THESIS

EDUCATIONAL ATTAINMENT POLYGENIC SCORES, SOCIOECONOMIC FACTORS, AND RESTING-STATE FUNCTIONAL CONNECTIVITY IN CHILDREN AND ADOLESCENTS

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ABSTRACT

EDUCATIONAL ATTAINMENT POLYGENIC SCORES, SOCIOECONOMIC FACTORS, AND RESTING-STATE FUNCTIONAL CONNECTIVITY IN CHILDREN AND ADOLESCENTS

Socioeconomic factors, such as family income and parental education, have been associated with resting-state functional connectivity (rsFC) in networks responsible for executive function in children and adolescents. Yet, children's socioeconomic context interacts with the genetics they inherit from their parents, and few studies of socioeconomic context and rsFC in children have considered genetics. Polygenic scores for educational attainment (PGS-EA) derived from genome-wide association studies (GWAS) reflect genetic predisposition to educational attainment. Yet, no studies have examined the associations between PGS-EA and rsFC. The goal of this study was to investigate how socioeconomic factors and PGS-EA jointly predict rsFC in neural networks associated with executive function, including the central executive (CEN), dorsal attention (DAN), salience (SN), and default mode networks (DMN) in children and adolescents. Participants are typically-developing 3- to 21-year-olds ($N = 245$, 51% female) from the previously-collected Pediatric Imaging, Neurocognition, and Genetics (PING) study. PGS-EA were computed based on the EA3 GWAS of educational attainment. Resting-state fMRI data were acquired, and system-level rsFC was computed. Findings indicated that family income was inversely associated with rsFC in the SN, while PGS-EA was positively associated with rsFC in the CEN. There were family income-by-age interactions for rsFC in the CEN and DAN, such that age was positively associated with rsFC in the CEN and DAN for children from higher income families and inversely associated with rsFC in the CEN for children from lower income families. These findings help to elucidate the independent genetic and socioeconomic contributions to connectivity in intrinsic functional neural networks underlying executive function.

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INTRODUCTION

Socioeconomic factors (e.g., family income, parental education) have long been established as robust and consistent predictors of cognitive and academic outcomes in children and adolescents (Duncan et al., 2017). Genetic factors also contribute to these outcomes (Hicks et al., 2021; Judd et al., 2020; Selzam et al., 2017), and research has uncovered interactions between socioeconomic and genetic factors in the prediction of cognitive and academic outcomes. Some findings have suggested that cognitive skills are more heritable within higher socioeconomic family environments in children and adolescents (Harden et al., 2007; Tucker-Drob & Harden, 2012; Turkheimer et al., 2003).

Recent progress in genetic research has provided new ways of investigating how genetic factors may interact with socioeconomic factors to influence academic and cognitive outcomes. Genome-wide association studies (GWAS) have made major breakthroughs in identifying single-nucleotide polymorphisms (SNPs) that are strongly linked to educational attainment (years of education completed) (Lee et al., 2018; Okbay et al., 2022; Rietveld et al., 2013). Polygenic scores for educational attainment (PGS-EA) derived from these GWAS have been consistently associated with academic achievement and general cognitive ability in independent samples (Hicks et al., 2021; Lee et al., 2018; Okbay et al., 2022; Rabinowitz et al., 2019; Selzam et al., 2017).

Building on this work, an emerging body of research has jointly considered socioeconomic factors and PGS-EA in relation to general cognitive outcomes as well as specific neurocognitive skills and brain structure (Judd et al., 2020; Merz et al., 2022; Mitchell et al., 2020; Raffington et al., 2019). However, the combined and potentially interactive influences of socioeconomic factors and PGS-EA on brain *function,* rather than structure, are not well understood. As such, the goal of this study was to use functional magnetic resonance imaging (fMRI) to investigate the joint and potentially interactive associations of socioeconomic factors and PGS-EA with resting-state functional connectivity (rsFC) in children and adolescents.

Socioeconomic Factors, Educational Attainment Polygenic Scores, and Neurocognitive Skills

Socioeconomic factors have been consistently associated with cognitive task performance in children and adolescents (Bradley & Corwyn, 2002; Duncan et al., 2017; McLoyd, 1998), with especially strong and consistent associations with executive function skills (Duncan & Magnuson, 2012; Hackman & Farah, 2009; Lawson et al., 2018; Noble et al., 2005, 2007). Specifically, higher socioeconomic status (SES) has been repeatedly associated with greater executive function skills, including working memory, attention shifting, and inhibitory control across childhood and adolescence (Lawson et al., 2018; Noble et al., 2005, 2007).

Similarly, studies have repeatedly found positive associations between PGS-EA and executive function skills (inhibitory control, working memory) in children and adolescents (de Zeeuw et al., 2014; Judd et al., 2020; Merz et al., 2022; Rea-Sandin et al., 2021). Moreover, recent studies have suggested that PGS-EA and socioeconomic factors have independent and additive associations with executive function skills (Judd et al., 2020; Loughnan et al., 2019; Merz et al., 2022; Rea-Sandin et al., 2021). Yet, the ways in which PGS-EA and socioeconomic factors may independently impact the neural underpinnings of executive function remain poorly understood.

Socioeconomic Factors, Educational Attainment Polygenic Scores, and Brain Structure

SES has been consistently associated with global and regional brain structure in children and adolescents (Farah, 2017). Research has linked higher SES with greater total cortical surface area in children and adolescents (McDermott et al., 2019; Noble et al., 2015). Socioeconomic differences have been found in the structure of widespread cortical regions and multiple subcortical structures, especially the hippocampus (Farah, 2017). Consistent evidence has linked higher SES with more gray matter in prefrontal cortical regions crucial to executive function (Farah, 2017; Merz et al., 2019).

PGS-EA has also been associated with global and regional brain structure in children and adolescents. Higher PGS-EA has been significantly associated with greater total cortical gray matter (total cortical surface area, volume) in children and adolescents (Alemany et al., 2019; Fernandez-Cabello et al., 2022; Judd et al., 2020; Merz et al., 2022). Higher PGS-EA has been significantly associated with greater cortical surface area in frontal (inferior frontal gyrus, medial orbitofrontal gyrus) (Merz et al., 2022) and parietal (intraparietal sulcus) regions (Judd et al., 2020) in children and adolescents.

Several studies have shown that socioeconomic factors and PGS-EA make significant independent contributions to brain structure (Judd et al., 2020; Merz et al., 2022; Mitchell et al., 2020; Raffington et al., 2019). For example, globally, higher SES has been associated with greater total cortical surface area in children and adolescents while controlling for PGS-EA (Judd et al., 2020; Merz et al., 2022). Regionally, higher SES has been associated with greater hippocampal volume (Raffington et al., 2019) and surface area in the parahippocampal gyrus (Merz et al., 2022) in children and adolescents while controlling for PGS-EA. Yet, to our knowledge, no studies have examined the independent associations of socioeconomic factors and

PGS-EA with brain *function* in children and adolescents. Based on previous work, research is especially needed that focuses on neural networks associated with executive function.

Resting-State Functional Connectivity

Resting-state functional connectivity (rsFC) refers to correlated fluctuations in blood-oxygen-level dependent (BOLD) signal in discrete brain regions while “at rest” or not performing a task (Fox & Raichle, 2007; Power et al., 2011). At all postnatal developmental stages, certain patterns of co-activation at rest within the brain tend to occur. Neural activity is largely synchronized within resting-state networks (RSNs), with distinct networks playing distinct roles in cognitive processes (Grayson & Fair, 2017; Seeley et al., 2007). Neuroimaging approaches that include measurement of rsFC are especially valuable in research focused on higher-order cognitive processes, which are the result of numerous and distributed brain regions working together.

Neural Networks Associated with Executive Function

Networks associated with executive function include the central executive network (CEN), dorsal attention network (DAN), salience network (SN), and default mode network (DMN) (Menon & D’Esposito, 2022). Researchers have differentiated between task control (or task-positive) networks (CEN, DAN, and SN) and the DMN, a “task-free” (or task-negative) network, with both types of networks important to executive function (Fox et al., 2005; C. Sripada et al., 2021). The CEN, a fronto-parietal network with primary hubs in the dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (Vincent et al., 2008), is predominantly known for its role in executive control, including working memory (Menon, 2011; Seeley et al., 2007).

The DAN is comprised of the intraparietal sulcus and the frontal eye fields, the junction of the precentral and superior frontal sulcus (Fox et al., 2005; Vossel et al., 2014). The DAN works together with the SN to enable attentional control and orientation through top-down processes (Freedman et al., 2020; Vossel et al., 2014).

The SN, which is often referred to as the cingulo-opercular network (CON) or ventral attention network (VAN), has main hubs in the anterior insula and dorsal anterior cingulate (Seeley et al., 2007). The SN is highly implicated in determining the importance of cognitive or emotional cues. It then signals to higher-order systems, such as the CEN, to recruit networks more directly involved in executive function (Goulden et al., 2014; Seeley et al., 2007). Additionally, the SN is thought to play a role in error monitoring and adaptation, especially in children (Dosenbach et al., 2008; Ham et al., 2013). The SN plays a vital role in executive function at a primary level by detecting salient stimuli and errors.

The DMN is activated when the brain is "at rest" and is anchored in the medial PFC, posterior cingulate cortex, and medial temporal cortex (Grayson & Fair, 2017; Greicius et al., 2003). The DMN is known for its role in social cognition including introspection and thinking about others' states of mind (Sherman et al., 2014), and rsFC in this network has been associated with performance on memory and cognitive tasks in adults (R. Li et al., 2018).

Socioeconomic Factors and rsFC in Networks Associated with Executive Function

Socioeconomic factors have been repeatedly examined in relation to rsFC in children and adolescents. These studies have employed a variety of different methodological approaches. Some have utilized a seed-based approach to measure rsFC such as seed-to-whole-brain (Turesky et al., 2019) and seed-to-seed methods with nodes in only the primary hubs of a network (Gellci et al., 2019; R. K. Sripada et al., 2014; Weissman et al., 2018). Only a few studies have focused on full *network* connectivity by extracting the connectivity between all pairs of nodes in the examined network(s) (Brody et al., 2019; Rakesh, Seguin, et al., 2021; Rakesh, Zalesky, et al., 2021; Tooley et al., 2020). This method allows for broader understanding of intrinsic functional connectivity over an entire neural network.

Broadly, in studies using various methods, socioeconomic factors have been associated with rsFC in networks related to higher-order cognitive function, attention, language (Brody et al., 2019; Rakesh, Seguin, et al., 2021; Rakesh, Zalesky, et al., 2021; R. K. Sripada et al., 2014; Su et al., 2021; Tooley et al., 2020; Turesky et al., 2019; Weissman et al., 2018), and reward and emotion processing (Brody et al., 2019; Hanson et al., 2019; Marshall et al., 2018; Turesky et al., 2019). More specifically, several studies have examined rsFC in neural networks associated with executive function. Studies using various methods have found that socioeconomic factors associate with rsFC in the SN (Cermakova et al., 2023; Gellci et al., 2019), although the directionality of these associations is mixed. Parental education has been positively (Gellci et al., 2019; Rakesh, Zalesky, et al., 2021) and negatively (Cermakova et al., 2023) associated with rsFC in the SN (also referred to as the CON). Other studies have not found significant socioeconomic differences in rsFC in the SN (Sripada et al., 2014). Socioeconomic factors have also been repeatedly associated with rsFC in the DMN. Childhood poverty has been associated with reduced connectivity in the DMN in adults (Sripada et al., 2014), and an increase in family income for children in socioeconomically disadvantaged families leads to a subsequent increase in DMN connectivity (Weissman et al., 2018).

The few prior studies that have used the full-network approach have found associations between socioeconomic factors and rsFC in the CEN, SN (also referred to as the CON and VAN), and the DAN. Socioeconomic disadvantage has been associated with decreased rsFC in the CEN (Brody et al., 2019), SN (Rakesh, Seguin, et al., 2021; Rakesh, Zalesky, et al., 2021), and DAN (Rakesh, Seguin, et al., 2021). Specifically, more time spent living in poverty during adolescence predicted less connectivity in the CEN during adulthood, but only among those who experienced low levels of supportive parenting (Brody et al., 2019). In a large-scale study of 9- to 10-year-olds, higher family income-to-needs ratio and parental education were both associated with greater connectivity in the CON (Rakesh, Zalesky, et al., 2021). In the same sample, higher neighborhood disadvantage was associated with lower rsFC in the CON and DAN (Rakesh, Seguin, et al., 2021).

Taken together, although evidence suggests that socioeconomic factors are associated with rsFC in networks associated with executive function, few studies have used a system-level approach to computing rsFC in these networks. In addition, associations between socioeconomic factors and rsFC in these networks while specifically controlling for genetic factors have yet to be examined. Furthermore, to our knowledge, the associations between PGS-EA and rsFC in these neural networks in children and adolescents are wholly unknown.

Age Differences in Associations of Socioeconomic Factors and PGS-EA with rsFC

Genetic differences in cognitive performance have been proposed to widen with age. In behavior genetics research, some suggest that the heritability of academic achievement and cognitive skills increases from childhood to young adulthood (Belsky et al., 2016; Harden et al., 2020; Haworth et al., 2010), indicating the importance of understanding the impact of PGS-EA on brain function across development. Similarly, socioeconomic differences in brain structure in the frontal, parietal, and temporal regions and limbic areas have been shown to increase with age (Grieve et al., 2011; Hanson et al., 2013; Noble et al., 2012), and age-related patterns of cortical thinning also differ by SES (Piccolo et al., 2016). Findings using functional neuroimaging show that socioeconomic differences in network connectivity may also widen throughout later childhood and adolescence, particularly for the limbic, somatomotor, and ventral attention systems (Tooley et al., 2020). Thus, more attention should be given to how socioeconomic factors and PGS-EA may impact age-related changes in rsFC in networks associated with executive function.

There is still much to understand concerning the normative development of RSNs. Most consistently, studies have found that the segregation of rsFC of higher-order networks (e.g., CEN, DAN, SN, and DMN) strengthens with age through childhood and adolescence (Grayson & Fair, 2017; Gu et al., 2015; C.-L. Li et al., 2019; Rohr et al., 2016), meaning that between-network rsFC decreases as within-network rsFC increases across development. This basic pattern has been observed for the CEN, DAN, SN, and DMN. Other studies have found no associations between age and whole-network connectivity throughout middle childhood and adolescence, potentially due to different developmental timing of subregions or individual connections (edges) within a network (Marek et al., 2015; Thomson et al., 2022).

The intrinsic connectivity of networks also may have nonlinear trajectories with different developmental bursts: the CEN having an increasing strength of within-network rsFC throughout childhood, with a decrease in early adolescence and subsequent larger increase in late adolescence; the SN/CON shows a more rapid increase in early adolescence with a levelling off; the DMN demonstrates a slight decrease in early adolescence and subsequent larger increase in late adolescence (Marek et al., 2015).

Gene-by-Environment Interactions

A growing body of research has investigated gene-by-environment (G x E) interactions in relation to cognitive development. Some of this research has focused on SES, and a prominent example comes from twin research. Twin studies have suggested that the heritability of intelligence (general cognitive ability) is suppressed under socioeconomically disadvantaged family environments in children and adolescents (Harden et al., 2007; Tucker-Drob & Harden, 2012; Turkheimer et al., 2003), suggesting that environmental influences may play a larger role in cognitive outcomes for children and adolescents in socioeconomically disadvantaged contexts. Higher SES may afford greater opportunities for children to benefit from learning experiences congruent with genetically-influenced intellectual interests and abilities. This interaction has not been consistently observed (Figlio et al., 2017; Grasby et al., 2019). It was most robust in nations with less access to equitable high-quality education and health care (Tucker-Drob & Bates, 2016). Although this example stems from the field of behavior genetics, polygenic scores can also be leveraged to investigate G x E interactions. In research using polygenic scores, it is important to consider whether gene-by-SES interactions may explain outcomes, such as brain structure and function.

Current Study

The goal of this study is to examine the independent associations of PGS-EA and socioeconomic factors (parental education, family income) with rsFC in neural networks associated with executive function (CEN, DAN, SN, DMN) in children and adolescents. In addition, three interactions were investigated in the prediction of rsFC in these networks: (1) PGS-EA-by-age interactions (controlling for socioeconomic factors), (2) socioeconomic-factor-by-age interactions (controlling for PGS-EA), and (3) PGS-EA-by-socioeconomic factor interactions. Participants were typically-developing 3- to 21-year-olds (50% male; *N* = 245 with complete fMRI, PGS-EA, and socioeconomic factor data) from the Pediatric Imaging, Neurocognition, and Genetics (PING) study (Jernigan et al., 2016).

Based on previous studies (de Zeeuw et al., 2014; Jansen et al., 2018; Judd et al., 2020; Merz et al., 2022; Mitchell et al., 2020; Rakesh, Seguin, et al., 2021; Rakesh, Zalesky, et al., 2021; Rea-Sandin et al., 2021), we hypothesized that higher PGS-EA and parental education (or family income) would be independently associated with greater rsFC in the CEN, DAN, SN, and DMN. We also tentatively hypothesized that these associations may differ by age, with associations between PGS-EA and rsFC the strongest among older children and adolescents.

Given that studies have often found independent or additive effects of PGS-EA and socioeconomic factors rather than PGS-EA-by-socioeconomic-factor interactions (Judd et al., 2020; Merz et al., 2022; Raffington et al., 2019; von Stumm et al., 2020), we expected we may also find additive rather than interactive effects. However, little is known about these interaction effects at the neural level, particularly in regard to neural function.

METHODS

Participants

For the PING study, typically-developing participants were recruited from ten locations throughout the United States (http://ping.chd.ucsd.edu) (Jernigan et al., 2016). Functional MRI data is publicly available for seven of those 10 sites (Cornell University; University of California, Davis; Kennedy Krieger Institute; Massachusetts General Hospital; University of California, San Diego; University of Massachusetts Medical School [UMMS]; Yale University). Eligibility criteria required the participants being between 3 and 20 years old and fluent in English. Exclusionary criteria included having a history of neurological disorders or head trauma, diagnosis of autism spectrum disorder, bipolar disorder, schizophrenia, or an intellectual disability, premature birth or prenatal exposure to illicit drugs for more than one trimester. Additionally, any individuals with contraindications for MRI were excluded from the study.

Sample Sizes

In total, 580 participants have complete socioeconomic and fMRI data, and 526 participants have genome-wide polygenic score data. The sample size was reduced for analyses involving polygenic score data because only participants with primarily European ancestry could be used in these analyses (see below). There were 252 participants with complete socioeconomic, fMRI, and polygenic score data. One participant was excluded due to the lack of time frames in their fMRI scan, and seven participants with excess motion detected during the preprocessing of their MRI data were also excluded, leading to a final sample of 245 participants.

Sample Characteristics

The final sample used in this study consisted of individuals between the ages of 3 and 21 years (51% female) (see Table 1). Analyses were conducted to compare the demographics in the fMRI subsample (*n* = 529) to those without fMRI data (*n* = 979). Family income did not significantly differ between the fMRI subsample and those without fMRI data, *t*(1506) = 1.13, *p* = .26. Parental education for the fMRI subsample (*M* = 15.11, *SD* = 2.26) was marginally higher than parental education for those without fMRI data (*M* = 14.88, *SD* = 2.27), *t*(1506) = 1.85, *p* = .06. Participants in the fMRI subsample (*M* = 13.41, *SD* = 4.93) were older on average than those without fMRI data (*M* = 10.44, *SD* = 4.42), *t*(1506) = 11.25, $p < .001$. A one-sample proportions test with continuity correction was conducted to compare the number of males vs. females between the fMRI subsample (49.3% female) and those without fMRI data (46.3% female). The results were non-significant, $X^2(1506) = 3.55$, *p* = .06.

Procedure

Written informed consent was provided by parents/guardians for all participants younger than 18 years of age and by the participants themselves if they were 18 years or older. Child assent was obtained for participants 7 to 17 years of age. The Institutional Review Board at each site approved the study. Parents/guardians of minor participants were responsible for completing the PING study demographics questionnaire, which included questions about income and education, while participants who were 18 years and older received a self-report version of the same questionnaire (Jernigan et al., 2016). Participants provided a saliva sample for DNA extraction and underwent neuroimaging which included a resting-state fMRI scan.

Measures

Socioeconomic Factors

The number of years of education completed for each parent in the home were averaged to compute the parental educational attainment score used in analyses. Parental education data were originally collected in bins. Parental education was then recoded as the means of the bins for analysis, following from previous work (Noble et al., 2015). Family income was also collected in bins, recoded as the means of bins, and log-transformed to correct for positive skew (Noble et al., 2015).

PGS-EA

The PING dataset includes 550,000 SNPs genotyped from saliva using Illumina Human660W-Quad BeadChip. The computation of the polygenic scores followed steps that have been covered in detail in previous studies (Khundrakpam et al., 2020; Merz et al., 2022). The data was prepared for imputation using the "imputePrepSanger" pipeline (https://hub.docker.com/r/eauforest/imputeprepsanger/) and implemented on CBRAIN (Sherif et al., 2014) using Human660W-Quad_v1_A-b37-strand chip as reference. Then, the data was imputed with Sanger Imputation Service (McCarthy et al., 2016) using default settings and the Haplotype Reference Consortium, HRC (http://www.haplotype-reference-consortium.org/) as the reference panel. The next step involved using Plink 1.9 (Chang et al., 2015), where the imputed SNPs were then filtered with the inclusion criteria: SNPs with unique names, only ACTG, and MAF > 0.05. All SNPs that were included had INFO scores R2 > 0.9 with Plink 2.0. Using the polygenic score software PRSice 2.1.2 (Euesden et al., 2015), additional ambiguous variants were excluded, resulting in 4,696,385 variants being available for polygenic scoring. We filtered to include individuals with .95 loadings to the European ancestry principal component (GAF_Europe variable in the PING dataset). This resulted in 526 participants that were then used to compute 10 principal components with Plink 1.9.

Each of the resulting ten polygenic scores include SNPs that have a p-value below a certain value, known as thresholding. These ten polygenic scores based on the EA3 GWAS (Lee et al., 2018) were used in analyses (see Table 2 for the number of SNPs in each polygenic score). A factor score computed based on all ten PGS-EA was used in analyses. This factor score computation approach uses a principal component analysis (PCA) (Allegrini et al., 2022; Coombes et al., 2020; Fernandez-Cabello et al., 2022) and intends to reduce Type I error while maintaining sufficient power.

Imaging Data

Image Acquisition

Resting-state fMRI data were acquired using 3 Tesla (3T) scanners manufactured by General Electric (GE), Siemens, and Philips (Jernigan et al., 2016). The sites with Siemens scanners acquired resting-state fMRI volumes with repetition time (TR) = 3000 ms, TE = 30 ms, and voxel size = 3 x 3 x 3.5 mm; the Philips scanners' resting-state fMRI volumes were acquired with TR = 2500 ms, TE = 30 ms, and voxel size = 2.67 x 2.67 x 3 mm; lastly, the GE scanners' resting-state fMRI volumes were acquired with TR = 3000 ms, TE = 30 ms, and voxel size = 3 x 3 x 3 mm. The pulse sequence parameters were optimized for equivalence in contrast properties (Jernigan et al., 2016). Participants were told to focus on a white fixation cross on a black background while laying still (Darki et al., 2019). Prospective motion correction (PROMO) was used to control for the real-time effects of motion during the acquisition itself (White et al., 2010).

Image Preprocessing

We used the preprocessed resting-state fMRI data provided through PING-in-a-Box (Jernigan et al., 2016). Brain extraction, or skull-stripping, was conducted using BET (Smith, 2002). The volumes were all normalized to standard MNI template after slice timing correction and realignment (Darki et al., 2019). Spatial smoothing using a Gaussian kernel of 5 mm and a grand-mean intensity normalization of the entire 4D dataset were performed. Finally, high pass temporal filtering was conducted (Gaussian-weighted least-squares straight line fitting, with sigma=75.0s). Additionally, the number of resting-state fMRI volumes differed across individuals, ranging from 19 to 300 volumes, due to the different scanning protocols (see Table 3). To ensure data quality, participants with fewer than 50 resting-state fMRI volumes were excluded from analyses (Darki et al., 2019).

Framewise Displacement

Six motion parameters—three translations and three rotations—were extracted for each participant and each volume using 3dvolreg in Analysis of Functional NeuroImages (AFNI) (Cox, 1996). The rotations were converted to radians. Framewise displacement (FD) was then calculated for each volume by taking the Euclidean distance of the translations and rotations, following Power et al. (2012). The following formula was used:

$$\mathbf{FD = \surd\ (dx)^2 + (dy)^2 + (dz)^2 + r\_x^2 + r\_y^2 + r\_z^2)}$$

where dx, dy, and dz are the absolute displacement values for translations in the x, y, and z directions, and r_x, r_y, and r_z are the absolute displacement values for rotation around x, y, and z axes, respectively. Mean FD was used as a measure of motion and included as a covariate in the regression analyses to account for motion-related artifacts in the data.

Computation of Network rsFC

For each node in a network, a region-of-interest (ROI) seed mask was created using the Yeo seven network parcellation scheme including 50 nodes (Yeo et al., 2011). Each ROI was then resampled using AFNI's 3dresample to match the MNI template resolution. Employing a general linear model (GLM) approach in AFNI (version 18.1.14) (Cox, 1996), time series data was extracted for each ROI using the 3dROIstats tool. Specifically, for each ROI, the time series data was extracted within that ROI using the 3dROIstats tool in AFNI by averaging the signal intensity at each time point across all voxels within the ROI. Next, the beta weights and t-statistics for all brain voxels at each time point was estimated using AFNI function 3dDeconvolve (Ward, 2002) while accounting for motion regressors. The regression coefficients were then converted into percent signal change by dividing the voxel-wise signal intensity in the ROI by the mean signal intensity in that ROI and multiplied by 100 using 3dcalc in AFNI (Cox, 1996; Cox & Hyde, 1997). The BOLD signal values were then extracted from the average time series in each ROI and correlated with the average time series in all other voxels of another ROI in the network over time using AFNI function 3dROIstats. Pairwise associations between nodes were then averaged across all pairs of nodes in a network to compute a final value reflecting the connectivity of all nodes of each network (see Table 4 for the nodes in each network).

Statistical Analyses

Descriptive statistics and multiple linear regression analyses were conducted in R (version 4.1.1). Multiple linear regression analyses were used to examine associations of socioeconomic factors (independent variable) and PGS-EA (independent variable) with rsFC in the specified neural networks (dependent variables) ($p < .05$ significance threshold). Separate regression models were conducted for family income and parental education and for rsFC in each of the focal networks (CEN, SN, DAN, DMN). Covariates included age, sex, mean FD, and a dummy codded site variable. Number of fMRI volumes was not included as a covariate because of its strong correlation with site. Analyses of associations between socioeconomic factors and rsFC controlled for PGS-EA, and analyses of associations between PGS-EA and rsFC controlled for socioeconomic factors. Additionally, analyses involving PGS-EA controlled for principal components 1-10 (PC1-10) to account for population homogeneity based on similarity in ancestry (Price et al., 2006).

Additionally, we tested interaction effects for rsFC in each network. First, we tested interactions between PGS-EA and age and between parental education/family income and age. Significant interactions were probed using a simple slopes analysis, which was conducted using the sim_slopes function in R (Bauer & Curran, 2005). Second, we tested interactions between socioeconomic factors and PGS-EA for rsFC in each network, using similar methods to those described above.

RESULTS

Descriptive Statistics

Descriptive statistics and zero-order correlations are provided in Table 5. Parental education and family income were significantly correlated, $r(242) = .42, p < .0001$. Family income, $r(243) = .19, p = .003$, and parental education, $r(243) = .31, p < .001$, were also both significantly correlated with PGS-EA.

Main Effects of PGS-EA on rsFC

Higher PGS-EA was significantly associated with higher rsFC in the CEN ($\beta = .002, p = .02$) (Figure 1). PGS-EA was not significantly associated with rsFC in the SN, DAN, or DMN.

Main Effects of Socioeconomic Factors on rsFC

Lower family income was significantly associated with higher rsFC in the SN ($\beta = -.002$, $p = .03$) (Figure 2). Family income was not associated with rsFC in the CEN, DAN, or DMN. Parental education was not significantly associated with rsFC in any networks while controlling for PGS-EA.

Socioeconomic-Factor-by-Age Interactions

There were significant family income-by-age interactions for rsFC in the CEN ($\beta = .002$, $p = .018$) and DAN ($\beta = .002, p = .016$). Simple slopes analyses revealed that age was positively associated with rsFC in the CEN for those in higher income families ($\beta = .005, p = .02$). Age was inversely associated with rsFC in the CEN for those in lower income families ($\beta = -.001, p = .04$) (Figure 3). A similar pattern of results was observed for rsFC in the DAN. Age was positively associated with rsFC in the DAN for those in higher income families ($\beta = .003, p = .048$). Age was not associated with rsFC in the DAN for those in middle- and lower-income families. There were no significant parental education-by-age or PGS-EA-by-age interactions.

Socioeconomic Factor-by-PGS-EA Interactions

There were no significant PGS-EA-by-parental education interactions or PGS-EA-by-family-income interactions for rsFC in any of the focal networks.

Sensitivity Analyses

Excluding Participants with Non-Standard Number of Volumes

There were 6 participants with non-standard numbers of fMRI volumes during acquisition. When removing those participants, all of the results remained significant.

Excluding Participants with > 1 mm Mean FD

There were 11 participants with mean FD greater than 1 mm. When removing those participants, all main effect results remained significant, but the interaction effects were no longer significant. Higher PGS-EA was significantly associated with higher rsFC in the CEN ($\beta = .002$, $p = .021$). Lower family income was significantly associated with higher rsFC in the SN ($\beta = -.002$, $p = .046$). The family-income-by-age interaction no longer met the significant treshold for rsFC in the CEN and DAN ($p = .068$, $p = .092$, respectively), yet could be considered still significant at a trend level.

Excluding Participants with > .5 mm Mean FD

There were 23 participants with mean FD greater than .5 mm. When removing those participants, main effect results for PGS-EA remained significant, while results for family income were no longer significant. Specifically, higher PGS-EA was significantly associated with higher rsFC in the CEN ($\beta = .002$, $p = .001$). Family income was no longer significantly associated with rsFC in the SN ($\beta = -.002$, $p = .083$). The family-income-by-age interaction was no longer significant for rsFC in the CEN or DAN ($p = .084$, $p = .059$, respectively).

DISCUSSION

This study aimed to investigate the independent associations of PGS-EA and socioeconomic factors (parental education, family income) with resting-state functional connectivity (rsFC) in neural networks related to executive function in children and adolescents. Secondary aims were to examine three interaction effects: PGS-EA-by-age, socioeconomic factor-by-age, and PGS-EA-by-socioeconomic factor interactions. Results indicated significant association between PGS-EA and rsFC in the CEN while controlling for parental education. In addition, family income was significantly associated with rsFC in the SN while controlling for PGS-EA. Additionally, interactions between family income and age were found for rsFC in the CEN and DAN while controlling for PGS-EA.

Educational Attainment Polygenic Scores and rsFC in the CEN

Genetic propensity for higher educational attainment was significantly associated with greater rsFC in the CEN in children and adolescents. These findings complement previous structural neuroimaging findings indicating that higher PGS-EA was associated with greater cortical surface area in the left medial orbitofrontal gyrus and inferior frontal gyrus (Merz et al., 2022), as both regions contain nodes in the CEN. Greater intrinsic connectivity in the CEN during middle childhood has been associated with higher cognitive skills (Sherman et al., 2014). Connectivity in the CEN may be part of the neural mechanisms underlying associations between PGS-EA and executive function (Rea-Sandin et al., 2021). These findings corroborate previous work suggesting that individual differences in the neural underpinnings of executive function arise in part from genetic variability.

Family Income and rsFC in the SN

Lower family income was associated with higher rsFC in the SN while controlling for PGS-EA. Previous findings for associations between socioeconomic factors and rsFC in the SN have been inconsistent (Cermakova et al., 2023; Gellci et al., 2019). Higher SES, measured by neighborhood-level factors and family income, has been associated with higher rsFC in the core nodes of the SN in one study (Gellci et al., 2019). In another study, which used a seed-to-voxel approach, lower maternal education at birth was associated with greater rsFC between several nodes of the SN during young adulthood (Cermakova et al., 2023). Other studies of the salience network have yielded null findings (Rakesh, Zalesky, et al., 2021; Sripada et al., 2014); however, one of these studies (Rakesh, Zalesky, et al., 2021) distinguished between the SN and CON and yielded significant findings for the CON, with higher SES being associated with higher intrinsic rsFC of the CON. Other forms of childhood adversity, particularly child maltreatment, have also been linked to increases in SN connectivity in older childhood and adolescence (Rakesh, Allen, et al., 2021). A novel contribution of the current study is that the association between lower family income and higher rsFC in the SN remained significant when controlling for PGS-EA.

These differences in results from previous studies could be partially due to differences in how rsFC in the SN was measured across studies. Some studies used key nodes of the salience network (Cermakova et al., 2023; Gellci et al., 2019) while others used whole-network approaches (Rakesh, Zalesky, et al., 2021; Sripada et al., 2014), Another key difference was the conflation of the SN and CON into a single network by some studies (Gellci et al., 2019), while other studies utilized parcellations that identified the SN and CON as two distinct networks (Rakesh, Zalesky, et al., 2021; Sripada et al., 2014).

In younger children, higher connectivity in the SN has been linked to lower cognitive and executive function skills (Hawkey et al., 2018). The SN is involved in error monitoring and determining the importance of cognitive or emotional cues then recruiting networks more directly involved in executing executive function skills (Goulden et al., 2014; Ham et al., 2013; Seeley et al., 2007). These findings are consistent with the idea that socioeconomic disadvantage may lead to lower executive function in part through disruption of connectivity in the SN.

Family Income-by-Age Interactions for rsFC in the CEN and DAN

There were family income-by-age interactions for rsFC in the CEN and DAN after controlling for PGS-EA. Age was positively associated with rsFC in the CEN and DAN for those in higher income families but negatively associated with rsFC in the CEN for those in lower income families. Although there is insufficient understanding of the pattern of development for rsFC, typical development seems to be characterized by protracted and increasing segregation and intrinsic strength of connectivity within brain networks (Fair et al., 2009; Teeuw et al., 2019). However, there has been variability on the relationship found between age and connectivity, with sensitive periods of more rapid development for entire networks and subregions of networks (Grayson & Fair, 2017). The CEN has shown non-linear patterns of development, increasing throughout childhood, with a slight decrease in within-network connectivity in early adolescence and more rapid increases in late adolescence (Grayson & Fair, 2017). In studies of the CEN and DAN, along with long-range increasing connectivity associated with age, there is a concomitant decrease in connection strength for short-range or spatially adjacent regions (Fair et al., 2007; Farrant & Uddin, 2015). This finding suggests that specific node to node connections may demonstrate different maturational patterns even within networks and should be further explored.

Only the children and adolescents in this sample from higher income backgrounds seemingly demonstrated increasing intrinsic strength of the CEN and DAN with development. This result suggests that children and adolescents in socioeconomic disadvantaged families may not demonstrate the same pattern of normative network segregation and maturation. More broadly, it suggests that age-related changes in rsFC during development may vary by socioeconomic context.

Particularly in the CEN, the children from lower income families even demonstrated an inverse association or the opposite trajectory from increasing strength within networks. These children also showed the highest connectivity at younger ages. These findings may be consistent with previously proposed hypotheses of early maturation of neural circuitry in response to early life stress, such as the stress acceleration hypothesis (Callaghan & Tottenham, 2016). This theory suggests that high levels of early life stress, induced by circumstances such as socioeconomic disadvantage, may lead to early maturation in brain function with subsequent altered developmental trajectories in brain network efficacy (Tooley et al., 2021). Early maturation of neural connectivity is theorized to occur as an adaptation to stressful environments that ultimately leads to less long-term efficiency in developed neural networks. This hypothesis, though recent, has been supported in a number of studies, especially for frontolimbic circuitry (Gee, 2021; Tooley et al., 2021).

The two networks in which these findings were present, the CEN and DAN, are particularly important for higher-order processes such as attentional control and executive function, such as working memory (Freedman et al., 2020; Menon, 2011; Seeley et al., 2007; Vossel et al., 2014). Accelerated maturation in these specific networks could ultimately lead to less efficient neural systems and diminished cognitive and executive function abilities in the long-term (Tooley et al., 2021).

Null Findings

There were unexpected null findings for associations between socioeconomic factors and rsFC in the DMN, counter to results previously found (Rakesh, Seguin, et al., 2021; Sripada et al., 2014). One study reported that the developmental trajectory of DMN connectivity is not uniform across all nodes (Supekar et al., 2010). Thus, average connectivity across the entire network may not reflect the changes that may be occurring if the edges were looked at separately. There were also null findings in terms of main effects of socioeconomic factors on rsFC in the DAN and CEN. However, the age effects may help to explain these null findings.

There were no PGS-EA-by-socioeconomic factor interactions for rsFC in the focal networks. Behavior genetics research has shown some evidence of differences in the heritability of cognitive skills as a function of socioeconomic context (Harden et al., 2007; Tucker-Drob & Harden, 2012; Turkheimer et al., 2003). But other previous research has often found additive rather than interactive effects of PGS-EA and socioeconomic factors on brain structure and cognitive outcomes (Judd et al., 2020; Merz et al., 2022; Raffington et al., 2019; von Stumm et al., 2020).

Sensitivity Analyses

The sensitivity analyses were designed to adhere to strict thresholds of motion. Head motion can introduce confounds to the measured signals, producing spurious changes in fMRI data, particularly in populations with higher motion, such as children (Power et al., 2012; Satterthwaite et al., 2012; Van Dijk et al., 2012). In all sensitivity analyses, the associations between PGS-EA and rsFC in the CEN remained significant. As the thresholds increasingly became stricter, the main effects of family income and family-income-by-age interactions for rsFC became non-significant. In a large-scale study of children, groups with the highest motion had higher prevalence rates of ethnic/racial minority backgrounds, lower parent education, and lower household incomes (Cosgrove et al., 2022). The authors suggest that motion-correction methods may inadvertently bias samples and results, particularly if motion relates to a variable of interest. In the current sample, mean FD was strongly correlated with age ($r = -.27$, $p < .0001$) but not family income ($r = -.099$, $p = .13$), parental education ($r = .008$, $p = .90$), or PGS-EA ($r = -.001$, $p = .98$). Yet, by restricting analyses to only those with extremely low motion, we may be erasing variability in the sample related to family income and age. Hence, this could explain why some of the main findings did not remain significant in the sensitivity analyses. For this reason, also, the sensitivity analyses are considered supplemental to the main results in this study.

Limitations

There were several limitations to consider when interpreting the findings from this study. First, due to the use of a cross-sectional, correlational design, no causal inferences can be made. In addition, inferences about development cannot be made based on studies using cross-sectional designs. Second, the findings from this study may be specific to samples of European ancestry and may not extend to individuals of different ethnic backgrounds. Large-scale GWAS, which are required for identifying SNPs used in calculating polygenic scores, have not been conducted that allow for the computation of reliable polygenic scores in populations of other ancestries at this time (Okbay et al., 2022). Third, this study did not over-sample for lower family incomes and parental educational attainments. Therefore, replication of the findings may be needed to ensure generalizability of the findings to populations experiencing greater socioeconomic disadvantage. Fourth, detection of interaction effects requires a great deal of power, and our smaller sample size may have reduced the ability to detect interaction effects.

Conclusion and Policy Implications

Despite these limitations, results suggest that PGS-EA and socioeconomic factors may make unique contributions to functional connectivity in neural networks that support executive function. Higher PGS-EA was significantly associated with greater connectivity in the central executive network. Lower family income was associated with greater connectivity in the salience network. Socioeconomic disadvantage may disrupt patterns of development and efficacy in multiple neural networks associated with executive function, including the central executive network and dorsal attention network, independent of genetic influences.

Investigating the unique and compounding nature of genetic and environmental contributions to alterations in brain function is an important pursuit for researchers. Findings from this study shed light on the neural mechanisms potentially underlying socioeconomic disparities in cognitive development while simultaneously considering genetic contributions. Research on genetic factors can help build policies and social interventions that create more social equality (Harden, 2021; Plomin & von Stumm, 2022). Findings from this research can be used in efforts in applied settings to design more effective prevention programs and interventions that reduce socioeconomic disparities in cognitive outcomes and academic achievement in children and adolescents.

TABLES

Table 1. Descriptive statistics for sample characteristics (*N* = 245)

	M	***SD***
Age (years)	13.05	4.78
Family income (U.S. dollars)	119,900	76,914
Parental education (years)	15.69	1.8
Mean FD	.22	.42
	%	***n***
Sex (female)	51.02	125
Scanner site		
Cornell University	7.34	18
University of California, Davis	15.92	39
Kennedy Krieger Institute/Johns Hopkins	20.41	50
Massachusetts General Hospital/Harvard	1.63	4
University of California, San Diego	29.39	72
University of Massachusetts Medical School	12.65	31
Yale University	12.65	31

Note. Although family income was log-transformed for use in analyses, family income raw data are provided here for ease of interpretation. FD, framewise displacement.

Table 2. The number of SNPs from the Lee et al. (2018) (EA3) GWAS included in each PGS-EA *p*-value threshold

***p*-value threshold**	**Number of SNPs from Lee et al. (2018) included**
$p < 5 \times 10^{-8}$	604
$p < 1 \times 10^{-7}$	694
$p < 1 \times 10^{-6}$	1067
$p < 1 \times 10^{-5}$	1795
$p < .0001$	3241
$p < .001$	6395
$p < .01$	14426
$p < .05$	28535
$p < .1$	38875
$p < .5$	80125
$p < 1$	99493

Note. SNP, single nucleotide polymorphism; GWAS, genome-wide association studies; PGS-EA, polygenic score for educational attainment

Table 3. Number of fMRI volumes acquired during the scan for each PING study site

Scanner site	**Number of fMRI volumes**
Cornell University	128
University of California, Davis	300
Kennedy Krieger Institute/Johns Hopkins	156
Massachusetts General Hospital/Harvard	128
University of California, San Diego	50
University of Massachusetts Medical School	156
Yale University	128

Note. fMRI, functional magnetic resonance imaging; PING, Pediatric Imaging, Neurocognition, and Genetics

Table 4. Nodes of the central executive, salience, dorsal attention, and default mode networks from the Yeo parcellation

	MNI coordinates		
Region	***x***	***y***	***z***
Central Executive Network			
Left inferior parietal lobule	-44	-51	48
Left inferior temporal cortex	-59	-49	-17
Left superior frontal gyrus	-22	13	60
Left inferior frontal gyrus	-41	35	19
Left middle orbital frontal gyrus	-28	43	-13
Left ventral prefrontal lobule	-30	22	-4
Left precuneus	-4	-71	46
Left middle cingulum	-5	-15	29
Left medial superior frontal gyrus	-5	26	45
Right inferior parietal lobule	50	-47	48
Right middle temporal cortex	62	-37	-15
Right ventral prefrontal cortex	32	23	-7
Right superior frontal gyrus	41	35	24
Right precuneus	7	-72	43
Right middle cingulum	6	-15	29
Right medial superior frontal gyrus	6	30	41
Salience Network			
Left parietal operculum	-59	-33	27
Left middle temporal gyrus	-57	-56	12
Left frontal operculum insula	-41	5	3
Left middle frontal gyrus	-29	41	31
Left dorsal anterior cingulate	-5	4	40
Right supramarginal gyrus	61	-30	26
Right precentral gyrus	51	0	49
Right frontal operculum insula	42	9	2
Right inferior frontal gyrus	52	39	2
Right middle frontal gyrus	30	45	30
Right dorsal anterior cingulate	5	8	41
Dorsal Attention Network			
Left superior parietal lobule	-27	-60	47
Left frontal eye field	-26	-4	55
Left precentral gyrus	-49	4	32
Right superior parietal lobule	29	-60	51
Right frontal eye field	28	-4	55

Right precentral gyrus	48	7	28
Default Mode Network			
Left angular gyrus	-48	-62	33
Left medial temporal gyrus	-58	-17	-14
Left medial superior frontal gyrus	-11	57	25
Left precuneus/ posterior cingulate cortex	-6	-53	30
Left parahippocampal cortex	-22	-30	-20
Right parietal	52	-55	29
Right medial temporal	57	-9	-17
Right ventral prefrontal cortex	46	29	-12
Right medial prefrontal cortex	8	52	22
Right precuneus/ posterior cingulate cortex	7	-53	28

Note. MNI = Montreal Neurological Institute.

Table 5. Descriptive statistics and zero-order correlations between variables of interest

	Variable	1	2	3	4	5	6	7
1	Parental education (years)	--						
2	Family income (U.S. dollars)	.42**	--					
3	CEN rsFC	.09	.01	--				
4	SN rsFC	-. 01	-.04	.72**	--			
5	DMN rsFC	.04	-.05	.73**	.57**	--		
6	DAN rsFC	-.03	-.03	.42**	.50**	0.35**	--	
7	PGS-EA	.31**	.19**	.14*	.09	.06	.05	--
	M (*SD*)	15.66 (1.82)	118,321 (75,166)	.10 (.00)	.10 (.00)	.01 (.00)	.09 (.00)	.02 (1.03)

Note. PGS-EA, polygenic score for educational attainment; CEN, central executive network; SN, salience network; DMN, default mode network; DAN, dorsal attention network; rsFC, resting-state functional connectivity.

* $p < .05$. ** $p < .01$.

FIGURES

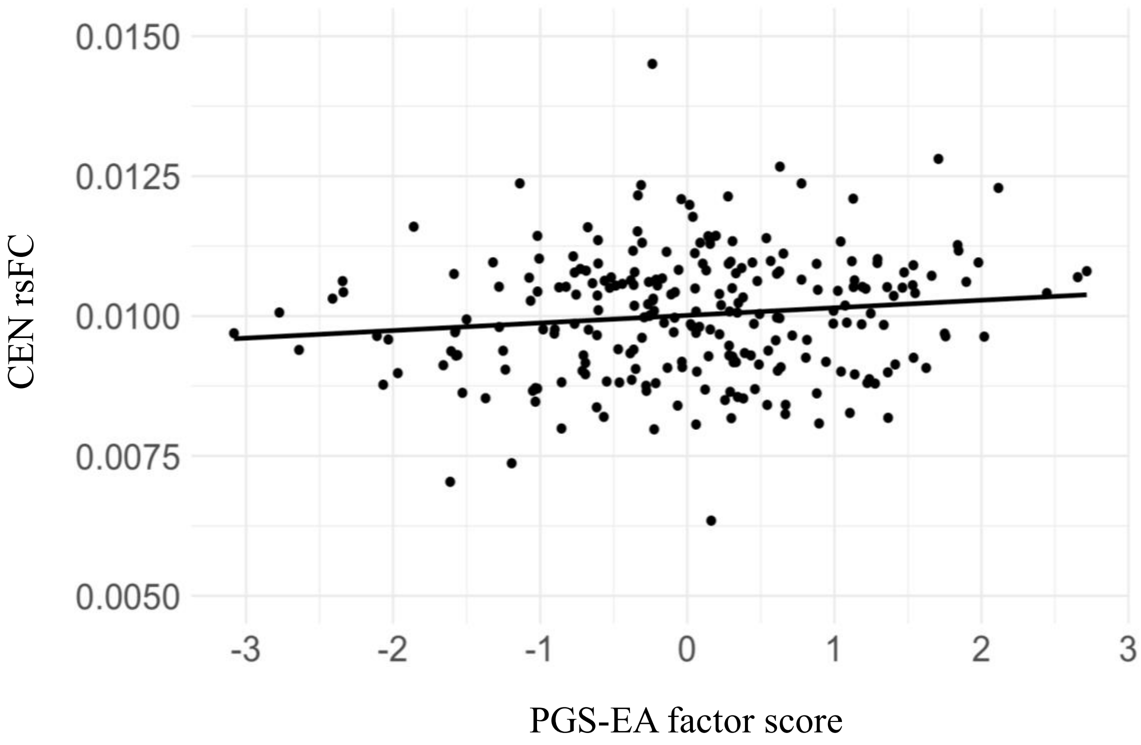

Figure 1. Higher educational attainment polygenic score (PGS-EA) was significantly associated with higher rsFC in the central executive network (CEN).

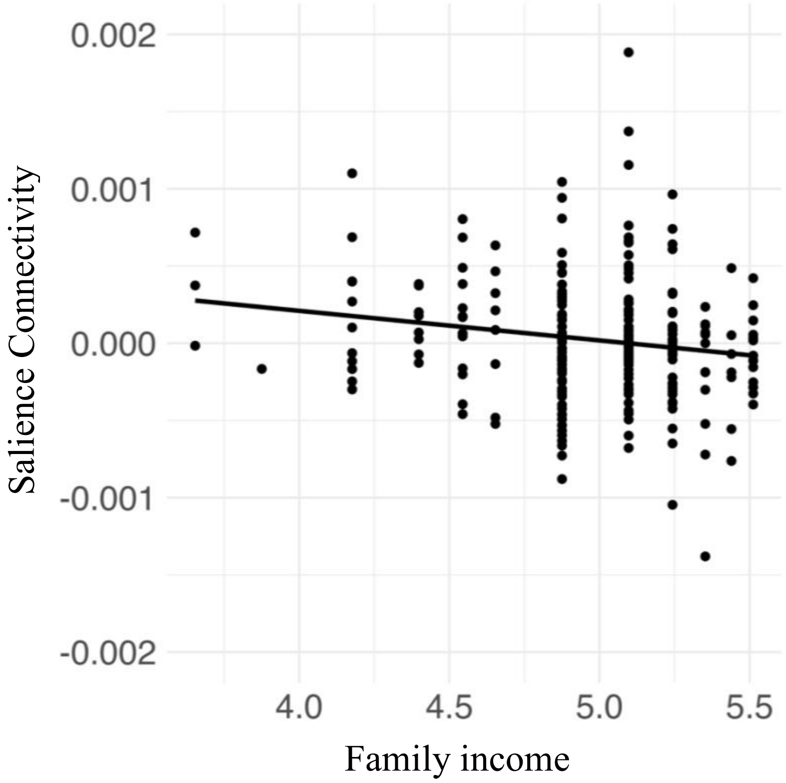

Figure 2. Scatterplot showing the residuals from a regression model with covariates plotted against the family income (log-transformed). The scatterplot visualizes the relationship between family income and the residuals, providing insight into salience network connectivity as a function of family income after accounting for the effects of the covariates.

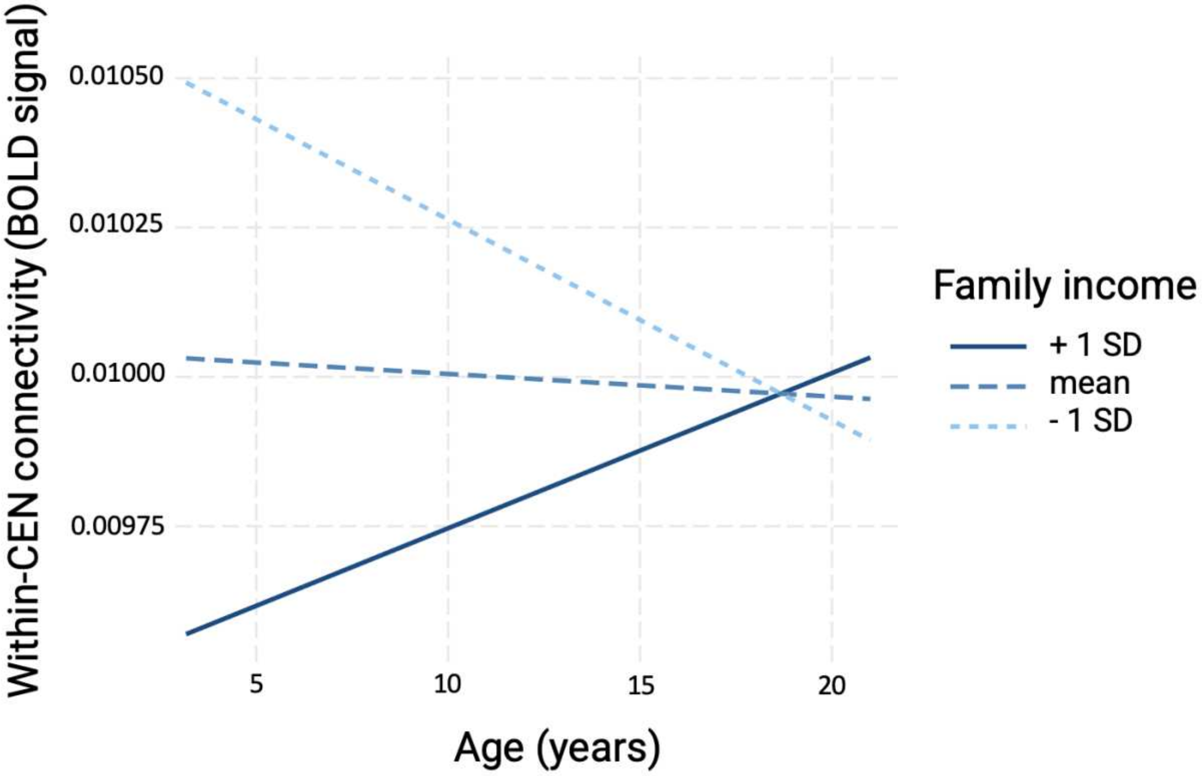

Figure 3. A simple slopes plot visualizing the interaction between family income and age for resting-state functional connectivity (rsFC) in the central executive network (CEN). Age was positively associated with rsFC in the CEN for children from higher income families and negatively associated with rsFC in the CEN for children from lower income families.

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