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Task fMRI paradigms may capture more behaviorally relevant information than resting-state functional connectivity

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Highlights:

- Functional connectivity (FC) patterns derived from fMRI tasks outperform resting-state FC at predicting individual differences in a measure of cognitive task performance and a task-derived behavioral inhibition measure.
- The improvement in behavioral prediction afforded by fMRI tasks over resting-state is largely associated with the FC of the task model fit.
- FC of the task model fit and task design model parameters contain shared and unique behavioral prediction power.

Abstract

Characterizing the optimal fMRI paradigms for detecting behaviorally relevant functional connectivity (FC) patterns is a critical step to furthering our knowledge of the neural basis of behavior. Previous studies suggested that FC patterns derived from task fMRI paradigms, which we refer to as task-based FC, are better correlated with individual differences in behavior than resting-state FC, but the consistency and generalizability of this advantage across task conditions was not fully explored. Using data from resting-state fMRI and three fMRI tasks from the Adolescent Brain Cognitive Development Study ® (ABCD), we tested whether the observed improvement in behavioral prediction power of task-based FC can be attributed to changes in brain activity induced by the task design. We decomposed the task fMRI time course of each task into the task model fit (the fitted time course of the task condition regressors from the single-subject general linear model) and the task model residuals, calculated their respective FC, and compared the behavioral prediction performance of these FC estimates to resting-state FC and the original task-based FC. The FC of the task model fit was better than the FC of the task model residual and resting-state FC at predicting a measure of general cognitive ability or two measures of performance on the fMRI tasks. The superior behavioral prediction performance of the FC of the task model fit was content-specific insofar as it was only observed for fMRI tasks that probed similar cognitive constructs to the predicted behavior of interest. To our surprise, the task model parameters, the beta estimates of the task condition regressors, were equally if not more predictive of behavioral differences than all FC measures. These results showed that the observed improvement of behavioral prediction afforded by task-based FC was largely driven by the FC patterns associated with the task design. Together with previous studies, our findings highlighted

the importance of task design in eliciting behaviorally meaningful brain activation and FC patterns.

Keywords: behavioral differences, predictive modeling, functional connectivity, cognitive development, behavioral inhibition

1. Introduction

An important aim of cognitive neuroscience is to understand how individual differences in behavioral attributes are associated with brain structure and function. With the availability of large neuroimaging datasets, recent work has pivoted towards building models that predict current or future behavior based on neuroimaging measures (Gabrieli, Ghosh, Whitfield-Gabrieli, 2015; Varoquaux & Poldrack, 2019; Finn & Rosenberg, 2021). Such predictive modeling approaches allow us to estimate better the degree to which behavioral differences are associated with individual differences in brain structure or function.

Trait differences can be predicted by individual differences in functional connectivity (FC), which measures the correlation of the BOLD response across regions of interests (ROIs) across brain regions by calculating the pairwise correlations of fMRI time series (Speer et al., 2021; Zhang et al., 2021). FC patterns are unique to an individual (Finn et al., 2015; Gratton et al., 2018), relatively stable across different mental states (Cole et al., 2014; Finn et al., 2015; Gratton et al., 2018), and sensitive to phenotypic differences including age (Dosenbach et al., 2010; Nielsen et al., 2019), cognitive abilities (Sripada et al., 2019, Moutoussis et al., 2021, Zhang et al., 2021; Chen et al., 2022), and mental health outcomes (Challis et al., 2015, Kim et al., 2016, Thomas et al., 2020; Chen et al., 2022).

FC is often estimated during resting-state fMRI acquisitions where participants are not engaged in a particular task but are simply instructed to either close their eyes or fixate on a crosshair and stay still. While resting-state fMRI has become the most common paradigm used for correlating FC patterns with behavioral traits or conditions, there is increasing evidence that rest may not always be the optimal condition to elicit FC patterns that are most relevant to differences in behavioral phenotypes in a particular domain (Rosenberg et al., 2016; Greene et al., 2018; Jiang et al., 2019; Finn, 2021). Naturalistic tasks or traditional fMRI tasks may have more utility for the prediction of trait or state differences as they can elicit cognitive states that are directly relevant to the behavioral domain of interest (Finn et al., 2017).

Direct comparisons between resting-state FC (rsFC) and task-fMRI FC suggest that the latter is better at predicting both fMRI attention task performance and trait measures of attention function (Rosenberg et al., 2016), measures of general cognitive ability (Greene et al., 2018; Elliot et al., 2019) and reading comprehension (Jiang et al., 2020). A similar advantage has been shown for more passive task fMRI with naturalistic paradigms such that FC during movie-watching paradigms outperformed rsFC in predicting individual differences in cognitive task performance and emotional health (Finn & Bandettini, 2021).

Why might FC patterns derived from task and naturalistic paradigms be more predictive of trait differences than FC patterns derived from rest? Finn and colleagues (Finn et al., 2017; Finn & Bandettini, 2021) proposed that task fMRI and naturalistic paradigms are better candidates than resting-state for the study of behavioral differences because tasks are tailored to engage a particular behavioral domain. Like a cardiac stress test where the heart's ability to respond to external stress is measured by inducing stress in a controlled environment, fMRI tasks and naturalistic paradigms can introduce cognitive and emotional challenges to simulate brain activity. It follows that an fMRI paradigm that engages the behavioral or cognitive processes involved in the behavioral phenotype of interest is likely to amplify brain-behavior relationships (Greene et al., 2020; Greene et al., 2018). In other words, the greater behavioral relevance of the FC derived from task fMRI paradigms may be attributable to the task effects.

Previous studies examining FC during fMRI tasks differ in whether they retain the task effects in the fMRI time course for FC estimation. With an explicit task design, the observed time course during a fMRI task can be decomposed into the part that is explained by the task, estimated by the task model fit, and the residual. If the task effect is retained (Vanderwal et al., 2017; Greene et al., 2018; Gao et al., 2019), the FC estimates, which we label the ***task-based FC***, capture the FC of the original and complete task fMRI time series (See Table 1 for a description of all fMRI measures used in this study). While numerous studies have reported the advantage of task-based FC at predicting behavioral traits (Greene et al., 2018; Elliot et al., 2019), task-state FC has been shown to be quantitatively different from rsFC as task-evoked signals may assert downstream effects on the correlation pattern of background brain regions (i.e. brain regions that are hypothesized to not be directly influenced by the fMRI task) (Al-Aidroors et al., 2012) or drive coincidental increases in the correlation patterns across brain regions that are otherwise absent at rest (Cole et al., 2019). While the implication of not removing the task evoked signals deserves further investigation, this study prioritizes its focus on the behavioral prediction performance of these FC measures.

If the task effect, estimated by the task model fit of subject-level general linear models (GLM) of task conditions, is removed (Arfanakis et al., 2000; Fair et al., 2007), the FC measures, which we label the ***task-model-residual FC***, capture the FC of the component of the task fMRI time series that is not explained by the task design. The task-model-residual FC has also been called “pseudo resting-state connectivity" (Jurkiewicz et al., 2018), “task FC” (Cole et al., 2014), “task-based FC” (Cole et al., 2019), and "background connectivity" (Al-Aidroos et al., 2012) in the literature. Because of its task-invariant nature, task-model-residual FC patterns have indeed been shown to resemble rsFC patterns (Jurkiewicz et al., 2018; Cole et al., 2019) and are predictive of behavioral differences across individuals (O'Halloran et al., 2018; Varangis, Habeck & Stern, 2020). If the task-model-residual FC does capture the same functional brain organization as resting-state FC as previous studies suggest (Jurkiewicz et al., 2018; Cole et al., 2019), the reported superior behavioral prediction of the task-state FC over rsFC may be attributable to the task effects that were removed from the task-model-residual FC. The task effects that are being removed from the task-model-residual time series are estimated with GLM models, where the beta estimates of task onsets and their temporal derivatives, which we refer to as the ***task model parameters***, capture the effect of task conditions on the time series of each ROI. We can manipulate data from fMRI tasks to study the behavioral sensitivity of the FC pattern of the task effects. By estimating the FC of the task model fit, which we call the ***task-model-fit FC***, we can directly assess and compare its behavioral relevance against the task-model-residual FC, the task-based FC, and the rsFC. These comparisons generate new hypotheses on the source of behavioral relevance in the task fMRI data and can provide additional information to guide the optimization of fMRI paradigms for the investigation of behavioral phenotypes.

fMRI paradigm	**Measure name**	**Definition**	**Name in other studies**
Resting-state fMRI	rsFC	Pairwise correlation of fMRI activity at rest	
fMRI tasks	Task-based FC	Pairwise correlation of the complete preprocessed task fMRI time series.	"Task-based FC" (Greene et al., 2018; Gao et al., 2019)

	Task-model-fit FC	Pairwise correlation of task-model-fit time series which is the task fMRI time series component explained by the task design. The task-model-fit time series is derived by multiplying the task design matrix by the beta estimates of the task condition regressors and their temporal derivative.	--
	Task-model-residual FC	Pairwise correlation of the task-model-residual time series which is the task fMRI time series component that cannot be explained by the task design. The task-model-residual time series is derived by subtracting the task-model-fit time series from the preprocessed task fMRI time series.	"Pseudo resting-state connectivity" (Jurkiewicz et al., 2018) "Task FC" (Cole et al., 2014) "Task-state FC" (Cole et al., 2019) "Background connectivity" (Al-Aidroos et al., 2012)
	Task model parameters	The beta estimates of the task condition regressors and their temporal derivative derived from subject-level GLM models.	

Table 1. Glossary for fMRI measures used in this study.

In this study, we leveraged the large sample of the Adolescent Brain Cognitive Development (ABCD) Study ® and compared the behavioral prediction performance of rsFC to the task-model-fit FC, task-model-residual FC, and task-based FC derived from the Emotional N-back (nBack) task, the Stop Signal Task (SST), and the Monetary Incentive Delay (MID) task.

We evaluated the out-of-sample prediction performance of each FC measure on three behavioral measures. The trait-like behavioral measure of interest was a measure of general cognitive performance, the total composite cognitive score of the NIH Cognition Toolbox. As examples of a more proximal, state-sensitive, behavioral measure we chose a behavioral inhibition measure derived from the SST fMRI task, the stop-signal reaction time (SSRT), and a working memory performance measure derived from the the nBack fMRI task, the 2-back accuracy measure. The behavioral prediction of the task model parameters, the beta estimates of the task condition regressors, was also estimated and contrasted with all task-derived FC measures. We also quantified how the prediction performance of FC measures changed with the amount of usable data and across sociodemographic variables, which are known to be associated with individual variability in cognitive (Korous et al., 2020) and brain outcomes (Farah, 2018; Taylor et al., 2020).

2. Methods

2.1 Participants

The ABCD Study is a longitudinal neuroimaging study that tracks brain and behavioral development of 11,880 children starting at 9 and 10 years old. The ABCD study used school-based recruitment strategies to create a demographically and ethnically diverse cohort (Garavan et al., 2018) with an embedded twin cohort and many siblings. Informed consent was obtained from parents/caretakers and assent was obtained from the children. Extensive descriptions of the recruitment, collection, and processing of the fMRI and the behavioral data of the ABCD study can be found in prior publications (Gavaran et al., 2018; Casey et al., 2018; Hagler et al., 2019). Participants with complete data across all the behavioral measures and covariates of interest were included in the analyses. To ensure accurate characterization of the FC matrices, participants were required to have at least 50% of usable data for each of the two runs of each fMRI task, and for each of the four resting state fMRI runs. The nBack task had the least number of participants that met the inclusion criteria (n = 3034). In order to match the number of participants across fMRI acquisitions for the behavioral prediction analysis, we randomly selected 3034 participants from each of the other fMRI acquisitions. Around 25% of the participants are shared between the final sample of each acquisition. The additional inclusion criteria and their effect on sample size is shown in Supplementary Table 1.

2.2 Behavioral measures

Here, we describe the behavioral measures used in the present study. The full neurocognition battery for the ABCD Study is detailed elsewhere (Luciana et al., 2018). The NIH Toolbox Cognition Battery measures a range of cognitive domains that show substantial development during childhood and adolescence. It consists of seven subtests, including measures of vocabulary size (Picture Vocabulary Task), single word reading ability (Oral Reading Task), rapid visual processing (Pattern Comparison Processing Speed Test), working memory capacity (List Sorting Working Memory Test), episodic memory (Picture Sequence Memory Test), attention and inhibitory control (Flanker Task), and cognitive flexibility (Dimensional Change Card Sort Task). The composite measure of the NIH Toolbox Cognitive Battery, the Total Composite Score is an arithmetic average of the 7 subtests summarizing the cognitive performance of an individual across the different cognitive domains. The age-uncorrected score of the composite measure, the total composite cognition score, was used as a primary behavioral outcome of this study. In the ABCD Study, participants perform the Stop Signal Task (SST) during fMRI scans. In this task, participants are instructed to inhibit a prepotent motor response to a Go Stimulus in response to a stop signal. A tracking algorithm varies the interval between the onset of the Go stimulus and the onset of the Stop stimulus (the Stop Signal Delay) based on individual performance. The Stop Signal Reaction Time (SSRT) quantifies the speed of the inhibitory process during the SST task, such that lower SSRT reflects more efficient response inhibition. The SSRT was calculated by subtracting participants' mean stop signal delay (SSD) from their mean reaction time during the SST fMRI task. The 2-back accuracy, derived from the nBack fMRI task, quantifies participants' working memory performance with participants' average accuracy on all 2-back conditions across two nBack runs. We chose the SSRT and the 2-back accuracy as additional behavioral outcomes because both measures quantify the performance of a specific cognitive processes during an fMRI task, in contrast to the general cognitive abilities assessed by the total composite cognition score. In addition, the measure was derived directly from performance during the task fMRI session enabling us to assess links between task performance and the miscellaneous FC measures obtained during that task.

2.3 Resting-state and task fMRI paradigms

The neuroimaging paradigms and acquisition parameters are detailed elsewhere (Casey et al., 2018), so a brief overview is provided here. Four 5-minute resting-state fMRI runs were acquired during which participants were instructed to fixate on a crosshair. Three task fMRI acquisitions were completed after the resting-state fMRI, with two runs of each of the following tasks: Emotional N-back task (nBack), Stop Signal Task (SST), and Monetary Incentive Delay Task (MID). The order of the tasks was counterbalanced across participants. These tasks have been shown to elicit anticipated patterns of brain activation in the ABCD Study baseline data consistent with previous literature (Chaarani et al., 2021).

The nBack engages the neural correlates of working memory and emotional regulation processes. To engage working memory, the task includes 0-back and 2-back conditions, presented in a block design. For the 2-back condition, participants were instructed to indicate with a button press whether the current stimulus matched the stimulus presented 2 trials back. For the 0-back condition, a target stimulus was presented at the beginning of the block and participants were instructed to press the button when they saw the target. To engage emotion regulation, the task stimuli included happy faces, fearful faces, neutral faces, and places, presented serially.

The SST engages the neural correlates of impulsivity and inhibitory control. In an event-related design, participants were instructed to indicate the direction of a leftward or rightward pointing arrow as quickly as possible. In 16.67% of the trials, the arrow was followed by a stop signal represented as an upward arrow, and participants were instructed to withhold their response. A tracking algorithm that varied the onset of the stimulus and the onset of the stop stimulus (the stop signal delay, SSD) was implemented to ensure approximately 50% successful and 50% unsuccessful stop trials.

The MID probes the neural correlates of reward processing. For each trial, participants could either win money, lose money, or earn nothing. Wins and losses were further subdivided into small or large amounts. At the start of each trial, participants were prompted with an incentive cue of five possible trial types (win $0.20, Win $5, Lose $5, Lose $0.20, $0-no money at stake) followed by a jittered anticipation period, during which participants fixated on a crosshair. Next, a target appeared to which participants made their button response. The trial ended with positive or negative feedback to inform participants about their performance. Since the MID task uses an adaptive algorithm that tracks to the performance of each participant, the behavioral outcome measures (e.g. reaction time) are not comparable across participants. As a result, no behavioral data from the MID task was used in this study.

2.4 Image acquisition and processing

2.4.1 Task and resting-state MRI acquisition and preprocessing

The ABCD MRI data were collected across 21 research sites using GE 750, Siemens Prisma, and Philips Achieva and Ingenia 3T scanners. Scanning protocols were harmonized across sites. The full details of the ABCD imaging acquisition and preprocessing protocols were described in Casey et al. (2018) and Hagler et al. (2019). Briefly, T1w sMRI images (1mm isotropic) were acquired with a 3D T1w inversion prepared RF-spoiled gradient echo scan, and fMRI acquisitions (rest and task) were collected with multiband EPI with slice acceleration factor 6 (2.4 mm isotropic, TR = 800ms). The preprocessing steps for fMRI data included (i) head motion correction, (ii) B0 distortion correction, (iii) gradient warping correction, (iv) within-scan motion correction, and (v) registration to T1w structural images. Initial frames (Siemens and Philips scanners: 8 TRs; GE DV25: 5 TRs; GE DV26: 16 TRs) were removed from the preprocessed task fMRI time course. Motion estimates were filtered to remove the effect of respiratory signals (Fair et al., 2018). The preprocessed time courses were normalized and sampled onto the cortical surface for each participant. Average time courses were calculated for a functionally defined parcellation scheme (Gordon et al., 2016) sampled from the atlas-space to individual subspace, and anatomically defined subcortical ROIs (Fischl et al., 2002).

2.4.2. Task model parameters, task-based fMRI time series, task-model-fit, and task-model-residual time series estimation

The task effects were estimated at the participant level using a GLM that included the stimulus timing for each task condition (Hagler et al., 2019) and the temporal derivative to capture any task related changes in the fMRI time course that is not captured by our task model. The GLM modeled each task condition with a bivariate gamma function and its first temporal derivative along with 4 nuisance regressors for baseline shifts and cubic trends and 12 regressors for the six motion estimates and their temporal derivatives. For the GLM estimation, time points with framewise displacement (FD) greater than 0.9 mm were censored (Siegel et al. 2014). For the behavioral prediction response of the task model parameters, both the beta estimates of the task condition regressors and the temporal derivative were included as predictors.

The task-based time series was the task fMRI time series after preprocessing. The task-model-fit time series was the component of the preprocessed task fMRI time series that was explained by the task design and was calculated by multiplying task design matrix to the beta estimates of task condition regressors and their temporal derivative. The task-model-residual time series was the component of the preprocessed task fMRI time series that was not explained by the task, calculated by subtracting the task-model-fit time series from the preprocessed task-based time series.

In matrix expression, $Y_{tr,roi}$ is the observed fMRI time series matrix of an fMRI task with *tr* as the number of TRs and *roi* as the number of ROIs. $X_{roi,cond}$ describes task condition onset at each ROI with *cond* as the number of task conditions. β is a *cond* by *roi* task model parameters matrix that quantifies the effect of each task condition. The task model parameters, β, were estimated as:

$$\hat{\beta} = X^{-1} Y ,$$

which estimated the effect of the task condition onset on the observed time series.

The task-model-fit time series matrix, $\hat{Y}$, was estimated as:

$$\hat{Y} = X^{-1} \hat{\beta} ,$$

and $\hat{Y}$ represented the estimated time series data at each ROI predicted by the task condition onset. The task-model-residual time series matrix was estimated with:

$$\hat{\varepsilon} = Y - \hat{Y},$$

which summarized the component of the observed time series that could not be explained by the task conditions.

The $\hat{\beta}$ corresponded to the task model parameters for behavioral prediction. The correlation of the estimated task-model-fit time series, $\hat{Y}$, corresponded to the task-model-fit FC. The correlation of the task-model residuals, $\hat{\varepsilon}$, corresponded to the task-model-residual FC. The correlation of the observed time series, Y, corresponded to the task-model-residual FC.

2.4.3 FC estimation

Several additional preprocessing steps were applied to the resting-state and task fMRI time series before the estimation of FC to reduce spurious signals that are unlikely to reflect functional brain activation. These steps included (1) censoring and residualization and removal of signals associated with cerebral white matter, ventricles, whole brain, and head motion estimates and their squares and derivatives (Power et al., 2014; Satterthwaite et al., 2012), (2) motion regression where frames with FD over 0.3mm were excluded (Power et al., 2014), and (3) band-pass filtering (0.009 and 0.08 Hz) (Hallquist et al., 2013). Motion traces were temporally filtered using an infinite impulse response (IIR) notch filter and the cutoffs are 0.31 and 0.43 Hz. Additional motion censoring was applied to exclude the following time points: time points with FD over 0.2mm, time points that were outliers with respect to the spatial variation across the brain, and time periods with less than 5 contiguous, sub-threshold time points. Average time courses were calculated for 333 cortical ROIs (Gordon et al., 2016) and 19 subcortical ROIs (Fischl et al., 2002) for each run and were concatenated. Pearson correlations were applied to calculate the pairwise correlations of these 352 ROIs. The r-to-z transformed correlation matrix formed the FC estimate of each time series.

2.5 Statistical analysis

2.5.1 Behavioral prediction algorithm

A nested 10-fold cross validation scheme was used to estimate the out-of-sample prediction performance of each set of fMRI measures. Participants from the same family were kept within the same training and testing set during the cross validation. Within each training set, the mass univariate beta estimates between each fMRI measure and a behavior were estimated using the Fast Efficient Mixed Effects Analysis (FEMA; Fan et al., 2021) where a general linear mixed effects model was estimated at each voxel or ROI. Compared to the traditional general linear models, FEMA explicitly adjusts for the effects of the nested family structure in the ABCD data and the covariates of no interest. The following sociodemographic and imaging acquisition variables were included in the FEMA models as covariates: age, biological sex, top 10 genetic PCs, highest parental education, household income, scanner ID (MRI device serial number) and software version. Mean framewise displacement (FD) and the number of usable time points were used as additional covariates for FC measures. A separate analysis was conducted without the inclusion of sociodemographic variables as covariates to probe the shared impact of sociodemographic variables on the imaging and the behavioral measure. For this analysis, only scanner ID and software version were used as covariates, along with mean FD and the number of usable time points for FC measures.

For behavioral prediction, the mass univariate beta estimates from FEMA were entered into a singular-value decomposition (SVD) based prediction method to predict the behavioral outcome of the unseen, test-set participants. Similar to our previous method, the Bayesian polyvertex score (PVSB, Zhao et al., 2021), the SVD-based prediction method applies shrinkage to the mass univariate beta estimates to improve out-of-sample prediction performance. The shrinkage factor was derived separately for each brain-behavior association with a 5-fold cross validation nested within each training set. Within each nested training set, SVD was applied to the imaging measure pre-residualized for sociodemographic covariates to approximate the covariance structure of the mass univariate beta estimates. From the SVD result, the top k singular vectors and their corresponding singular values were used to calculate a shrinkage factor that was used to reweight the mass univariate beta estimates from FEMA. One hundred k values were selected at equal distances between 1 and the dimension of the predictor space. The best performing k value was selected as the shrinkage factor for the full training set. The reweighted mass univariate estimates were then applied to the test set imaging data to calculate the predicted behavioral score for each test set participant. A separate cross validation procedure that was based on ABCD sites (i.e. leave-one-site-out) was also implemented (see S.I. Methods) to examine the effect of the chosen cross validation procedure on behavioral prediction.

The predicted behavioral score summarizes the variability in the behavioral outcome that is attributable to individual differences of the imaging measure. Squared correlation between the predicted and the observed behavioral score was used as the metric for out-of-sample behavioral prediction performance of each imaging measure. The ninety-five percent confidence interval of the behavioral prediction performance of each fMRI measure was generated with bootstrap resampling (Elliot et al., 2019) using the ci_cor function (confintr package) in R. The predicted behavioral scores were also used in subsequent analyses to probe the shared and unique behavioral variance explained by different FC measures.

All usable data from each modality were included in the behavioral prediction analysis. As resting-state fMRI was collected with 4 runs while the task-fMRI was collected with 2 runs of data, we investigated how the behavioral prediction performance of each FC measure was affected by scan length, i.e. the number of runs in supplementary analysis (Supplementary Methods).

2.5.2 Quantification of shared and unique behavioral variance explained by the task-model-fit FC and the task-model-residual FC

As the task-model-fit FC and task-model-residual FC were derived as complementary subcomponents of the same task fMRI time series, we examined if they contained unique information for behavioral differences by estimating their shared and unique behavioral variance explained. In this set of analysis, we used the predicted behavioral scores of each FC measure on each behavior as the predictor because they captured the prediction effects of FC measures on behaviors while reducing the predictor dimensionality to a single measure. We first estimated the out-of-sample behavioral prediction performance of the predicted behavioral scores of task-model-fit FC and of the task-model-residual FC individually with generalized additive mixed models (GAMMs) with sociodemographic factors as fixed effects covariates and family ID as random effects. These *univariate models*, with only one brain predictor in the model, gave us an estimate of the behavioral variance explained by each FC in isolation. Then, we estimated their total prediction effect by including the predicted behavioral scores of both FC measures as predictors in an *augmented model*, with sociodemographic factors as fixed effects covariates and family ID as random effects.

The unique variance explained by the task-model-fit FC (unique R^2 adjusted for task-model-residual FC) was calculated as the difference in R^2 between the univariate model with the predicted behavioral score of the task-model-residual FC as the only FC predictor and the augmented model with the predicted scores of both the task-model-fit FC and the task-model-residual FC. The unique variance explained by the task-model-residual FC (unique R^2 adjusted for task-model-fit FC) was estimated as the difference in R^2 between the univariate model with the predicted behavioral score of the task-model-fit FC and the augmented model. The gamm4 (gamm4 package) function was used to perform GAMMs in R and the r.squaredGLMM (MuMIn package) function was used to estimate the behavioral variance explained (fixed effects pseudo-r-squared) of the fMRI predictors from GAMMs.

2.5.3 Quantification of shared and unique behavioral variance explained by the task-model-fit FC and the task model parameters

Both task-model-fit FC and task model parameters capture the task effects on brain activity. We assessed whether these two task effects measures explained unique behavioral variance by quantifying the shared and unique variance explained of the predicted behavioral scores of the task-model-fit FC and the task model parameters. An augmented model that included both measures was performed to estimate the total prediction effect of the task-model-fit FC and the task model parameters. The unique variance explained by the task-model-fit FC (unique R^2 adjusting for task model parameters) was estimated as the difference in R^2 between the augmented model and the univariate model with task model parameters. The unique variance explained by the task model fit (unique R^2 adjusting for task-model-fit FC) was estimated as the difference between the augmented model and the univariate model with task-model-fit FC. Family relatedness was modeled as a random effect and sociodemographic factors were used as fixed effects covariates for all the above-mentioned models.

2.5.4 The effect of sociodemographic factor adjustment on behavioral prediction performance

To understand how sociodemographic factor adjustment changes the behavioral prediction performance of fMRI measures, we reran the above behavioral prediction models without the adjustment of sociodemographic factors and only including scanner ID, scanner software version, mean FD, and the number of usable timepoints as covariates in FEMA. The unadjusted mass univariate beta estimates of all FC and task model parameters were used to calculate the behavioral prediction performance of all fMRI measures without the adjustment of sociodemographic differences in our sample. The prediction performance of each fMRI measure with and without sociodemographic adjustment was compared.

2.6 Data Statement

Data used in this article were obtained from the Adolescent Brain Cognitive Development (ABCD) Study (https://abcdstudy.org), held in the NIMH Data Archive (NDA).

3. Results

3.1 Task-model-fit FC and task-based FC conferred task-specific advantage at predicting individual differences in behavior over rsFC and task-model-residual FC.

Prediction performance of rsFC and the three task-derived FC measures on individual differences in total composite cognition score, SSRT, and 2-back accuracy are shown in Figure 1. After adjusting for sociodemographic variables, the squared correlation between the rsFC and the total composite cognition was 0.036. The squared correlations between the nBack, SST, and MID task-model-residual FC estimates and the total composite cognition were 0.033, 0.021, and 0.034, respectively.

Increased behavioral prediction was observed for the task-based FC and the task-model-fit FC derived from the nBack and the MID task. The squared correlations between the total composite cognition and the nBack task-based FC and task-model-fit FC were 0.062 and 0.067, and the squared correlations of the MID task-based FC and task-model-fit FC were 0.064 and 0.064. We did not observe an increase in prediction for the SST task-based and the task-model-fit FC on total composite cognition (SST task-model-fit FC squared correlation: 0.014; SST task-based FC squared correlation: 0.025). Behavioral prediction performance of fMRI measures estimated using leave-one-site out cross validation followed similar patterns as the 10-fold cross validation.

We observed a task-specific effect of SST-derived FC measures on SSRT. Only FC measures derived from the SST task were significantly predictive of the individual differences in SSRT. Among the SST task FC measures, we observed an advantage for the SST task-model-fit FC relative to the SST task-model-residual FC. The squared correlation between the SST task-model-fit FC and SSRT was 0.095, while the squared correlation of the SST task-model-residual FC was 0.049. We compared the FEMA z-score map of the SST task-model-residual FC on SSRT to the effect size map of the SST task-model-fit FC, the SST task-based FC, and the rsFC (Figure 2). The mass univariate beta estimates of the SST task-model-residual FC bore greater resemblance to the effect size map of the SST task-model-fit FC than to the rsFC, suggesting that the SST task-model-residual FC captured a similar predictive pattern as the SST task-model-fit FC. The mass univariate beta estimates of other brain-behavior associations are shown in Supplementary Figures (SI. Figure 1-4).

A similar task-specific advantage was also observed for the nBack FC measures at predicting 2-back accuracy. While the squared correlation between the rsFC and the 2-back accuracy was 0.016, the squared correlations of the nBack task-model-residual FC, the nBack task-state FC, and the nBack task-model-fit FC were 0.07, 0.135, and 0.132, respectively. The

FC measures derived from the SST task demonstrated similar prediction performance as the rsFC. For the MID task, we also observed a greater association between the MID-derived FC measures and the 2-back accuracy than the rsFC and the SST-derived FC measures. The squared correlations of the MID task-model-residual FC, task-state FC, and task-model-fit FC were 0.024, 0.046, and 0.048, respectively.

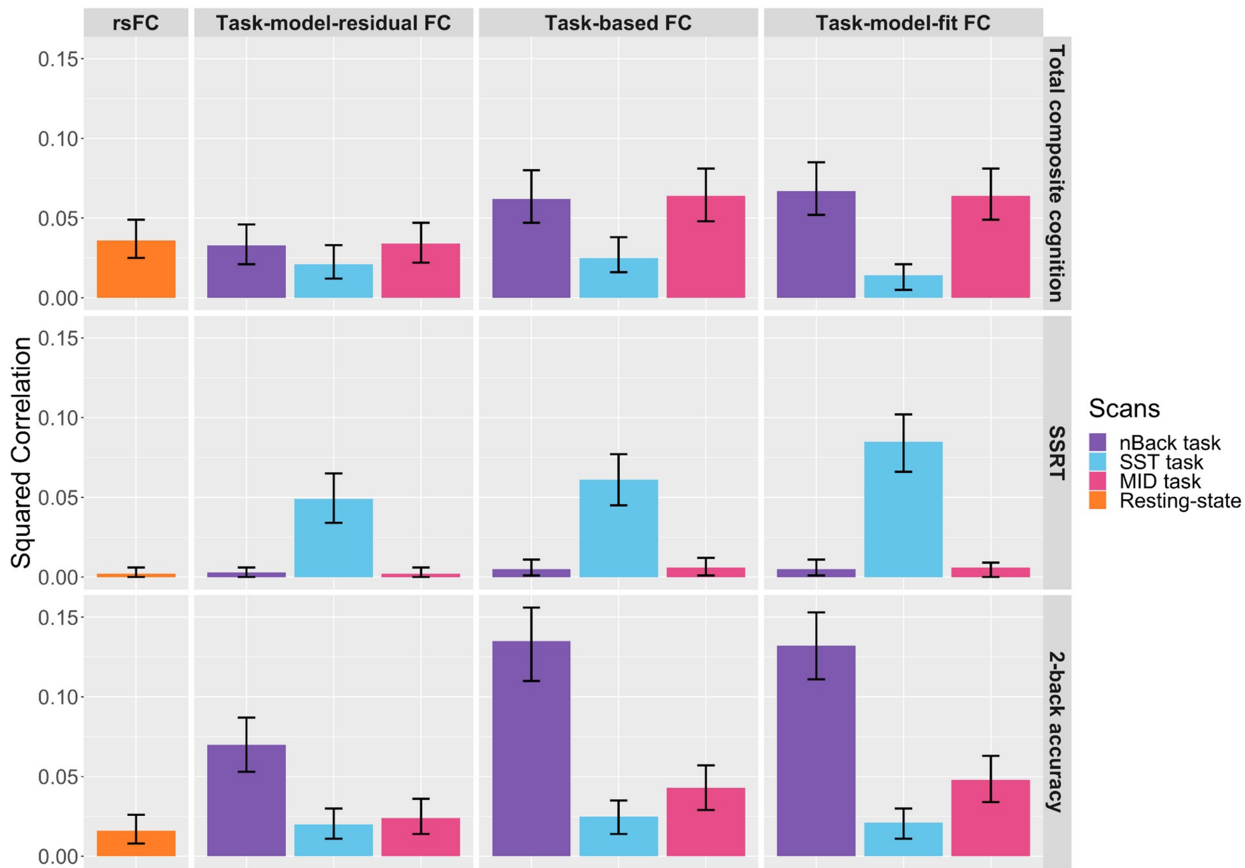

Figure 1. The task-based FC and task-model-fit FC outperformed rsFC and task-model-residual FC at predicting individual variability in total composite cognition, SSRT, and 2-back accuracy. For total composite cognition (top row), rsFC (first column) and the task-model-residual FC measures (second column) showed similar behavioral prediction performance. Task-based FC (third column) and task-model-fit FC (fourth column) of the nBack and MID task, on the other hand, outperformed rsFC and task-model-residual FC explaining behavior differences in total

composite cognition. For the SSRT (middle row), only task-derived FC measures from the SST task were predictive. All SST task FC measures were predictive of the SSRT, while rsFC was not. For the 2-back accuracy (bottom row), the nBack-derived task FC measures outperformed the rsFC and the task-derived FC measures from the other two fMRI tasks. Error bars show the ninety-five percent confidence intervals estimated with bootstrap resampling.

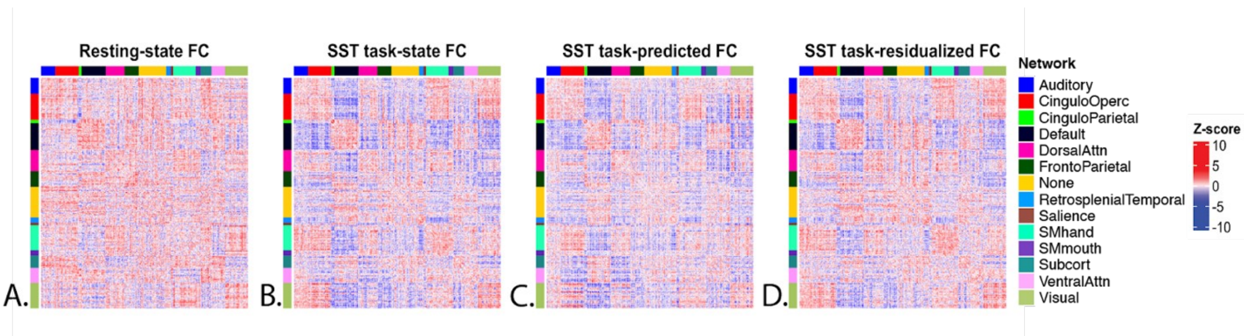

Figure 2. The effect size matrices of the SST task FC measures on SSRT were more similar to each other than to rsFC. 352 ROIs x 352 ROIs effect size matrices, organized by functional network, are shown. Each cell corresponds to the mass univariate z-score of each ROI pair on SSRT derived from FEMA analyses.

We conducted post-hoc correlation analyses on the behavioral outcome variables to examine whether the task-specific advantage of the nBack and the SST task was due to a high correspondence between the in-scanner cognitive behaviors and out-of-scanner behavioral outcomes. If the in-scanner behavior of an fMRI task is highly correlated with the out-of-scanner behavior of interest, we expect to observe that that fMRI task is better at predicting the out-of-scanner behavior of interest.

The correlation between the total composite cognition, SSRT, and the 2-back accuracy was estimated in the sample of participants who were sampled for the rsFC prediction analysis. The 2-back accuracy measure was highly correlated with the total composite cognition ($r = 0.46$) but not with SSRT ($r = -0.07$). This could contribute to the greater prediction performance of the nBack-derived FC measures on total composite cognition. The SSRT, on the other hand, was not positively correlated with either the total composite cognition ($r = -0.12$) or the 2-back accuracy. This lack of in-scanner behavior and out-of-scanner behavior correlation might contribute to the minimum association between the SST-derived FC measures and the other behavioral measures.

3.2 Task-model-fit FC accounted for the behavioral variance predicted by the task-model-residual FC.

Given that the task-model-fit FC and task-model-residual FC were derived from complementary subcomponents of the task fMRI time series, we examined whether these FC measures contributed unique information to behavioral prediction (Table 2) by quantifying the shared and unique variance explained by the predicted behavioral scores of the two FC measures. For the prediction of total composite cognition by the nBack and MID tasks, task-model-residual FC contributed minimal unique variance explained ($R^2 < 1\%$) after adjusting for task-model-fit FC. On the other hand, the nBack and MID task-model-fit FC each explained 4.1% variance in total composite cognition after adjusting for task-model-residual FC. Therefore, task-model-fit FC predicted unique behavioral variance, while task-model-residual FC did not. By contrast, SST task-model-fit FC did not contribute unique variance to predicting total composite cognition, while the SST task-model-residual FC uniquely explained 1.3% of the variance. For the SST-SSRT association, after adjusting for the shared behavioral variance explained, both the SST task-model-fit FC and the SST task-model-residual FC predicted unique variance in SSRT (SST task-model-fit FC: unique R^2 = 4.5%; SST task-model-residual FC: unique R^2 =1.1%). We believe that the unique association between SSRT and the SST task-model-residual FC might be attributable to the insufficient modeling and removal of the SST task effect. For the prediction of 2-back accuracy, both nBack task-model-fit FC and the nBack task-model-residual FC predicted unique behavioral variance, although the unique variance explained by the task-model-fit FC was much greater than the task-model-residual FC (nBack task-model-fit FC: unique R^2 = 7.9%; nBack task-model-residual FC: unique R^2 =1.8%).

fMRI tasks	**Task-model-fit FC**		**Task-model-residual FC**	
	R^2	**Unique R^2 adjusted for task-model-residual FC**	**R^2**	**Unique R^2 adjusted for task-model-fit FC**
Behavior: Total composite cognition				
nBack	6.4%	4.1%	3.1%	0.8%
SST	1.1%	0.4%	2.0%	1.3%
MID	6.6%	4.1%	3.1%	0.6%
Behavior: SSRT				
nBack	0.4%	0.4%	0.2%	0.1%
SST	7.9%	4.5%	4.5%	1.1%
MID	0.2%	0.1%	0.3%	0.2%
Behavior: 2-back accuracy				
nBack	12.9%	7.9%	6.9%	1.8%
SST	1.9%	0.9%	1.9%	0.9%
MID	4.5%	2.6%	2.3%	0.3%

Table 2. The shared and unique variance explained (R^2) of the task-model-fit FC and the task-model-residual FC for each brain-behavior association.

3.3 Similar to the task-model-fit FC, task model parameters also exhibited a task-specific prediction advantage over the task-model-residual FC and rsFC.

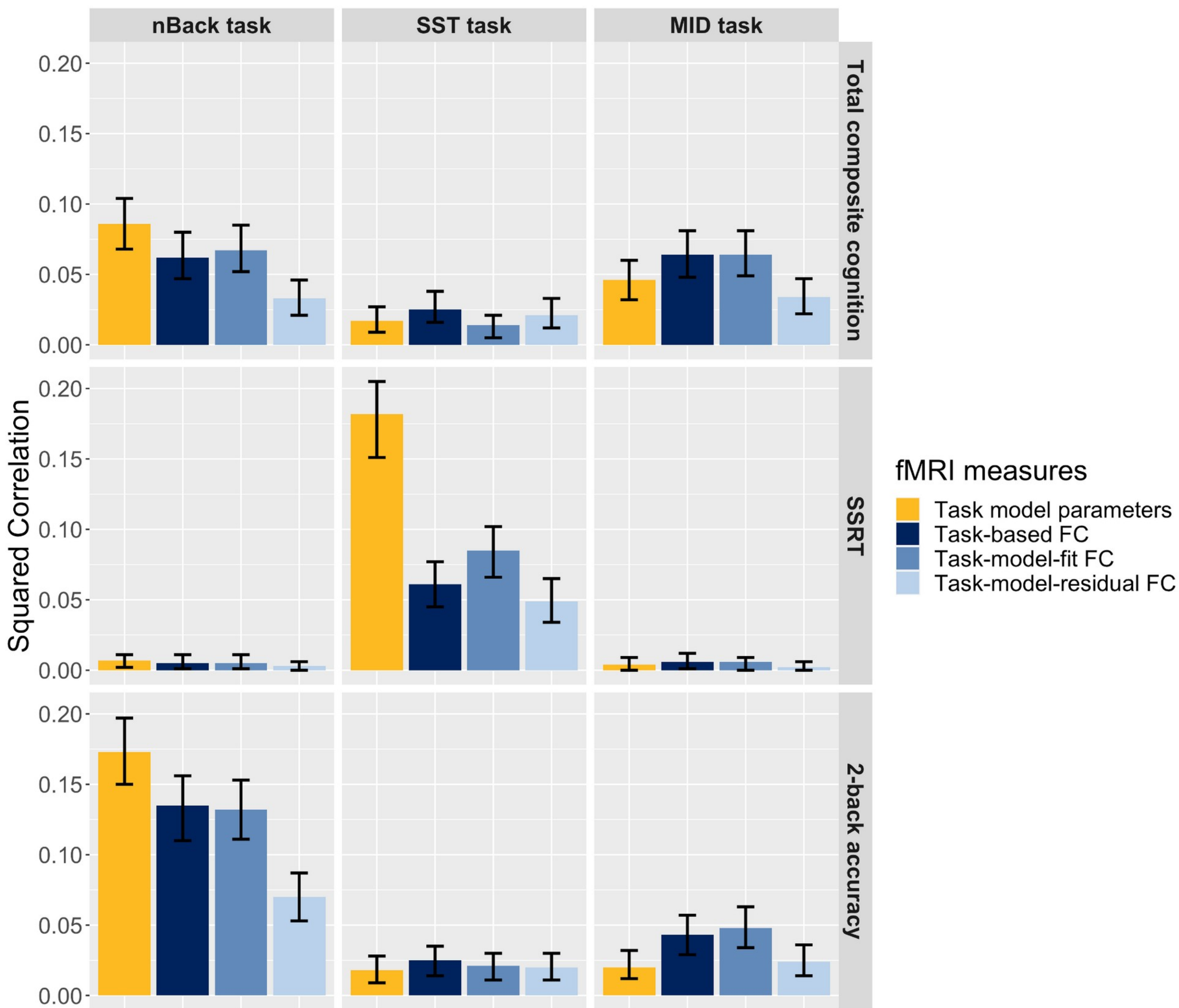

Figure 3. Task model parameters outperformed task-model-residual FC at predicting behavioral differences. Similar to the task-model-fit FC, task model parameters (yellow) demonstrated task-specific advantage over the task-model-residual FC at predicting total composite cognition (top row), SSRT (middle row), and 2-back accuracy (bottom row).

The task model parameters were equally, if not more predictive, than the task-model-fit FC and significantly outperformed the task-model-residual FC (Figure 3) at predicting behavioral differences. For total composite cognition, the nBack task model parameters were more predictive than the nBack task-model-fit FC (squared correlation: 0.084), and the MID task model parameters were less predictive of total composite cognition (squared correlation: 0.043). For SSRT, the SST task model parameters showed the best predictive performance of all fMRI measures (squared correlation: 0.182) and doubling the prediction effect of SST task-model-fit FC. For 2-back accuracy, the nBack task-model-parameters (squared correlation: 0.167) again outperformed the task-model-fit FC (squared correlation: 0.067). Across all task-derived FC measures, the task-model-residual FC was the least predictive across all brain-behavioral measures.

3.4 Task model parameters and task-model-fit FC explained both shared and unique behavioral variance.

We next examined whether the task model parameters and task-model-fit FC offered redundant functional brain information relevant for behavior by quantifying the unique behavioral variance explained by the predicted behavioral score of each brain measure after adjusting for the prediction effect of the other (Table 3). We observed a decrease in unique variance explained (unique R^2) for both measures, suggesting that a proportion of the behavioral association was shared between the task model parameters and the task-model-fit FC. Though there was this decrease, both measures were uniquely associated with behavior, still explaining meaningful variance after adjusting for the effect of the other measure. For example, the nBack task model parameters explained 8% of the variance in total composite cognition. After adjusting for the effect of the task-model-fit FC, it uniquely explained 3.1% of behavioral variance. The nBack task-model-fit FC explained 6.4% of the behavioral variance in total composite cognition, and after adjusting for the effect of task model parameters, its unique R^2 dropped to 1.5%.

fMRI task	Task model parameters		Task-model-fit FC	
	R^2	Unique R^2 adjusted for task-model-fit FC	R^2	Unique R^2 adjusted for task model parameters
Behavior: Total composite cognition				
nBack	8.0%	3.1%	6.4%	1.5%
SST	1.5%	1.1%	1.3%	0.8%
MID	4.3%	1.7%	6.4%	3.9%
Behavior: SSRT				
nBack	0.5%	0.3%	0.4%	0.2%
SST	16.7%	11.6%	7.6%	2.5%
MID	0.3%	0.3%	0.4%	0.3%
Behavior: 2-back accuracy				
nBack	16.7%	6.6%	13.0%	2.9%
SST	1.6%	1.0%	2.0%	1.3%
MID	1.9%	0.5%	4.9%	3.4%

Table 3. Task model parameters and task-model-fit FC explained both shared and unique variance in individual differences in behaviors. The R^2 columns display the individual variance explained for each fMRI measure, corresponding to the data shown in Figure 1 and Figure 4. The R^2 adjusted columns display the unique variance explained after adjusting for the effect of the other fMRI measure.

3.5 Adjusting for sociodemographic factors reduced the behavioral prediction performance of FC and task model parameters.

Sociodemographic variables accounted for a proportion of the unadjusted behavioral association of fMRI measures, and the effect was more prominent for the prediction of total composite cognition (Figure 4). When not controlling for sociodemographic factors, the squared correlation between rsFC and total composite cognition was 0.127. That number dropped to 0.036 after the adjustment for sociodemographic differences. A similar reduction in prediction performance was observed for the task-derived FC measures and task model parameters. The prediction performance for 2-back accuracy also showed a significant reduction when adjusting for sociodemographic variables. For the association between the SSRT and the SST task, we observed a more moderate effect of sociodemographic adjustment. The SST task model parameters had a squared correlation of 0.211 with SSRT without the adjustment of sociodemographic covariates. After covarying for sociodemographic factors, its squared correlation was 0.182.

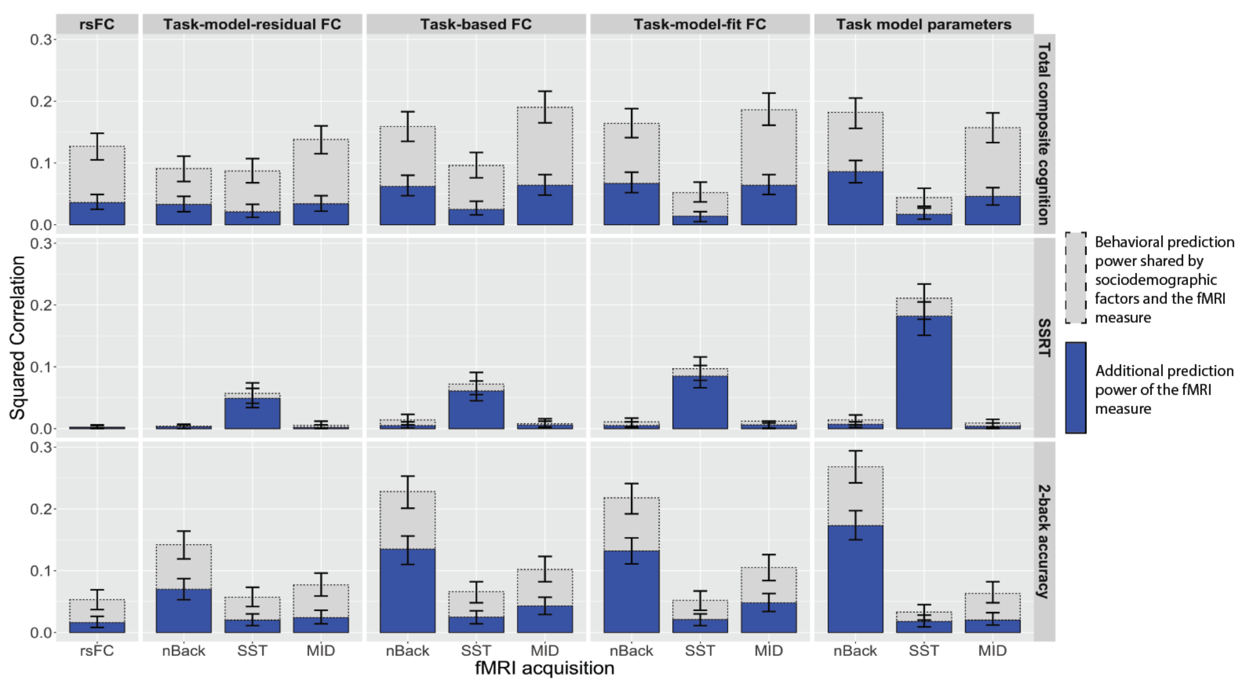

Figure 4. A proportion of the behavioral prediction power of task model parameters and FC measures was explained by sociodemographic variation across individuals. The unadjusted

prediction squared correlation or each behavioral outcome, represented by the total height of the bar, was partitioned into two components, a variance component that was shared with sociodemographic factors (shown in gray) and a variance component that was additive to the effect of sociodemographic factors (shown in blue), i.e.,the prediction effect after adjusting for sociodemographic covariates.

4. Discussion

Characterizing the optimal fMRI measures that capture variance in behavioral differences is a critical step to develop reliable neuroimaging biomarkers for the detection and treatment of brain and behavioral disorders. This study addressed this issue by comparing the behavioral prediction performance of resting-state and task-derived fMRI measures including resting-state FC, task-based FC, task-model-fit FC, task-model-residual FC, and task model parameters. Previous findings have suggested that task fMRI is better than resting-state fMRI at capturing behaviorally relevant FC signals (Rosenberg et al., 2016; Greene et al., 2018; Finn & Bandettini, 2021). We hypothesized that fMRI tasks better reproduce neural processes required to meet the cognitive demands that individuals experience in real life and thus elicit changes in FC patterns that are better associated with individual differences in behavioral phenotypes. We found that, when an fMRI task captured similar cognitive constructs as the behavior of interest, task-model-fit FC and task model parameters were better than rsFC and the task-model-residual FC component at predicting individual differences in that behavior.

4.1 Behavioral differences are better predicted by FC patterns derived from task fMRI than resting-state fMRI.

Consistent with previous findings (Rosenberg et al., 2016; Greene et al., 2018; Finn & Bandettini, 2021), we observed an advantage for the task fMRI paradigms over resting-state fMRI at predicting individual differences in both trait-level behavioral measures, such as the total composite cognition, and state-level behavioral outcomes, such as the SSRT and 2-back accuracy. This finding corroborates the previous result that task manipulation accentuates the functional correlation patterns of the brain that are behaviorally relevant (Cole et al., 2021). This behavioral prediction advantage of task-derived FC measures is also task-specific, such that only fMRI tasks that evoke relevant cognitive demands and content to the behavior of interest confer this advantage (Greene et al., 2018; Finn et al., 2017). In our study, this was demonstrated by the double dissociation of the nBack and the SST task in the prediction of total composite cognition and SSRT. We also found a greater association between 2-Back accuracy and the total composite cognition, which could reflect that children with strong working memory abilities also performed better on language tasks and tasks tapping into fluid intelligence (Rosenberg et al., 2020). A previous study (Marek et al., 2022) has shown that the prediction advantage of fMRI tasks over rest can be explained by the correlation between in-scanner task behaviors (e.g. working memory during the nBack task) and the out-of-scanner behavior of interest (e.g. total composite cognition). Consistent with what was found in Marek et al., we found there was a high correlation between our in-scanner behavior (2-back accuracy) and out-of-scanner behavior (total composite cognition). However, we do not believe this constitutes a confound as it has previously been interpreted; rather, it helps explain why we see some generalizability of in-scanner functional brain measures to out-of-scanner behavioral performance. Among all fMRI modalities examined in this study, in-scanner behaviors of the resting-state fMRI (i.e. lying still and staring at a crosshair) bore minimum resemblance with our behavioral measures of interest, which might explain the moderate association between rsFC and all behavioral outcome variables. While resting-state fMRI has been indispensable for the characterization of large-scale brain networks and provides a convenient paradigm for cross-study data aggregation, task fMRI might be a better vehicle to probe behaviorally relevant FC signals.

To assess the shared and unique information resided in different task-derived FC measures, our analysis focused on comparing the shared and unique behavioral variance explained by the task-model-fit FC and the task-model-residual FC as they are mutually exclusive, subcomponents of the task-state FC. Our analysis showed that the behavioral prediction advantage of task fMRI paradigms is driven by task-model-fit FC, that is, changes in FC patterns in response to cognitive demand, and the task-model-residual FC, FC fluctuations that are not explained by task demands, contributed little unique information at predicting behavioral differences. While task-elicited FC fluctuations are modest compared to the individual-specific functional connectome identified at rest (Laumann et al., 2017; Gratton et al., 2018), these task-induced modulations improve the modeling and detection of behavioral differences because they directly reflect changes in the functional brain patterns when a behavior is being performed.

4.2 Task model parameters are equally, if not more predictive, than the task-model-fit FC, and both measures confer complementary information on behavioral differences.

The task model parameters were equally, if not more predictive, than the task-model-fit FC at predicting individual differences of both behavioral measures. The squared correlation of the SST task model parameters and SSRT was 0.2, which is a significant improvement relative to the SST task-model-fit FC, the best predicting FC measure from the same fMRI task. A similar magnitude of prediction performance was achieved by the nBack task-model-parameters and the

2-back accuracy (squared correlation: 0.167). Despite the excitement of using FC measures to behavioral differences in the literature, our results suggest that fMRI task activations are at least as good, if not better, than FC measures at capturing individual differences in behavior.

We also showed that task model parameters and task-model-fit FC contained shared and unique information for predicting behavioral differences, an observation consistent with previous reports (Larabi et al., 2018; Kowalski et al., 2019). Characterizing the behavioral relevance of both task fMRI measures allowed us to uncover unexpected behavioral association patterns with fMRI tasks. For example, we did not expect to observe an association between the MID task FC and the total composite cognition score given limited theories connecting the two measures. However, we found that the MID task-model-fit FC was equally predictive of total composite cognition score as the nBack task, a working memory task previously associated with cognitive development (Sripada et al., 2020; but also see Kardan et al., 2022). This unexpected finding was supported by studies reporting similar cognitive performance prediction accuracy for FC measures derived from a working memory task and a reward processing task that captures similar cognitive constructs as the MID task, in the Human Connectome Project (HCP) (Greene et al., 2018; Jiang et al., 2020). As both the task model parameters and task-model-fit FC measures can be readily derived from existing task fMRI data, we suggest future studies assess the behavioral relevance of both, as they might yield additive information about the neural correlates of complex behavioral phenotypes.

4.3 Sociodemographic factors treatment is crucial and yields differential implications for behavioral prediction studies of fMRI measures

Importantly, we found that adjusting for sociodemographic covariates, including age, sex at birth, ancestry, ethnicity, income, and education, significantly impacted the behavioral prediction effect of FC measures and task model parameters, and such effects were more prominent for total composite cognition and 2-back accuracy than for the SSRT. This is consistent with previous findings that sociodemographic factors account for substantial individual variability in fMRI phenotypes (Yaple & Yu, 2020; Rakesh, Zalesky, Whittle, 2021) and in measures of cognitive performance (Bradley & Corwyn, 2002; Korous et al., 2020), and that adjusting for sociodemographic factors reduces the effect sizes of rsFC measures on cognitive task performance (Marek et al., 2022).

Controlling for sociodemographic factors can substantially alter estimates of the power of brain phenotypes to predict behavioral differences. An investigator's choice to include these variables as covariates, and which to include, should be guided by the specific prediction goal of the analysis. Because sociodemographic variables are so robustly linked to both neuroimaging and behavioral phenotypes in the ABCD Study, it will probably be necessary to consider the pattern of associations across many models to begin to understand these underlying relationships. Here we have chosen to present both the model with no adjustment and the model with adjustment for all the sociodemographic variables listed above. For our predictions of the total composite cognition score in the general population, the results suggest robust association between this measure and functional brain phenotypes. However, the results with the full model (including covariates) suggest that when only differences among peers of the same age, sex, ancestry, ethnicity, and parental income/education are considered in the model, the associations with functional brain phenotypes are much more modest. This trend was also observed in an earlier study of ABCD participants involving structural brain phenotypes (Palmer et al. 2021). While these discrepancies in the results can sometimes lead to confusion for scientists and other stakeholders, it is important to emphasize that the different models both answer different questions about prediction and raise new questions about the factors that reduce generalizability across groups within the population. To address this uncertainty, it may be helpful for researchers to develop standards for presenting several covariate models in each publication to help readers understand better the context of their estimates of prediction from neuroimaging phenotypes (see Wagenmakers et al., 2022).

4.4 Limitations

We used a correlation-based FC estimation framework to quantify the behavioral relevance of resting-state and task fMRI data. Graph-theory derived network properties of FC measures have also been associated with behavioral outcomes (Liu et al., 2012; Khazaee, Ebrahimzadeh, Babajani-Feremi, 2015; Qian et al., 2018) and might have provided evidence for additional prediction power. The out-of-sample behavioral prediction in this study could be an underestimation of the behavioral relevance of resting-state fMRI and task fMRI data as other network-based fMRI properties might introduce additional behavioral prediction power relative to the correlation-based FC measures. This limitation, however, would not change our conclusions regarding the relative advantage of task-related FC over rsFC for capturing behaviorally relevant differences, as all FC measures were processed with the same censoring and filtering criteria and were applied to the same prediction pipeline. Similarly, our choice of prediction method may also have impacted the reported out-of-sample prediction performance. Other analytical methods, such as machine learning based prediction methods, could potentially yield different estimates of the behavioral prediction performance of FC measures. We also acknowledge that there were differing numbers of frames across modalities. However, we included this as a covariate in our analysis, which would eliminate any linear effects of the number of frames on the prediction performance of each modality. Although our results were similar with both 10-fold and leave-one-site-out cross validation, we acknowledge that cross-validation with an independent study would be a fruitful endeavor, especially as more large-scale population datasets are collected and made available to the scientific community. Finally, other behavioral outcomes could be considered in the future, for instance through extraction of more nuanced measures from the SST beyond reaction times, such as using drift diffusion modeling, as well as modeling meaningful behaviors from the MID task that could be compared between individuals.

5. Conclusion

In summary, by comparing the behavioral prediction performance of FC measures derived from task fMRI to that from rsFC, we provide additional evidence that fMRI tasks that evoke neural processes relevant to the behavioral phenotypes of interest are better predictors of those phenotypes than FC measures from resting-state fMRI. To maximize the ability to detect behaviorally relevant FC patterns of the brain, efforts should be made to select fMRI tasks that recruit similar cognitive processes relevant to the behavioral phenotypes of interest. This work provides further support for the utility of the task activation and FC analysis frameworks for the identification of functionally relevant brain signals. It also highlights the need for consistent reporting of the results of behavioral prediction studies to examine the impact of sociodemographic covariates on the prediction, and to describe more clearly the prediction context to which the models could be expected to generalize, based on these covariates.

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Disclosure of competing interests

Dr. Dale reports that he was a Founder of and holds equity in Cor-Techs Labs, Inc., and serves on its Scientific Advisory Board. He is a member of the Scientific Advisory Board of Human Longevity, Inc. He receives funding through research grants from GE Healthcare to UCSD. The terms of these arrangements have been reviewed by and approved by UCSD in accordance with its conflict-of-interest policies. Dr. Dale also reports that he has memberships with the following research consortia: Alzheimers Disease Genetics Consortium (ADGC); Enhancing NeuroImaging Genetics Through Meta-analysis (ENIGMA); Prostate Cancer

Association Group to Investigate Cancer Associated Alterations in the Genome (PRACTICAL); Psychiatric Genomics Consortium (PGC). All other authors have no conflicts of interest.

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