What is an adaptive pattern of brain activity for a child? It depends on their environment

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Abstract.

Prior fMRI research indicates that lower resting-state functional connectivity between
two specific brain networks is linked to better cognitive test performance in children and
adults. However, most study samples are skewed towards higher-socioeconomic status
individuals – and what is adaptive for one population may not be for another. In a pre-
registered study, we analyzed resting-state fMRI data from 6839 children ages 9-10
years. For children above the federal poverty line, we replicated the prior finding: better
cognitive performance was related to weaker connectivity between the lateral
frontoparietal and default mode networks. However, for children living in poverty, this
relation trended in the opposite direction. Follow-up cross-validated predictive analyses
revealed that these results were driven by several key features of a child's environment.
Thus, "optimal" brain function depends in part on the external pressures children face,
highlighting the need for more diverse samples in research on the human brain and
behavior.
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Introduction

In the United States, one fifth of children are estimated to live below the poverty line

(Semega et al., 2019). Relative to children living just above poverty, these children are

least likely to have access to the federal social safety net, and they are at heightened

risk for poor health and educational outcomes (Hoynes & Schanzenbach, 2018;

Reardon, 2016). Compared to their peers whose families earn more money, children

living in poverty tend to perform worse on tests of cognitive functioning (for a review,

see Farah, 2017), itself a risk factor for later outcomes (e.g., Spengler et al., 2015).

However, such broad comparisons obscure substantial variability *within* the group of

children living in poverty, a large segment of whom score on par with their higher-

income peers. Here, we seek to understand this form of resilience—high cognitive test

performance in the face of structural barriers to success. One way to begin to address

this question is to identify sets of experiences that may be protective for children in

poverty, given the wide range of experiences they have (DeJoseph et al., 2020;

Gonzalez et al., 2019). Another way is to probe differences in brain function, to gain

insight into the mechanisms underlying resilience. In this study, we examine the neural

and environmental correlates of resilience in a sample of over 1,000 children across the

United States likely to be living in poverty.

In one of the most influential theories of development, Waddington proposed that

ontogenetic trajectories are variable across individuals and not inherently fixed at birth

(Johnson & de Haan, 2015; Waddington, 1957). Instead, both biological and

environmental influences interact across development to constrain the ultimate

expression of cells in our bodies. This means that in some cases, environmental

pressures, especially early in life, may cause two individuals with the same biological

constraints to develop different phenotypes. In other cases, two individuals may take

distinct developmental trajectories, but ultimately still develop the same phenotype

(Edelman & Gally, 2001). Extending this metaphor to the current study, it is possible

that two children who display the same level of performance on a cognitive test might

achieve this through different developmental trajectories, if they grow up under different

external pressures. The optimal developmental trajectory for a child, therefore, may be

influenced by the child's environment.

Accumulating evidence suggests that the brain is able to adapt flexibly to the

constraints of the environment, especially in early life. Both humans and nonhuman

animals develop skills that best suit the needs of their contexts. For example, in one set

of studies, adults who had grown up in unpredictable early environments performed

better on tests of task shifting, which may be an adaptive skill to possess during periods

of instability (Mittal et al., 2015). Similar findings have been observed in humans and

nonhuman animals across a wide range of early experiences and cognitive domains

(Ellis et al., 2017; Frankenhuis et al., 2019; Young et al., 2018). The result of this

flexibility may be that higher-level cognitive skills such as executive functions and

reasoning develop in context-sensitive ways.

Thus, neural differences between groups of children growing up in different

contexts need not indicate behavioral deficits or neural inefficiencies for either group—in

some cases, they may point to alternate routes toward the development of these higher-

level cognitive skills. Children living in poverty can have vastly different experiences,

including varying levels of exposure to threatening circumstances or deprivation of

resources (Humphreys & Zeanah, 2015; McLaughlin et al., 2014). Understanding the

ways in which their brains may have been tuned by their respective environments can

lend insight into mechanisms of adaptation, and, ultimately, how best to support each

child within the specific constraints of their lives.

Strikingly, while much research has characterized the trajectories of brain

development that support cognitive test performance for upper-middle class children—

most of whom who tend to be living in urban places close to universities in the United

States—only in the last decade has research begun to focus on children from lower

socioeconomic status (SES) backgrounds. This new thrust of research has begun to

uncover neural differences between higher- and lower-SES children in brain structure

and function, beginning from an early age (e.g., Hair et al., 2015; Hanson et al., 2013;

S. B. Johnson et al., 2016; Leonard et al., 2019; Mackey et al., 2015; Noble et al., 2015;

Noble et al., 2006). However, even while this field of the developmental cognitive

neuroscience of SES has grown, children living below the poverty line tend to be under-

represented within the population considered to be lower SES. In addition, many studies

group children considered lower SES together and compare them to a group of higher

SES children, obscuring variability within the lower SES group. Characterizing optimal

brain development for children living below poverty helps shift our questions away from

how these children differ from children above poverty, and toward a closer

understanding of mechanisms underlying variability among children who are

underrepresented in cognitive neuroscience. Ultimately, this brings us toward a fuller

understanding of brain development across the full spectrum of life experiences.

In line with the hypothesis that children may achieve the same behavior or

phenotype through different developmental routes, studies examining brain function

during higher-level cognitive tasks often find qualitatively different brain-behavior

relations as a function of children's family income. These differences appear particularly

in lateral prefrontal cortex (PFC) and parietal regions—two regions involved in higher

cognitive function which show protracted development (Casey et al., 2000), and are

likely to be sensitive to environmental input (Farah, 2017; Mackey et al., 2013; Merz,

Maskus, et al., 2019).

For example, an early study by Sheridan et al. found that nine-year-olds who fell

below the median of their sample on the federal income-to-needs ratio (mean of 1.75 in

the lower-income group) showed *stronger* lateral PFC activation when performing a

novel rule-learning task. Further, increased levels of activation appeared to be

marginally positively related to learning for the lower-SES children, while the opposite

pattern was found among the higher-SES children (Sheridan et al., 2012). In another

study, however, Finn et al. found that children who qualified for free or reduced lunch

(those whose families made less than 185% of the federal poverty level) showed

weaker activation of lateral PFC than their higher income peers as working memory

load increased. Further, these differences in activation were related to children's

performance on a standardized math test (Finn et al., 2017).

Collectively, these and other studies suggest that children with lower versus

higher family incomes may recruit different patterns of neural circuitry—particularly in

lateral prefrontal and parietal regions—to complete tasks such as working memory, rule

learning, and attention (see Merz, Wiltshire, & Noble, 2019 for a review). These

differences in brain function are typically thought to reflect differences in either the

cognitive mechanisms by which children approach the task or efficiency of neural

processing. However, differences in tasks and task demands make it difficult to

generalize across studies showing lower or higher PFC activation as a function of SES.

When children are performing a specific task, differences in brain function cannot reveal

whether there are differences in attentional allocation or strategies used to solve the

task, or in the underlying neural systems that support that behavior.

One way to reconcile these findings of SES differences in brain function may be

to measure the activity of large-scale brain networks in the absence of specific task

demands to investigate how these more global patterns relate to cognitive performance.

In this vein, researchers have probed large-scale brain networks by measuring brain

function at "rest"—that is, they have measured patterns of low-wave fluctuations in

neural activity over time while participants simply lay awake in the scanner. This

approach, called resting-state fMRI, has revealed high correlations over time among

anatomically distal brain regions. Brain regions that are highly correlated are thought to

work in tandem with one another, forming several networks across the brain that each

become more cohesive and segregated from one another across development (Power

et al., 2010). Patterns of temporal coupling within and across networks are thought to

reflect a prior history of co-activation, offering insight into recent thought patterns

(Guerra-Carrillo et al., 2014). Indeed, there is evidence that children and adolescents

living in disadvantaged neighborhoods show baseline differences in resting-state

connectivity patterns (Marshall et al., 2018). Here, we sought to investigate the relations

between resting-state connectivity and both cognitive performance and specific

environmental factors.

In studies of higher-level cognition in adults, these large-scale brain network

dynamics have been found to predict cognitive test performance (Barber et al., 2013;

Hampson et al., 2010; Keller et al., 2015; Kelly et al., 2008). One such network, the

lateral frontoparietal network (LFPN), includes regions in the lateral prefrontal and

parietal areas, and is consistently activated in higher-level cognitive tasks, such as

those taxing executive functions or reasoning. LFPN is more active during performance

of externally directed tasks than during opportunities for unconstrained, internally

directed thought (Vincent et al., 2008). In contrast, the default mode network (DMN),

including regions in the medial frontal and medial parietal areas, is consistently de-

activated during external tasks, relative to other brain networks. The DMN is more

active during internally oriented processing (Raichle et al., 2001), as well as during

tasks that require mentation outside of the here-and-now (Spreng, 2012).

In prior adult fMRI studies, stronger connectivity within LFPN and weaker

connectivity between LFPN and DMN has been associated with higher cognitive

performance (Barber et al., 2013; Hampson et al., 2010; Keller et al., 2015; Kelly et al.,

2008). This set of findings has led to the view that, in order to perform well, individuals

must practice focusing narrowly on the task at hand while inhibiting internally-directed or

self-referential thoughts (Raichle et al., 2001; Simpson et al., 2001a, 2001b; Weissman

et al., 2006). As with developmental work, however, the vast majority of participants in

adult fMRI studies are relatively high in SES.

Consistent with adult research, studies focusing on generally higher-income

children suggest that relations between LFPN and DMN are related to children's

cognitive test performance. As children develop, LFPN and DMN become more

segregated from one another (Chai et al., 2014), and increased LFPN within-network

correlation and diminished LFPN-DMN correlation at rest each predict better cognitive

test performance at ages 10 and 13 (Sherman et al., 2014). In addition, increased LFPN

activation and decreased DMN activation during a working memory task were related to

improvements in working memory between ages 8 and 22, mediating age-related

improvement, cross-sectionally (Satterthwaite et al., 2013). Reduced anticorrelations—

that is, tighter coupling—between key nodes in these networks at age 7 have even been

shown to predict attentional problems at age 11 (Whitfield-Gabrieli et al., 2020). Taken

together, the literature suggests that it is adaptive for DMN to function largely

independently from LFPN during performance of a cognitively challenging task, and that

the development of this dissociation may promote stronger focus on externally directed

tasks.

Drawing from a large behavioral and brain imaging dataset including over 10,000

children across the United States (ABCD Study; Casey et al., 2018), we asked whether

the patterns of connectivity that are adaptive among higher SES children also help to

explain why some children living in poverty are more resilient than others. Specifically,

in a set of pre-registered analyses, we tested whether characteristics of LFPN and DMN

connectivity predict cognitive test performance for over 1,000 children from this larger

dataset estimated to be living in poverty. We combined measures of children's abstract

reasoning (Matrix reasoning task), inhibition (Flanker task), and shifting (Dimensional

Card Sort task), to capture children's performance on higher-level cognitive tasks that

did not task verbal skill, given well-established SES differences in verbal performance.

Given prior evidence from higher SES children and adults, we predicted that

weaker LFPN-DMN between-network connectivity (decreased LFPN-DMN temporal

coupling) and stronger within-network LFPN connectivity (LFPN-LFPN coupling) would

be related to higher cognitive test performance even for children living in poverty.

However, it is also plausible that children in poverty might develop different brain-

behavior links in order to contend with different barriers. In line with theories that

children could achieve the same phenotype through alternate developmental

trajectories, one might expect that higher cognitive test scores would be predicted by

different patterns of network connectivity among children in poverty. To preview our

findings, our analyses revealed a different pattern in children in poverty than had been

observed in prior studies. As a result, we conducted follow-up analyses involving the

higher-income children in this sample to test whether their data would replicate prior

findings, and confirmed that it did.

In a second set of pre-registered analyses, we probed demographic variables to

better understand features of children's environments which might explain variability

both in their cognitive test performance, and in the relation between LFPN-DMN

connectivity and cognitive test performance. We looked at a set of 29 variables that

span home, school, and neighborhood contexts to see whether they could predict

variability in children in poverty's test performance. We also included interactions

between LFPN-DMN connectivity and each of these variables, to see if patterns of

brain-behavior relations could be explained by any particular set of experiences.

To our knowledge, this is the largest sample of children living below the poverty

line whose brain development has been studied. Moreover, the tight age range in this

dataset—all children were between 9 and 10 years old—complements prior studies that

have considered children across a much wider age range. Ultimately, examining

relations between patterns of brain activity and cognitive test performance could help to

elucidate the mechanisms through which high-performing children in poverty are able to

contend with structural barriers in their environments.

Results

We identified 1,034 children between ages 9 and 10 with usable data on

cognitive test performance, resting state connectivity, and family income, who were

likely to be living below the poverty line in 2016-2018, when the data were collected. We

made this determination by comparing children's combined household income to the

Supplemental Poverty Level for 2015-2017 averaged across study sites, which adjusts

for variation in the cost of living in different locations, as well as household size (L. Fox,

2017). We considered children to be in poverty if they were part of a family of 4 with a

total income of less than $25,000. An additional 5,805 children from the same study

sites had usable cognitive test, resting state, and family income data and were likely to

be living *above* the poverty line, based on their combined household income (ranging

from $25,000 to over $200,000) and number of individuals in the home. Participant

information is displayed in Tables 1 and 2.

Children's scores on the three cognitive tests (Matrix reasoning, Flanker task,

and Dimensional Card Sort task) were moderately correlated with each other, $r = 0.23 -$

0.43 in the whole sample, $r = 0.25 - 0.39$ for children living in poverty alone. We created

summary cognitive test scores by summing children's standardized scores on all three

tests, as pre-registered. We first tested whether there was an association between

income and cognitive test scores, using a linear mixed effects model with a random

intercept for study site. For this analysis, income was defined as a continuous variable

using the median income level in each income bracket. Results replicated prior studies

(e.g., Duncan & Magnuson, 2012; Farah, 2018; Noble et al., 2015): on average, children

whose families had higher incomes tended to perform better on cognitive tests, $B =$

0.008, SE = 0.0004, $p < 0.001$, $r = 0.24$, a moderate effect size, though it accounts for

only 6% of the variance in children's cognitive test scores. As shown in Figure 1,

however, there was large individual variability in cognitive test scores within each

income bracket. It is this individual variability we sought to explore further.

LFPN-DMN connectivity. Working from our pre-registered analysis plan

(https://aspredicted.org/blind.php?x=3d7ry9), we tested the relation between LFPN-

DMN connectivity and nonverbal cognitive test performance in our sample of children in

poverty. We used linear mixed effects models to predict cognitive test performance from

LFPN-DMN connectivity, controlling for children's age and head motion in the scans,

with a random intercept for study site (see Methods). Contrary to previously published

results, we did not find a negative association between LFPN-DMN connectivity and test

performance. In fact, the estimated direction of the effect was positive, though this was

not statistically significant, B = 2.11, SE = 1.12, t (1028) = 1.88; χ_2 (1) = 3.52, p = 0.060.

This numerically positive association was still observed when using a robust linear

mixed effects model, which detects and accounts for outliers or other sources of

contamination in the data that may affect model validity, B = 1.78, SE = 1.09, t = 1.64.

Thus, this unexpected pattern was not driven by outliers. This effect was most

pronounced for Matrix Reasoning and least evident for Flanker, but the estimate was

positive for all three tests (see Supplement).

Given this unexpected result, we next explored whether the expected association

between LFPN-DMN connectivity and test performance was present in higher-income

children in the larger dataset. To this end, we analyzed the 5,805 children from the

same study sites were likely to be living *above* the poverty line. Consistent with prior

studies (Satterthwaite et al., 2013; Sherman et al., 2014; Whitfield-Gabrieli et al., 2020),

children living above the poverty line showed a negative association between LFPN-

DMN connectivity and cognitive test performance, B = -1.41, SE = 0.45, t (5794) = -

3.14; χ_2 (1) = 9.85, p = 0.002. A direct comparison between the groups confirmed that

the association between LFPN-DMN connectivity and test performance differed as a

function of whether or not children were living in poverty, χ_2 (1) = 8.99, p = 0.003 (Figure

2). For children living above poverty, having higher LFPN-DMN connectivity appeared to

be risk factor for low cognitive test performance, while for children living below poverty,

this was more protective (see Supplementary Figure 1).

To further investigate the reliability of this dissociation, we performed several

follow-up tests. Our first test was designed to probe how frequently the parameter

estimate observed in the children in poverty would be expected to be observed in a

larger sample of children living above poverty. Using a bootstrapping procedure (see

Methods), we estimated the expected distribution of LFPN-DMN coefficients for the

prediction of cognitive test scores among the higher-income children in the dataset. The

results of this analysis confirmed that the observed estimate for children in poverty fell

outside of the 95% CI, and was higher than 987 out of 999 bootstrapped samples, p =

0.013. Repeating this bootstrapping procedure for children living below poverty revealed

a similar effect (see Supplement); the bootstrapped distributions from the two samples

are plotted side by side in Figure 3. Permutation testing further confirmed this

dissociation; a model trained on children above poverty consistently over-estimated the

performance of children living below poverty, well outside of what would be expected by

chance (see Supplement). These results confirm that the relation between LFPN-DMN

connectivity and cognitive performance differed for children living below and above

poverty.

We performed several additional follow-up analyses to ensure that these results

were not driven by differences in head motion or age. First, head motion—which is

known to influence functional connectivity estimates (Power et al., 2015)—differed

significantly as a function of poverty status (see Table 1) and was correlated with

cognitive test performance (B = -1.91, SE = 0.16, p < 0.001). Thus, we repeated these

analyses with only those children who met a stringent motion criterion of less than or

equal to 0.2 mm of average framewise displacement (N = 4444; 589 below poverty).

Results were consistent, and even stronger, in this subsample of low-motion children

(see Supplement). Second, given prior evidence that LFPN and DMN become less

correlated across age, we asked whether this relation was true in the current study.

Indeed, even within this very restricted age range, LFPN-DMN connectivity was lower

among older children across the entire sample, B = -0.0003, SE = 0.0001, t (6832) = -

2.93 p = 0.003, a pattern which was consistent for both children below poverty and

those above (see Supplementary Figure 2). We note that, while children in poverty had

marginally higher LFPN-DMN connectivity overall (see Table 1), this difference was

eliminated when accounting for group differences in child age; on average, children

living above poverty were approximately 17 days older than children living below

poverty (see Table 1).

LFPN-LFPN connectivity. Following our pre-registration, using linear mixed

effects models, we next tested whether children in poverty would show the positive

correlation between LFPN *within-network* connectivity and cognitive test performance

that has previously been documented in higher-SES children. The relation between

LFPN-LFPN connectivity and test scores was not significant for children in poverty, B =

0.24, SE = 0.87, t (1028) = 0.28; χ_2 (1) = 0.08, p = 0.783, or for the higher income

children in the larger study, B = 0.34, SE = 0.36, t (5797) = 0.94; χ_2 (1) = 0.89, p =

0.346. Thus, strength of resting-state functional connectivity within the LFPN network

was not a predictor of cognitive performance in this large sample of 9 to 10-year-olds.

Environmental variables. To further explore the dissociation observed for

LFPN-DMN connectivity, we next asked whether features of children's environments

might explain why the brain-behavior link differed as a function of poverty status. Even

among children living in poverty, different children are exposed to very different

experiences in their homes, neighborhoods, and schools. Under what environmental

constraints might it be optimal (with respect to cognitive test performance) for the LFPN

to work more closely with the DMN? To answer this question, we considered 29

demographic variables chosen to reflect features of children's home, school, and

neighborhood environments (Table 2). To test whether any of these variables could

explain the observed group interaction, we performed Ridge regression. Specifically, we

used nested cross-validation to predict cognitive test performance from an interaction

between LFPN-DMN connectivity and these demographic variables, in addition to main

effects of each of these variables. Briefly, Ridge regression is a regularization technique

that penalizes variables that do not contribute to model fit, thus giving more weight to

the most important variables. This approach allows for the inclusion of many variables in

a model while reducing the chances of overfitting, and deals with issues of

multicollinearity. We pre-registered this second step of analyses prior to examining the

data further (https://aspredicted.org/blind.php?x=tg4tg9), given the substantial analytic

flexibility possible with such a large set of variables.

We trained our model in a training set of two-thirds (N = 670, after removing

missing data) of the children in poverty, using 5-fold cross-validation. Next, we tested

whether these demographic and neural model parameters could be used to predict

cognitive test scores in the held-out test set: the remaining one-third (N = 329) of

children in poverty. Indeed, we found that our model performed above chance (cross-

validated R_2 > 0), explaining 6% of the variance in children's cognitive test scores in this

held-out sample. While 6 percent is small, it bears mentioning that this is a pure

indicator, unlike the R_2 of models that have been fit to the data themselves and are thus

likely to be inflated because they are overfit. More importantly, this prediction is based

on a relatively restricted sample of children: those who live in poverty, whose total family

income is below $35,000. As we report below, the model is far more predictive when

applied to the highly heterogeneous sample of children living above the poverty line.

Exploring the model parameters revealed that the strongest predictors of test

performance for children in poverty included parents' highest level of education;

children's race/ethnicity; youth-reported school disengagement (a negative predictor);

strength of parents' ethnic identification (a positive predictor); generational status—that

is, the number of generations the family has been in the United States (a negative

predictor); and a number of more structural characteristics, particularly related to the

composition of children's neighborhoods (Table 3). Thus—even within this relatively

restricted sample of children living in poverty—individual, home, neighborhood, and

school variables helped to predict children's cognitive test scores.

When considering interactions between functional connectivity and demographic

variables, we found that a small number of characteristics of children's experiences

interacted with LFPN-DMN connectivity to predict cognitive test scores. Specifically,

variables related to school type, neighborhood safety, child's race/ethnicity, and parents'

highest level of education contributed to model fit (see Table 3). To better understand

these results, we plotted the relation between cognitive test scores and LFPN-DMN

connectivity for the factors showing significant interaction effects (Figure 4). Visualizing

the interaction for neighborhood safety revealed that children living in safer

neighborhoods showed a negative relation between LFPN-DMN connectivity and test

performance, whereas those who lived in particularly dangerous neighborhoods showed

a positive relation. With regard to schooling, the relation between LFPN-DMN

connectivity was more positive for children attending public schools than those

attending other types of schools (predominantly charter, *N* = 79, and private, *N* = 40).

Thus, the brain-behavior relation for children in poverty living in safer neighborhoods, or

attending non-public schools, more closely resembled that of the higher-income sample.

Similar results were true for levels of parental education and race, such that subsets of

children whose parents were more highly educated and children who were white

showed a more similar pattern of brain-behavior relations as children living above

poverty.

Given that this model achieved predictive power even in a held-out sample of

children in poverty, we wondered whether the relations between these demographic,

brain, and cognitive variables would hold across a broader spectrum of socioeconomic

status. Thus, as an exploratory analysis, we tested whether these initial model

parameters, trained on the two-thirds of children living in poverty, could also be used to

predict cognitive test performance in the higher-income children. Again, we found that

the model performed above chance; in fact, it explained 19% of variance in cognitive

test scores in this large, diverse sample.

Finally, we conducted a confirmatory factor analysis to test whether the

demographic variables could be split into individual and home, neighborhood, and

school factors based on our *a priori* categorization. This categorization did not meet our

pre-registered criteria for a good model fit (our CFI was considerably lower than 9); as a

result, we did not continue with this portion of the analysis. Thus, our data-driven

approach provided insights that would have been missed by simply categorizing

variables based on our prior assumptions.

Discussion

Prior research in both adults and children suggests that, in order to perform well

on cognitively demanding tasks, the LFPN must operate independently from the DMN

(Chai et al., 2014; Sherman et al., 2014; Whitfield-Gabrieli et al., 2020). Given that the

LFPN and DMN have been linked to externally and internally focused attention,

respectively, these findings are generally taken to suggest that it is optimal for

individuals engaged in a cognitively demanding task to focus narrowly on the task at

hand while inhibiting internally-directed or self-referential thoughts (Raichle et al., 2001;

Simpson et al., 2001a, 2001b; Weissman et al., 2006). However, the majority of the

research that led to this conclusion has been conducted with non-representative

samples of individuals from higher-income backgrounds. Given the large heterogeneity

of experiences and outcomes for children living in poverty, we focused on this relatively

under-studied population.

In this study, we tested the relation between patterns of brain connectivity and

nonverbal cognitive test performance for over 1,000 American children estimated to be

living in poverty. Although children in poverty scored lower on average than their higher-

income peers from the same study sites, there was large variability. Indeed, many of the

children in poverty scored on par with children whose family incomes were considerably

higher. In contrast to prior research, we did not find that higher cognitive test scores

were associated with stronger anti-correlations between the LFPN and DMN within this

group; in fact, these children showed a weakly positive relation between cognitive

performance and functional connectivity between these networks. By contrast, for the

children in the sample living above poverty, we replicated the negative relation observed

in prior studies (e.g., Sherman et al., 2014). Thus, for children living above poverty,

having higher LFPN-DMN connectivity could be a risk factor for lower cognitive test

performance, while for children living below poverty, it could be protective.

Further confirming the reliability of this dissociation, both a bootstrapping analysis

and permutation testing showed that models trained on the data from the children living

above poverty did a poor job of predicting test performance for the children below

poverty. It is important to note that the fact that we see statistically trending but

numerically small group differences in overall LFPN-DMN functional connectivity, as

well as no evidence of group differences in LFPN-LFPN connectivity. As such, the most

salient difference between children below and above poverty in our analyses was not

overall brain connectivity, but rather the relationship between connectivity and cognitive

performance.

This pattern of results is also in line with prior structural and task-based brain

imaging studies showing interactions between SES and neural variables in predicting

test performance (Leonard et al., 2019; Merz, Wiltshire, et al., 2019). For example,

several studies have found SES differences in lateral prefrontal and parietal activation

during cognitive tasks, core nodes of the LFPN (e.g., Finn et al., 2017; Sheridan et al.,

2012). Together, these findings support the idea that which patterns of brain function

are adaptive with respect to cognitive test performance depends on the environments

that children must contend with.

One interpretation of this unexpected interaction is that the relation between

LFPN-DMN connectivity and test performance depends in part on the demands of

children's daily experiences. It may be optimal under some circumstances to engage in

thought patterns that more frequently co-activate the LFPN and DMN (e.g., Christoff et

al., 2009; Fornito et al., 2012; Prado & Weissman, 2011). For example, while DMN is

generally thought to be suppressed during goal-directed tasks, it is active during a

variety of goal-directed tasks that require internal mentation, or projection outside of the

here-and-now (e.g., thinking about the past or the future). In particular, the DMN has

been found to support performance on tasks involving autobiographical memory,

prospective memory (planning), and introspecting about one's own and others' thoughts

(Buckner & Carroll, 2007; Spreng, 2012).

Thus, stronger temporal coupling between the LFPN and DMN for the higher-

performing children living in poverty could be related to drawing on past experiences

and planning for the future, which may be more important for children who grow up

under circumstances in which a path toward achieving success is less clear-cut.

Additionally or alternatively, it may be beneficial for disadvantaged children to reflect on

their own performance or behavior to contend with being evaluated negatively within or

outside of school (e.g., Batruch et al., 2017), and/or introspecting about others' mental

states. We expand on these ideas below in relation to specific environmental variables.

In contrast to our findings with LFPN-DMN connectivity, we found no significant

association between within-network LFPN connectivity and test performance—either in

the children living below or above poverty. These results were unexpected, given prior

studies reporting that connectivity within the LFPN is positively related to cognitive test

performance in both adults and children (Langeslag et al., 2013; Li & Tian, 2014;

Sherman et al., 2014; Song et al., 2008). For example, Sherman and colleagues found

that for 10-year-olds, higher IQ was correlated with higher connectivity between the

dorsolateral prefrontal cortex and the posterior parietal cortex, two hub regions of the

LFPN. One reason for the non-significant effect in our study may be that we examined

connectivity within the LFPN as a whole, rather than looking at particular regions or

subnetworks within LFPN. Thus, the entire network might not be developed enough by

ages 9 to 10 to see this relation on a global scale.

To better characterize the positive relationship between LFPN-DMN and test

performance among the children living in poverty, we examined a number of

demographic variables. While poverty status tends to be associated with a higher

likelihood of particular experiences, such as racial or ethnic discrimination, more

crowding in the home and financial strain, unsafe neighborhoods, and underfunded

public schools, there is large variation in the experiences of children who live in poverty

(DeJoseph et al., 2020). Moreover, experiences that are on average associated with

worse cognitive outcomes (such as being deprived of caregiver support in early life)

can, under some circumstances, produce *better* cognitive outcomes (Nweze et al.,

2020), suggesting there may be different routes to achieving high cognitive performance

in these cases. Thus, we predicted that differences in environmental influences *among*

children in poverty would explain whether strong LFPN-DMN connectivity was adaptive

or maladaptive for cognitive test performance.

Our analyses suggested that demographic variables could not be well fit to a pre-

determined factor structure based on variables relating to the individual, home,

neighborhood, and school; therefore, we took a data-driven approach to examine the

effects of environmental variables. Because many of these variables are correlated with

each other, we adopted an analytic approach—Ridge regression—that allows for

collinearity. The results of this analysis suggested that, even within the population of

children in poverty alone—children who are often conceptualized as a homogenous

group—variation in their environments was predictive of their cognitive test

performance. We note, however, that this was far from deterministic; a model trained on

two-thirds of the children in poverty explained 6% of the variance in the held-out third,

suggesting these variables accounted for a small amount of variance overall.

The most predictive variables in the model were main effects of children's

race/ethnicity, their parents' highest level of education, and neighborhood-level

characteristics such as the percent of people in their census tract who were

unemployed, had not completed their high school degree by age 25, and were living in

poverty. There is ample evidence that living in an under-resourced neighborhood

severely restricts opportunity (Badger & Bui, 2018; Chetty et al., 2016; Neuman &

Moland, 2019). Further, while both race and parental education are individual-level

variables, they are also indicators of the kinds of structural barriers that children face,

including access to resources and institutions, such as high-quality schools, jobs, and

healthcare and stable housing in safe neighborhoods, and experiences of racism within

these systems (Alexander, 2012; Chetty et al., 2018; Desmond & Kimbro, 2015; Kraus

et al., 2019; Shedd, 2015). Thus, the strongest predictors of low-income children's

cognitive performance reflect structural constraints on children's lives. However, our

data also suggest that being raised by parents with strong ethnic identification may

provide some psychological buffer against these and other threats, in line with other

research (Cardoso & Thompson, 2010; Chen et al., 2015; Costigan et al., 2010; Simons

et al., 2002; Varner et al., 2018).

In addition to these main effects, we found several interactions between

environmental variables and LFPN-DMN connectivity that contributed to the model's

predictive power. Given what is known about the functions of these brain networks as

well as the types of challenges that children in poverty face, we offer some hypotheses

as to why stronger LFPN-DMN connectivity could be beneficial for them.

Children who attended public schools were more likely to show a positive relation

between LFPN-DMN connectivity and cognitive performance. Many public schools are

economically segregated, meaning that the public schools attended by children in

poverty are particularly likely to be under-funded (Reardon & Owens, 2014). The

constraints children face in these kinds of public schools likely require them to learn

under different circumstances than in charter or private schools. For example, there are

likely to be more students in a public school classroom, and therefore more potential for

distraction, or less feedback provided by teachers (Horng, 2005; Orfield & Lee, 2005).

Thus, children who achieve high cognitive test scores even in these environments may

do so by recruiting LFPN and DMN together more frequently to engage in thought

patterns like monitoring their own learning or performance.

In addition, children living in poverty who were white were more likely to show the

expected pattern between LFPN-DMN connectivity and performance based on the

literature, particularly compared to children who were Black, who were the next best

represented in our sample. In line with the idea that Black children face disproportionate

barriers to success, these children typically have to deal with a different set of daily

constraints than their white peers in particular (Shedd, 2015). Indeed, rich qualitative

data suggests that Black mothers are vigilant about planning for potential experiences

of racism (e.g., making decisions about how to dress in order to be treated well by store

clerks), and self-monitoring in these situations (Nuru-Jeter et al., 2009), both thought

patterns that would likely co-activate LFPN and DMN.

Along with type of schooling and race, several neighborhood characteristics

interacted with LFPN-DMN connectivity to predict children's cognitive test performance.

The safer children's parents reported their neighborhood to be, the more negative the

relation between LFPN-DMN connectivity and test performance, mirroring the average

relation for higher-income children. The same pattern of results was found for children

who lived in neighborhoods in which people were more likely to have plumbing or higher

levels of education. The effect of neighborhood safety could be related to mentalizing

about the goals and intentions of others in the service of monitoring potential threats in

their environment. Of course, further research is needed to test each of these

hypotheses, and they are not mutually exclusive.

While our study benefited from the ABCD dataset's rich objective measures of

the large-scale environment, there are other potential environmental and individual level

variables that should be considered in future research (Pollak & Wolfe, 2020). Our

research assessed only self-reported parenting styles, but there is ample evidence that

more specific parenting behaviors such as language use relate to children's cognitive

development (Hart & Risley, 1995). In addition, genetic variability contributes to

individual differences in brain development, cognitive test performance, and even

parenting, something worth exploring in future research. Future research could also

benefit from a more sensitive measure of poverty. Because the dataset did not specify

which of the 19 study sites corresponded to which American city, due to concerns about

confidentiality, we determined a cut-off for our poverty threshold based on cost-of-living

across study sites. Because cities across the United States vary substantially in cost-of-

living, we selected a stringent cutoff for the poverty line. Thus, there are almost certainly

families in the above-poverty group that belong in the below-poverty group. If anything,

this suggest that the use of a more sensitive measure would likely increase the group

difference that we report.

Further, while we focused on three tests of non-verbal cognitive test

performance, future studies should examine a broader range of cognitive systems, as

these may be differentially affected by the environment (Rosen, Meltzoff, et al., 2019).

For example, a systematic review of the literature suggests that experiences of threat

and deprivation have distinct effects on medial and lateral prefrontal cortex

development, respectively (McLaughlin et al., 2019); these effects may be mediated in

part by lower-level visual and attentional processes (Rosen, Amso, et al., 2019).

Clearly, there is a need for research which investigates the precise mechanisms

through which the environment affects specific neural and cognitive systems. In

addition, there is evidence children's performance on cognitive tests can fluctuate from

day to day for a variety of reasons (Dirk & Schmiedek, 2016; Könen et al., 2015),

including motivation (Somerville & Casey, 2010), which is a likely source of noise in our

models. Moreover, the cognitive tests used in the current study, while predictive of

children's later outcomes (e.g., Pagani et al., 2017), have been argued to be culturally

biased (Suzuki & Aronson, 2005). Notably, our emphasis is not on overall differences

cognitive test performance between groups, but rather differences in the way cognitive

performance is related to brain network connectivity. Nonetheless, an important area of

research is to look beyond these more canonical cognitive tasks to identify assessments

or testing contexts for which children living in poverty might be particularly adapted to

excel (Frankenhuis et al., 2020). Doing so might reveal that some children who

underperformed on the cognitive measures in the current study have strengths in other

domains as a result of adaptation to their environments.

This study opens several questions about the neural underpinnings of these

findings that should be further examined. Given individual variability in network

topography (Seitzman et al., 2019), future studies should examine whether this

variability contributes to our findings. In addition, LFPN and DMN are both summary

network measures; there could be qualitative differences in node-to-node connectivity,

or smaller interactions between sub-networks, that we are not capturing in the current

study (Buckner & DiNicola, 2019; Dixon et al., 2018; Fornito et al., 2012; Lopez et al.,

2020). Moreover, it would be helpful to look at children's task-based activation and

functional connectivity to examine whether children in poverty are more likely to activate

DMN during neutral, externally driven cognitive tasks outside of their daily

environments. Finally, given that these metrics only explain a small amount of variance,

it is important to look at the contribution of other neural indices of both anatomical and

functional brain network connectivity. In particular, it would be interesting to test whether

the group interaction could be explained by differential engagement of the cingulo-

opercular (so-called "salience") network, given theories that it is involved in coordinating

the engagement of DMN and LFPN (Sridharan et al., 2008), and evidence that

connectivity between the three networks changes across age (Uddin et al., 2010).

Taken together, the results of our study suggest that "optimal" patterns of brain

development depend in part on the external pressures that children face. Children living

in poverty did not show the expected negative relation between LFPN-DMN connectivity

and test performance based on prior research in higher-income populations. Features of

children's environments helped to explain which children showed more positive versus

more negative associations, suggesting that different patterns of brain development

may be adaptive under different circumstances. These results go against the idea that

different patterns of brain activation for children living in poverty necessarily imply a

deficit (Ellwood-Lowe et al., 2016), and instead point to the ways in which children adapt

to various constraints. Still, it is unclear whether patterns of brain development that

appear adaptive in middle childhood will continue to be adaptive over time; an important

next step will be to follow these children longitudinally to see how LFPN-DMN

connectivity and its relation with cognitive test performance changes across

adolescence.

Given that the structures that govern success have been largely created around

the needs of middle- and upper-middle class families, understanding the strengths of

families in poverty—and how children may thrive in spite of these structural barriers—is

critical. Altogether, these results highlight the substantial variability of experiences of

children living in poverty, who are often conceptualized as a single, homogenous group

and compared to higher-SES children. Moreover, they suggest that our field's

assumptions about generalizability of brain-behavior relations are not necessarily

correct. Looking beyond convenience samples of children will ultimately lend more

insight into the neural underpinnings of cognition, and may show that there is not a

general guiding principle about what is optimal in the ways we have thus far assumed.

Not only would this advance benefit developmental cognitive neuroscience as a field,

but it may ultimately allow us to better serve disadvantaged youth.

Methods

Analysis plans were pre-registered prior to data access

(https://aspredicted.org/blind.php?x=3d7ry9, https://aspredicted.org/blind.php?x=tg4tg9)

and analysis scripts are openly available on the Open Science Framework

(https://osf.io/hs7cg/?view_only=d2acb721549d4f22b5eeea4ce51195c7). All deviations

from the initial analysis plan are fully described in the Supplement.

Participants. Participants were selected from the larger, ongoing Adolescent

Brain Cognitive Development (ABCD) study, which was designed to recruit a cohort of

children who closely represented the United States population (http://abcdstudy.org; see

Garavan et al., 2018). We planned to restrict our primary analyses to children who fell

below the poverty line on the supplemental poverty measure, which takes into account

regional differences in cost-of-living (L. Fox, 2017). For example, while the federal

poverty level in 2018 was $25,465 for a family of four, the supplemental poverty level in

Menlo Park, CA—one of the ABCD study sites—was estimated to be over $37,000

around the same time period. However, upon reviewing the data after our pre-

registration, we found that study site in the ABCD data was de-identified for privacy

reasons, and as a result we could not use study site-specific poverty cut-offs. Instead,

we estimated each child's poverty status based on their combined family income

bracket, the number of people in their home, and the average supplemental poverty

level for the study sites included in the sample.

Based on these factors, we considered children to be in poverty if they lived in

families of fewer than five people and their combined family income was less than

$25,000, or if they lived in families of five or more people and their combined family

income was less than $35,000. We excluded children who did not provide information

about family income and complete data on all three cognitive tests, and/or if their MRI

data did not meet ABCD's usability criteria (see below). In addition, due to a scanner

error, we excluded post-hoc all children who were scanned on Philips scanners. This

left us with 1034 children identified as likely to be living below poverty (6839 across the

whole sample). Table 1 provides a breakdown of sample demographics.

Cognitive test performance. Children's performance was measured on three

non-verbal cognitive tests. Specifically, children completed two tests from the NIH

Toolbox (http://www.nihtoolbox.org): Flanker, a measure of inhibitory control (Eriksen &

Eriksen, 1974), and Dimensional Change Card Sort (DCCS), a measure of shifting

(Zelazo et al., 2013); and the Matrix Reasoning Task from the Wechsler Intelligence

Test for Children-V (WISC-V), a measure of abstract reasoning (Wechsler, 2014). More

details on each of these tests and their administration in the current study is described

elsewhere (Luciana et al., 2018). We created a composite measure of performance

across these three domains by creating z-scores of the raw scores on each of these

tests and summing them, as pre-registered; the tests were moderately correlated, 0.23

$< r <$ 0.43, in the whole sample.

MRI Scan Procedure. Scans were typically completed on the same day as the

cognitive battery, but could also be completed at a second testing session. After

completing motion compliance training in a simulated scanning environment,

participants first completed a structural T1-weighted scan. Next, they completed three to

four five-minute resting state scans, in which they were instructed to lay with their eyes

open while viewing a crosshair on the screen. The first two resting state scans were

completed immediately following the T1-weighted scan; children then completed two

other structural scans, followed by one or two more resting state scans, depending on

the protocol at each specific study site. All scans were collected on one of three 3T

scanner platforms with an adult-size head coil. Structural and functional images

underwent automated quality control procedures (including detecting excessive

movement and poor signal-to-noise ratios) and visual inspection and rating (for

structural scans) of images for artifacts or other irregularities (described in Hagler et al.,

2019); participants were excluded if they did not mean quality control criteria.

672   **Scan parameters**. Scan parameters were optimized to be compatible across

scanner platforms, allowing for maximal comparability across the 19 study sites. All T1-

weighted scans were collected in the axial position, with 1mm$_3$ voxel resolution, 256 x

256 matrix, 8 degree flip angle, and 2x parallel imaging. Other scan parameters varied

by scanner platform (Siemens: 176 slices, 256 x 256 FOV, 2500 ms TR, 2.88 ms TE,

1060 ms TI; Philips: 225 slices, 256 x 240 FOV, 6.31 ms TR, 2.9 ms TE, 1060 ms TI;

GE: 208 slices, 256 x 256 FOV, 2500 ms TR, 2 ms TE, 1060 ms TI). All fMRI scans

were collected in the axial position, with 2.4mm$_3$ voxel resolution, 60 slices, 90 x 90

matrix, 216 x 216 FOV, 800ms TR, 30 ms TE, 52 degree flip angle, and 6 factor

MultiBand Acceleration. Motion was monitored during scan acquisition using real-time

procedures to adjust scanning procedures as necessary (see Casey et al., 2018).

683   **Resting state fMRI processing**. Data processing was carried out using the

ABCD pipeline and carried out by the ABCD Data Analysis and Informatics Core; more

details are reported by Hagler et al. (2019). Briefly, T1-weighted images were corrected

for gradient nonlinearity distortion and intensity inhomogeneity, and rigidly registered to

a custom atlas. They were run through FreeSurfer's automated brain segmentation to

derive white matter, ventricle, and whole brain ROIs. Resting state images were first

corrected for head motion, displacement estimated from field map scans, B$_0$ distortions,

and gradient nonlinearity distortions, and registered to the structural images using

mutual information. Initial scan volumes were removed, and each voxel was normalized

and demeaned. Signal from motion, quadratic trends, and mean time courses of white

matter, gray matter, and whole brain, plus first derivatives, were regressed out, and

frames with greater than 0.3mm displacement were excluded. While the removal of

whole brain signal (global signal reduction) is controversial in the context of interpreting

anti-correlations (Chai et al., 2012; Murphy & Fox, 2017), we note that we are able to

replicate prior studies showing that a more negative link between our networks of

interest is related to test performance in our higher-income sample (see Results),

lending credence to the inclusion of this step in the analysis pipeline for our purposes.

The data underwent temporal bandpass filtering (0.009 – 0.08 Hz). These time courses

were projected onto FreeSurfer's cortical surface, upon which 13 functionally-defined

networks (Gordon et al., 2016) were mapped and time cources for FreeSurfer's

standard cortical and subcortical ROIs extracted (Desikan et al., 2006; Fischl et al.,

2002). Correlations for each pair of ROIs both within and across each of the 13

networks were calculated. These were z-transformed and averaged to calculate within-

network connectivity for each network (the average correlation of each ROI pair within

the network) and between-network connectivity across all networks (the average

correlation of pairs of each ROI in one network with each ROI in another network).

Here, we examined only within-network connectivity for LFPN and between-network

LFPN-DMN connectivity.

Analysis. Analyses were performed using R version 3.6.0 (R Core Team, 2017).

We performed two separate linear mixed effects models using the *lme4* package (Bates

et al., 2015) to test the relation between cognitive test scores and (1) LFPN-DMN

connectivity, and (2) LFPN within-network connectivity. In our initial pre-registration, we

did not consider the nested structure of the data or potential confounds. To determine

whether to include these in our model in a data-driven fashion, we tested whether each

of the following variables contributed significantly to model fit: (1) nesting within study

site, (2) nesting within families, (3) child age, and (4) mean levels of motion in resting

state scan. All except (2) contributed to model fit at a level of $p < 0.01$ and were thus

retained in final models. We note that our reported results are similar when we perform

simple linear regression with no covariates, exactly as pre-registered. To determine the

significance of our neural connectivity metrics, we tested whether these contributed to

model fit. In all cases, we compared models without the inclusion of the variable of

interest to models with this variable included, and calculated whether the variable of

interest contributed significantly to model fit, using the *anova* function for likelihood ratio

test model comparison.

In our second set of analyses, we sought to explore the unexpected results from

our first set of analyses by asking whether certain environmental variables determine

whether LFPN-DMN connectivity is positively or negatively associated with cognitive

test performance across individuals. To do this, we gathered 31 environmental variables

of interest, spanning home, neighborhood, and school contexts. Upon examining the

data, we learned that three of these were not collected at the baseline visit and thus

could not be included. Moreover, we made the decision to include ethnicity separate

from race, as it was collected, to retain maximal information. The final 29 environmental

variables are listed in Table 2. In preparation for our subsequent analyses, we mean-

centered and standardized these variables in the larger dataset to allow for potential

comparisons across the high- and low-income children. Levels of each factor variables

were broken down into separate dummy-coded variables for inclusion in factor and

ridge analyses. When data were missing, they were interpolated using the *mice*

package in R (van Buuren & Groothuis-Oudshoorn, 2011).

We first performed a confirmatory factor analysis using the *lavaan* package in R

(Rosseel, 2012) to see whether individual and home, neighborhood, and school

variables can be separated into distinct factors. If this achieved adequate fit

(significantly better fit than a single factor model and CFI>9), we planned to perform a

linear mixed effects model predicting cognitive test performance from an interaction

between LFPN-DMN connectivity and each factor score.

We next performed a ridge regression using the *glmnet* package in R (Friedman

et al., 2010). This analysis technique penalizes variables in a model that have little

predictive power, shrinking their coefficient closer to zero, thus allowing for the inclusion

of many potential predictors while reducing model complexity. These models also

include a bias term, reducing the chances of overfitting to peculiarities of the data, a

common pitfall of ordinary least squares regression. Finally, ridge regression also deals

well with multi-collinearity in independent variables; in contrast to alternatives such as

Lasso, if two variables are highly correlated and both predictive of the dependent

variable, coefficients of both will be weighted more heavily in ridge.

We fit ridge regressions predicting cognitive test score residuals, which partialled

out the covariates included in our basic linear mixed effects models (random intercept

for study site, fixed effects for age and motion), from an interaction between LFPN-DMN

connectivity and each environmental variable of interest. This analysis used nested

cross-validation. Specifically, we first split the data into a training (2/3) and testing (1/3)

set. We then tuned parameters of the ridge regression on the training set using 5-fold

cross-validation. Ultimately, we used the best-performing model to predict cognitive test

scores in the held-out testing set and assessed model fit using R_2 cross-validated. An

R_{2CV} above 0 indicates that the model performed above chance; otherwise, it will be

below 0. We evaluated the significance of specific variables in our model by plugging in

the lambda parameter from the best-performing model to the linearRidge function in the

ridge package in R (Cule & Moritz, 2019), on the whole sample of children in poverty.

Robustness analyses. We did several additional analyses to test the

robustness of our results. First, we repeated our primary analyses as robust linear

mixed effects models, using the *robustlmm* package in R (Koller, 2016). These models

detect outliers or other sources of contamination in the data that may affect model

validity, and performs a de-weighting procedure based on the extent of contamination

introduced. These analyses are reported in the main text, and bolster our primary

analyses.

Next, we performed a bootstrapping procedure intended to probe how frequently

the parameter estimate observed in the children in poverty alone would be expected to

be observed in a larger population of children living above poverty. In order to derive an

estimate for observed parameter estimates in a population of higher-income children,

we randomly sampled 500 data points from the children living above poverty, with

replacement. For these 500 data points, we fit our primary linear mixed effects model to

the data, predicting children's cognitive test scores, and calculated the average

parameter estimate for LFPN-DMN connectivity. We repeated this process 999 times,

generating a distribution of parameter estimates likely within the larger population of

higher-income children from which our participants were drawn. Next, we compared

these bootstrapped parameter estimates to the parameter estimate observed for

children in poverty in our sample. If the brain-behavior relation does not differ

systematically as a function of poverty status—in other words, if the observed relation

between LFPN-DMN connectivity and cognitive test scores for the children in poverty

would be likely to be observed in a larger, population-level sample of children above
poverty—the parameter estimate for children in poverty should fall within the 95%
confidence interval of the bootstrapped parameter estimates.

To further confirm this dissociation, we also performed a permutation procedure
to examine the extent to which the model parameters from the higher-income children
alone could explain the data in the children in poverty. Briefly, we used the model
parameters generated from the higher-income children to predict test performance in
the children in poverty, and calculated the mean difference (observed values minus
predicted values). We next randomly permuted the labels of each group, such that
assignment into the higher- versus lower-income group was now arbitrary. We repeated
the process above, now fitting model parameters to our arbitrary "higher-income" group
and using them to predict cognitive test performance in our arbitrary "lower-income"
group. Again, we calculated the mean error between observed and predicted values.
This permutation and prediction procedure was repeated 999 times, generating a
distribution of mean differences when the distinction between the two groups was
arbitrary. If the model parameters generated from our actual higher-income group could
reasonably be applied to our actual lower-income group, we would expect that the mean
error would fall within the 95% confidence interval of our distribution of permuted mean
errors.

Finally, given that children living in poverty had significantly more motion than
children living above poverty, we repeated our primary analyses with only those children
who met an extremely stringent motion threshold of 0.2mm. These results are reported
in the Supplement.

Additional R packages used for data cleaning, analysis, and visualization include:
dplyr (Wickham et al., 2019); *ggplot2* (Wickham, 2016); *car* (J. Fox & Weisberg, 2011);
corrplot (Wei & Simko, 2017); *MuMIn* (Bartoń, 2019); *tidyr* (Wickham & Henry, 2019);
summarytools (Comtois, 2019); *finalfit* (Harrison et al., 2019); *fastDummies* (Kaplan,
2019); *caret* (from Jed Wing et al., 2019); *scales* (Wickham, 2018); *foreign* (R Core
Team, 2018); *MASS* (Venables & Ripley, 2002); *sjPlot* (Lüdecke, 2019); *tableone*
(Yoshida, 2019); *gtools* (Warnes et al., 2018).

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Figure 1. Illustration of the variability of cognitive test performance within every level of

family income in the sample (N = 6839). Colors indicate whether children were classified as

living in poverty, based on a combination of their family income and number of people in

the home. Replicating prior studies, higher income is associated with higher cognitive test

performance (R = 0.24); however, it is important to acknowledge this substantial variability

within and overlap between children at each level of family income.

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Figure 2. Relations between resting state network metrics and cognitive test score residuals, for
children living above poverty (dark blue) and below poverty (light blue). Models include fixed
effects for age and motion and a random effect for study site. Panel A: Children living above
poverty show an expected, negative, relation between LFPN-DMN connectivity and test
performance, $B = -1.41$, SE = 0.45; $p = 0.002$, while children living below poverty show the
opposite pattern, $B = 2.11$, SE = 1.12; $p = 0.060$, interaction: $X_2(1) = 8.99$, $p = 0.003$. Panel B:
Children across the sample show a non-significant positive relation between LFPN-LFPN within-
network connectivity and test performance, above poverty: $B = 0.34$, SE = 0.36; $p = 0.346$;
below poverty: $B = 0.24$, SE = 0.87; $p = 0.783$; interaction: $X_2(1) = 0.0005$, $p = 0.982$. Networks
functionally defined using the Gordon parcellation scheme; on left, LFPN is shown in yellow and
DMN shown in red, figures adapted from (Gordon et al., 2016).
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Figure 3. Bootstrapped distributions for LFPN-DMN connectivity parameter estimates in the
models predicting cognitive test performance, for children above (dark blue) and below (light
blue) poverty. Estimates calculated from models run on 500 data points drawn with replacement
from each sample separately, repeated 999 times. Bootstrapped coefficients for children above
poverty ranged from -6.47 to 3.74, with a mean of -1.41, 95% CI [-1.50, -1.31], mirroring our
observed parameter estimate for the higher-income group. The observed estimate for children
in poverty fell outside of the 95% CI, and was higher than 987 out of 999 bootstrapped samples,
p = 0.013.

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Figure 4. Interactions between demographic variables and LFPN-DMN connectivity in
predicting cognitive test scores, for children below poverty. The majority of non-public schools
were charter and private schools. In addition, only white and Black/African American race are
displayed as these were the most represented in the current sample. 89% level confidence
intervals for predicted effects calculated and displayed using the sjPlot package in R (Lüdecke,
2019).

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1308 **Table 1.** Participant characteristics. Demographic information in plain text; brain and cognitive
1309 variables italicized.

	Above poverty (*n* = 5805)	Below poverty (*n* = 1034)	p-test
Age in months (mean (SD))	119.44 (7.54)	118.89 (7.50)	0.032
Sex at birth (%)			0.055
Other/did not disclose	0 (0.0)	1 (0.1)	
Female	2913 (50.2)	511 (49.4)	
Male	2892 (49.8)	522 (50.5)	
Primary caregiver in study (%)			<0.001
Biological mother	4904 (84.5)	920 (89.0)	
Biological father	645 (11.1)	54 (5.2)	
Adoptive parent	137 (2.4)	18 (1.7)	
Custodial parent	43 (0.7)	23 (2.2)	
Other	76 (1.3)	19 (1.8)	
Site (de-identified) (%)			<0.001
site02	429 (7.4)	19 (1.8)	
site03	285 (4.9)	130 (12.6)	
site04	369 (6.4)	122 (11.8)	
site05	203 (3.5)	42 (4.1)	
site06	395 (6.8)	16 (1.5)	
site07	170 (2.9)	42 (4.1)	
site08	177 (3.0)	14 (1.4)	
site09	250 (4.3)	24 (2.3)	
site10	297 (5.1)	101 (9.8)	
site11	224 (3.9)	67 (6.5)	
site12	298 (5.1)	73 (7.1)	
site13	361 (6.2)	61 (5.9)	
site14	434 (7.5)	15 (1.5)	
site15	127 (2.2)	85 (8.2)	
site16	820 (14.1)	70 (6.8)	
site18	208 (3.6)	19 (1.8)	
site20	422 (7.3)	76 (7.4)	
site21	314 (5.4)	54 (5.2)	
site22	22 (0.4)	4 (0.4)	
RSfMRI mean framewise displacement (mean (SD))	*0.19 (0.15)*	*0.23 (0.18)*	*<0.001*
LFPN-DMN connectivity (mean (SD))	*0.058 (0.06)*	*0.061 (0.06)*	*0.061*
LFPN-LFPN connectivity (mean (SD))	*0.21 (0.07)*	*0.21 (0.08)*	*0.286*
Matrix reasoning raw score (mean (SD))	*18.67 (3.51)*	*16.35 (3.89)*	*<0.001*
Flanker raw score (mean (SD))	*95.34 (8.03)*	*91.92 (10.24)*	*<0.001*
Card sort raw score (mean (SD))	*94.09 (8.58)*	*89.83 (9.79)*	*<0.001*

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1312 **Table 2.** Wider environmental information. Variables included in the ridge regression predicting
1313 cognitive test scores. All except income were used in primary models; additional tests confirmed
1314 that income did not add predictive power above and beyond these variables.

	Above poverty (n = 5805)	Below poverty (n = 1034)	p-test
Combined family income (%)			<0.001
Less than $5,000	0 (0.0)	187 (18.1)	
$5,000 through 11,999	0 (0.0)	219 (21.2)	
$12,000 through $15,999	0 (0.0)	154 (14.9)	
$16,000 through $24,999	0 (0.0)	280 (27.1)	
$25,000 through $34,999	215 (3.7)	194 (18.8)	
$35,000 through $49,999	579 (10.0)	0 (0.0)	
$50,000 through $74,999	972 (16.7)	0 (0.0)	
$75,000 through $99,999	1050 (18.1)	0 (0.0)	
$100,000 through $199,999	2157 (37.2)	0 (0.0)	
$200,000 and greater	832 (14.3)	0 (0.0)	
Parents' highest level of education (n, %)			<0.001
3rd grade	1 (0.0)	0 (0.0)	
4th grade	0 (0.0)	1 (0.1)	
5th grade	0 (0.0)	1 (0.1)	
6th grade	4 (0.1)	13 (1.3)	
7th grade	1 (0.0)	2 (0.2)	
8th grade	1 (0.0)	8 (0.8)	
9th grade	6 (0.1)	24 (2.3)	
10th grade	10 (0.2)	26 (2.5)	
11th grade	12 (0.2)	34 (3.3)	
12th grade	13 (0.2)	47 (4.5)	
High school graduate	167 (2.9)	169 (16.3)	
GED or equivalent	66 (1.1)	91 (8.8)	
Some college	590 (10.2)	297 (28.7)	
Associate degree: occupational	374 (6.4)	135 (13.1)	
Associate degree: academic	297 (5.1)	63 (6.1)	
Bachelor's degree	1818 (31.3)	86 (8.3)	
Master's degree	1677 (28.9)	32 (3.1)	
Professional school degree	364 (6.3)	4 (0.4)	
Doctoral degree	403 (6.9)	1 (0.1)	
People living in home (mean (SD))	4.76 (1.64)	4.97 (2.89)	0.001
Any siblings (yes, %)	1905 (32.8)	269 (26.0)	<0.001
Hours/week spent at another household (mean (SD))	5.34 (19.45)	5.45 (21.63)	0.869
Financial stress (0-7; mean (SD))	0.28 (0.85)	1.32 (1.61)	<0.001
Race (%)			<0.001

Native American/Alaska Native	17 (0.3)	14 (1.4)	
Asian	126 (2.2)	8 (0.8)	
Black/African American	495 (8.5)	377 (36.5)	
Pacific Islander	8 (0.1)	1 (0.1)	
Other	159 (2.7)	74 (7.2)	
White	4263 (73.4)	386 (37.3)	
Mixed	696 (12.0)	141 (13.6)	
Refuse to answer	41 (0.7)	33 (3.2)	
Hispanic/Latino ethnicity (no, %)	4776 (83.1)	682 (67.3)	<0.001
Parent marital status (%)			<0.001
Married	4621 (79.7)	302 (29.6)	
Widowed	33 (0.6)	22 (2.2)	
Separated/divorced	600 (10.4)	232 (22.7)	
Never married	319 (5.5)	369 (36.1)	
Living with partner	223 (3.8)	96 (9.4)	
Generational status (%)			<0.001
Parent born outside U.S.	708 (12.2)	201 (19.5)	
Grandparent born outside U.S.	933 (16.1)	90 (8.7)	
Child born outside U.S.	118 (2.0)	32 (3.1)	
Parents and grandparents born in U.S.	4043 (69.7)	709 (68.7)	
School setting (%)			<0.001
Not in school	19 (0.3)	6 (0.6)	
Regular public school	4836 (83.3)	891 (86.2)	
Regular private school	346 (6.0)	40 (3.9)	
Charter school	412 (7.1)	79 (7.6)	
Vocational/tech school	2 (0.0)	1 (0.1)	
Cyber school	7 (0.1)	2 (0.2)	
Home school	112 (1.9)	2 (0.2)	
School for behavioral/emotional problems	7 (0.1)	3 (0.3)	
Other	63 (1.1)	10 (1.0)	
Youth-reported supportive school environment (6-24; mean (SD))	19.95 (2.63)	19.96 (3.22)	0.949
Youth-reported school involvement (4-16; mean (SD))	13.11 (2.25)	13.22 (2.44)	0.162
Youth-reported school disengagement (2-8; mean (SD))	3.66 (1.39)	3.79 (1.57)	0.006
Census: % of people over age 25 with at least a high school diploma (mean (SD))	91.13 (8.76)	81.30 (12.11)	<0.001
Census: income disparity (mean (SD))	1.81 (1.17)	3.13 (1.34)	<0.001
Census: % of occupied units without complete plumbing (mean (SD))	0.28 (0.64)	0.44 (0.83)	<0.001
Census: % of families below the poverty level (mean (SD))	8.35 (8.68)	20.93 (14.61)	<0.001

Census: % of labor force aged >=16 y unemployed (mean (SD))	7.69 (4.52)	13.15 (7.49)	<0.001
Census: uniform crime reports (mean (SD))	43774.47 (69634.30)	43204.49 (57108.32)	0.81
Census: adult violent crime reports (mean (SD))	2660.87 (6271.58)	2642.93 (5030.45)	0.933
Census: estimated lead risk (1-10; mean (SD))	4.40 (2.98)	6.77 (2.89)	<0.001
Parent-reported neighborhood safety (1-5; mean (SD))	4.05 (0.85)	3.34 (1.11)	<0.001
Parent self-reported aggressive behavior (0-30; mean (SD))	3.14 (3.27)	4.47 (4.58)	<0.001
Parent self-reported intrusive behavior (0-12; mean (SD))	1.01 (1.43)	1.08 (1.43)	0.198
Parent self-reported withdrawn behavior (0-18; mean (SD))	1.35 (1.85)	2.46 (2.83)	<0.001
Parent ethnic identification (1-5; mean (SD))	2.71 (0.86)	2.58 (0.94)	<0.001
Youth-reported family conflict (0-9; mean (SD))	1.93 (1.92)	2.45 (2.04)	<0.001
Youth-reported parental monitoring (1-5; mean (SD))	4.43 (0.46)	4.31 (0.59)	<0.001
Youth-reported parental acceptance (1-3; mean (SD))	2.80 (0.29)	2.76 (0.33)	<0.001

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1317 **Table 3.** Estimated coefficients from Ridge regression predicting children's cognitive test
1318 scores, when controlling for fixed effects of age and motion and random effects of study site, for
1319 all children below the poverty line. Interactions with and main effect of LFPN-DMN connectivity
1320 italicized.

	Estimate	Scaled estimate	Std. Error (scaled)	t value (scaled)	Pr(>|t|)
(Intercept)	-0.75	NA	NA	NA	NA
Black race	-0.14	-2.17	0.36	6.00	0.000
Parents' highest level of education (years)	0.06	2.13	0.43	4.97	0.000
White race	0.11	1.62	0.37	4.37	0.000
Census: % of people over age 25 with >= high school diploma	0.04	1.40	0.38	3.66	0.000
Asian race	0.50	1.42	0.44	3.25	0.001
Census: estimated lead risk	-0.04	-1.12	0.37	3.03	0.002
Third generation American	-0.06	-0.94	0.33	2.87	0.004
Census: % of labor force aged >=16 y unemployed	-0.02	-1.06	0.37	2.84	0.005
Youth-reported school disengagement	-0.03	-1.16	0.41	2.80	0.005
Parent ethnic identification	0.03	1.11	0.43	2.56	0.011
Census: % of families below the poverty level	-0.02	-0.83	0.34	2.47	0.013
Census: income disparity	-0.03	-0.84	0.34	2.47	0.014
LFPN-DMN x Public school	*0.33*	*0.65*	*0.28*	*2.35*	*0.019*
LFPN-DMN x Parent-reported neighborhood safety	*-0.25*	*-0.87*	*0.38*	*2.27*	*0.023*
LFPN-DMN x Parents' highest level of education	*0.22*	*0.76*	*0.36*	*2.10*	*0.036*
First generation American	0.06	0.72	0.35	2.04	0.041
LFPN-DMN x White race	*0.48*	*0.69*	*0.37*	*1.88*	*0.060*
LFPN-DMN x Black race	*-0.40*	*-0.61*	*0.33*	*1.84*	*0.066*
Parent never married	-0.04	-0.68	0.38	1.79	0.074
LFPN-DMN x Mixed race	*0.84*	*0.73*	*0.41*	*1.78*	*0.076*
LFPN-DMN x Census: % of occupied units without complete plumbing	*0.24*	*0.74*	*0.43*	*1.72*	*0.085*
LFPN-DMN	*0.19*	*0.38*	*0.24*	*1.57*	*0.116*
LFPN-DMN x Not in school	*-4.10*	*-0.62*	*0.41*	*1.53*	*0.127*
Mixed race	0.06	0.62	0.41	1.50	0.133
LFPN-DMN x Parent self-reported intrusive behavior	*0.22*	*0.59*	*0.41*	*1.46*	*0.146*
LFPN-DMN x Hours/week spent at another household	*-0.20*	*-0.64*	*0.44*	*1.45*	*0.146*
Parent married	0.04	0.56	0.39	1.45	0.148
Second generation American	0.07	0.59	0.41	1.44	0.150
Parent-reported neighborhood safety	0.02	0.58	0.41	1.41	0.160
LFPN-DMN x non-Hispanic	*0.21*	*0.39*	*0.28*	*1.38*	*0.167*
LFPN-DMN x First-generation American	*0.38*	*0.46*	*0.36*	*1.28*	*0.199*
LFPN-DMN x Youth-reported school involvement	*0.16*	*0.48*	*0.38*	*1.28*	*0.202*

Other race	-0.06	-0.52	0.41	1.26	0.208
LFPN-DMN x Private school	*-1.08*	*-0.53*	*0.43*	*1.26*	*0.209*
LFPN-DMN x Youth born outside U.S.	*1.23*	*0.53*	*0.44*	*1.22*	*0.222*
LFPN-DMN x Second-generation American	*-0.66*	*-0.48*	*0.41*	*1.17*	*0.244*
Native American/Alaska Native	0.13	0.48	0.43	1.12	0.263
LFPN-DMN x Census: % of people over age 25 with >= a high school diploma	*0.10*	*0.37*	*0.35*	*1.06*	*0.290*
Any siblings	-0.03	-0.46	0.44	1.05	0.296
LFPN-DMN x Parent separated/divorced	*0.31*	*0.39*	*0.38*	*1.01*	*0.311*
LFPN-DMN x Financial stress	*-0.09*	*-0.40*	*0.41*	*0.98*	*0.330*
LFPN-DMN x Census: uniform crime reports	*-0.14*	*-0.35*	*0.36*	*0.97*	*0.331*
LFPN-DMN x Census: income disparity	*0.08*	*0.28*	*0.29*	*0.94*	*0.347*
Other school setting	0.11	0.40	0.43	0.92	0.357
Youth-reported parental acceptance	-0.01	-0.38	0.42	0.91	0.361
LFPN-DMN x Youth-reported school disengagement	*-0.12*	*-0.37*	*0.41*	*0.90*	*0.369*
LFPN-DMN x Parent ethnic identification	*0.12*	*0.38*	*0.43*	*0.89*	*0.373*
Youth-reported parental monitoring	-0.01	-0.36	0.42	0.84	0.402
LFPN-DMN x People living in home	*-0.08*	*-0.34*	*0.40*	*0.84*	*0.403*
Hispanic ethnicity	0.02	0.25	0.31	0.80	0.422
Non-hispanic ethnicity	-0.02	-0.25	0.31	0.80	0.422
Not in school	-0.15	-0.32	0.41	0.80	0.425
LFPN-DMN x Census: adult violent crime reports	*-0.12*	*-0.27*	*0.35*	*0.78*	*0.438*
LFPN-DMN x Youth-reported parental monitoring	*-0.09*	*-0.30*	*0.41*	*0.73*	*0.466*
Parent separated/divorced	0.02	0.29	0.40	0.72	0.471
LFPN-DMN x Youth-reported supportive school environment	*0.08*	*0.28*	*0.40*	*0.70*	*0.486*
Youth-reported family conflict	-0.01	-0.26	0.42	0.61	0.543
Youth-reported supportive school environment	-0.01	-0.24	0.40	0.60	0.546
LFPN-DMN x Parent married	*0.16*	*0.22*	*0.37*	*0.59*	*0.553*
Youth-reported school involvement	-0.01	-0.23	0.39	0.59	0.555
LFPN-DMN x Third-generation American	*0.09*	*0.17*	*0.29*	*0.58*	*0.565*
LFPN-DMN x Asian race	*0.48*	*0.23*	*0.41*	*0.57*	*0.569*
LFPN-DMN x Other race	*-0.29*	*-0.23*	*0.40*	*0.56*	*0.574*
Home school	-0.16	-0.22	0.39	0.56	0.574
Parent widowed	-0.05	-0.24	0.44	0.56	0.576
LFPN-DMN x home school	*-2.77*	*-0.21*	*0.39*	*0.54*	*0.590*
Hours/week spent at another household	-0.01	-0.23	0.45	0.51	0.607
School for behavioral/emotional problems	0.14	0.24	0.47	0.51	0.613
People living in home	0.00	-0.20	0.40	0.50	0.617
LFPN-DMN x Native American/Alaska Native	*0.53*	*0.20*	*0.42*	*0.47*	*0.639*
LFPN-DMN x Youth-reported parental acceptance	*0.06*	*0.18*	*0.40*	*0.46*	*0.648*
LFPN-DMN x Any siblings	*0.13*	*0.18*	*0.40*	*0.44*	*0.661*

Parent self-reported intrusive behavior	0.01	0.18	0.41	0.43	0.668
LFPN-DMN x Youth-reported family conflict	*0.06*	*0.18*	*0.42*	*0.43*	*0.669*
LFPN-DMN x Charter school	*-0.24*	*-0.18*	*0.41*	*0.43*	*0.669*
Census: adult violent crime reports	0.01	0.15	0.35	0.42	0.677
LFPN-DMN x School for behavioral/emotional problems	*-2.24*	*-0.19*	*0.47*	*0.40*	*0.688*
LFPN-DMN x Census: % of families below the poverty level	*0.03*	*0.12*	*0.30*	*0.40*	*0.689*
LFPN-DMN x Parent self-reported withdrawn behavior	*0.04*	*0.14*	*0.39*	*0.37*	*0.714*
Parent self-reported aggressive behavior	0.00	0.14	0.38	0.36	0.722
Private school	-0.02	-0.14	0.42	0.34	0.731
Financial stress	0.00	0.12	0.44	0.28	0.782
LFPN-DMN x Parent living with partner	*-0.13*	*-0.11*	*0.41*	*0.26*	*0.797*
LFPN-DMN x Parent self-reported aggressive behavior	*0.03*	*0.10*	*0.38*	*0.25*	*0.799*
Child born outside U.S.	-0.02	-0.10	0.44	0.24	0.812
Census: uniform crime reports	0.00	-0.05	0.36	0.14	0.888
LFPN-DMN x Census: % of labor force aged >=16 y unemployed	*-0.01*	*-0.05*	*0.33*	*0.14*	*0.890*
Parent living with partner	-0.01	-0.05	0.42	0.13	0.901
LFPN-DMN x Census: estimated lead risk	*0.01*	*0.03*	*0.33*	*0.09*	*0.929*
LFPN-DMN x Parent never married	*0.02*	*0.03*	*0.36*	*0.08*	*0.936*
LFPN-DMN x Other school setting	*0.10*	*0.03*	*0.42*	*0.07*	*0.948*
Public school	0.00	0.02	0.37	0.05	0.957
Charter school	0.00	-0.01	0.40	0.04	0.972
Census: % of occupied units without complete plumbing	0.00	0.01	0.44	0.02	0.983
Parent self-reported withdrawn behavior	0.00	0.00	0.39	0.01	0.992
LFPN-DMN x Hispanic ethnicity	*0.00*	*0.00*	*0.34*	*0.01*	*0.991*
LFPN-DMN x Parent widowed	*0.00*	*0.00*	*0.44*	*0.00*	*0.998*

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