly reduced the amount of data used for analysis; albeit, to a similar degree in males and females. However, sex differences in state functional connectivity were observed with medium effect sizes, indicating that there was sufficient power to detect meaningful effects.

In spite of numerous sex differences in functional connectivity, the number of behavioral sex differences in the current study was very sparse. Indeed, a group difference in errors of omission during Post-SRP Incongruent Flanker trials was the only finding where boys and girls differed in their responding in a context specific to SRP. Notably, this finding, which was pursued due to *a priori* hypotheses, was detected post-hoc despite a lack of a significant interaction between sex and task condition. Therefore, this particular finding must be interpreted with caution. It is possible that sex differences in Flanker performance are not as robust as sex differences in functional connectivity. Indeed, this may be the case given that the current sample was generally healthy, and sex differences in cognitive control performance are not commonly found in healthy youth despite sex differences in brain activation (Alarcon et al., 2014; Christakou et al., 2009; Cservenka et al., 2015; Hjelmervik et al., 2014; Li et al., 2010; Rubia et al., 2010; Rubia et al., 2013; Schweinsburg et al., 2005; Weiss et al., 2003; White et al., 2014). Likewise, a lack of sex differences in the identification with positively- and negatively-valenced self-relevant statements may also be due to a small sample size, given that previous studies have reported sex differences in self-esteem during adolescence (Allgood-Merten et al., 1990; McClure et al., 2010; Moksnes and Espnes, 2013). Replication of this study with a larger sample may reveal more sex differences in behavioral responding.

The design of the current study did not permit analysis of cognitive control performance or functional connectivity based on the domains and/or valence of the SRP statements. In every SRP block, statements were presented randomly and consecutively in order to sustain an SRP effect that would carry over to the subsequent set of Flanker trials. Thus, the effects of domain and valence across SRP trials were averaged and their unique effects cannot be measured. It is likely that either valence or domain of the SRP phrases may have differentially influenced SRP BOLD signal and its sustained effect on Flanker trials. Given that adolescents in the present study reported identifying with more positive than negative phrases, it is possible that negatively-valenced statements were not contributing to the SRP effect as readily as positively-valenced cues; however, because the effects of individual statements on cognitive control trials could not be determined, this conclusion must be confirmed with a different task design. Future studies may consider separating positive and negative SRP conditions into separate blocks to measure their unique effects. Additionally, personalizing statements to reflect positive or negative self-relevant thoughts of each individual (Carew et al., 2013) may increase the effect of SRP on cognitive control.

Functional connectivity is generally considered a relatively stable measure (i.e. trait functional connectivity) (Braun et al., 2012; Chen et al., 2015; Chou et al., 2012; Du et al., 2015; Franco et al., 2013; Guo et al., 2012a; Hjelmervik et al., 2014; Rzucidlo et al., 2013; Shah et al., 2016; Song et al., 2012; Zuo and Xing, 2014) across participants and mental states (Calhoun et al., 2008; Cole et al., 2014; Krienen et al., 2014; Smith et al., 2009), which has made it possible to examine its relationship to behavioral correlates (Baur et al., 2013; Fulwiler et al., 2012; Modi et al., 2015; Pan et al., 2016; Takeuchi et al., 2013). However, recent work demonstrates that there is an appreciable difference in network functional connectivity between task and resting states, such that state functional connectivity effects explain as much or more of the variance in inter-individual connectivity than trait effects (Geerligs et al., 2015). Moreover, differences in functional connectivity between individuals are not static, but greatly depend on the mental state during which these measurements are obtained. The results of the present study support this assertion by demonstrating that sex differences in functional connectivity occurred across task conditions and between task and rest conditions. This suggests that consideration must be given to the participant’s mental state when determining under what context the functional connectivity architecture of an individual provides the most meaningful association to the behavioral correlate being studied.

There are a variety of analytic approaches used to measure task-based functional connectivity, including removal of linear task effects with regression (Fair et al., 2007), removal of task-induced variance with independent component analysis (Arfanakis et al., 2000) and psychophysiological interaction (O'Reilly et al., 2012), with the latter options being most effective for block designs. Linear regression of task effects is not restricted by the experimental design as long as task effects are effectively modeled and removed. Indeed, previous work has shown that this approach may not remove all task-related signal (Fair et al., 2007); however, this very signal may represent altered functional connectivity due to task engagement (Fair, 2007; Fransson, 2006; Hampson et al., 2004; Lowe et al., 2000; Zhang and Li, 2010; Zhang and Li, 2012c) (i.e. state functional connectivity). Even so, the possibility that nonlinear task effects remain and alter correlation coefficients cannot be ruled out.

4.5 Future Directions and Implications for Major Depressive Disorder (MDD)

Studying the transition from internally- to externally-directed thought will be an important avenue of research to continue in the field of MDD (Belleau et al., 2015; Jacobs et al., 2014; Wagner et al., 2015). The inability to deactivate DMN or decouple from FPN has been linked to a decline in cognitive control performance in healthy individuals (Anticevic et al., 2010; Hampson et al., 2010; Keller et al., 2015; Kelly et al., 2008; Li et al., 2007) and individuals in remission from MDD (Bartova et al., 2015; Jacobs et al., 2014); however, the utility of this mechanism for understanding risk for major depression is unknown. Researchers have posited that the imbalance between DMN and FPN, as well as other task-relevant networks, such as the cingulo-opercular and salience networks, are associated with internally-focused cognitive styles (i.e. rumination) and a failure to attenuate DMN activity in transitions from rest to task (Hamilton et al., 2011; Marchetti et al., 2012). Understanding this mechanism in at-risk youth may provide an avenue for early intervention, such as mindfulness training, which has been shown to alter the functional connectivity of DMN-FPN functional connectivity and activation (Creswell et al., 2016; Tomasino and Fabbro, 2016). In particular, elucidating sex differences in this mechanism may help explain the disproportionate risk afflicting girls and young women.

Implementing more sophisticated functional connectivity methods may provide additional insight about the pervasiveness of the sex differences reported here. One approach involves graph theory-based functional connectivity analyses to elucidate more global properties of functional connectivity architecture that may help predict onset of MDD. Although many studies have begun to study aberrations in brain functional connectomics that differentiate patients with MDD (Guo et al., 2012b; Luo et al., 2015; Qin et al., 2014; Wang et al., 2014; Ye et al., 2015; Zhang et al., 2014; Zheng et al., 2015), including adolescents with MDD (Jin et al., 2011), no studies have examined whether sex differences in functional global network architecture confer risk for MDD, even though sex differences in global and nodal network topology have been reported previously in healthy participants (Casanova et al., 2012; Tian et al., 2011). In fact, one study reported sex differences in the association between past childhood maltreatment and inhibitory control network functional connectivity, as measured with graph theory methods (Elton et al., 2013). Childhood maltreatment, especially sexual abuse, is one risk factor for MDD that occurs more commonly in girls, compared to boys (Dunn et al., 2012; Kessler, 2000); thus, findings from studies like Elton and colleagues' (2013) provide further information about network topology using graph theory methods in order to understand discrepancies in the risk for MDD across the sexes.

Moreover, it is possible to examine changes in functional connectivity at a smaller time-scale using dynamic functional connectivity. Many studies have now used this approach to track changes in functional connectivity and cognitive states over the course of seconds (Allen et al., 2014a; Gonzalez-Castillo et al., 2015; Hutchison et al., 2013; Larson-Prior et al., 2011; Rissman et al., 2004; Sakoglu et al., 2010). Future research may consider using dynamic functional connectivity to assess the temporal profile of the sustained effect of SRP on cognitive control, as measured by DMN-FPN functional connectivity, and sex differences therein. Indeed, one study using dynamic functional connectivity reported that functional coupling between the DMN and the salience network, specifically the insular cortex, is linked with rumination in patients diagnosed with MDD (Kaiser et al., 2016). Similar approaches should be employed with youth at risk for developing MDD to track if and how these mechanisms confer risk for MDD.

CHAPTER 5: SUMMARY AND CONCLUSIONS

Healthy male and female adolescents demonstrated a differential impact of affective SRP on cognitive control task performance that was mirrored by DMN-FPN functional coupling. Specifically, induction of an affective SRP state interfered with the expected pattern of anti-correlation between DMN and FPN and led to worse cognitive control performance in girls only. Importantly, sex differences in this pattern of connectivity were absent in Control conditions, indicating that these effects were due to the affective SRP induction. Although behavioral effects were small, results indicated that girls' performance (i.e. errors of omission) suffered more than boys' during cognitive control trials that were preceded by the affective SRP induction.

Importantly, co-rumination, which was endorsed to a larger degree by girls than boys, mediated the effect of sex on Post-SRP Incongruent Flanker errors of omission, while DMN-FPN trait functional connectivity mediated sex differences in co-rumination. Thus, co-rumination may be a mechanism through which trait functional connectivity between FPN and DMN impairs cognitive control performance in emotionally salient and personally relevant contexts. However, a causal effect of DMN-FPN trait functional connectivity on co-rumination cannot be assumed, in fact, bidirectional effects are likely present, providing two potential avenues for intervention – neural and environmental. Together, these findings suggest that sex differences in both co-rumination and DMN-FPN trait functional connectivity may be important for understanding sex differences in risk for MDD. Future studies must determine their relevance using similar experimental paradigms longitudinally and with adolescents who are at risk for MDD.

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APPENDICES

Appendix A. Affective SRP-Flanker Task Exit Questionnaire

1. Did you understand the task instructions? (circle one)

   YES NO

2. How often did you identify with the statements presented in the task? (circle one)

   1) Never

   2) A few times

   3) Sometimes

   4) Many times

   5) All the time

4. Identifying with the statements made you feel:

   1) Very upset

   2) Somewhat upset

   3) No emotion

   4) Somewhat happy

   5) Very happy

3. What strategies did you use to help you decide what direction the arrow was pointing?

5. How important was it for you to do well on this task?

1) Not important at all

2) Moderately unimportant

3) Neither important nor unimportant

4) Moderately important

5) Very important

6. How did you feel during the task?

1) Very tense

2) Somewhat tense

3) Neither tense or relaxed

4) Somewhat relaxed

5) Very relaxed

7. How interested were you in doing the task?

1) Not at all

2) A little

3) Moderately

4) Very

8. Comments?

Appendix B. Affective SRP Stimuli

Academic positive	Physical positive	Social positive
Fast learner	Very good-looking	Very popular
Studies hard	Has great hair	Easy to talk to
Really intelligent	In good shape	Goes to parties
Honor student	Has clear skin	Has a best friend

Academic negative	Physical negative	Social negative
Isn’t very smart	Unattractive	Socially awkward
Has failed a test	Has really bad skin	Kind of a loner
Gets bad grades	Overweight	Is a liar
Skips class a lot	Has crooked teeth	Gets teased

Appendix C. Affective SRP-Flanker Task Instructions

During this task, you will be completing three different types of trials. During the first type of trial, you will first see a cue that reads, “DOES THIS DESCRIBE YOU?” followed by a series of short phrases. You must decide whether they describe you and choose YES or NO. If YES, press button 1, and if NO, press button 2. You must choose one option even if don’t completely agree with the YES and NO options. Please only respond when you see YES and NO on the screen. There is no right answer, we only want to know whether the phrase describes you or not.

During the second type of trial, you will first see a cue that says, “CAN THIS CHANGE?” followed by similar short phrases. This time, you must decide whether these qualities or facts can change in *other* people. If the answer is YES, press button 1 and if the answer is NO, press button 2. You must choose one option even if don’t completely agree with the YES and NO options. Please only respond when you see YES and NO on the screen. There is no right answer; we only want to know your opinion about whether these traits and facts can change in *other* people.

Lastly, during the third type of trial, you will do something very different. First, you will see a cue that reads, “CENTER ARROW” followed by a row of arrows in the middle of the screen. Your job is to press button 1 if the *center* arrow is pointing left or button 2 if the *center* arrow is pointing right, regardless of where the other arrows are pointing. These trials move very fast, so be sure to focus your attention and try your best. Also make sure you respond before the arrows disappear from the screen, otherwise the computer will mark your response as incorrect.

These trials will appear in a different order than I have described, so make sure you pay attention to the cues, “DOES THIS DESCRIBE YOU?”, “CAN THIS CHANGE?” or “CENTER ARROW”, so that you know what to do.

Do you have any questions?