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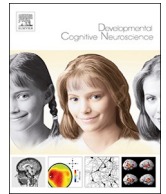
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Income change alters default mode network connectivity for adolescents in poverty

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ABSTRACT

Experiencing poverty during childhood and adolescence may affect brain function. However, income is dynamic, and studies have not addressed whether income change relates to brain function. In the present study, we investigated whether intrinsic functional connectivity of default mode network (DMN) regions was influenced by mean family income and family income change. Parents of 68 Mexican-origin adolescents (35 females) reported family income annually when adolescents were 10–16 years old. Intercept and slope of income at each of these ages were calculated for each participant. At age 16 years, adolescents completed a resting state functional neuroimaging scan. Adolescents from high and low income families did not differ in their functional connectivity, but for adolescents in families with lower incomes, their connectivity patterns depended on their income slope. Low-income adolescents whose income increased demonstrated greater connectivity between the posterior cingulate cortex (PCC) and the medial prefrontal cortex (mPFC), both DMN regions, and between the PCC and the right inferior frontal gyrus. Increases in income were associated with greater connectivity of the mPFC with the right inferior frontal gyrus and the left superior parietal lobule regardless of mean income. Increases in income, especially among adolescents in poverty, may alleviate stressors, influencing the development of brain networks.

1. Introduction

Growing up in poverty is associated with numerous contextual stressors (Evans, 2004) and can have pernicious effects on later behavior and physiology. However, incomes are dynamic across the lifespan (Duncan, 1996), and income volatility has itself been found to be predictive of child outcomes, particularly for children in lower income families (Dearing et al., 2001). Income losses across middle childhood are associated with increased risk of developing internalizing and externalizing problems, while income gains are associated with decreased risk of developing externalizing problems (Miller and Votruba-Drzal, 2016). These behavioral outcomes are likely mediated in part by brain structure and function. Family income during childhood is associated with alterations to brain structure and function in adolescence and adulthood (for comprehensive reviews, see Brito and Noble, 2014; Johnson et al., 2016), but income change has not been examined in relation to the brain. In the present study, we investigated how both mean income and income change across adolescence are associated

with the brain's intrinsic functional connectivity.

Brain activity is coordinated through large-scale brain networks. The regions that make up each network demonstrate correlated activity, or connectivity, at rest (Yeo et al., 2011). Aberrant connectivity within the default mode network (DMN), one of the core brain networks, is associated with low income, elevated stress hormones, and numerous psychiatric disorders (Buckner et al., 2008; Menon, 2011; Sripada et al., 2014). The DMN includes the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), ventral prefrontal cortex, and medial temporal lobe. These regions demonstrate high correlated activity at rest and show activity in response to tasks involving autobiographical memory, prospection, theory of mind, and self-referential processing (Buckner et al., 2008; Spreng et al., 2009). Connectivity among regions within the DMN increases from childhood to adulthood, indicating more integration, or coordinated activity with age (Fair et al., 2008), while connectivity between DMN nodes and other networks decreases, or becomes more segregated, indicating more efficient between-network communication with age (Stevens et al., 2009). Given

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the DMN's function and these developmental patterns suggestive of both structural and functional fine-tuning, DMN connectivity and its associated functions may be sensitive to the effects of income and income change across adolescence.

One study to date investigated the effects of childhood family income on later patterns of DMN connectivity. Sripada et al. (2014) examined the effects of age 9 family income-to-needs ratio on DMN connectivity in early adulthood, controlling for concurrent income. They found that family income-to-needs ratio at age 9 was positively correlated with PCC connectivity to hippocampus, vmPFC, and the adjacent PCC, indicating that higher family income in late childhood predicted greater connectivity within the DMN in young adulthood. However, these results should be interpreted in light of the fact that current income and childhood family income were highly correlated in the sample, and thus variance attributed to current income must be interpreted in light of this multicollinearity (Kraha et al., 2012). Examining income change as a variable of interest may more closely represent income dynamics and help disentangle contributions from past and current income. In addition, while Sripada et al. (2014) used only a PCC seed, use of both PCC and mPFC seed regions is typical in seed-based resting state functional connectivity analysis of the DMN (e.g. Greicius et al., 2003; Sherman et al., 2014), and both PCC and mPFC have been found to show distinct connectivity patterns with regions outside of the DMN (Uddin et al., 2009).

In the current study, we investigated whether DMN intrinsic connectivity patterns in relation to childhood family income, similar to those reported by Sripada et al. (2014), were evident in a sample of Mexican-origin late adolescents from families of low to moderate income. Because family income is dynamic, and the effects of poverty can vary based on its timing and volatility, we examined the effects of mean family income, change in family income across adolescence, and their interaction. A positive income slope would indicate that family income-to-needs ratio increased across adolescence, while a negative income slope would indicate that family income-to-needs ratio did not change. In addition, for adolescents whose mean income was low, a positive income slope would mean that they experienced greater poverty earlier in adolescence than they did later, while a negative income slope would mean that they experienced greater poverty later in adolescence than they did earlier.

We expected that both greater mean income and a more positive slope of income across adolescence would be associated with increased connectivity between the PCC and mPFC seed regions. Furthermore, we expected that the effects of changes in income and differential socioeconomic experiences across the adolescent years would be more pronounced for adolescents in poverty. We therefore hypothesized that mean income and income slope would interact in predicting connectivity between PCC and mPFC, such that income slope would have a stronger effect on connectivity within the DMN for adolescents with lower mean family income. We also used a whole brain analysis approach to explore whether mean income and income change would influence connectivity between each of the two DMN seed regions and the rest of the brain. We expected that high income and income gains would be associated with increased connectivity with other regions within the DMN and decreased connectivity with regions outside the DMN.

2. Method

2.1. Participants

As described in previous work (Weissman et al., 2015), participants were 73 Mexican-origin adolescents (40 female, $M_{Age} = 16.26$ years, $SD = 0.50$) enrolled in a functional neuroimaging sub-study of the California Families Project (CFP), a 10-year, prospective, longitudinal study of risk for and resilience to substance use problems. Participants in the main CFP study included 674 single- and two-parent families of

Mexican origin with a fifth grade child ($M_{Age} = 10.85$, 50% female) who were drawn at random from school rosters of students during the 2006–2007 and 2007–2008 school years. All adolescents in the CFP completed the Woodcock-Johnson III IQ test (Woodcock et al., 2001) on the first visit in fifth grade. Verbal intelligence was assessed using the Verbal Comprehension subscale, and fluid intelligence was assessed using the Visual Matching subscale. Individuals with a total score ≤ 70 on these subscales were ineligible to participate in the current study. Participants were recruited from the parent study based on their responses on two substance use scales completed in the 9th grade (ages 14–15) (Elliott et al., 1982; Shaffer et al., 2000). Adolescents met criteria for the user group ($N = 37$) if during the 9th grade they reported using alcohol, marijuana or other drugs three or more times within the three months prior to their annual CFP assessment. Adolescents met criteria for the abstainer group ($N = 36$) if in grade 9 they reported that they had never used substances and had no intention to use substances in the future. Simple random sampling without replacement using these grouping criteria was used to select an equal proportion of users and abstainers. This selection approach over a fully randomized strategy was used to ensure variability in substance use in the adolescents who completed the neuroimaging study. Nonetheless, the rate of substance use in our present sample was fairly low and predominantly subclinical (Table 1). Four adolescents met criteria for a diagnosis of alcohol abuse. Two met criteria for a diagnosis of alcohol dependence. One met criteria for marijuana abuse, and one met criteria for marijuana dependence. Finally, one adolescent met criteria for both marijuana and alcohol abuse. Overall, patterns of use in the sample are similar to the distributions found in studies of substance use prevalence in Latino youth (Atherton et al., 2016; Johnston et al., 2014; Weissman et al., 2015). Because substance use was not a variable of interest in this study, recruitment status was used as a covariate in all analyses. One adolescent was excluded from analyses because of missing income-to-needs ratio data. Four adolescents were excluded from analyses due to excessive movement in the scanner, resulting in a sample of 68 youths for all reported analyses.

2.2. Measures

Mothers reported their annual household income yearly when adolescents were 10–16 years old, to the nearest \$5000 increment (i.e., \$30,001–\$35,000), with $\geq \$95,001$ as the highest reporting option. Each increment corresponded with a number between 1 = less than \$5000 and 20 = \$95,001 or more. They also reported their household roster. Their income value was then divided by the income value that corresponded with the poverty line for their family size as indicated by the U. S. Census Bureau (www.census.gov/hhes/www/poverty/data/threshld/). For example, in 2010, the poverty threshold for a family of three was \$17,552, corresponding to income value 4 = \$15,001–\$20,000. A family of three reporting an income between \$15,001–\$20,000 would have an income-to-needs ratio of 1 for that year. A family of three reporting an income of \$20,001–\$25,000 would have an income-to-needs ratio of 1.25. Ordinary least squares regression was used to calculate the intercept and slope of each participant's family income-to-needs ratio for the 7 waves of data collection relative

Table 1
Substance use frequency in the past 3 months among “high risk” youth ($N = 35$).

	Cigarettes		Alcohol		Marijuana	
	N	%	N	%	N	%
Never	30	88	14	41	19	58
Less than once a week	3	9	16	47	11	33
Once per week	1	3	2	6	0	0
Two or three times a week	0	0	2	6	1	3
Almost every day	0	0	0	0	2	6

to the wave, centered at wave 4 (age 13) so that the intercept represented the mean income over the 7 waves, and the slope represented the linear pattern of change.

2.3. Resting state fMRI

Participants underwent fMRI resting-state procedures whereby they were instructed to lie still in the scanner with their eyes open and to focus on a white fixation cross presented on a black screen for 7 min 24 s. Scanning occurred with a Siemens 3T TIM Trio MRI scanner with a 32-channel head coil. Parameters for image acquisition were: voxel size = $3.5 \times 3.5 \times 3.5$ mm, slices = 35, slice thickness = 3.5 mm, repetition time = 2000 ms, echo time = 27 ms, flip angle = 80° , interleaved slice geometry, field of view = 224 mm. Images were T2 wted. The first three volumes were discarded to ensure magnet stabilization, leaving 220 vol.

2.4. fMRI data preprocessing

Preprocessing was conducted using the FMRIB Software Library (FSL; Smith et al., 2004) and Analysis of Functional NeuroImaging (AFNI) software (version 17.1.1, updated June 6, 2017; Cox, 1996). Preprocessing consisted of slice timing correction, rigid body motion correction with six degrees of freedom, and spatial smoothing with a 6 mm half-maximum Gaussian kernel. “Denoising” of the data was accomplished through independent component analysis using FSL’s MELODIC, with components rated as either signal or noise using criteria for visual inspection described by Kelly et al. (2010). The noise components were filtered out of the functional data. Each participant’s functional data were then co-registered with their brain-extracted structural images and normalized to Montreal Neurological Institute (MNI) stereotaxic space using FSL’s two-stage registration method via FLIRT. Alignment was visually confirmed for all participants. AFNI was then used for de-spiking, band-pass filtering above 0.1 Hz and below 0.01 Hz, concurrent with regression of the 6 motion parameters, and censoring of volumes with head motion greater than 0.3 mm from the previous volume, resulting in the aforementioned exclusion of four participants for whom censoring resulted in the removal of more than 44/220 vol (i.e., 20% of the data). Mean framewise displacement, including censored volumes, was calculated for each participant as an indicator of subject movement for use as a control variable in group-level analyses ($M = 0.10$ mm, $SD = 0.059$).

2.5. fMRI data analysis

Based on prior work (Spreng et al., 2009; Sripada et al., 2014), two spherical seeds were defined within a 6 mm radius to assess DMN connectivity, one in PCC (MNI: $-7, -51, 31$), and one in mPFC (MNI: $-1, 47, -1$). Average time course of the voxels in each ROI was extracted using AFNI’s *3dmaskave*.

Seed-to-seed connectivity was derived by calculating the correlation between the two time courses. Correlation coefficients were transformed using Fisher’s z' transformation. Multiple regression analysis was used to determine the effect of income-to-needs ratio intercept and slope (each mean-centered) and their interaction effect on the z' -transformed correlation between PCC and mPFC activity, representing seed-to-seed connectivity for each participant, controlling for gender, recruitment status, and movement.

Whole brain connectivity of each seed was determined by finding the correlation between the seed time course and the time course of every voxel in the brain for each participant using AFNI’s *3dfim+*. Correlation coefficients were transformed using Fisher’s z' transformation. More positive values in the resulting z' -transformed score for each voxel indicated more similarity between the BOLD time course of the ROI and that voxel, while more negative values indicated anticorrelation between the BOLD time courses.

Table 2
Descriptive statistics and Pearson correlation coefficients for sample characteristics.

Variable	N	M	SD	1	2	3	4
1. Gender (1 = female)	68	0.51	–	–			
2. Substance use status (1 = users)	68	0.51	–	–0.18	–		
3. Mean income-to-needs ratio	68	1.34	0.66	0.03	–0.09	–	
4. Income-to-needs ratio slope	68	0.02	0.11	–0.06	–0.34*	0.16	–

M = mean; SD = standard deviation; * $p < .05$.

Cluster thresholding was determined using AFNI’s *3dClustSim* program (updated 7/2016; Cox et al., 2017), which generates Monte Carlo simulations to determine appropriate cluster sizes, and AFNI’s *3dFWHMx* program, which accounts for the number of voxels and the intrinsic spatial autocorrelation in the data residuals. Based on output from these programs, a voxel-wise threshold of $t = 2.912$, $p = .005$, and a minimum cluster size of 590 voxels produced an overall alpha < 0.05 . Regression analyses were conducted using AFNI’s *3dttest++* to determine the effect of income-to-needs ratio intercept and slope (each mean-centered) and their interaction on the z' -transformed correlation maps representing connectivity for each ROI for each participant, controlling for gender, recruitment status, and movement.

3. Results

3.1. Income dynamics

The mean income-to-needs ratio of 1.35 indicated that the average participant’s family income was just above the poverty line (Table 2). Of the 68 families in the sample, 23 had mean income-to-needs ratios below the poverty line. On average, income-to-needs ratio within the sample increased marginally over time ($M_{\text{slope}} = 0.024$, $t = 1.88$, $p = .07$). However, there was considerable variability in the slopes of income-to-needs ratio ($SD = 0.11$, range = -0.28 to 0.29). Income slope was negatively associated with recruitment status, such that adolescents whose family income-to-needs ratio increased more across adolescence were less likely to have used substances at age 14–15 years.

3.2. Head movement

Movement was not correlated with mean income ($r = -0.06$) or income slope ($r = 0.06$), nor did it differ significantly by gender or recruitment status.

3.3. Connectivity of PCC and mPFC

PCC and mPFC were strongly connected with one another ($M_{z'} = 0.54$, $SD_{z'} = 0.28$). Connectivity patterns were also very similar for the two seed regions. PCC demonstrated more extensive and stronger connectivity with posterior parietal and medial temporal cortex. The mPFC demonstrated significant positive connectivity with ventrolateral PFC, insula, and subcortical regions (in particular basal ganglia), which were not significantly connected with PCC. For visualization, regions demonstrating connectivity with the seed region at a $z' > 0.25$ are highlighted, with green depicting overall positive connectivity, red denoting a positive association with income slope, and blue highlighting a negative association with the interaction of mean income and income slope (Fig. 1). There was no negative connectivity detected of $z' < -0.25$ for either seed region.

3.4. Income dynamics and PCC-mPFC connectivity

Neither mean income nor income slope had significant main effects on PCC-mPFC connectivity, but there was a significant mean

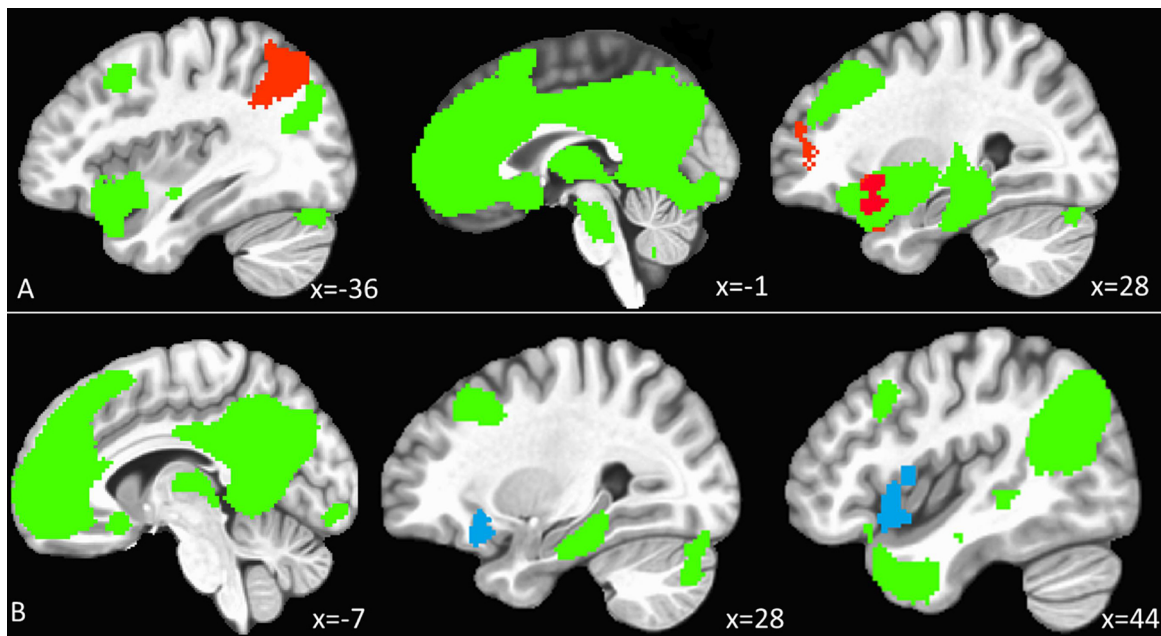


Fig. 1. Positive PCC and mPFC connectivity and relations to income dynamics. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
 (A) Positive medial prefrontal cortex (mPFC) connectivity, thresholded at $z' > 0.25$, is shown in green. Clusters where connectivity with mPFC was positively and significantly related with income slope are shown in red. (B) Positive posterior cingulate cortex (PCC) connectivity, thresholded at $z' > 0.25$, is shown in green. The cluster where the interaction between mean income and income slope was significantly related to connectivity with PCC is shown in blue. $N = 68$.

Table 3
 Multiple regression analysis of the relation between income dynamics and mPFC-PCC connectivity.

	B	SE
Intercept	0.583**	0.087
Gender	-0.084	0.070
Head movement	0.477	0.596
Substance use status	-0.075	0.075
Mean income-to-needs ratio	0.008	0.053
Income-to-needs ratio slope	0.386	0.372
Mean income x income slope interaction	-1.136*	0.481

$N = 68$; * $p < .05$, ** $p < .01$, SE = standard error.

income \times income slope interaction effect (Table 3). Plotting the simple slopes of this interaction revealed that when mean income was higher (1 SD above the mean), connectivity between the PCC and mPFC was significantly greater than 0, but did not vary significantly as a function of income slope. However, when mean income was lower (1 SD below the mean), more connectivity between PCC and mPFC was still

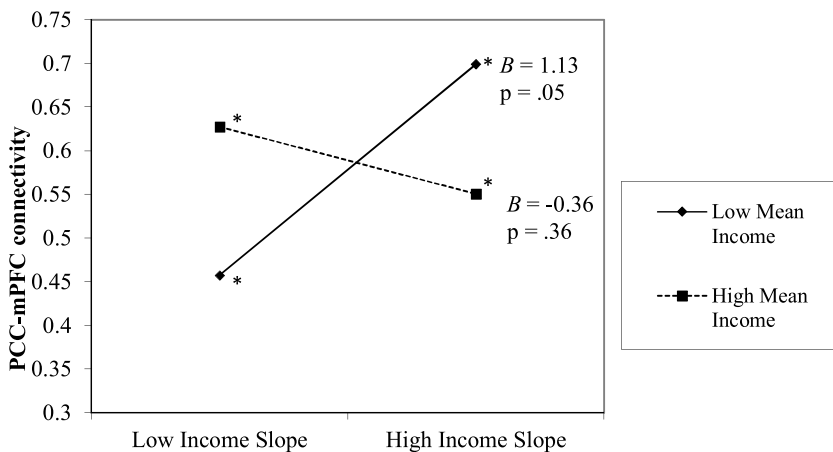


Fig. 2. Mean income \times income slope interaction in relation to PCC-mPFC connectivity.

Interaction of mean income and income slope in relation to PCC-mPFC connectivity. Low Mean Income = 0.69, High Mean Income = 2.01, Low Income slope = -0.09, High Income Slope = 0.13. PCC = posterior cingulate cortex, mPFC = medial prefrontal cortex. $N = 68$; *Significantly different from 0 at $p < .05$.

significantly greater than 0, and a more positive income slope (increasing income) was associated with greater positive connectivity between the PCC and mPFC (Fig. 2).

3.5. Income dynamics and mPFC whole brain connectivity

Mean income-to-needs ratio was not significantly associated with mPFC connectivity with any part of the brain. Two regions demonstrated a significant positive relation between income slope and the strength of connectivity with the mPFC seed (Table 4). A more positive income slope was associated with greater connectivity of the mPFC with clusters centered in the left superior parietal lobule (LSPL) and right inferior frontal gyrus (RIFG). Both regions demonstrated small to moderate connectivity with the mPFC on average (Table 4). A more positive income slope was associated with greater positive connectivity, and a more negative income slope was associated with less positive connectivity. Mean income and income slope did not interact in predicting mPFC connectivity with any other part of the brain.

Table 4
Results of whole brain analyses of the relations among income dynamics and mPFC and PCC connectivity.

Voxels	Peak (x, y, z)	Region	BA	Mean Connectivity (z score)
Clusters with significant positive relations between income-to-needs slope and mPFC connectivity				
1213	28, 20, -16	Right Inferior Frontal Gyrus	47	0.25
1039	-36, -70, 54	Left Superior Parietal Lobule	7	0.13
Clusters with a significant mean income-to-needs ratio x income-to-needs ratio slope interaction in relation to PCC connectivity				
599	28, 22, -16	Right Inferior Frontal Gyrus	47	0.03

mPFC = medial prefrontal cortex; PCC = posterior cingulate cortex; MNI coordinates for the voxel with the highest coefficient within each cluster; BA = Brodmann's area; $N = 68$; Voxel-wise threshold: $t = 2.912$, $p = .005$, minimum cluster = 590 voxels, $\alpha < 0.05$.

3.6. Income dynamics and PCC whole brain connectivity

Neither mean income-to-needs ratio nor income slope were significantly independently associated with PCC connectivity with any part of the brain. There was a significant mean income x income slope interaction predicting PCC connectivity with a cluster centered in RIFG, and in the right anterior insula. This region demonstrated no connectivity with PCC on average (Table 4).

Plotting the simple slopes of these interactions revealed that when mean income was higher (1 *SD* above the mean), connectivity between the PCC seed and RIFG did not differ significantly from 0 and did not vary significantly as a function of income slope. However, when mean income was lower (1 *SD* below the mean), there was a significant positive association between income slope and connectivity between PCC and RIFG. More positive income slope (increasing income) was associated with greater positive connectivity between the PCC seed and RIFG, while a more negative income slope (decreasing income) was associated with less positive and more negative connectivity, albeit not significantly different from 0 when income slope was 1 *SD* below the mean (Fig. 3).

3.7. Post hoc tests within substance abstaining adolescents only

To ensure that these effects were not influenced by the significant association between income slope and substance use recruitment, post-hoc multiple regression analyses were conducted using the mean z' -transformed scores of mPFC-PCC connectivity and each significant cluster as outcome variables among the subset of adolescents who had



Fig. 3. Mean income x income slope interaction in relation to PCC-RIFG connectivity.

Interaction of mean income and income slope in relation to PCC-RIFG connectivity. Low Mean Income = 0.69, High Mean Income = 2.01, Low Income slope = -0.09, High Income Slope = 0.13. PCC = posterior cingulate cortex, RIFG = right inferior frontal gyrus. $N = 68$; *Significantly different from 0 at $p < .05$.

never engaged in substance use. The regressors in these multiple regressions were sex, head movement, mean income, income slope, and the mean income x income slope interaction. The mean income x income slope interaction in relation to mPFC-PCC connectivity was no longer significant in this regression, but the effect size was slightly higher in magnitude ($B = -1.312$, $S.E. = 0.783$, $p = .105$) suggesting that this null result was due to reduced power not the influence of substance use. All results reported in Sections 3.5 and 3.6 were significant in these regressions, indicating that effects were not driven by substance use history.

4. Discussion

4.1. Main findings

This study investigated the effects of mean income-to-needs ratio and income change across seven years of adolescence on resting state functional connectivity of the DMN, based on seed regions in the mPFC and PCC. Income change interacted with mean income in relation to mPFC-PCC connectivity, such that income slope was positively related to connectivity only among adolescents with low mean income. In addition, whole brain analyses revealed that mPFC connectivity with the RIFG and the LSPL were positively associated with income change and that income change interacted with mean income in relation to PCC connectivity with the RIFG. Overall, these results suggest that ongoing integration and segregation of the brain's functional connectivity during adolescence may be sensitive to relative change in income, especially among low-income adolescents.

More positive connectivity between mPFC and PCC may be indicative of greater integration between the posterior and anterior sub-networks of the DMN among impoverished adolescents whose family income increased. Given the function of the DMN, increased connectivity between network subcomponents may serve an adaptive function, by improving social cognition and prospection, allowing adolescents to navigate increasingly complicated social environments and apply past experiences to future decisions. In addition, greater connectivity between anterior and posterior components of the DMN has been found to be associated with better executive function (Hampson et al., 2006), perhaps because it allows for more coherent deactivation during attention-demanding tasks (Greicius et al., 2003). Better executive function is consistently associated with higher socioeconomic status (Hackman and Farah, 2009). Greater connectivity between the anterior and posterior DMN among adolescents, especially those near the poverty line, who experience increases in family income may therefore be predictive of improved cognitive and behavioral outcomes for those adolescents relative to their comparatively impoverished peers who experience decreases in family income.

While the PCC and mPFC are typically considered the hubs of the

DMN (Greicius et al., 2003; Sherman et al., 2014) and are highly correlated with one another, they have been found to have distinct connectivity patterns. In particular, connectivity with the right insula has been found to be positive for mPFC but negative for PCC (Uddin et al., 2009). The insula is thought to be a primary hub in the salience network, important for switching between activation of the DMN and anticorrelated control networks (Menon and Uddin, 2010; Sridharan et al., 2008). RIFG and insula to PCC connectivity was more positive among low-income youth whose income was lower in early adolescence and increased across adolescence and less positive or more negative in low income youth whose income was higher in earlier adolescence and decreased later. Higher income youth demonstrated connectivity between PCC and RIFG that was not significantly different from 0 and did not differ significantly as a function of income slope. This suggests that the timing of poverty exposure could lead to differential patterns of connectivity between the posterior DMN and the salience network, with exposure early in adolescence leading to hyperconnectivity and exposure late in adolescence leading to hypoconnectivity.

One potential explanation of our findings is that chronic poverty-related stress and economic hardship caused by diminishing family income may disrupt the development of PCC connectivity. The Family Stress Model posits that economic pressure and hardship can disrupt family processes, thereby negatively impacting adolescent adjustment (Conger et al., 2002; Conger et al., 1994). Poverty duration is also positively associated with multiple indicators of physiological stress in adolescents (Evans and Kim, 2007), including elevated cortisol, which is associated with decreased DMN connectivity (Sripada et al., 2014). However, the nature of the disruptions may be dependent on when in adolescence the poverty was experienced. Adolescents who experienced more poverty early in adolescence, but whose income improved demonstrated more connectivity between the two DMN seeds, but also demonstrated more connectivity between the PCC and RIFG and insula, a hub of the salience network. Conversely, adolescents whose income decreased and therefore experienced more poverty later in adolescence, demonstrated less connectivity between the DMN seeds but also more negative connectivity between PCC and the salience network. Poverty-related stress may therefore disrupt the development of connectivity within the DMN and between the DMN and the salience network in a divergent manner depending on the timing of exposure.

In addition to poverty-related stress exposure, social cognitions may play an important role in the relation between income change and connectivity of DMN regions. Growing up in poverty and experiencing financial hardship can have profound effects on social cognition, including children's attributions for others' views of them, and their view of themselves relative to others (Heberle and Carter, 2015). Adolescents may be particularly neurobiologically sensitive to their social context (Blakemore and Mills, 2014; Schriber and Guyer, 2016), including their subjective social status. Regions of the DMN are associated with social cognition and self-reflective processes (Mars et al., 2012; Spreng et al., 2009), and there is some evidence that negative perceptions of one's own social status relate to reduced grey matter volume of DMN regions (Gianaros et al., 2007) and heightened activity in mPFC and PCC when evaluating social information (Muscatell et al., 2012). Adolescents who experience greater income change may be more cognizant of their social status relative to others, and greater engagement in social comparison may alter connectivity within the DMN.

The positive relation between income slope mPFC connectivity with the RIFG and LSPL did not differ significantly in whole brain analyses as a function of mean income. RIFG and LSPL demonstrated overall positive connectivity with mPFC across the whole sample, consistent with prior findings (Buckner et al., 2008; Uddin et al., 2009). It is possible that income change had a similar impact on mPFC connectivity with RIFG and LSPL, regardless of mean income because the development of connectivity between these regions is more impacted by adolescents' experiences of income change relative to what they had experienced previously, and consequentially their perceptions of their own

subjective social status.

4.2. Limitations and future directions

Although our study had several strengths including the sample size, demographics, and longitudinal income data, it is not without limitations. First, while multiple time points of income data allowed for an investigation of both cumulative income and income change across adolescence, these measures did not capture family income before age 10, which may also significantly influence patterns of DMN connectivity in late adolescence. Second, relying on a single time point of neuroimaging data precludes determining whether the observed differences in DMN connectivity reflect stable differences, or variability in developmental timing. As such, future work with additional time points of neuroimaging data will help to address these questions. Finally, although substance use in our sample fell within typical usage rates among adolescents (Atherton et al., 2016; Johnston et al., 2014; Weissman et al., 2015), our recruitment criteria were significantly correlated with income slope and may therefore constitute a confound, despite controlling for it in our analyses. However, recruitment status did not correlate with DMN connectivity measures, and analyses within the non-use group showed results comparable to those found for the full sample.

Although the present findings suggest that change in income across adolescence may influence patterns of DMN connectivity, the proximate mechanisms responsible for these differences remain undetermined. Future work should examine how family, neighborhood, and peer processes impacted by change in income contribute to alterations in brain function. Moreover, we intend to follow up with these adolescents in the future to determine what behavioral and psychosocial manifestations relate to the different patterns of DMN connectivity we observed. We anticipate that dissociation in behavioral phenotypes, such as cognitive empathy, social competence, and attention control, based on age of exposure to poverty may result from the different functional connectivity patterns we observed.

4.3. Conclusion

That change in income across adolescence predicted alterations in DMN connectivity in this study, especially for adolescents in poverty, suggests that neurodevelopmental outcomes are still sensitive to contextual influences experienced in adolescence. Furthermore, the brain regions of the DMN involved in social cognition processes may be especially susceptible to contextual influences during the adolescent period as suggested by prior frameworks (Blakemore and Mills, 2014; Schriber and Guyer, 2016). Policies targeted at improving the material resources of families in poverty may therefore have a profound effect on influencing adolescents' neurobiology, and therefore their social and cognitive functioning.

Conflict of interest

None.

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References

- Atherton, O.E., Conger, R.D., Ferrer, E., Robins, R.W., 2016. Risk and protective factors for early substance use initiation: a longitudinal study of Mexican-origin youth. *J. Res. Adolesc.* 26 (4), 864–879. <http://dx.doi.org/10.1111/jora.12235>.
- Blakemore, S.-J., Mills, K.L., 2014. Is adolescence a sensitive period for sociocultural processing? *Annu. Rev. Psychol.* 65 (1), 187–207. <http://dx.doi.org/10.1146/annurev-psych-010213-115202>.
- Brito, N.H., Noble, K.G., 2014. Socioeconomic status and structural brain development. *Front. Neurosci.* 8, 276. <http://dx.doi.org/10.3389/fnins.2014.00276>.
- Buckner, R.L., Andrews-Hanna, J.R., Schacter, D.L., 2008. The brain's default network: anatomy, function, and relevance to disease. *Ann. N. Y. Acad. Sci.*
- Conger, R.D., Ge, X., Elder, G.H., Lorenz, F.O., Simons, R.L., 1994. Economic stress, coercive family process, and developmental problems of adolescents. *Child Dev.* 65 (2), 541–561. <http://dx.doi.org/10.1111/j.1467-8624.1994.tb00768.x>.
- Conger, R.D., Wallace, L.E., Sun, Y., Simons, R.L., McLoyd, V.C., Brody, G.H., 2002. Economic pressure in African American families: a replication and extension of the family stress model. *Dev. Psychol.* 38 (2), 179–193. <http://dx.doi.org/10.1037/0012-1649.38.2.179>.
- Cox, R.W., Chen, G., Glen, D.R., Reynolds, R.C., Taylor, P.A., 2017. fMRI clustering and false-positive rates. *Proc. Natl. Acad. Sci. U. S. A.* 114 (17), E3370–E3371. <http://dx.doi.org/10.1073/pnas.1614961114>.
- Cox, R.W., 1996. AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Comput. Biomed. Res.* 29 (3), 162–173. <http://dx.doi.org/10.1006/cbmr.1996.0014>.
- Dearing, E., McCartney, K., Taylor, B.A., 2001. Change in family income-to needs matters more for children with less. *Child Dev.* 72 (6), 1779–1793. <http://dx.doi.org/10.1111/1467-8624.00378>.
- Duncan, G.J., 1996. Income dynamics and health. *Int. J. Health Serv.: Plan. Admin. Eval.* 26 (3), 419–444. <http://dx.doi.org/10.2190/1KU0-4Y3K-ACFL-BYU7>.
- Elliott, D.S., Ageton, S.S., Huizinga, D., 1982. *Explaining Delinquency and Drug Use*. Behavioral Research Inst, Boulder, CO.
- Evans, G.W., Kim, P., 2007. Childhood poverty and health: cumulative risk exposure and stress dysregulation. *Psychol. Sci.* 18 (11), 953–957. <http://dx.doi.org/10.1111/j.1467-9280.2007.02008.x>.
- Evans, G.W., 2004. The environment of childhood poverty. *Am. Psychol.* 59 (2), 77–92. <http://dx.doi.org/10.1037/0003-066X.59.2.77>.
- Fair, D.A., Cohen, A.L., Dosenbach, N.U.F., Church, J.A., Miezin, F.M., Barch, D.M., et al., 2008. The maturing architecture of the brain's default network. *Proc. Natl. Acad. Sci.* 105 (10), 4028–4032. <http://dx.doi.org/10.1073/pnas.0800376105>.
- Gianaros, P.J., Horenstein, J.A., Cohen, S., Matthews, K.A., Brown, S.M., Flory, J.D., et al., 2007. Perigenual anterior cingulate morphology covaries with perceived social standing. *Soc. Cogn. Affect. Neurosci.* 2 (3), 161–173. <http://dx.doi.org/10.1093/scan/nsm013>.
- Greicius, M.D., Krasnow, B., Reiss, A.L., Menon, V., 2003. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* 100 (1), 253–258. <http://dx.doi.org/10.1073/pnas.0135058100>.
- Hackman, D.A., Farah, M.J., 2009. Socioeconomic status and the developing brain. *Trends Cogn. Sci.* 13 (2), 65–73. <http://dx.doi.org/10.1016/j.tics.2008.11.003>.
- Hampson, M., Driesen, N.R., Skudlarski, P., Gore, J.C., Constable, R.T., 2006. Brain connectivity related to working memory performance. *J. Neurosci.* 26 (51), 13338–13343. <http://dx.doi.org/10.1523/JNEUROSCI.3408-06.2006>.
- Heberle, A.E., Carter, A.S., 2015. Cognitive aspects of young children's experience of economic disadvantage. *Psychol. Bull.* 141 (4), 723–746. <http://dx.doi.org/10.1037/bul0000010>.
- Johnson, S.B., Riis, J.L., Noble, K.G., 2016. State of the art review: poverty and the developing brain. *Pediatrics* 137 (4). <http://dx.doi.org/10.1542/peds.2015-3075>.
- Johnston, L.D., O'Malley, P.M., Miech, R. a., Bachman, J.G., Schlenberg, J.G., 2014. Monitoring the Future National Results on Adolescent Drug Use: Overview of Key Findings. Institute for Social Research, the University of Michigan, pp. 1–7. <http://dx.doi.org/10.1111/j.1530-0277.2010.01235.x>.
- Kelly, R.E., Alexopoulos, G.S., Wang, Z., Gunning, F.M., Murphy, C.F., Morimoto, S.S., et al., 2010. Visual inspection of independent components: defining a procedure for artifact removal from fMRI data. *J. Neurosci. Methods* 189 (2), 233–245. <http://dx.doi.org/10.1016/j.jneumeth.2010.03.028>.
- Kraha, A., Turner, H., Nimon, K., Zientek, L.R., Henson, R.K., 2012. Tools to support interpreting multiple regression in the face of multicollinearity. *Front. Psychol.* 3, 44. <http://dx.doi.org/10.3389/fpsyg.2012.00044>.
- Mars, R.B., Neubert, F.-X., Noonan, M.P., Sallet, J., Toni, I., Rushworth, M.F.S., 2012. On the relationship between the default mode network and the social brain. *Front. Hum. Neurosci.* 6, 189. <http://dx.doi.org/10.3389/fnhum.2012.00189>.
- Menon, V., Uddin, L.Q., 2010. Saliency, switching, attention and control: a network model of insula function. *Brain Struct. Funct.* 214 (5–6), 655–667. <http://dx.doi.org/10.1007/s00429-010-0262-0>.
- Menon, V., 2011. Large-scale brain networks and psychopathology: a unifying triple network model. *Trends Cogn. Sci.* 15 (10), 483–506. <http://dx.doi.org/10.1016/j.tics.2011.08.003>.
- Miller, P., Votruba-Drzal, E., 2016. The role of family income dynamics in predicting trajectories of internalizing and externalizing problems. *J. Abnorm. Child Psychol.* 1–14. <http://dx.doi.org/10.1007/s10802-016-0181-5>.
- Muscattell, K.A., Morelli, S.A., Falk, E.B., Way, B.M., Pfeifer, J.H., Galinsky, A.D., et al., 2012. Social status modulates neural activity in the mentalizing network. *Neuroimage* 60 (3), 1771–1777. <http://dx.doi.org/10.1016/j.neuroimage.2012.01.080>.
- Schriber, R.A., Guyer, A.E., 2016. Adolescent neurobiological susceptibility to social context. *Dev. Cognit. Neurosci.* 19, 1–18. <http://dx.doi.org/10.1016/j.dcn.2015.12.009>.
- Shaffer, D., Fisher, P., Lucas, C.P., Dulcan, M.K., Schwab-Stone, M.E., 2000. NIMH diagnostic interview schedule for children version IV (NIMH DISC-IV): description, differences from previous versions, and reliability of some common diagnoses. *J. Am. Acad. Child Adolesc. Psychiatry* 39 (1), 28–38. <http://dx.doi.org/10.1097/00004583-200001000-00014>.
- Sherman, L.E., Rudie, J.D., Pfeifer, J.H., Masten, C.L., McNealy, K., Dapretto, M., 2014. Development of the Default Mode and Central Executive Networks across early adolescence: a longitudinal study. *Dev. Cognit. Neurosci.* 10, 148–159. <http://dx.doi.org/10.1016/j.dcn.2014.08.002>.
- Smith, S.M., Jenkinson, M., Woolrich, M.W., Beckmann, C.F., Behrens, T.E.J., Johansen-Berg, H., et al., 2004. Advances in functional and structural MR image analysis and implementation as FSL. *Neuroimage* 23, S208–S219. <http://dx.doi.org/10.1016/j.neuroimage.2004.07.051>.
- Spreng, R.N., Mar, R.A., Kim, A.S.N., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J. Cogn. Neurosci.* 21 (3), 489–510. <http://dx.doi.org/10.1162/jocn.2008.21029>.
- Sridharan, D., Levitin, D.J., Menon, V., 2008. A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proc. Natl. Acad. Sci. U. S. A.* 105 (34), 12569–12574. <http://dx.doi.org/10.1073/pnas.0800005105>.
- Sripada, R.K., Swain, J.E., Evans, G.W., Welsh, R.C., Liberzon, I., 2014. Childhood poverty and stress reactivity are associated with aberrant functional connectivity in default mode network. *Neuropsychopharmacology* 39 (9), 2244–2251. <http://dx.doi.org/10.1038/npp.2014.75>.
- Stevens, M.C., Pearlson, G.D., Calhoun, V.D., 2009. Changes in the interaction of resting-state neural networks from adolescence to adulthood. *Hum. Brain Mapp.* 30 (8), 2356–2366. <http://dx.doi.org/10.1002/hbm.20673>.
- Uddin, L.Q., Clare Kelly, A.M., Biswal, B.B., Xavier Castellanos, F., Milham, M.P., 2009. Functional connectivity of default mode network components: correlation, anticorrelation, and causality. *Hum. Brain Mapp.* 30 (2), 625–637. <http://dx.doi.org/10.1002/hbm.20531>.
- Weissman, D.G., Schriber, R.A., Fassbender, C., Atherton, O., Krafft, C., Robins, R.W., et al., 2015. Earlier adolescent substance use onset predicts stronger connectivity between reward and cognitive control brain networks. *Dev. Cogn. Neurosci.* 16, 121–129. <http://dx.doi.org/10.1016/j.dcn.2015.07.002>.
- Woodcock, R.W., McGrew, K.S., Mather, N., 2001. *Woodcock-Johnson III Tests of Achievement*. Test Vol. 2001.
- Yeo, B.T.T., Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, D., Hollinshead, M., et al., 2011. The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *J. Neurophysiol.* 106 (3), 1125–1165. <http://dx.doi.org/10.1152/jn.00338.2011>.