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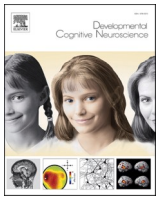

Brain network connectivity during peer evaluation in adolescent females: Associations with age, pubertal hormones, timing, and status

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ABSTRACT

Despite copious data linking brain function with changes to social behavior and mental health, little is known about how puberty relates to brain functioning. We investigated the specificity of brain network connectivity associations with pubertal indices and age to inform neurodevelopmental models of adolescence. We examined how brain network connectivity during a peer evaluation fMRI task related to pubertal hormones (dehydroepiandrosterone and testosterone), pubertal timing and status, and age. Participants were 99 adolescents assigned female at birth aged 9–15 ($M = 12.38$, $SD = 1.81$) enriched for the presence of internalizing symptoms. Multivariate analysis revealed that within Salience, between Frontoparietal – Reward and Cinguloopercular – Reward network connectivity were associated with all measures of pubertal development and age. Specifically, Salience connectivity linked with age, pubertal hormones, and status, but not timing. In contrast, Frontoparietal – Reward connectivity was only associated with hormones. Finally, Cinguloopercular – Reward connectivity related to age and pubertal status, but not hormones or timing. These results provide evidence that the salience processing underlying peer evaluation is jointly influenced by various indices of puberty and age, while coordination between cognitive control and reward circuitry is related to pubertal hormones, pubertal status, and age in unique ways.

1. Introduction

1.1. Puberty onset as a sensitive period of development

Puberty is associated with changes in brain functioning that support the development of social behavior (Crone et al., 2020; Crone and Dahl, 2012a; Nelson et al., 2005a, 2016; Pfeifer and Allen, 2021a; Vetter--O'Hagen and Spear, 2012; Vijayakumar et al., 2018a). Preclinical animal studies indicate that hormonal changes impact secondary sex characteristics and also shift brain functioning during adolescence, ultimately influencing the development of social behaviors (Schulz et al., 2009; Schulz and Sisk, 2006). Specifically, testosterone directly impacts social behaviors necessary to facilitate sexual reproduction such as play, aggression, and flank-marking (Schulz and Sisk, 2016a). Female animal hormones are less well researched, but available evidence indicates that pubertal hormones also play a role in defining adult social behavior necessary for reproduction (Schulz and Sisk, 2006, 2016a). These behavioral changes may result from hormonal modulation of cellular

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functioning in subcortical and prefrontal brain regions including the amygdala, hypothalamus, hippocampus, ventral striatum, and anterior cingulate cortex (Ahmed et al., 2008; Blakemore et al., 2010; Goddings et al., 2019; Piekarski et al., 2017). This research has culminated in theories positing that during puberty, widespread brain circuitry is honed and perhaps even solidified – permanently impacting the development of social behavior (Schulz et al., 2009). This theory is currently being applied to human research to better understand how puberty may alter brain functioning supporting social behavior and mental health trajectories. However, despite ongoing efforts, our knowledge remains limited as to how different aspects of puberty relate to brain functioning in humans.

In humans, puberty is a developmental process driven by neuroendocrine changes. Adrenarche begins with the secretion of androgens in the adrenal cortex around age 6 and represents the initiation of puberty. Later, beginning anywhere from age 9–15 years of age, the secretion of gonadotropin-releasing hormone in the hypothalamus gives rise to the gonadarche phase, culminating in complete physical maturation (Dai and Scherf, 2019; Dorn et al., 2019). The neuroendocrine changes characterized by the release and rise of hormones including dehydroepiandrosterone (DHEA) and testosterone (Biro et al., 2014).

During adolescence, shifting pubertal hormones coincide with changing external body traits (Rudolph, 2014; Susman and Dorn, 2009), rapid reorganization of brain circuitry (Crone et al., 2020; Nelson et al., 2016; Tamnes et al., 2017), and new social priorities (Goddings et al., 2012; Quevedo et al., 2009) where adolescents begin to focus on forming and maintaining close social bonds with peers. For some adolescents, puberty is also associated with significant increases in risk for psychopathology. Existing research indicates that several markers of the pubertal transition including changes to pubertal hormones (Andersen et al., 2023; Byrne et al., 2017; Dorn et al., 2019; Susman et al., 1987), adolescents' self-reported external body changes (i.e. perceived pubertal status) (Angold and Rutter, 1992; Kilkenny et al., 2008), and the timing of these bodily changes (i.e. perceived pubertal timing) (Barendse et al., 2022; Barendse and Pfeifer, 2021; Ellis et al., 2019; Ullsperger and Nikolas, 2017) all may play a role in the onset of psychopathology (Mendle, 2014; Rudolph, 2014). Despite the causal evidence from animal models implicating puberty as driving alterations to brain functioning, it remains unclear how the different markers of the pubertal transition are associated with specific brain circuitry functions. This knowledge gap makes it difficult to mechanistically link different components of puberty to social behavior and mental health.

1.2. Puberty, brain functioning, and social behavior

Neurodevelopmental models postulate that the transition to adolescence is characterized by heightened social-affective and reward circuit sensitivity (Blakemore and Mills, 2014; Braams et al., 2015; Crone and Dahl, 2012a; Galvan, 2013; Ladouceur et al., 2019), increased engagement of cognitive control networks (Marek et al., 2022) and strengthening of integration among these brain circuits (Luna et al., 2015; Marek and Dosenbach, 2018). Together, these changes to brain circuitry are thought to contribute to heightened sensitivity to peers in novel social contexts – providing opportunities to engage a maturing cognitive control system (Casey et al., 2016; Crone et al., 2020; Crone and Dahl, 2012a; Luna et al., 2015). Although this broad understanding of the neurodevelopmental processes supporting changes in social behavior exists, the specific mechanisms driving these changes (e.g., puberty, age, environment) remain unclear.

As with animal work, associations between puberty, brain functioning, and social behavior have been observed in humans. This research has typically examined the brain's response to socially salient tasks (Dai and Scherf, 2019; Pfeifer and Allen, 2021b) such as peer rejection (Masten et al., 2013), affective face processing (Scherf et al., 2012), and self/other evaluation (Dai and Scherf, 2019; Jankowski et al., 2014; Pfeifer and Allen, 2021b; Silk et al., 2014). Consistent with the animal literature, human findings implicate the amygdala and prefrontal cortex as being closely linked to the pubertal process (Dai and Scherf, 2019; Delevich et al., 2021; Ferri et al., 2014) and further suggest puberty as having far reaching effects on social-affective, attention, salience, and cognitive control circuitry (Dai and Scherf, 2019; Vijayakumar et al., 2018b).

Peer evaluation paradigms are powerful tools for testing the link between puberty and brain functioning supporting social behavior, and are particularly informative with adolescent girls given that girls may experience increased sensitivity to peers relative to boys (Rudolph, 2014, 2002). Peer evaluation paradigms also capitalize on the social re-orientation of adolescence, which is characterized by rapid neurodevelopment and a growing prioritization of peer opinions and interactions, often manifesting as hypersensitivity to peer evaluation (Crone et al., 2020; Crone and Dahl, 2012b; Ladouceur et al., 2019; Nelson et al., 2005b; Silk et al., 2014). The timing of adolescent social re-orientation parallels puberty, prompting researchers to theorize that social re-orientation and puberty are integrally related (Crone and Dahl, 2012b; Pfeifer and Allen, 2021b). fMRI evaluation tasks elicit brain activation within the prefrontal cortex, ACC, insula, striatum, and temporal and parietal cortices (Crone et al., 2020; Somerville et al., 2013) – regions that are separately associated with puberty (Goddings et al., 2019). Together, this work suggests that probing puberty and brain function associations during a peer evaluation task may be a fundamental step in understanding how puberty relates to brain functions supporting social behavior.

1.3. Advancing puberty and brain functioning research

Current research examining the association between puberty and brain function have several limitations. First, most studies investigating associations between puberty and brain function solely measure status and statistically remove the effect of age (Pfeifer and Allen, 2021b). This focus on status may limit our knowledge of how different pubertal indices and age relate to brain circuitry. For example, although evidence suggests that hormones, pubertal status, and pubertal timing are each associated with reward, salience, and social-affective brain regions (Dai and Scherf, 2019; Pfeifer and Allen, 2021b; Sisk and Zehr, 2005; Urošević et al., 2014), other work reported that perceived pubertal timing and hormones may be uniquely related to cognitive control regions (Laube et al., 2020). One study also showed that hormonal effects on the brain are significantly larger than pubertal status effects (Braams et al., 2015).

Second, no studies to date have disentangled how different markers of puberty are associated with brain functioning during peer evaluation tasks. Specifically, hormone levels and brain functioning associations during peer evaluation fMRI tasks provide insight into how biological antecedents of puberty may affect brain circuitry that is essential for adolescent social behavior. Perceived pubertal status associations with brain functioning during peer evaluation fMRI tasks would inform how general processes such as perception of bodily changes link with socially relevant brain circuitry. Tests of how perceived pubertal timing (i.e., status relative to same-aged peers) relate to brain function may inform how the perception of physically maturing earlier or later than one's peers may manifest at the level of the brain.

Third, most studies do not attempt to disentangle sex and age effects. Differences in pubertal processes based on biological sex are well established (Susman and Dorn, 2009); one way to address this concern is to isolate analyses to only one biological sex. Chronological age effects are difficult to isolate from puberty (Dai and Scherf, 2019); thus, testing alternative statistical models beyond the typical approach of including age as a covariate is one means of expanding knowledge of unique age and puberty effects.

Finally, most existing puberty research focuses on brain activation of specific regions (Dai and Scherf, 2019). Given that brain regions do not function in isolation of one another, connectivity approaches may

provide complimentary data needed to refine neurodevelopmental models of social behavior (Casey et al., 2016). Specifically, a brain network perspective would include probing how well-known brain circuitry involved in social, reward, salience/attention, and cognitive control (i.e., processes honed during adolescence and relevant to social behavior) relate to hormones, pubertal status, and pubertal timing. This network-based method would limit inconsistencies generated by probing specific, often variably defined regions, and provide a broader test of how puberty relates to brain function. Overall, examining areas of specificity in which pubertal indices are associated with brain connectivity during a peer evaluation task may identify novel targets for further evaluation and eventual intervention.

1.4. The present study

In the present study we incorporated a multimodal assessment of puberty and extracted network connectivity during a peer evaluation fMRI task. Although peer evaluation fMRI tasks may more strongly elicit networks involved in social processes (e.g. Default, Reward, Salience) relative to cognitive control networks, we nonetheless probed broad brain networks with regions known to support processes relevant to social behavior and puberty (Crone and Dahl, 2012b), including Default Mode (DM), Reward, CinguloOpercular (CO), FrontoParietal (FP), Salience (SN), Ventral Attention (VAN), and Dorsal Attention (DAN) networks. We identified significant associations among brain network connectivity and five developmental outcomes – dehydroepiandrosterone (DHEA), testosterone, perceived pubertal status, perceived pubertal timing, and age – in girls transitioning to adolescence. Given the relatively nascent state of the literature linking puberty with brain connectivity (Dai and Scherf, 2019; Gracia-Tabuenca et al., 2021), and the recent guidance on improving brain-behavior association studies (Marek et al., 2022), we chose to conduct a data-driven analysis combining multivariate statistical learning with cross-validation to test how pubertal factors and brain network connectivity are related.

Based on existing neurodevelopmental models and prior research (Blakemore and Mills, 2014; Crone and Dahl, 2012b; Goddings et al., 2012; Luna et al., 2015; Pfeifer and Allen, 2021b; Urošević et al., 2014; van Duijvenvoorde et al., 2016; Vijayakumar et al., 2018b), we hypothesized that the strongest associations across our pubertal indices would be evident with the DMN, Reward, and Salience networks given the peer evaluation context (Crone et al., 2020; Somerville et al., 2013; van Duijvenvoorde et al., 2016) and existing preliminary work emphasizing puberty's potential impact on social-affective circuitry during the transition into adolescence (Goddings et al., 2019, 2012; Ladouceur et al., 2019). Further, based on prior work, we hypothesized that perceived pubertal timing and hormones would show more robust associations with cognitive control and reward networks (Ladouceur et al., 2019; Laube et al., 2020). Given data indicating that cognitive control functions continue to be refined into adulthood relative to the already sensitized social-affective circuitry in early adolescence (Luna et al., 2015; Marek et al., 2015; Marek and Dosenbach, 2018), we anticipated cognitive control networks would most strongly link with age. Finally, we posited that hormones would show the largest effects with brain network connectivity based on theoretical and empirical research (Braams et al., 2015; Byrne et al., 2017; Goddings et al., 2012; Ladouceur et al., 2019; Vijayakumar et al., 2018b) and preclinical research in animals (Schulz and Sisk, 2006, 2016a; Sisk and Zehr, 2005).

2. Material and methods

2.1. Participants

Participants were recruited as part of a larger, longitudinal study on the biological and behavioral stress response and risk for internalizing symptoms and self-injurious thoughts and behaviors in adolescent girls. This larger sample included 229 adolescents assigned female sex at birth ($M = 12.38$, $SD = 1.81$; range 9–15 years old). The sample was enriched for internalizing symptoms; adolescent females with a history of life stress including chronic peer problems (e.g., bullying), changes in home/family, depressive symptoms, and/or prior suicidal thoughts were recruited from local community clinics, inpatient units, outpatient mental health agencies, high schools, and the general community using flyers and mass email advertisements. Exclusionary criteria included pervasive developmental disorders, psychosis history, intellectual disability, chronic medical disease (e.g. autoimmune disorder, diabetes), or factors preventing study completion (e.g. English fluency, proximity to lab).

This inclusion criteria resulted in a sample of adolescent females with a wide range of clinical symptoms. Because of this clinical diversity, this sample is consistent with what might be expected for a group of adolescent females, where there is an increase in psychopathology and particularly internalizing symptoms (Centers for Disease Control and Prevention, 2021; Costello et al., 2011).

The final analytical subsample was comprised of participants that were eligible and interested in completing an fMRI scanning session ($n = 138$; 60% percent). Demographic differences between this subsample and the larger 229 sample were minimal and are reported in the supplemental material. Within the scanned subsample, participants were excluded for missing pubertal data ($n = 11$), quality issues with neuroimaging ($n = 24$; see below for details) or both ($n = 4$), resulting in a final sample of $n = 99$ for this investigation. Time between the initial baseline visit and the fMRI scan session for the 99 participants was, on average, 17 weeks ($SD = 27.56$). For the present sample (n = 99), participants self-identified as Black or African American ($n = 37$), Asian ($n = 2$,), White ($n = 38$), Hispanic/Latinx ($n = 5$), American Indian or Alaska Native ($n = 2$), or more than one race/other (n = 15) (see Supplemental Material for more detail on race, ethnicity, and gender reporting). 78 percent of the sample reported taking a medication, which included psychotropic (29%), allergy (8%), or both (5%). Of the 99 participants included in primary analyses, approximately 58% self-reported that they had experienced menarche. A portion of this sample has been analyzed in one prior study using the same fMRI task (Pelletier-Baldelli et al., 2023); this prior study focused on identifying social goals and associated brain connectivity, with no attention to puberty and age links with brain function. Participants' assent and caregiver consent was obtained according to the Declaration of Helsinki, and all consent and study procedures were pre-approved by the University's Institutional Review Board.

2.2. Puberty measures

2.2.1. Pubertal hormones

All hormones were collected from saliva at the initial visit, separate from the subsequent scanning session. We collected DHEA and testosterone given that these hormones have been linked with brain changes in adolescence (Byrne et al., 2017; Goddings et al., 2019; Ladouceur et al., 2019; Maninger et al., 2009; Nguyen et al., 2013; Vijayakumar et al., 2018b). The selection of DHEA and testosterone hormones was based on literature stating that both hormones rise with pubertal development (Biro et al., 2014) but are not as influenced by the menstrual cycle compared to other commonly investigated hormones including estradiol and progesterone. Further, both hormones are mostly considered part of adrenarche in females, and existing research supports adrenarche as a sensitive period of neurodevelopment impacting mental health (Byrne et al., 2017).

Testosterone levels were collected with salivary swab while DHEA was collected via passive drool. Consistent with prior approaches (Herting et al., 2021), we accounted for the effect of caffeine, birth control, BMI, and time of sample by extracting residuals from models where these variables predicted each hormone level separately. Residuals from models accounting for the effect of these confounds were included as DHEA and testosterone outcomes of interest.

2.2.2. Perceived pubertal status

The Pubertal Development Scale (PDS) was used to assess perceived pubertal status (Petersen et al., 1988). For both adolescents and the caregiver, a mean rating was generated based on the five items rated on a four-point scale (Cheng et al., 2021; Herting et al., 2021). Higher scores indicate more advanced perceived pubertal status. Consistent with prior work (Giletta et al., 2015; Rudolph, 2008) we used the combined average of self-report and caregiver scores (r =0.86).

2.2.3. Perceived pubertal timing

Perceived pubertal timing was calculated by extracting the residuals from a model where age predicted perceived pubertal status (Barendse and Pfeifer, 2021; Dorn, 2006; Rudolph, 2014). This perceived pubertal timing score was used a dependent variable in subsequent analyses.

2.3. fMRI measures

2.3.1. fMRI Task

Brain function was examined using a social evaluation fMRI task (Miller et al., 2019; Pelletier-Baldelli et al., 2023; Somerville et al., 2013). Participants were told that the task examined how their brains responded to an initial interaction with a similar aged, same-sex peer. During the task, participants passively viewed a screen that indicated whether a peer was monitoring them via camera in real-time ("video on") or not ("system off"). The "video on" condition reflected an active evaluation condition while the "system off" condition was an evaluation anticipation condition as participants were told the camera could turn back on at any moment. The resulting task was block design with the two pseudo-random conditions (i.e. "video on" and "system off") for a total task time of 5 minutes and 45 seconds. Participants were not actually monitored and were debriefed following task completion in accordance with our approved IRB protocol.

2.3.2. fMRI preprocessing and postprocessing

Imaging data were minimally preprocessed using fMRIPrep v.1.5.3 (Esteban et al., 2019). This approach included intensity correction, skull-stripping, spatial normalization, segmentation, slice time correction, motion correction, and co-registration. Next, scans were corrected for noise related to motion parameters, white matter, cerebrospinal fluid, and global signal. Motion was accounted for by censoring timepoints with framewise displacement greater than.2 mm. Within the larger 138 scanned sample, 24 participants were excluded for quality checks as follows: 9 participants were excluded from analyses due to scanner or task administration issues and 15 participants were excluded because greater than 50% of their imaging data was motion censored. The average framewise displacement in the final sample was.1.

2.3.3. Brain network connectivity

To examine connectivity, we first extracted regional brain signal across task conductions using an established functional brain atlas (Power et al., 2011; Seitzman et al., 2020). We chose to collapse across the "video on"/evaluation and "system off"/anticipation conditions and model connectivity across task conditions for several reasons: first, the across task analysis increased power and second, we hypothesized that participants were attuned to peer evaluation even when the screen indicates they were not being observed, which is supported by prior work using this task that showed similar activations across the anticipation and evaluation conditions (Somerville et al., 2013). Finally, existing research indicates that similar intrinsic networks to those analyzed here are generated using task-based fMRI, resting-state, and the combination (Elliott et al., 2019). Regional brain activation extraction resulted in a 138 (volume) × 300 (region) timeseries matrix for each participant, where each column represented activation of a single brain region. We next reduced the timeseries matrix to the regions belonging to brain networks we believed most relevant to peer evaluation and puberty based on existing literature (Crone et al., 2020; Crone and Dahl, 2012b; Somerville et al., 2013). These networks included the SN, VAN/DAN, FP, DMN, Reward, and CO networks, with regions identified as belonging to each network based on prior work (Power et al., 2011; Seitzman et al., 2020). This timeseries matrix was then transformed to create a large correlation matrix reflecting correlations among all regions. The full connectivity matrix was then partitioned to isolate within (7 networks) and between-network (21 networks) connectivity. Between network connectivity reflected every possible between network comparison using the original 7 networks (e.g., default – salience or reward – ventral attention connections only). These 28 within and between correlation matrices were used as predictors in subsequent analyses (Rudolph et al., 2018).

2.4. Analysis plan

2.4.1. Multivariate partial least-squares regression approach

2.4.1.1. Overall approach. The primary analyses included the two pubertal hormones – DHEA and testosterone, perceived pubertal timing, and perceived pubertal status as outcomes and the brain connectivity matrices as predictors in a multivariate (i.e., multi-response) partial least-squares regression (PLSR); age was included as a fifth outcome of interest to test specificity of results (Fig. 1). The multivariate PLSR approach was based on existing work (Abdi and Williams, 2013; Krishnan et al., 2011; Rudolph et al., 2018, 2017). Broadly, PLSR is a data reduction technique, where we reduce the brain connectivity correlation matrices to a limited number of orthogonal components that most significantly relate to our pubertal and age outcomes. In this way, we identify meaningful relations between high-dimensional patterns brain connectivity and puberty while limiting the number of tests conducted, further reducing the false positive rate through means of multivariate modeling (Marek et al., 2022). This PLSR analyses was conducted using a stepwise approach to further reduce the number of tests. The first step was the multivariate analyses in which we tested all within- and between-network connectivity relations across all developmental outcomes. The second step focused on the within- and between-network combinations that performed well in the first step after corrections for multiple comparisons. The second step provided information on specificity of associations (see supplement for details).

2.4.1.2. Model Performance. To assess overall model performance, we applied permutation testing (Rudolph et al., 2018). As in prior work (Rudolph et al., 2018), significant models were identified by having a Kolmogorov–Smirnov (KS) p value passing Bonferroni correction and an effect size >0.2. All significant findings and included post-hoc sensitivity analysis where we determined the potential influence of motion, medication, and time between the baseline puberty/age assessment and MRI scan on our findings. Specifically, we reran the PLSR analyses with one model accounting for the effect of motion, and a second model that accounted for the effects of both medication and time between assessments (see supplement for details). Thus, models meeting our significance criterion across all sensitivity analyses from the first step were examined in the second step where we evaluated specificity of network connectivity patterns and each developmental outcome of interest.

2.4.1.3. Model predictive features. For visualization purposes, we probed the network connectivity patterns among the three networks that were robustly associated with our developmental outcomes. Specifically, we extracted the top 10 connections from each network connectivity pattern that robustly linked with our five developmental outcomes. The top 10 connections were identified based on the absolute value of β weights. The top 10 connections were then extracted for visualization with a standardized brain surface using Surface software (McCausland Center for Brain Imaging., 2021).

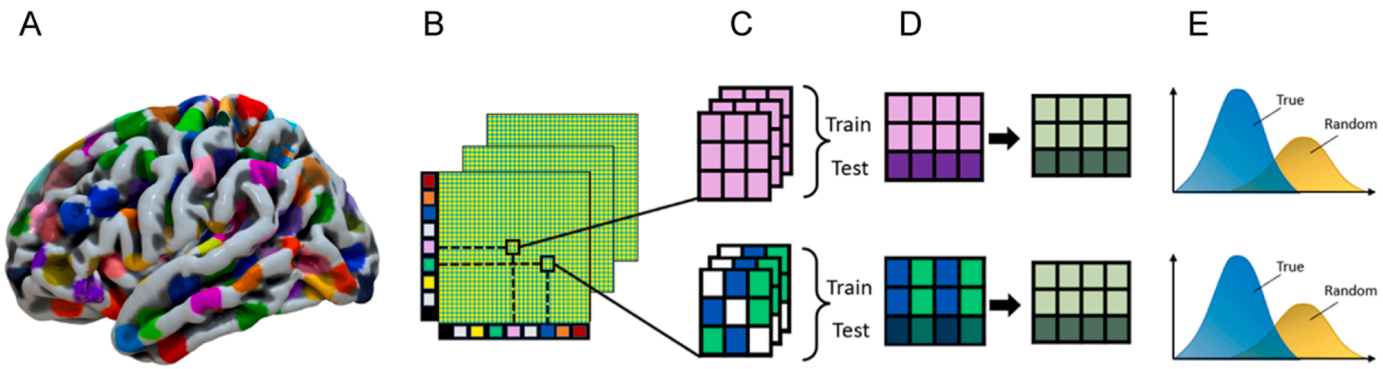

Fig. 1. Overview of multivariate partial least square regression (PLSR) analysis. (A) Average regional timeseries were extracted using an existing parcellation (Power et al., 2011; Seitzman et al., 2020) (B) Timeseries were used to create pair-wise correlation matrices for regions involved in seven *a priori* social-affective, attention/salience, reward, and cognitive control networks. (C) 28 within (top panel) and between (bottom panel) network combinations were extracted and used as input features for multivariate PLSR models with pubertal hormones, timing, status, and age as outcomes. Components for the PLSR model were estimated using 5-fold internal cross-validation. (D) A repeated (k = 5000) hold-out random resampling procedure was used to partition the sample into testing (80%) and training (20%) samples. (E) The "true" distribution of correlations between observed and predicted outcomes are then plotted against a null (i.e., "random") distribution of correlations generated from randomly permuting our data. The PLSR model was conducted across all outcomes (i.e. multivariate) and then separately for each outcome. Figure is adapted with permission from Rudolph et al. (2018).

3. Results

3.1. Developmental factors

Correlations among DHEA, testosterone, perceived pubertal timing, status, and age revealed small-to-large effects (Table 1). Descriptive statics indicated a range of development within the sample (Table 2). All hormone values are within a range similar to existing literature for the age and sex of the present sample (Gray et al., 2010; Herting et al., 2021).

3.2. Brain network connectivity associations across all developmental outcomes

When examining *within* connectivity of the seven large scale social-affective, cognitive-control and attention networks assessed, connectivity of the SN, FP, and VAN initially exhibited the strongest associations across all four developmental factors. Of the 21 *between* network combinations analyzed, nconnectivity involving the CO, FP, Reward, VAN, and DAN were initially associated with all developmental factors. However, only *within* SN and *between* connections involving Reward with both the CO and FP network remained significant across all sensitivity analyses that accounted for motion, medication, and time between initial puberty/age assessment and MRI scan session (Table 3). These findings aligned with our hypotheses that predicted overall associations involving SN and Reward connectivity. However, we did not anticipate that cognitive control networks would have such a robust effect across all developmental outcomes. We also did not find any anticipated significant results involving the DMN.

Table 1
Correlations among developmental factors.

	DHEA	Testosterone	Timing	Status	Age
DHEA	—	—	—	—	—
Testosterone	**0.49**	—	—	—	—
Pubertal Timing	**0.26**	**0.23**	—	—	—
Pubertal Status	**0.46**	**0.33**	**0.63**	—	—
Age	**0.42**	**0.27**	0.07	**0.81**	—

Note. DHEA = Dehydroepiandrosterone. Timing and Status are derived from the Petersen Development Scale and represent perceived measures of status and timing. Bolded pearson correlations values are significant at $p < 0.001$.

Table 2
Descriptive statistics for developmental factors.

Variable	Mean	SD	Range
DHEA	158.87	94.56	13.16–492.29
Testosterone	66.82	22.57	15.23 – 142.65
Pubertal Timing	-0.01	0.49	-1.25–1.12
Pubertal Status	2.77	0.82	1.2–4
Age	12.38	1.81	9.16–15.08

Note. The hormone values are pg/mL and are presented without accounting for the effect of time of collection, caffeine, BMI, and birth control although these were controlled for in analyses. Pubertal timing represents the residual values from a model whereby age predicted status. Values are shown for the primary subsample of $n = 99$.

3.3. Specificity of brain network connectivity associations with hormones, perceived pubertal status, perceived pubertal timing, and age

The second step of analysis, which focused on the three networks surviving all sensitivity analyses from Table 3, revealed specificity of network associations with the five developmental outcomes of interest. Table 4 shows these networks and the associated effect size specific to each developmental outcome. DHEA and testosterone were linked with SN and FP – Reward connectivity exclusively (Fig. 2, Supplemental Tables 1–2), which aligned with hypotheses that predicted cognitive control and reward associations with hormones. However, we did not anticipate seeing such strong effects between SN and hormones. Perceived pubertal status and age only related to SN and CO – Reward connectivity (Fig. 3, Supplemental Tables 3–4), which is in partial support of our hypothesis that age would link with cognitive control circuitry. DHEA, testosterone, perceived pubertal status, and age all showed medium effects with cognitive control connectivity; the perceived pubertal status associations were unanticipated. Also contrary to hypotheses, there were no associations involving perceived pubertal timing that remained significant when accounting for potential confounds in sensitivity analyses.

4. Discussion

For years, researchers have sought to clarify how adolescent development provides a sensitive window of opportunity for changes to the brain, social behavior, and mental health. Various accounts emphasize pubertal indices such as pubertal timing (Barendse et al., 2022; Pfeifer and Allen, 2021b; Ullsperger and Nikolas, 2017), whereas others focus

Table 3
Within- and between-brain network connectivity significantly associated with hormones, pubertal status, pubertal timing, and age.

Networks	Cohen's *d*	ROIs	Components	Train *r*	Train SD	Test *r*	Test SD
Salience*	0.703	13	1	0.13	0.22	-0.02	0.22
CO-Reward*	0.516	38	1	0.06	0.2	0.11	0.2
FP – Reward*	0.336	44	3	0.1	0.21	0.11	0.21
FP	0.33	36	3	0.13	0.21	0.11	0.21
VAN	0.311	11	1	0.11	0.18	0.06	0.21
CO-Salience	0.269	43	5	-0.04	0.21	-0.06	0.21
VAN - DAN	0.201	27	1	0.07	0.2	-0.01	0.19

Note. Cohen's *d* represents the difference in model fit statistics (i.e. correlation between observed and predicted outcomes) of the true & random distributions; it is an indicator of model accuracy. Higher *d* = better performance of model relative to chance. All models are $d > 0.2$ and $p < 0.001$. Asterisks (*) indicate that the networks remained at $p < 0.001$ and $d > 0.2$ across all sensitivity analyses that controlled for motion, timing between assessments, and medication. Brain network abbreviations are as follows: FP – Frontoparietal; VAN – Ventral Attention; DAN – Dorsal Attention; CO – Cinguloopercular.

Table 4
Specificity of associations between brain network connectivity and hormones, pubertal timing, status, and age.

	DHEA	Testosterone	Timing	Status	Age
Salience	**0.386***	**0.261***	**0.25**	**0.519***	**0.568***
FP - Reward	**0.3***	**0.395***	**0.253**	-0.038	0.013
CO-Reward	**0.2**	0.139	0.19	**0.343***	**0.518***

Note. Cohen's *d* values are shown for each association between every developmental factor and specific brain network connectivity. Higher *d* = better performance of the model that tested the link between brain connectivity and the developmental factor. Bolded effects are significant at $d > 0.2$ and $p < 0.001$. Items with asterisks indicate that the networks remained at $d > 0.2$ and significant for the respective developmental factor across all sensitivity analyses. Brain network abbreviations are as follows: FP – Frontoparietal; CO – Cinguloopercular.

on age and the environments associated with being an adolescent (Costello et al., 2011; Ortuño-Sierra et al., 2021; Rothenberg et al., 2023). Given that peer evaluation is a particularly salient and shifting experience during puberty, we used a peer evaluation context to probe specificity in how different pubertal indices and age relate to brain connectivity. During intermittent peer evaluation, within SN connections and cognitive control – reward connections showed the most robust associations across all pubertal indices and age, which was in partial support of hypotheses. As anticipated, we found that adolescent females exhibit both shared and unique associations between brain networks and pubertal hormone levels, perceived pubertal status, and age. DHEA and testosterone were exclusively associated with within SN and FP - Reward connectivity. In contrast, pubertal status and age were uniquely linked to within SN and CO – Reward connectivity. Contrary to hypotheses, there were no associations involving perceived pubertal timing. These findings support animal and human models that suggest puberty hones brain circuitry relevant to peer evaluation (Barendse and Pfeifer, 2021; Crone et al., 2020; Crone and Dahl, 2012a; Nelson et al., 2005b; Pfeifer and Allen, 2021b; Schulz and Sisk, 2006, 2016a) and provides evidence of general and specific ways in which brain connectivity and puberty relate.

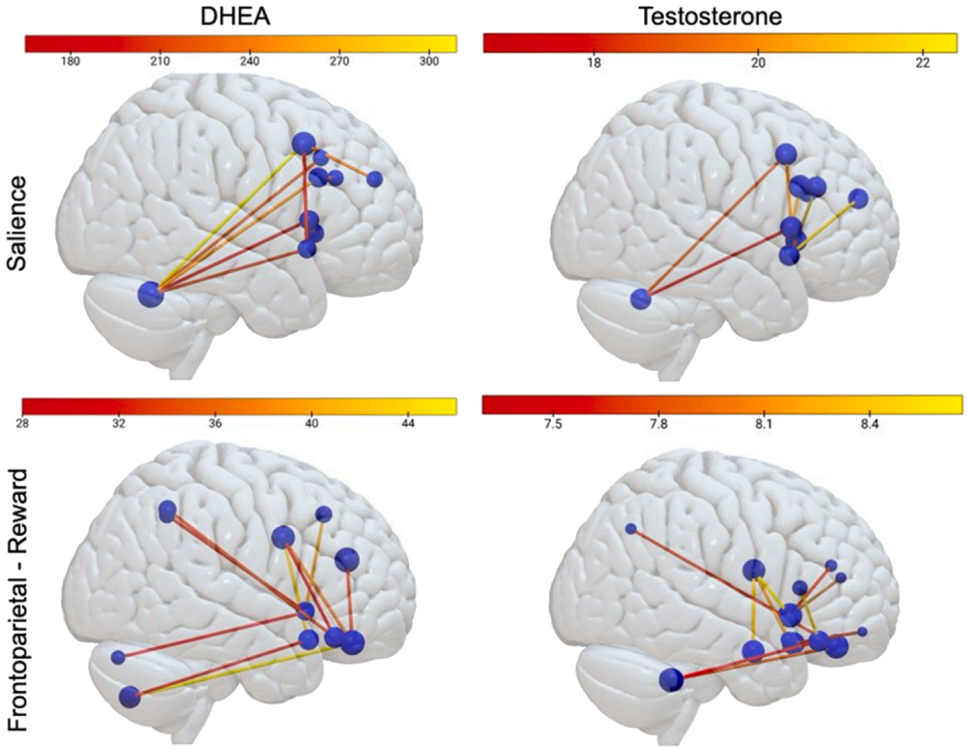

Fig. 2. Within Salience network (top panel) and between Frontoparietal – Reward (bottom panel) connectivity significantly associated with both DHEA and testosterone. The top ten connections that influenced the models for DHEA and testosterone are presented. Colors indicate the extent of the influence of each connection. Regions that appear more transparent are more medial.

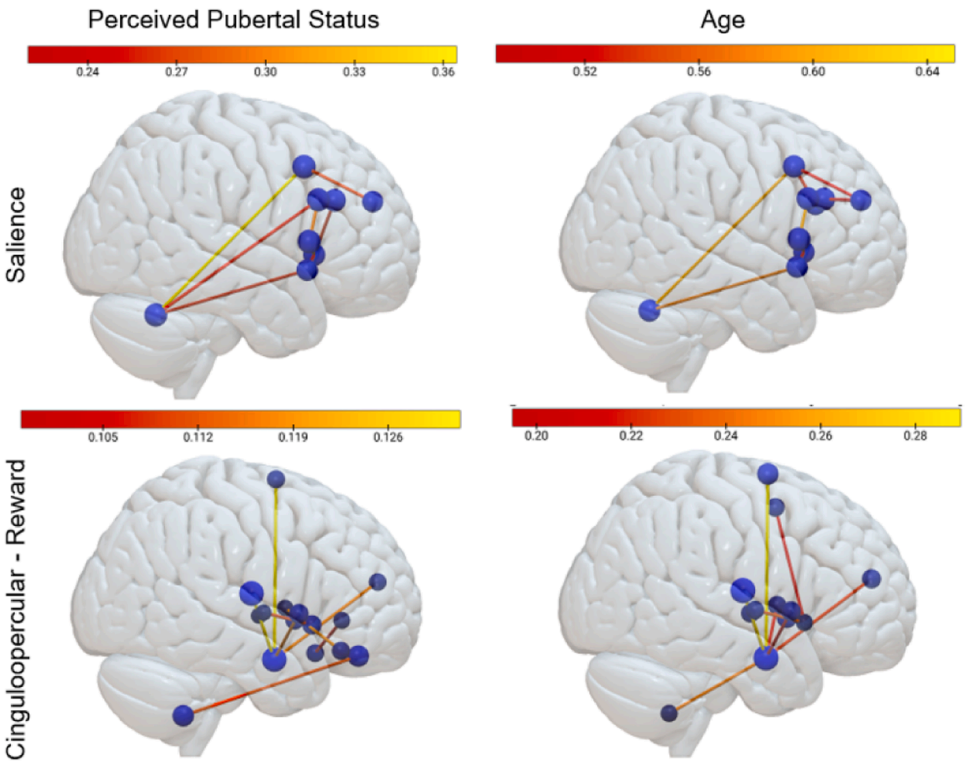

Fig. 3. Within Salience network (top panel) and between Cinguloopercular – Reward (bottom panel) connectivity significantly associated with both perceived pubertal status and age. The top ten connections that influenced the models for status and age are presented. Colors indicate the extent of the influence of each connection. Regions that appear more transparent are more medial.

4.1. Salience network connectivity supporting peer evaluation is associated with most pubertal indices and age

Within SN connectivity showed the strongest associations across all developmental factors, specifically with both DHEA and testosterone, perceived pubertal status, and age. Notably, although significant, the model performance was variable, with perceived pubertal status and age showing the largest effects. Developmental models of adolescence underscore the salience of peer evaluation (Nelson et al., 2005b; Somerville et al., 2013; Stroud et al., 2009), the increased self-evaluation of this period of life (Pfeifer and Berkman, 2018) and engagement of the SN (Rosen et al., 2018). Peer evaluation paradigms have revealed heightened activation within salience regions, potentially reflecting the processing of salient contextual cues relevant to peer evaluation (Somerville et al., 2013). Other work has indicated that SN regions can become engaged when individuals are rejected (Crone et al., 2020). Within this context, our finding suggests that SN connectivity subserving the processing of salient cues and experiences relevant to peer evaluation information may be part of a broader developmental processes jointly influenced by puberty and age. Notably, we did not find any association with perceived pubertal timing and Salience network connectivity. Although further research is needed, it may be that adolescent girls perceived pubertal status relative to peers is less impactful to the processing of salience of peer evaluation. Together, our findings support a theory that the heightened adolescent salience of peers subserved by SN functioning may be driven in part by pubertal hormones, perception of physical changes to the body, and environmental impact related to one's age as opposed to where girls are in their developmental trajectory relative to peers.

The lack of DMN associations across puberty and age outcomes was unanticipated. The DMN is implicated in self-referential thinking, processing information about others, and rumination (Andrews-Hanna et al., 2014, 2010; Raichle, 2015) – cognitive process that are relevant to the experience/anticipation of peer evaluation (Kumar et al., 2019). It may be that DMN functioning during intermittent peer evaluation is less related to puberty and age and more impacted by other environmental variables not measured here (e.g. social network, home environment/caregiver, educational and other resources) (Colich et al., 2021). Further, several studies report that medications including anti-depressants and stimulants alter DM connectivity (Posner et al., 2013; Schulz and Sisk, 2006; Silberstein et al., 2016). Although we accounted for the potential influence of medication on connectivity in our analyses, most of our sample was taking some form of medication which could have impacted results. Future work will need to be done in other developing adolescent samples to identify how puberty, age, and DMN connectivity may interact to influence the processing of peer evaluation.

Finally, there were no findings involving perceived pubertal timing, which may be a result of limited measurement (Barendse et al., 2022) although there are mixed findings linking pubertal timing with the brain (Goddings et al., 2019; Vijayakumar et al., 2018b). Some have argued that perceived pubertal timing is more reflective of social environment, given that advancing later/earlier than peers can shift interpersonal dynamics. While null findings should be interpreted with caution, it may be that the brain circuitry elicited during peer evaluation may be primarily influenced by the biological components of puberty as opposed to social. The younger age of the sample may also have inhibited our ability to find significant associations involving pubertal timing given that this measure relies on the awareness of one's physical traits relative to same-aged peers. It may also be that any effects of pubertal timing occur later in development. Future research with broader pubertal timing measurement will address these remaining questions.

4.2. Cognitive control and reward network connectivity supporting peer evaluation exhibits unique relations with hormones, pubertal status, and age

Although multivariate analyses showed that cognitive control –

reward connectivity was related to all developmental outcomes, there were also specific associations involving DHEA, testosterone, status, and age. Existing data suggests that the activation of cognitive control and reward networks during evaluation may indicate self-regulation of emotional response to peer evaluation, planning for action, experience of social acceptance, and/or motivation for approach behaviors (Crone et al., 2020). Reward circuitry is thought to be hypersensitive during adolescence (Blakemore and Mills, 2014; Braams et al., 2015; Galvan, 2013; Ladouceur et al., 2019; van Duijvenvoorde et al., 2016), providing a biological mechanism to support adolescent's seeking out novel peer relationships and experiences. Neurodevelopmental models suggest that the integration between cognitive control and reward networks develops throughout adolescence (Luna et al., 2015; Marek et al., 2015; Marek and Dosenbach, 2018). Within the context of this existing literature, our finding suggests that the coordination between self-regulation and a putatively heightened motivation/emotional response to peer evaluation is collectively influenced by DHEA, testosterone, perceived pubertal status, and age.

However, the specificity of our findings suggests that there may be unique ways in which pubertal hormones relate to cognitive control and reward networks relative to perceived pubertal status and age. We found that DHEA and testosterone were uniquely related to FP – Reward connectivity while perceived pubertal status and age were associated with CO – Reward connectivity.

The shared link between DHEA and testosterone with FP-Reward connectivity is consistent with the fact that testosterone is a metabolite of DHEA. Further, receptors targeted by DHEA and testosterone exist in frontal and limbic regions of the brain (Höfer et al., 2013; Maninger et al., 2009; Vijayakumar et al., 2018a). DHEA levels impact regions within the FP network (Nguyen et al., 2013) and testosterone have been repeatedly linked with reward circuitry (Braams et al., 2015; de Macks et al., 2011; Ladouceur et al., 2019; Spielberg et al., 2015), further corroborating the present findings. The FP network functions as a cognitive control "hub" (Marek et al., 2015; Marek and Dosenbach, 2018) to coordinate task initiation, adaptation, and error correction (Dosenbach et al., 2007; Marek et al., 2015; Marek and Dosenbach, 2018). Thus, the present findings suggest that DHEA and testosterone in girls may have a specific impact on the coordination between the FP cognitive control "hub" and affective/motivational processes subserved by reward circuitry work in response to intermittent peer evaluation. In addition to future work testing causality, it will be important to gather more hormonal data in a wider age range to identify whether adrenarche and/or gonadarche may represent the most sensitive window for the influence of DHEA and testosterone on FP-Reward connectivity.

In contrast, CO - Reward connectivity was associated with status and age. The CO is thought to have unique functions related to the facilitation and maintenance of tonic alertness – a self-driven, sustained attentional process (Sadaghiani and D'Esposito, 2015). In the context of peer evaluation, connectivity between this CO network and reward circuitry could represent an exchange of information regarding maintaining alertness toward motivating and valued components of peer feedback. Thus, the present result may indicate that perceived pubertal status and age are uniquely linked to this set of cognitive processes.

Our finding that the CO-Reward connectivity was shared between status and age aligns with the well-known variance shared by these two variables, with some researchers considering that these two measures both serve as a broad proxy of general development. And yet, it is noteworthy that DHEA and testosterone did not relate to CO – Reward connectivity given that hormones are the antecedents of pubertal development. Perceived social status and age as measured here could be reflective of a variety of factors including awareness of the self/body and environmental experiences. Thus, it may be that the associations with status and age here are indicative of CO-Reward connections during peer evaluation being most impacted by social/environmental factors relative to biological pubertal processes.

4.3. Future considerations

The present study is characterized by a number of strengths including the use of data driven approach, multiple puberty indices, analysis of separate models for puberty versus age, and a focus on brain network connectivity that acknowledges that brain regions do not function in isolation. There are several ways forward to disentangle how pubertal markers link with adolescent brain function that include broadening hormone measurement and testing directionality of associations found here. First, future studies would benefit from a more comprehensive hormone collection procedure. The present study included one sample of DHEA and testosterone, which may not reflect the actual levels of circulating hormones. Longitudinal hormone collection, including multi-day assessment over at least one month, in a wider age range is needed due to hormone variability and potential limited specificity of hormones in pre- and peri-pubertal girls, along with studies using both saliva and blood collection given the questionable reliability between these methods (Dai and Scherf, 2019). Such an approach would aid in identifying how specific hormones and/or hormones relevant to a specific pubertal phase or menstrual cycle timing link with brain function.

Second, the present study interpreted results using animal models as the foundation (Schulz and Sisk, 2016b, 2006), which propose puberty as the causal mechanism driving shifts in brain functioning supporting social behavior. However, longitudinal research is needed to identify directionality of the findings reported here as it is also probable that the experience of peer evaluation influences brain function, which in turn, influences indices of puberty. While existing work using the fMRI task implemented in the present study suggests similar neural activation during anticipation of and experience of peer evaluation (Somerville et al., 2013), future work could disentangle connectivity during these conditions to ascertain a more nuanced understanding of the relations between pubertal development and peer evaluation processes. Finally, although perceived pubertal status measured in the present study was a combination of parent and girls' report, early adolescents tend to over-report status, which could have influenced our results given our age range of 9–15. Thus, future research should also test how these puberty and brain network connectivity findings manifest in a wider age range, within typically developing adolescents including those not taking psychotropic medication, and ultimately identify how these connectivity patterns relate to psychopathology.

4.4. Conclusion

In conclusion, researchers have postulated that puberty engenders a second period of sensitive development during adolescence where brain function and behavior can be altered, ultimately influencing social behavior and mental health trajectories. Peer evaluation is a particularly salient experience during this adolescent sensitive period of development. The present study brought together separate lines of research on peer evaluation and puberty and found evidence for specificity in how various pubertal indices and age link with brain network connectivity during an intermittent peer evaluation fMRI task. Our findings indicate that although there appear to be broad ways in which development and the brain intersect, there are unique ways in which puberty and age are associated with brain connectivity. Continuing to unravel the specificity of these developmental and brain connectivity associations will advance mechanistic understanding of how social behavior and mental health unfolds during adolescence.

Data Statement

Components of the data are publicly available on the National Database Archive (#2310). The remaining data and code are available upon request.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2024.101357.

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