

## RESEARCH ARTICLE

# Investigating cognitive neuroscience theories of human intelligence: A connectome-based predictive modeling approach

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## Abstract

Central to modern neuroscientific theories of human intelligence is the notion that general intelligence depends on a primary brain region or network, engaging spatially localized (rather than global) neural representations. Recent findings in network neuroscience, however, challenge this assumption, providing evidence that general intelligence may depend on system-wide network mechanisms, suggesting that local representations are necessary but not sufficient to account for the neural architecture of human intelligence. Despite the importance of this key theoretical distinction, prior research has not systematically investigated the role of local versus global neural representations in predicting general intelligence. We conducted a large-scale connectome-based predictive modeling study ( $N = 297$ ), administering resting-state fMRI and a comprehensive cognitive battery to evaluate the efficacy of modern neuroscientific theories of human intelligence, including spatially localized theories (Lateral Prefrontal Cortex Theory, Parieto-Frontal Integration Theory, and Multiple Demand Theory) and recent global accounts (Process Overlap Theory and Network Neuroscience Theory). The results of our study demonstrate that general intelligence can be predicted by local functional connectivity profiles but is most robustly explained by global profiles of whole-brain connectivity. Our findings further suggest that the improved efficacy of global theories is not reducible to a greater strength or number of connections, but instead results from considering both strong and weak connections that provide the basis for intelligence (as predicted by the Network Neuroscience Theory). Our results highlight the importance of considering local neural representations in the context of a global information-processing architecture, suggesting future directions for theory-driven research on system-wide network mechanisms underlying general intelligence.

## KEYWORDS

cognitive neuroscience, connectome, fMRI, individual differences, intelligence, network neuroscience theory

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## 1 | INTRODUCTION

A central and enduring aim of research in the psychological and brain sciences is to elucidate the information-processing architecture of human intelligence (for a review, see Barbey et al., 2021). Does intelligence originate from a specific brain structure (e.g., the lateral prefrontal cortex [PFC]; Duncan et al., 2000), a primary brain network (e.g., the frontoparietal network; Jung & Haier, 2007), or instead reflect system-wide network mechanisms for flexible and efficient information processing (Barbey, 2018)? Accumulating evidence in network neuroscience (Bassett & Sporns, 2017) suggests that spatially localized accounts of human intelligence may miss the forest for the trees, failing to capture the importance of global network topology and dynamics in human cognition (Dubois et al., 2018; Gallos et al., 2012; Shine et al., 2016). Thus, new approaches in network neuroscience propose that intelligence emerges from connectivity across a global information-processing architecture (Barbey, 2018), contrasting with spatially localized theories that account for individual differences in intelligence by appealing to a single brain region (Duncan & Owen, 2000; Duncan et al., 2000), primary brain network (Duncan et al., 2000; Jung & Haier, 2007), or the overlap among specific networks (Kovacs & Conway, 2016). Despite this major source of contention among modern theories, prior research has not systematically investigated the predictions of local versus global theories of intelligence within a comprehensive, connectome-wide association study.

Localist theories posit that intelligence originates from spatially localized neural mechanisms. For example, Lateral PFC Theory (Duncan & Owen, 2000; Duncan et al., 2000) proposes that general intelligence ( $g$ ) primarily depends on functional activity within the PFC, drawing upon a wealth of evidence supporting the role of the dorsolateral PFC in goal-directed behavior (e.g., Barbey et al., 2014). Parieto-Frontal Integration Theory (P-FIT; Jung & Haier, 2007) predicts that intelligence emerges from integrated neural activity within a broader frontoparietal network, with meta-analyses also highlighting the functional involvement of medial PFC regions, occipital lobe, and subcortical structures (Basten et al., 2015). More recently, Multiple Demand (MD) Theory (Camilleri et al., 2018; Duncan, 2010) has proposed that intelligence depends on activity within the MD network, which entails a core set of regions in midcingulate cortex, bilateral anterior insula, inferior frontal gyrus, right middle frontal gyrus, right inferior parietal cortex, and intraparietal sulcus. Finally, Process Overlap Theory (POT; Kovacs & Conway, 2016) predicts that intelligence depends on the functional overlap among multiple brain regions and networks that are selectively engaged on the basis of task demands.

Recent discoveries in network neuroscience motivate a growing headwind for standard localist theories, suggesting that intelligence emerges from global brain network topology (Deco et al., 2015; Sporns et al., 2000b) and dynamics (Cabral et al., 2017; Shine et al., 2016; Sporns et al., 2000a), rather than relying solely on a specific brain region or primary network. Drawing from this literature, the Network Neuroscience Theory (NNT) of Intelligence (Barbey, 2018) proposes that  $g$  reflects individual differences in system-wide network mechanisms for efficient and flexible information processing, and therefore depends on global profiles of functional connectivity.

The community structure of the human brain is also known to rely on weak functional connections that enable an efficient, small-world topology (Bertolero et al., 2018; Gallos et al., 2012) and support brain network flexibility and dynamics. Thus, the NNT predicts that global profiles of weakly connected functional edges will also be important predictors of  $g$  (Dubois et al., 2018; Santarnecchi et al., 2014). The emphasis on whole-brain, multi-network connectivity and the inclusion of weak connections motivates the prediction that intelligence will depend on functional connections that are distributed globally across the entire connectome.

### 1.1 | Aims

The aim of this study is to investigate the information-processing architecture of general intelligence, conducting a systematic evaluation of modern cognitive neuroscience theories that center on the recruitment of local or global brain mechanisms. Of primary interest is whether global profiles of functional connectivity will outperform local connectivity profiles when predicting individual differences in  $g$ . To investigate this hypothesis, this study deployed a predictive modeling framework in resting-state functional connectivity data ( $N = 297$ ) to directly compare the generalizability, reliability, and predictive accuracy of local versus global functional connectivity profiles that have been theorized to underpin intelligence.

We directly compared functional connectivity profiles by investigating their predictive accuracy using a connectome-based predictive modeling (CPM) framework (Finn et al., 2015; Shen et al., 2017), as each theory makes testable predictions about the spatial profile of functional connections underlying intelligence. The use of resting-state functional connectivity in this study is motivated by a wealth of prior evidence suggesting that resting-state data enable the prediction of individual differences in general intelligence and further inform the topology and dynamics of information processing (Bolt et al., 2017; Schultz & Cole, 2016; Thiele et al., 2022, see also Cole et al., 2013). Thus, resting-state connectivity is well-established in this context (Dubois et al., 2018; Feilong et al., 2021; Jiang et al., 2020; Saxe et al., 2018; Xu et al., 2022), and provides a powerful framework for understanding individual differences in high-level cognition (Dubois & Adolphs, 2016).

Localist theories of intelligence derive their predictions primarily from task-based fMRI paradigms, identifying regional correlates of intelligence without addressing broader profiles of network connectivity or dynamic interactions between predicted regions. As localist theories do not make strong claims about network topology or dynamics, an analysis based on functional topology or dynamic connectivity would not provide the desired direct comparison across all theories, motivating our decision to instead use CPM in the present study. Furthermore, CPM is capable of jointly interrogating all functional edges possible under each theory while accounting for Type I errors during feature selection, allowing this approach to make model comparisons that consider all possible theoretical specifications of edges within a functional connectivity profile that may support general intelligence. These attributes allow CPM to directly compare

evidence for the spatial and functional localization of each theory, objectively comparing the accuracy, generalizability, and reliability of predictions in intelligence across all modern theories.

This study investigated three primary hypotheses. First, we hypothesized that localist theories of intelligence would produce accurate and reliable predictions. Second, based on current evidence in the field of network neuroscience and recent predictive modeling studies using functional connectivity (Dubois et al., 2018; Feilong et al., 2021; Jiang et al., 2020), we predicted that global theories would outperform local theories, providing novel evidence that global profiles of functional connectivity produce more accurate and more reliable predictions of general intelligence. Third, we hypothesized that global connectivity patterns would show that weakly connected functional edges important for maintaining network topology (Bertolero et al., 2018; Gallos et al., 2012) are a reliable predictor of general intelligence. We sought to assess these hypotheses by examining prediction models based on each theory with respect to four quantitative metrics: (a) correlation between predicted and observed intelligence scores; (b) permutation test of prediction significance; (c) prediction *F*-statistics; and (d) the difference in prediction's mean absolute error (MAE) and confidence intervals.

## 2 | MATERIALS AND METHODS

### 2.1 | Participants

Data were collected from a sample of healthy young adults in Illinois as part of a larger study investigating the efficacy of multimodal interventions to enhance fluid intelligence (previously described in Daugherty et al., 2020; Zwilling et al., 2019). This study reports preintervention resting-state fMRI data that were acquired prior to the intervention (and therefore not affected by the larger project). All subjects gave written informed consent in accordance with the Declaration of Helsinki. Study inclusion criteria recruited adults (1) aged 18–44 years; (2) fluent in English; (3) possessing at least a high-school diploma; (4) with normal or corrected to normal vision and hearing; (5) free of any psychoactive medication; (6) without history of neurological, psychological, or endocrine disease; (7) without history of concussion for the past 2 years; (8) not having learning disorders; (9) not smoking >10 cigarettes a day; (10) with a body mass index < 35; and (11) with at least one positive response on the revised Physical Activity Readiness Questionnaire (Thomas et al., 1992). All subjects reported in the present analysis were randomly assigned to brain imaging data collection and were right-handed.

### 2.2 | Estimating general intelligence

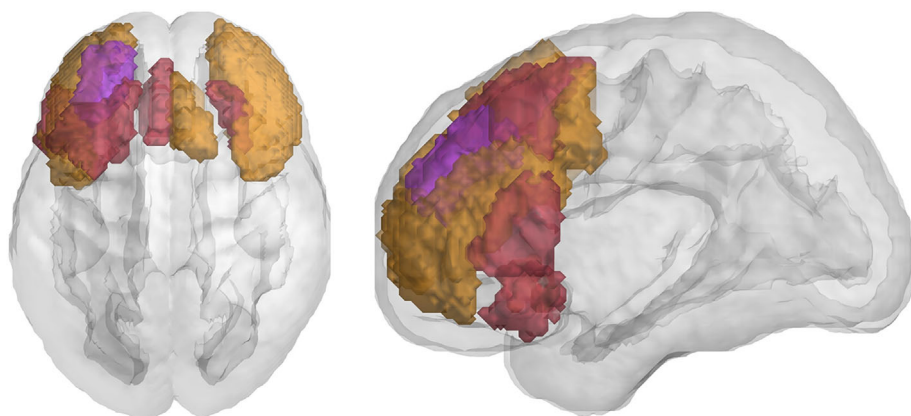
Subjects were administered a comprehensive psychometric battery of fluid and crystallized intelligence tasks, including a figure series completion test of fluid intelligence (Kyllonen et al., 2019), the Law School Admissions Test Logical Reasoning Battery (Mackey et al., 2015),

Shipley-2 Vocabulary (Winfield, 1953), and the Adult Decision-Making Competence battery (Bruine de Bruin et al., 2007, 2020), collectively composing up to 3 hours of psychometric measurement administered over two days. Previous work demonstrates a high degree of overlap and redundancy between the Adult Decision-Making Competence battery and other canonical measures of intelligence (Blacksmith et al., 2019; Bruine de Bruin et al., 2020; Missier et al., 2010; Román et al., 2019), providing further evidence that the battery provides a valid and reliable measure of general intelligence. Descriptive statistics of the psychometric battery have been detailed in prior work (see Román et al., 2019). Here, we employed structural equation modeling (SEM; Muthén, 2002) to identify shared variance across the entire battery and to derive a latent measurement of psychometric *g* (Jensen, 1993) for each subject. Our analysis approach also accounted for the potential sex effects that have been demonstrated in functional connectivity data (Jiang et al., 2020; Satterthwaite et al., 2014; Zhang et al., 2018) by fitting a linear model to *g* scores and controlling for both sex and age and using the residuals as inputs to the neuroimaging analysis.

### 2.3 | Neuroimaging analysis and modeling

We acquired 10-min resting-state echoplanar imaging (EPI) scans using a Siemens Magnetom 3 Tesla Trio scanner with a 32-channel head coil (for a prior example of this sequence, see Talukdar et al., 2018). Structural brain images were acquired as a multiecho T1-weighted magnetization prepared gradient echo (0.9 mm isotropic resolution, TR = 1900 ms, TI = 900 ms, TE = 2.32 ms), with GRAPPA and an acceleration factor of 2 (Auerbach et al., 2013). Resting-state images were acquired using accelerated gradient EPI sequence: TR = 2000 ms, TE = 30 ms, FOV = 240 mm, 90° flip angle, 10 min acquisition, or 300 volumes, 1.9 × 1.9 × 2.0 mm voxel size and 56 slices with 10% slice gap. Participants fixated on a white crosshair presented on a black background for the duration of the scan.

All MRI data processing was performed using containerized processing pipelines for reproducible analysis of neuroimaging data. Preprocessing steps were performed using *fMRIPrep* 20.2.0 (Esteban et al., 2018, 2019) and XCP Engine 1.0 (Ciric et al., 2017; Lydon-Staley et al., 2019). As intelligence has been significantly correlated with head motion (Siegel et al., 2017), we deployed ICA-AROMA denoising (Pruim et al., 2015), a best-performing algorithm for confound regression and robust control of motion artifacts (Parkes et al., 2018). Head motion in the study was generally low, with subjects displaying an absolute head displacement of 0.29 mm per scan on average. Preprocessing entailed: slice timing correction, motion correction, spatial smoothing (3 mm FWHM kernel), nuisance signal regression, temporal bandpass filtering, linear registration of functional images to structural images, and nonlinear registration of structural images to a standard-space MNI152 brain template (2 mm isotropic voxel resolution). Head-motion parameters were accounted for using ICA-AROMA analysis (Pruim et al., 2015). All nuisance variables were modeled via a single GLM (Satterthwaite et al., 2013), to



**FIGURE 1** Functional regions included in the Lateral PFC connectivity map, colored by intrinsic connectivity network. Purple, ventral attention; orange, frontoparietal; red, default mode

remove spurious correlations and noise introduced by head motion as well as variables of no interest such as CSF and white matter signal. In addition to ICA-AROMA components classified as noise, these variables of no interest also included head motion correction parameters, individual volume motion outliers estimated using DVARS (Power et al., 2014) with outliers flagged above 1.5 standardized DVAR or Framewise Displacement exceeding 0.5 mm, and mean white matter and cerebrospinal fluid signals averaged across all voxels identified during image segmentation. The fully preprocessed resting-state BOLD timeseries data were taken as the deconfounded residuals from the final GLM model. The residual image was transformed into normalized MNI152 space and resampled to 4 mm isotropic voxels. To investigate the effect of using multiple imaging atlases on the results, resting-state images were parcellated using both a 200 and 400 ROI network-based atlas of cortical gray matter (Schaefer et al., 2018). Subcortical nuclei were also labeled and extracted based on the Harvard-Oxford subcortical atlas (Makris et al., 1999). Undirected functional connectivity edges reflected full Pearson correlations between pairwise BOLD timeseries and were fisher-transformed for normality prior to the predictive modeling analysis.

To compare the predictions of modern neuroscientific theories of intelligence, we identified and labeled the set of anatomical brain regions specified for each theory, treating all functional edges between these nodes as possible connectivity candidates for feature selection in our predictive model. To provide a more comprehensive test of each theory and to account for possible effects of parcellation resolution on model fidelity, we generated connectivity profiles for each theory at both 200 and 400 ROI levels of resolution (Dadi et al., 2019; Pervaiz et al., 2020). We briefly review the neural mechanisms predicted by each theory below.

## 2.4 | Lateral PFC Theory

Early studies investigating the neurobiology of *g* provided evidence for the importance of the lateral PFC in cognitive control functions for goal-directed behavior (Barbey et al., 2013; Barbey et al., 2014; Duncan & Owen, 2000; Duncan et al., 2000). Using cortical region labels as reported in Schaefer et al. (2018), we constructed a profile of PFC connectivity that included all functional edges within and

between bilateral rostral, caudal, medial, and dorsolateral PFC regions (Figure 1), therefore examining the contributions of PFC connectivity to general intelligence.

## 2.5 | Parieto-Frontal Integration Theory

In addition to emphasizing the importance of the lateral PFC, subsequent research revealed a more broadly distributed network of regions underlying general intelligence. P-FIT proposes that connectivity of a distributed frontoparietal network accounts for intelligence by enabling the integration of knowledge between frontal and parietal areas to support hypothesis generation and problem solving (Jung & Haier, 2007). A meta-analysis of 16 functional and 12 structural studies further identified several correlates of P-FIT connectivity (Basten et al., 2015), providing the basis for the selection of cortical regions included in our predictive model (Figure 2). Regions identified by P-FIT connectivity were further inspected to ensure conformation to existing anatomical maps (Martinez & Colom, 2021).

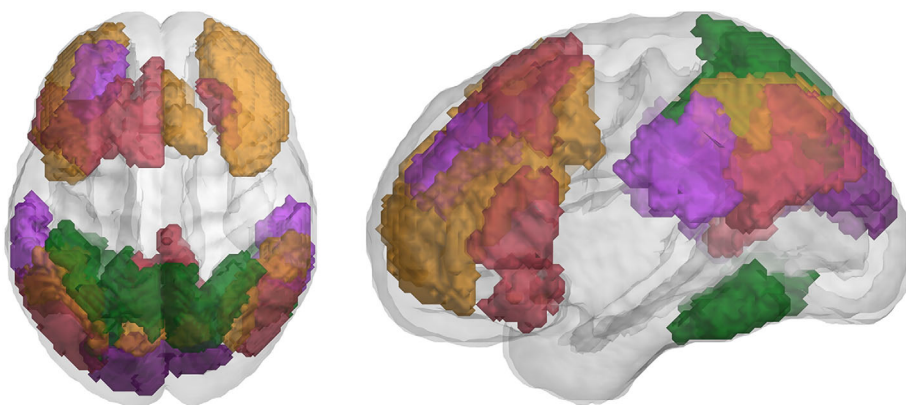
## 2.6 | Multiple Demand Theory

The MD Theory incorporates more recent advances in understanding the network architecture of general intelligence by appealing to an even broader network of frontoparietal and cinguloopercular regions (Camilleri et al., 2018; Duncan, 2010). To generate an anatomical mask of MD regions, we overlaid the Schaefer atlas with a published cortical atlas of the extended MD network (Diachek et al., 2020) generated from experimental data via a watershed method (Fedorenko et al., 2011). This atlas displays robust agreement with existing reports of MD regions (Camilleri et al., 2018; Fedorenko et al., 2013). Here, we include signal from all possible MD functional edges overlapping with MD network regions reported in Diachek et al. (2020; Figure 3).

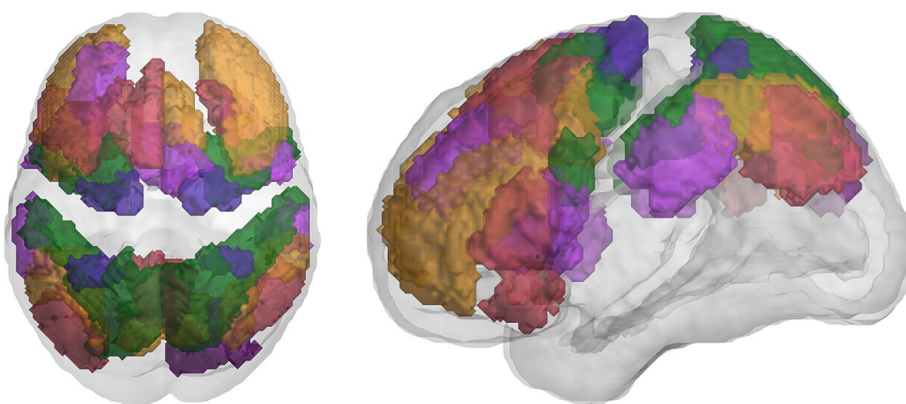
## 2.7 | Process Overlap Theory

POT provides a novel framework centered on the idea that general intelligence reflects the engagement of multiple cognitive processes

**FIGURE 2** Functional regions included in the Parieto-Frontal Integration Theory (P-FIT) connectivity map, colored by intrinsic connectivity network. Green, dorsal attention; purple, ventral attention; orange, frontoparietal; red, default mode



**FIGURE 3** Functional regions included in the Multiple Demand (MD) Theory connectivity map, colored by intrinsic connectivity network. Green, dorsal attention; purple, ventral attention; orange, frontoparietal; red, default mode



represented by the overlap (or shared connections) among brain networks (Kovacs & Conway, 2016). POT builds upon evidence for the central role of frontoparietal network in general and fluid intelligence (Barbey et al., 2014; Jung & Haier, 2007), expanding this account by suggesting that a hierarchy of cognitive abilities is instantiated in an overlapping hierarchy of brain networks (cf. Román et al., 2014). According to Kovacs and Conway (2016), “the positive manifold is caused by the overlap of executive processes that are involved in both working memory and intelligence,” with the neural correlates of those processes “activated in an overlapping fashion that is in agreement with the tenets of [Process Overlap] theory”, such that “the overlap the theory proposes appears to actually take place in the human brain.” We therefore trained CPM models of POT using only right-tailed functional edges, where higher general intelligence is associated with positive functional connectivity (reflecting integration and overlap). As a comparison, we similarly investigated predictions of intelligence generated from a complementary left-tailed feature selection procedure in CPM (that instead identifies the contribution of weak functional connections).

## 2.8 | Network Neuroscience Theory

NNT proposes that  $g$  emerges from individual differences in the network topology and dynamics of the human connectome. The theory emphasizes the importance of global system-wide network

mechanisms in intelligence (Bassett & Bullmore, 2006, 2017). A key respect in which this view differs from POT (and other network sampling approaches) is by emphasizing the constraints that brain network architecture places on flexibly reconfiguring brain networks during goal-directed behavior (e.g., Bolt et al., 2017; Dehaene et al., 1998; Gu et al., 2015; Kitzbichler et al., 2011) and across development (Byrge et al., 2014; Zuo et al., 2017). Rather than depend exclusively on overlapping brain networks (as proposed by POT), NNT posits that weak connections enable flexible information processing (Barbey, 2018) and will therefore also play an important role in predicting general intelligence. Unlike for POT, CPM models of global functional connectivity were trained to include both left- and right-tailed functional edges, where greater intelligence may be associated with significantly higher and/or lower connectivity (as was also the case in our analysis of localist theories of intelligence).

## 2.9 | Predictive modeling

We quantified the relationship between functional connectivity profiles and intelligence using CPM. CPM feature selects brain regions using mass-univariate statistical thresholding with respect to a dependent outcome (i.e., through the use supervised learning methods). This approach maximizes the proportion of true positive connections included after feature selection in the model. The feature-selected functional connections are summarized (added) to create a single

value per subject, allowing CPM to collapse across differences in the cardinality of functional edges and compare theories of intelligence without being confounded by the spatial extent of a connectivity profile. CPM then fits an unregularized linear model between summed connectivity data and the behavioral outcome.

This study deployed CPM due to its ease of use, reliance on interpretable linear relationships, and ability to account for Type I errors made during feature selection. The use of cross-validation in CPM to generate predictions affords a within-sample test of each theory's ability to generalize to external subjects (Finn & Rosenberg, 2021; Gabrieli et al., 2015; Hofman et al., 2021), as does the use of permutation testing and nonparametric bootstrapping. We deployed CPM on each of the predicted local or global functional connectivity profiles to directly compare the reliability, generalizability, and accuracy of their underlying functional connectivity profile for predicting general intelligence.

Predictions of general intelligence are made by applying feature selection to possible functional edges within a given connectivity profile (as Type I errors in feature selection will have a negative impact on cross-validated predictive performance). During feature selection, correlation thresholds of  $p < .01$  and  $p < .05$  were used to select functional edges for inclusion in the training model at both 200 and 400 ROI parcellations, thus accounting for the possible effects of parcellation resolution and feature selection threshold on model fidelity. For each model, we additionally performed permutation testing, randomly shuffling intelligence scores and repeating CPM 1000 times to determine if the observed predictive performance was higher than would be expected by chance from the subset of functional connections included in a connectivity profile. Testing model performance against a null distribution of connectivity values in this way affords an assessment of the reliability of the underlying connectivity profiles, reflecting the extent to which connections within a connectivity profile are reliably modeling sources of individual difference in general intelligence within this sample. We further investigated the performance of each prediction by assessing the fit of a linear model between predicted and ground-truth data, as better-fitting models reflect lower prediction error across the entire sample. Finally, we performed a nonparametric bootstrap of difference in the MAE between the best-performing model overall and other best-performing models within each theory, and computed confidence intervals to determine the extent to which full-sample differences in absolute model performance generalize to subpopulations within the dataset.

To summarize, we examine a comprehensive set of metrics for comparing the predictions made by CPM, including (1) the predictive accuracy of leave-one-out validated CPM models at two feature selection thresholds ( $p < .01$  and  $p < .05$ ) and two parcellation resolutions (200 ROI and 400 ROI); (2) the permutation test significance ( $p_{1000}$ ) that the observed predictive performance is higher than would be expected by chance from the functional edges included in a functional connectivity profile; (3)  $F$ -statistics of a significant model fit between CPM predictions and ground truth intelligence scores as compared against an intercept-only restricted model; and (4) a nonparametric bootstrap of the difference in MAE and confidence interval observed between the best-performing models for each theory.

Predictions made by CPM will be more accurate to the extent that models are trained on a higher proportion of true-positive edges connections (Shen et al., 2017). Naturally, localist theories of intelligence will also consider fewer input features than global theories. To investigate whether differences in model performance reflect differences in the proportion of true-positive connections—not differences in the total number of connections used as input features, we further conducted validation testing that varies the number of features included in the model. We perform (1) a grid search that increases the number of randomly permuted edges included in a connectivity profile, and (2) a grid search that examines predictive performance while decreasing the number of true-positive connections included in a global connectivity profile (by relaxing the  $p$ -value threshold during feature selection). This analysis provides a critical assessment of how prediction accuracy is affected by (1) altering the proportion of true-positive connections (i.e., selecting fewer sensitive edges via lower feature selection thresholds), and (2) altering the absolute number of null input features included in a model.

## 3 | RESULTS

### 3.1 | Psychometric battery

Descriptive statistics and pairwise correlations for the psychometric battery are reported in Table 1 and Table 2, respectively. During SEM modeling, we observed that a single latent factor,  $g$ , demonstrated the highest and most parsimonious model fit for variance in the psychometric battery, accounting for 62% of the variance across the entire cognitive battery, with RMSEA = 0.014 and CFI = 0.995, suggesting excellent fit (Hu & Bentler, 1999). Following prior research and conventions in the field, two Adult Decision-Making Competence battery subtests were excluded from this analysis: (1) Path Independence was not collected in this sample, due to the subtest's low reliability and validity (Bruine de Bruin et al., 2007), and (2) Under/Over Confidence was removed during analysis, due to nonsignificant, negative variance with the general factor (Blacksmith et al., 2019; Brown, 2015). While we explored hierarchical representations of general intelligence within the battery (Haier et al., 2009), including bifactor approaches (Mansolf & Reise, 2016),

**TABLE 1** Descriptive statistics for scales in the psychometric battery.

Battery subtest	$\mu$	$\sigma$	Range
Figure Series Completion	2.02	1.49	[-2.95 to 5.85]
Law School Admission Test	12.6	4.03	[1–25]
Shipley-2 Vocabulary	111	9.30	[73–131]
Applying Decision Rules	0.82	0.16	[0.33–1]
Resistance to Sunk Costs	4.32	0.70	[2–6]
Recognizing Social Norms	0.47	0.21	[-0.41 to 0.88]
Consistency in Risk Perception	0.74	0.11	[0.40–1]
Resistance to Framing	4.18	0.42	[2.5–5]

Note:  $N$ , sample size;  $\mu$ , mean;  $\sigma$ , SD.

**TABLE 2** Pearson correlation matrix for scales in the psychometric battery.

	FS	LSAT	S	DR	SC	RSN	CRP	RF
Figure Series Completion	1.000							
Law School Admission Test	0.337	1.000						
Shipley-2 Vocabulary	0.156	0.486	1.000					
Applying Decision Rules	0.411	0.463	0.355	1.000				
Resistance to Sunk Costs	0.225	0.187	0.028	0.213	1.000			
Recognizing Social Norms	0.137	0.178	0.221	0.203	0.149	1.000		
Consistency in Risk Perception	0.213	0.347	0.223	0.346	0.196	0.176	1.000	
Resistance to Framing	0.232	0.387	0.307	0.293	0.106	0.197	0.293	1.000

Abbreviations: CRP, consistency in risk perception; DR, applying decision rules; FS, figure series completion; LSAT, law school admission test; RF, resistance to framing; RSC, resistance to sunk costs; RSN, recognizing social norms; S, Shipley-2 vocabulary.

**TABLE 3** Model coefficients for factor analysis of *g* in psychometric battery.

Battery subtest	Factor loading with <i>g</i>
Figure Series Completion	0.51
Law School Admission Test	0.73
Shipley-2 Vocabulary	0.55
Applying Decision Rules	0.70
Resistance to Sunk Costs	0.34
Recognizing Social Norms	0.32
Consistency in Risk Perception	0.49
Resistance to Framing	0.43

model fit indices were highest for a single latent factor of *g*. Model coefficients for this factor structure are reproduced in Table 3.

Tables 4 and 5 illustrate the accuracy and reliability of *N*-fold predictions of intelligence generated from cognitive neuroscience theories via CPM using 200 or 400 ROI parcellations, respectively. The observed findings display several convergent patterns. First, most theories generated the best predictions from 200 ROI parcellations feature selected at  $p < .01$ . For the Lateral PFC Theory, this model displayed roughly equivalent accuracy to 400 ROI models. Second, predictive accuracy was roughly equivalent for the three highest-performing 200 ROI models (P-FIT, MD, and NNT), at  $r = .25$ . Third, only the Lateral PFC Theory and NNT displayed significant predictions at both 200 and 400 ROI levels of resolution. Fourth, for the P-FIT, MD, and Process Overlap Theory, only the 200 ROI and  $p < .01$  models produced predictions that significantly outperformed a permutation test baseline. For all other model specifications, these theories produced nonsignificant predictions. Fifth, the prediction performance for POT, where CPM considered only positive, right-tailed relationships between connectivity strength and general intelligence, was notably low compared with the positive- and negative-tailed edges considered by NNT. Finally, NNT produced the most significant prediction of intelligence (400 ROI,  $p_{1000} < .001$ ), and produced significant predictions for three out of four possible model specifications.

Reviewing the significance and confidence intervals of these predictions shows that 8/20 models investigated produce significant

( $p_{1000}$ ) predictions of intelligence, all sharing overlapping confidence intervals. All  $p < .01$  at 200 ROI analyses are significant (and share overlapping confidence intervals), in addition to one Lateral PFC model ( $p < .05$  at 400 ROI) and two Network Neuroscience models ( $p < .05$  at both 200 ROI and 400 ROI).

The significance values ( $p_{1000}$ ) reported in Tables 4 and 5 and discussed in this manuscript are uncorrected, providing a baseline index of how reliably each model is able to leverage individual differences in connectivity profiles to predict general intelligence. Applying a Benjamini-Hochberg FDR correction to control for familywise error rate across models would have declared only  $p_{1000} \leq .01$  prediction models to be statistically significant. Applying a Bonferroni correction across this family of null distributions would have declared only NNT predictions from the 400 ROI and  $p < .05$  model to be statistically significant.

These findings suggest that true-positive functional connections underlying *g* are indeed captured by local connectivity profiles but are observed more reliably (across multiple ROI resolutions and  $p$ -thresholds) using profiles of global connectivity. Among neuroscience theories of intelligence, Lateral PFC and NNT are the only models to make accurate and reliable predictions using parcellations that reflect both a coarse (200 ROI) and more fine-grained (400 ROI) cortical topography, suggesting these theories characterize both local and global profiles of functional connectivity underlying general intelligence (see Barbey, 2018). Comparing predictions from POT and NNT demonstrates that global connectivity profiles including both strong and weak connections produce more accurate and reliable predictions, providing key evidence to support the network neuroscience perspective. Our findings suggest that intelligence depends on local and global integration, and also on weakly connected edges important for maintaining global network topology (Bertolero et al., 2018; Gallos et al., 2012).

### 3.2 | Predictive fit and direct model comparisons

Table 6 displays *F*-statistics for the significance of an unregularized model of full-sample *N*-fold predictions and observed intelligence scores compared against an intercept-only restricted model. In two

Theory	ROI	$r$ ( $p < .01$ )	$r$ ( $p < .05$ )
Lateral Prefrontal Cortex Theory	200	.21* [0.10, 0.32]	-.01 [-0.12, 0.1]
Parieto-Frontal Integration Theory	200	.25* [0.14, 0.35]	.15 [0.04, 0.26]
Multiple Demand Theory	200	.25** [0.14, 0.35]	.12 [0.01, 0.23]
Process Overlap Theory	200	.11* [0.00, 0.22]	-.02 [-0.09, 0.13]
Network Neuroscience Theory	200	.25** [0.14, 0.35]	.16* [0.047, 0.27]

Note: Permutation test significance ( $p_{1000}$ ) marked as \*  $p < .05$ , \*\*  $p < .01$ , and \*\*\*  $p < .001$ . 95% confidence intervals are displayed after each model.

Theory	ROI	$r$ ( $p < .01$ )	$r$ ( $p < .05$ )
Lateral Prefrontal Cortex Theory	400	.22 [0.11, 0.33]	.25** [0.14, 0.36]
Parieto-Frontal Integration Theory	400	.03 [-0.08, 0.14]	.08 [-0.03, 0.19]
Multiple Demand Theory	400	.07 [-0.04, 0.18]	.18 [0.01, 0.23]
Process Overlap Theory	400	-.02 [-0.13, 0.09]	.02 [-0.09, 0.13]
Network Neuroscience Theory	400	.17 [0.06, 0.28]	.22*** [0.11, 0.33]

Note: Permutation test significance ( $p_{1000}$ ) marked as \*  $p < .05$ , \*\*  $p < .01$ , and \*\*\*  $p < .001$ . 95% confidence intervals are displayed after each model.

**TABLE 6**  $F$ -statistic of significant model fit versus an intercept-only restricted model. Best-fitting predictions for each neuroscience theory are highlighted in bold.

Theory	ROI	$F$ ( $p < .01$ )	$F$ ( $p < .05$ )
Lateral Prefrontal Cortex Theory	200	14	0.03
	400	15.9	<b>20.9</b>
Parieto-Frontal Integration Theory	200	<b>19.7</b>	7.5
	400	0.5	1.8
Multiple Demand Theory	200	<b>19.6</b>	4.9
	400	1.5	10.3
Process Overlap Theory	200	<b>4.1</b>	0.3
	400	0.2	0.0
Network Neuroscience Theory	200	<b>20.3</b>	7.9
	400	6.4	14.9

out of four combinations of connectome resolution and CPM threshold (200 ROI at  $p < .01$ , 200 ROI at  $p < .05$ ), we observed that the best-fitting predictions (highest  $F$ -statistic) across all subjects are produced using NNT edges. In the remaining two model combinations, Lateral PFC connectivity showed the best model fit (400 ROI at  $p < .01$ , 400 ROI at  $p < .05$ ). These model-fit statistics demonstrate that global functional connectivity profiles specified by NNT produce the best-fitting estimates of general intelligence at a more coarse-grained level of connectome resolution, while Lateral PFC Theory produces the best-fitting estimates of general intelligence when viewed at a more fine-grained level of connectome resolution.

Table 7 displays the average number of positive and negative edges identified by feature selection in CPM across all folds of leave one out cross-validation. The number of significant edges retained by CPM increases when lowering the  $p$ -threshold or increasing the number of brain regions considered by model. From the perspective of

**TABLE 4** Correlation coefficient between  $N$ -fold predictions and ground truth values of  $g$ , using 200 ROI parcellations with feature selection at  $p < .01$  and  $p < .05$ .

**TABLE 5** Correlation coefficient between  $N$ -fold predictions and ground truth values of  $g$ , using 400 ROI parcellations with feature selection at  $p < .01$  and  $p < .05$ .

parsimony, the Lateral PFC models require drastically fewer edges to reliably predict individual differences in general intelligence, highlighting the importance of these regions. From the perspective of systems neuroscience, Network Neuroscience models demonstrate that a drastically larger number of whole-brain functional edges neglected by localist theories also correlate with intelligence and contain true positive signal, supporting the NNT prediction that individual differences in intelligence emerge from system-wide network topology and dynamics. CPM eliminates the dimensionality of input edges before fitting predictive models, prohibiting a test of model parsimony that considers the true number of edges included in a model.

Table 8 displays bootstrapped confidence intervals around the estimated difference in MAE observed between the significant predictions of each theory when compared to the NNT (at 200 ROI and  $p < .01$ ). Using  $N$ -fold predictions generated in the full sample, we observed the following MAE for the best-performing models of each theory: Lateral PFC = 0.79; P-FIT = 0.77; MD = 0.73; POT = 0.84; NNT = 0.72. Global connectivity profiles specified by the NNT demonstrated the lowest MAE (i.e., the highest predictive performance). To make inferences about the generalizability of observed differences in prediction error between models, differences in prediction MAE were computed across 1000 bootstrap replicates, where bootstrap samples were drawn consistently for every model in each fold to facilitate direct comparison across consistent subpopulations. In all cases, the average bootstrapped difference in MAE is lower for predictions using global connectivity profiles based on the NNT. We observed no cases where 95% confidence intervals crossed the origin, suggesting that the lower MAE of NNT would be observed across almost all samples drawn independently from this population. Overall, these data suggest that the greater absolute prediction performance observed for the NNT model at 200 ROI represents a consistent increase in prediction accuracy over all other neuroscientific theories of intelligence examined.



**TABLE 7** Average number of positive and negative edges surviving feature selection at each ROI resolution and  $p$ -threshold.

Theory	ROI	$p$ -value	Positive edges	Negative edges
Lateral Prefrontal Cortex Theory	200	<.01	2	33
Lateral Prefrontal Cortex Theory	200	<.05	5	94
Lateral Prefrontal Cortex Theory	400	<.01	6	59
Lateral Prefrontal Cortex Theory	400	<.05	29	206
Parieto-Frontal Integration Theory	200	<.01	8	163
Parieto-Frontal Integration Theory	200	<.05	35	620
Parieto-Frontal Integration Theory	200	<.01	17	463
Parieto-Frontal Integration Theory	200	<.05	101	1652
Multiple Demand Theory	200	<.01	14	378
Multiple Demand Theory	200	<.05	45	968
Multiple Demand Theory	400	<.01	29	706
Multiple Demand Theory	400	<.05	175	2060
Process Overlap Theory	200	<.01	85	–
Process Overlap Theory	200	<.05	388	–
Process Overlap Theory	200	<.01	321	–
Process Overlap Theory	200	<.05	1693	–
Network Neuroscience Theory	200	<.01	85	1560
Network Neuroscience Theory	200	<.05	388	5183
Network Neuroscience Theory	200	<.01	321	4861
Network Neuroscience Theory	200	<.05	1693	16,655

**TABLE 8** Bootstrapped prediction accuracy comparisons between 200 ROI models at  $p < .01$  across 1000 draws.

Theory	$\Delta$ MAE vs. Network Neuroscience Theory				
	$\mu$	$\sigma$	CI	Minimum	Maximum
Lateral Prefrontal Cortex Theory	−0.071	0.035	[−0.075, −0.066]	−0.200	0.038
Parieto-Frontal Integration Theory	−0.039	0.031	[−0.043, −0.036]	−0.225	0.038
Multiple Demand Theory	−0.042	0.033	[−0.046, −0.039]	−0.255	0.036
Process Overlap Theory	−0.113	0.048	[−0.119, −0.108]	−0.294	−0.053

Note: The table illustrates average decrease in predictive performance (mean absolute error [MAE]) observed for significant 200 ROI models compared with Network Neuroscience Theory ( $\mu$ , mean;  $\sigma$ , SD; CI, 95% confidence interval). 95% CIs do not cross the origin, suggesting that predictions of Network Neuroscience Theory are reliably higher than other theories across the majority of subpopulations in our sample.

### 3.3 | Subtest score predictions

Table 9 displays predictions of individual subtest scores from 200 ROI models feature selected at ( $p < .01$ ; i.e., for which predictions from all models consistently outperform a null baseline). One prediction from the intelligence literature is that larger, multi-network representations of intelligence will show an increasing relationship with cognitive performance as task complexity increases. Previous work using gray matter volumetrics supports this prediction (Colom et al., 2006). Interestingly, we do not observe this phenomenon. Instead, we found a more evenly distributed relationship between functional connectivity and cognitive ability, such that performance on tasks with both a higher and lower  $g$  loading covaries with the connectome. This implies that the connectome organization and topology are important

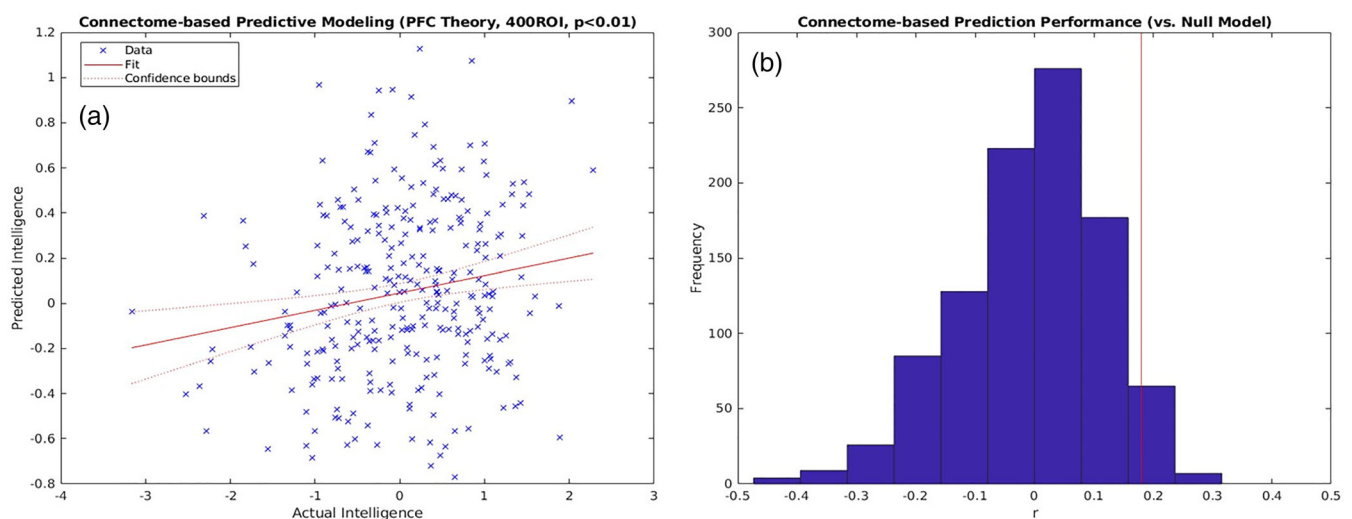
regardless of the specific (i.e., narrow) facets of intelligence being addressed. POT predicts that general intelligence emerges from the spatial overlap between regions that support specific executive functions, motivating the prediction that cognitive processes that are less dependent upon executive function (e.g., Shipley Vocabulary) will demonstrate less spatial overlap and association with intelligence (compared with tasks that are more strongly tied to executive functions, such as Applying Decision Rules and Figure Series Completion). Our results do not provide evidence to support this prediction, suggesting again that intelligence depends both on global and local organization in the functional connectome (consistent with predictions of NNT).

We will now further review the performance of CPM predictions for each theory.

Battery subtest	Loading	PFC	P-FIT	MD	POT	NNT
Law School Admission Test	0.73	-0.13	0.15	0.22	-0.08	0.16
Applying Decision Rules	0.7	0.01	0.08	0.12	-0.05	0.14
Shipley-2 Vocabulary	0.55	0	0.02	0.12	0.05	0.18
Figure Series Completion	0.51	0.04	0.16	0.08	0.02	0.18
Consistency in Risk Perception	0.49	0.02	0.23	0.19	0.09	0.17
Resistance to Framing	0.43	-0.09	0.23	0.17	0.04	0.18
Resistance to Sunk Costs	0.34	0.03	0.21	0.28	0.1	0.27
Recognizing Social Norms	0.32	-0.05	-0.04	-0.25	-0.01	0.04

**TABLE 9** Subtest-level predictions using CPM at 200 ROI and  $p < .01$ . Subtests are ordered according to their loading with the general factor of intelligence observed in our sample.

Abbreviations: CPM, connectome-based predictive modeling; MD, Multiple Demand; NNT, Network Neuroscience Theory; PFC, prefrontal cortex; P-FIT, Parieto-Frontal Integration Theory; POT, Process Overlap Theory.



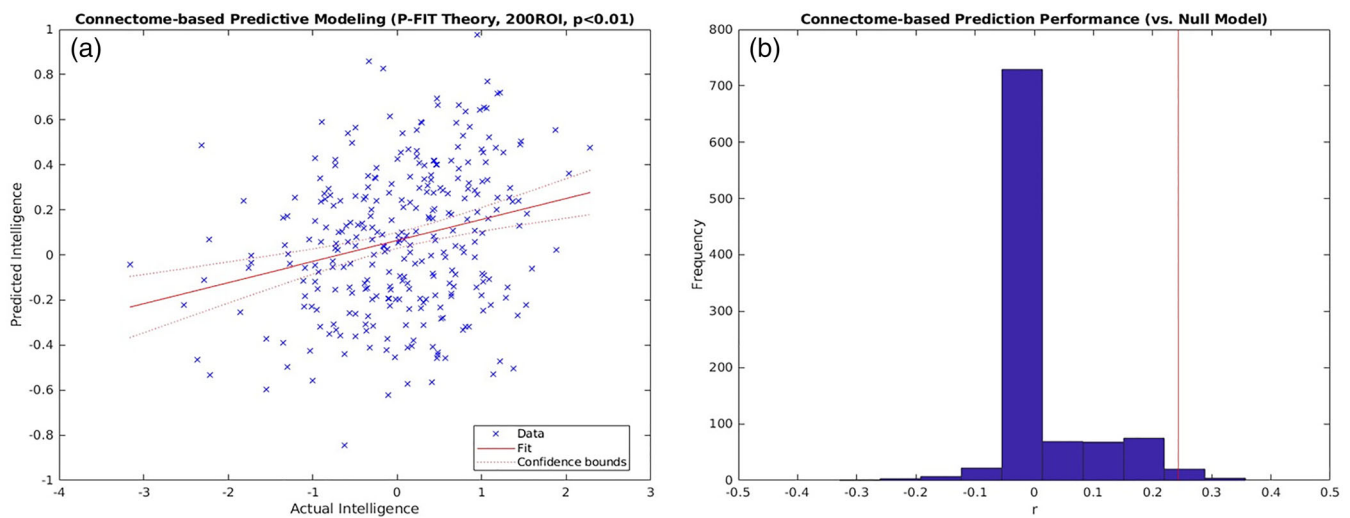
**FIGURE 4**  $N$ -fold cross-validated performance for connectome-based predictive modeling (CPM) predictions of  $g$  using functional edges from Lateral Prefrontal Cortex (PFC) Theory. (a) CPM results predict  $g$  from PFC edges at  $r = .25$  (400 ROI,  $p < .05$ ). (b) Permutation test significance ( $p_{1000} = .008$ ) suggests a significant association between edges used for prediction and psychometric  $g$  at 400 ROI and  $p < .05$ .

### 3.4 | Lateral PFC Theory

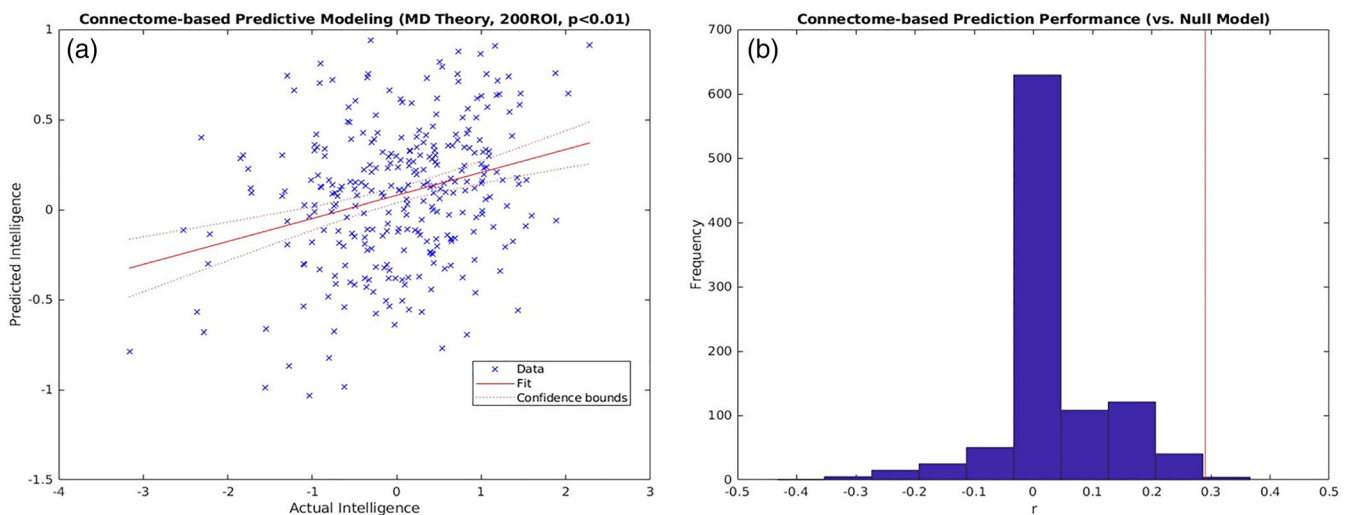
For profiles of lateral PFC connectivity, we observed the most robust predictive performance at a threshold of  $p < .05$  and 400 ROI (Figure 4a). Prediction performance was also significantly more reliable compared with the null distribution for the 200 ROI model feature selected at  $p < .01$ . These findings suggest that more fine-grained representations of functional connectivity (Feilong et al., 2021) may be better suited to capture generalizable signals of intelligence within the lateral PFC, aligning with previous research showing granular functional specialization in the lateral PFC during task-based cognition (Gilbert et al., 2010; Kamigaki, 2019; Yamasaki et al., 2002). Further, the presence of two statistically significant and reliable models suggests that intelligence depends on the organization and connectivity of lateral PFC at multiple levels of resolution, further highlighting the importance of these regions for the prediction of general intelligence.

### 3.5 | Parieto-Frontal Integration Theory (P-FIT)

For connectivity profiles based on P-FIT, we observed the most robust predictive performance at a threshold of  $p < .01$  (Figure 5a). Only a 200 ROI parcellation feature selected at  $p < .01$  produced reliable predictions of  $g$ , suggesting that more coarse-grained representations of functional connectivity may be better suited for predicting general intelligence with respect to P-FIT models. This coarse-grained connectivity profile would be best suited for characterizing network topology that supports more general task-based activation and connectivity, aligning with previous research implicating frontoparietal network activity across a variety of cognitive tasks (Cole et al., 2013, 2014; Vakhtin et al., 2014). Permutation testing suggests that model performance is statistically significant at  $p_{1000} = .02$  for only a 200 ROI model feature selected at  $p < .01$  (Figure 5b).



**FIGURE 5** N-fold cross-validated performance for connectome-based predictive modeling (CPM) predictions of  $g$  using functional edges from frontoparietal cortex. (a) CPM results predict  $g$  from Parieto-Frontal Integration Theory edges at  $r = .25$  (200 ROI,  $p < .01$ ). (b) Permutation test significance ( $p_{1000} = .02$ ) suggests a significant association between edges used for prediction and psychometric  $g$  at 200 ROI and  $p < .01$ .



**FIGURE 6** N-fold cross-validated performance for connectome-based predictive modeling (CPM) predictions of  $g$  using functional edges from the cortical extended Multiple Demand (MD) network. (a) Connectome-based predictive modeling results predict  $g$  from extended MD network at  $r = .18$  (200 ROI,  $p < .01$ ). (b) Permutation test significance ( $p_{1000} = .008$ ) suggests a reliable association between edges used for prediction and psychometric  $g$  at 200 ROI and  $p < .01$ .

### 3.6 | Multiple Demand (MD) Theory

For connectivity profiles based on MD Theory, we observed the most robust predictive performance at a threshold of  $p < .01$ , when CPM was trained with 2926 unique functional edges and 77 vertices from a 200 ROI parcellation (Figure 6a). Permutation testing demonstrates significance at  $p_{1000} = .008$  (Figure 6b), suggesting that the observed predictive performance is less likely to have occurred under the null distribution than was observed for previous models. Using this model specification, prediction accuracy of localist connectivity based on the MD network is equivalent to P-FIT and NNT-based models using the same ROI set and  $p$ -threshold. This model (200 ROI,  $p < .01$ ) is the only model of MD network connectivity

that produces statistically significant predictions, suggesting that only coarse-grained representations of highly significant MD functional edges are able to make generalizable predictions of  $g$  using CPM.

### 3.7 | Process Overlap Theory (POT)

For positive (right-tailed) global connectivity profiles specified by POT (i.e., connections that represent functional overlap), we find evidence that whole-brain functional edges do a relatively poor job at predicting  $g$  compared with other connectivity profiles, with the best-performing model (Figure 7a) generating predictions of  $r = .11$  and

$p_{1000} = .01$  based on 200 vertices and 19,900 unique functional edges (200 ROI,  $p < .01$ ).

Performing a complimentary analysis of weak connections (i.e., left-tailed edges; Figure 7b) revealed that these connections outperform strong connections, generating more accurate predictions at  $r = .15$ . This finding is consistent with emerging evidence in network neuroscience to suggest that brain network flexibility depends on weak connections (Bertolero et al., 2015, 2018; Gallos et al., 2012). Permutation testing for this model specification also demonstrated significance at  $p_{1000} < .01$ , suggesting that both strong and weak edges in global connectivity profiles are sensitive to individual differences in this sample. Consistent with POT, these findings suggest that whole-brain functional edges supporting spatial overlap (i.e., strong connections) are sensitive and generalizable predictors of psychometric  $g$ . However, weak connections that facilitate brain network flexibility are at least if not more predictive of individual differences in  $g$ , implying that functional edges important to maintaining aspects of global network topology are also a reliable neurobiological predictor of intelligence. This overall pattern of findings therefore conflicts with the predictions of POT.

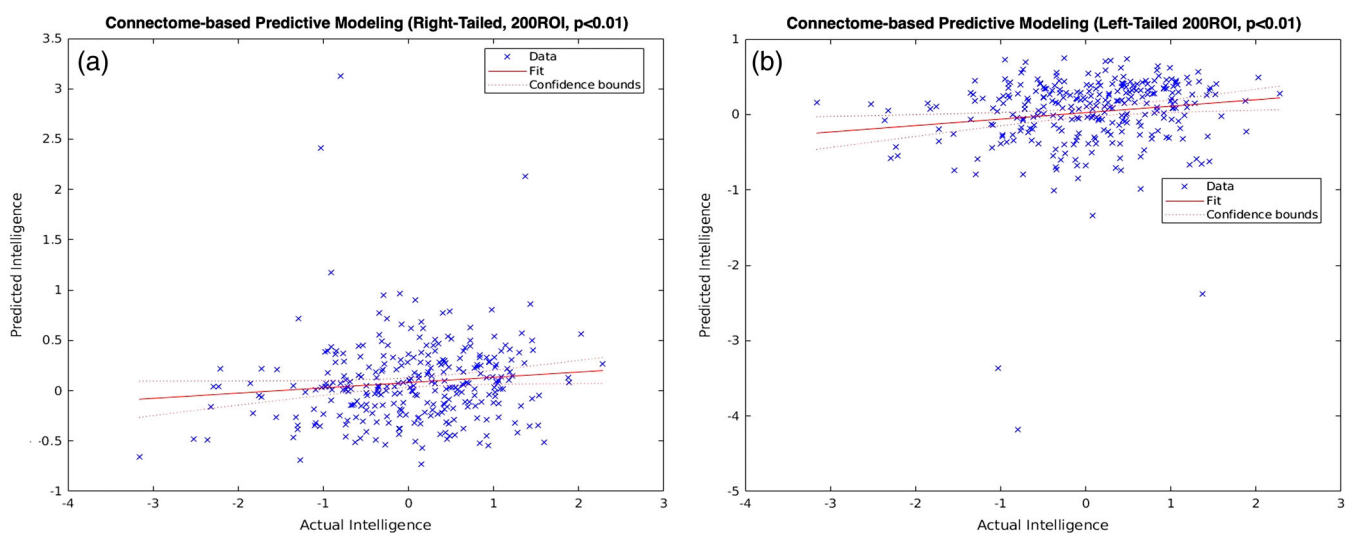
### 3.8 | Network Neuroscience Theory (NNT)

For profiles of global functional connectivity predicted by NNT, we find evidence that jointly modeled left- and right-tailed functional edges produce the most robust predictions of general intelligence, with the best-performing model (Figure 8a) generating predictions of  $r = .25$  based on 200 vertices and 19,900 unique functional edges (200 ROI,  $p < .01$ ). Permutation testing suggests that the model is sensitive to individual differences in intelligence, producing predictions that are significant at  $p_{1000} = .005$  under permutation testing

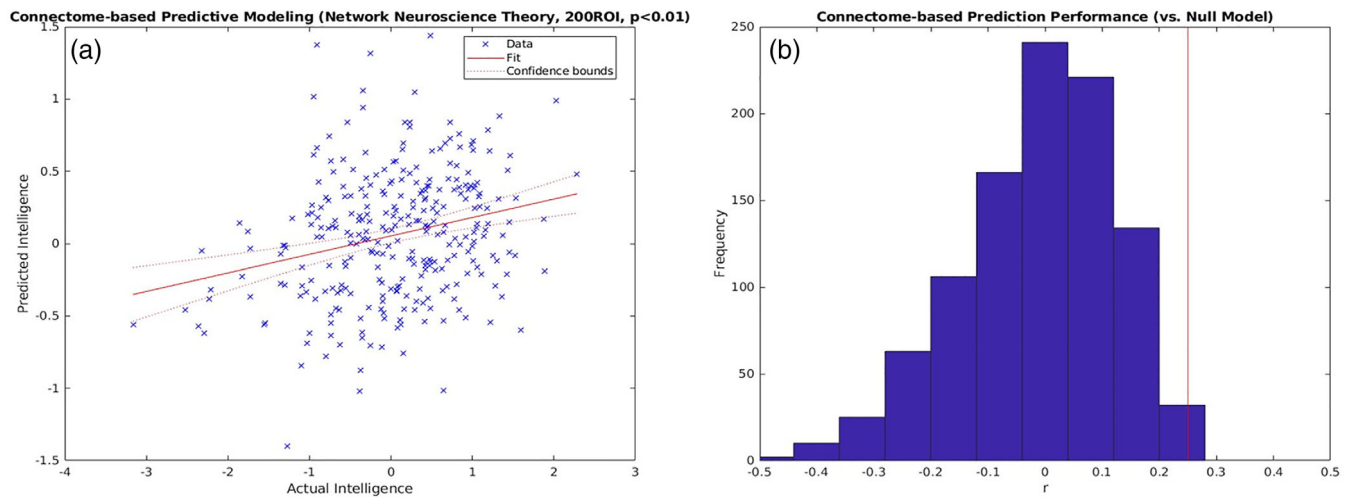
(Figure 8b). Unlike local connectivity profiles, global profiles of whole brain connectivity data produce significant prediction performance for multiple model specifications, with a 400 ROI CPM analysis feature selected at  $p < .05$  generating predictions at  $r = .22$  and  $p_{1000} < .001$ , and a 200 ROI CPM analysis feature selected at  $p < .05$  generating predictions at  $r = .16$  and  $p_{1000} = .026$ . In addition to accounting for a greater proportion of variance compared with previous models and theories, NNT models can also predict intelligence from both more fine-grained and coarse-grained representations of functional connectivity. Thus, NNT demonstrates the best overall performance among the theories we have examined.

### 3.9 | Feature dimensionality and true-positive ratio

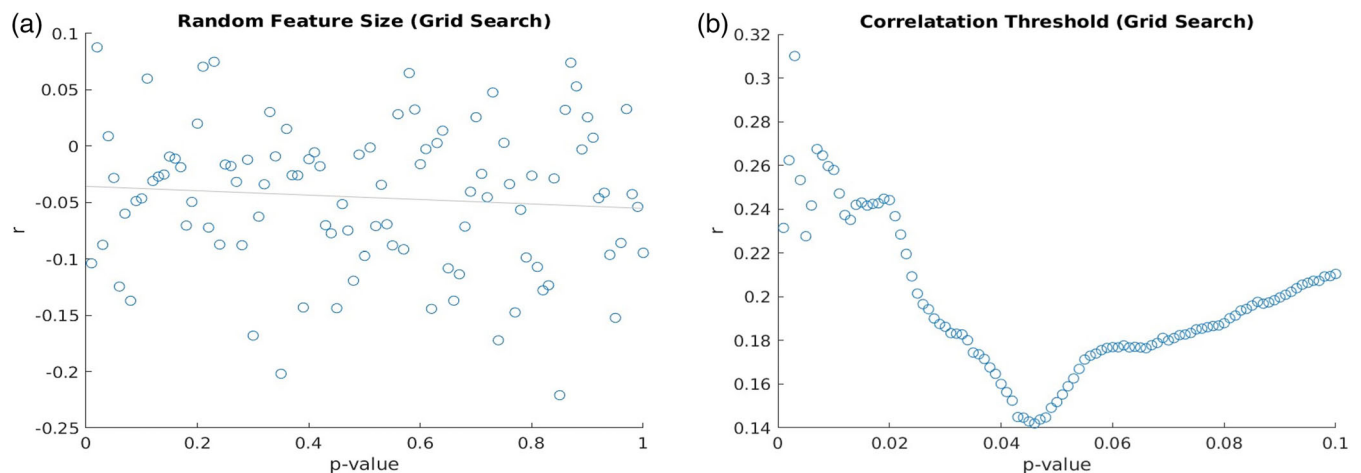
It is important to establish that the observed pattern of findings (greater prediction accuracy and reliability for profiles of global connectivity) is not a result of trivial differences in the input space of functional edges considered during feature selection. To examine this issue, we performed validation testing via a grid search across an increasing proportion of randomly permuted edges in CPM (Figure 9a), demonstrating that arbitrarily increasing the dimensionality of the input feature space by including edges from  $p < .001$  to  $p = 1$  does not generate higher predictive accuracy. Additionally, we tested the effect of varying the ratio of potentially true-positive edges in CPM by performing a grid search over increasingly liberal  $p$ -thresholds from  $p < .001$  to  $p < .1$  using observed global connectivity data at 400 ROI (Figure 9b). We found that including larger numbers of non-random edges (i.e., potentially lowering the ratio of true-positive edges in our predictions) systematically decreased predictive performance, until predictions become nonsignificant ( $p_{1000} > .05$ ) at  $p = .034$  and prediction accuracy began to increase. Taken together,



**FIGURE 7** N-fold cross-validated performance for connectome-based predictive modeling (CPM) predictions of  $g$  using functional edges from the Process Overlap Theory (POT). (a) CPM results predict  $g$  from right-tailed process overlap edges at  $r = .11$  and  $p_{1000} = .01$  (200 ROI,  $p < .01$ ). (b) The comparable connectome-based predictive modeling analysis predicts intelligence from left-tailed (i.e., weak) edges at  $r = .15$  and  $p_{1000} = .01$  (200 ROI,  $p < .01$ ), providing evidence that is inconsistent with the predictions of POT.



**FIGURE 8**  $N$ -fold cross-validated performance for connectome-based predictive modeling (CPM) predictions of  $g$  based on network neuroscience theory (NNT). (a) CPM results predict  $g$  based on NNT at  $r = .25$ . (b) Permutation test significance ( $p_{1000} = .005$ ) suggests a significant association between edges used for prediction and psychometric  $g$  at 200 ROI and  $p < .05$ .



**FIGURE 9** Connectome-based predictive modeling (CPM) validation tests demonstrate that larger feature spaces do not produce a more reliable prediction of  $g$ . (a) Larger input features spaces in  $N$ -fold CPM do not result in more accurate predictions of  $g$ . (b) Relaxing the  $p$ -value threshold to include additional (non-random) significant edges reduces accuracy when predicting  $g$ . Resulting CPM predictions of  $g$  become nonsignificant at  $p = .034$ .

these results suggest that the observed differences in CPM performance between local and global connectivity profiles are not an artifact of differences in input feature size. Instead, this analysis demonstrates that our findings reflect differences in the underlying ratio of true-positive functional edges for predicting  $g$ .

Furthermore, our findings suggest that the comparable prediction accuracy of NNT and localist theories is a more difficult test of NNT, as global whole-brain connectivity necessarily entails all edges contained in localist theories, in addition to many other edges that would need to produce generalizable predictions of intelligence. For example, if true-positive edges existed only within the MD network, and error across the remaining connections was normally distributed, we would expect a greater proportion of false-positives from global edges and would expect lower prediction accuracy from global

connectivity profiles during  $N$ -fold validation (which we do not observe). Thus, our findings suggest that the improved performance of NNT does not result from trivial differences in the input space of functional edges, illustrating how the performance of the NNT reflects a comprehensive examination of all connections and therefore may present a more difficult test than the theories to which it is compared.

## 4 | DISCUSSION

Emerging evidence in network neuroscience suggests that localist theories of general intelligence may in fact be incomplete without also addressing the contribution of system-wide brain network topology

and dynamics. To investigate this hypothesis, we deployed a CPM framework to directly compare evidence for localized and global connectivity profiles predicted to underlie general intelligence by current cognitive neuroscience theories. We compared predictions of each theory based on four quantitative metrics: prediction correlation, permutation test significance, *F*-statistics, and difference in MAE. We found that global connectivity profiles specified by NNT (1) produced predictions that largely meet or exceed the accuracy of predictions derived from localist theories, and (2) exceeded the reliability of predictions derived from localist connectivity profiles. Comparing (3) *F*-statistics and (4) bootstrapped MAE also supported the reliability and generalizability of global connectivity profiles for predicting intelligence above those derived from localist connectivity profiles. These findings provide a strong empirical case to suggest that global profiles of functional connectivity produce robust and generalizable estimates of general intelligence, outperforming predictions made by localist neuroscience theories of intelligence in many contexts.

Consistent with existing neuroscience data, localist theories of intelligence do produce reliable predictions of *g*. However, these standard localist theories display lower predictive performance, lower model fit, lower statistical significance, and individually do so for fewer of the model specifications we examined—suggesting that localist theories may fail to fully capture underlying sources of variance in the functional connectome important to individual differences in general intelligence.

#### 4.1 | Local connectivity profiles predict general intelligence

We observed that both localized lateral PFC and frontoparietal network edges produce reliable predictions of *g* during N-fold validation, consistent with the wealth of evidence for the importance of the PFC in general intelligence (Barbey et al., 2012, 2013; 2014; Braun et al., 2015; Cole et al., 2012; Daugherty et al., 2020; Duncan & Owen, 2000; Duncan et al., 2000; Gilbert et al., 2010; Jung & Haier, 2007; Kamigaki, 2019; Vakhtin et al., 2014; Yamasaki et al., 2002). By a small margin, we observed the highest localist theory prediction accuracy and reliability from connectivity profiles specified by the MD Theory (Diachek et al., 2020; Duncan, 2010). While many frontoparietal network connections are also entailed by MD system, MD additionally includes vertices implicated in attentional networks (Mineroff et al., 2018) and the cingulo-opercular system (Camilleri et al., 2018). The higher predictive performance of the MD network compared with other localist network accounts may therefore reflect the inclusion of both the frontoparietal network and the cingulo-opercular network, which are together known to support key facets of cognitive control (Crittenden et al., 2016). Lateral PFC connectivity produced arguably the best predictions of localist theories, in that multiple model specifications (in terms of both ROIs and feature selection significance) produced significant high predictions of intelligence (notably, while requiring only a small number of functional edges).

#### 4.2 | Global connectivity profiles predict general intelligence

We observed that globally distributed functional connectivity profiles predicted by POT (Kovacs & Conway, 2016) produced the lowest observed predictive performance for three out of four model specifications, critically including predictions generated by the 200 ROI at  $p < .01$  model. As the edges predicted by POT are positive in nature (i.e., representing spatial overlap), this connectivity profile entails the omission of weakly connected edges also important for network architecture and topology (Bertolero et al., 2018; Gallos et al., 2012). Separately examining left-tailed edges demonstrated that functional connections supporting overlap are in fact the least important globally for predicting *g*, contradicting the predictions of POT. Our results instead indicate that the inclusion of weak functional connections enables more accurate predictions of *g*, supporting the role of network flexibility in general intelligence (Bassett & Bullmore, 2017; Bertolero et al., 2015, 2018; Gallos et al., 2012; Hilger et al., 2017; Langer et al., 2012). Indeed, weak edges appear to play a critical role in modifying network topology to support general intelligence and system-wide flexibility of information processing (e.g., see Gu et al., 2015; Santarnecchi et al., 2014), as predicted by NNT.

Small world networks enable the optimal balance of local and global efficiency (Gallos et al., 2012; Watts & Strogatz, 1998), resulting in a hierarchically organized modular network architecture (Barbey et al., 2015; Meunier et al., 2010) that supports both efficient integration (Achard & Bullmore, 2007; Avena-Koenigsberger et al., 2019; Khambhati et al., 2018) and specialization of cognitive abilities (Spearman, 1904, 1927; van den Heuvel et al., 2009). According to NNT, the resulting topological balance of segregation and integration (Cohen & D'Esposito, 2016; van Vreeswijk & Sompolinsky, 1996; Wang et al., 2021), and the critical dynamics that accompany balanced states (Beggs, 2008; Fekete et al., 2021; Vázquez-Rodríguez et al., 2017), facilitate brain network dynamics that give rise to both efficient and specialized information processing (Bassett et al., 2011; Braun et al., 2015; Finc et al., 2020; Shine et al., 2016).

Consistent with NNT, our findings suggest that network properties supporting intelligence are not isolated within specific brain regions or networks identified by localist theories of intelligence. Instead, we observed that global profiles of functional connectivity are the most robust predictors of general intelligence, providing evidence that both strongly connected functional edges supporting integration and weakly-connected functional edges supporting segregation play an important role.

For each cognitive neuroscience theory of intelligence, we observed differences in prediction performance across feature selection thresholds and parcellation resolutions, suggesting that properties of network organization associated with individual differences in intelligence may operate at multiple levels of resolution (see Khambhati et al., 2018), depending on the neural system being investigated. We observed that the most accurate predictions for most models were derived from 200 ROI connectivity profiles feature selected at  $p < .01$ . This level of resolution may be well-suited to identify more

generalizable properties of network organization and topology, reflecting large-scale brain network connectivity patterns that are present generally across many subjects. Models trained on global connectivity profiles also displayed accurate and reliable predictions for other model specifications, suggesting that global connectivity can identify individual differences at multiple levels of resolution and across a greater range of true-positive rates. We observed that a more fine-grained 400 ROI representation of whole-brain functional connectivity produced the most statistically significant prediction of  $g$ , emphasizing the importance of granular profiles of functional connectivity. We also observed that generalizable predictions of  $g$  can be made using global functional edges at multiple feature selection thresholds.

### 4.3 | Integrating local and global representations

Our findings provide evidence for the importance of both localized lateral PFC connectivity and global functional brain network connectivity. CPM models based on the Lateral PFC Theory and NNT produce the only predictions that are significant at multiple levels of connectome resolution. The Lateral PFC models require very few functional edges to produce accurate predictions of intelligence, highlighting the central role of these regions and functional connections in general intelligence. In contrast, NNT Models identify a substantially larger set of significant edges, providing evidence that regions important for intelligence are also distributed across the entire connectome. Differences between the number of significant localist and global edges are too large to result from only edges incident with nodes specified by localist connectivity masks (Zalesky et al., 2012), pointing to the globally distributed nature of regions associated with intelligence. Notably, subtest-level predictions using lateral PFC edges greatly underperform localist network and global connectivity profiles, providing evidence that lateral PFC regions may not explain individual differences in specific facets of general intelligence.

The domain-general role of lateral PFC in intelligence resonates with prior research on prefrontal contributions to high-level cognition. Previous research indicates that the PFC embodies a hierarchy of functional connectivity gradients—moving from rostral to caudal regions—to facilitate goal-directed behavior (Badre & D'Esposito, 2009; Badre & Nee, 2018; Koechlin et al., 2003). Our findings further illustrate the importance of examining global brain network connectivity and align with recent proposals that elucidate how complex, goal-directed behavior is constructed from the interaction(s) among multiple brain networks (e.g., organized in a nested hierarchy from local to global representations; Barbey, 2018; Colom et al., 2006; Kievit et al., 2016; Protzko & Colom, 2021; Román et al., 2014; Soreq et al., 2021). Our results contribute to this emergent view by highlighting the critical importance of individual differences in globally distributed weak functional edges as predicted by NNT.

### 4.4 | Limitations

While these findings suggest that global profiles of functional connectivity best predict individual differences in  $g$ , several limitations and

challenges remain. First, while CPM has been extensively used and validated in many neuroscience contexts, it is by no means the only approach for predictive modeling (e.g., Dubois et al., 2018; Feilong et al., 2021), nor would we expect it to robustly discover and predict all forms of possible statistical relationships (e.g., it would not account for nonlinear relationships). Second, resting-state fMRI data are not the only imaging modality that could be used in such an analysis, for example here, we neglect structural network topology and task-based functional dynamics. Third, while the region and network definitions provided by Schaefer et al. (2018) are widely used, other schemes for network parcellation exist (e.g., Kozák et al., 2017; Uddin et al., 2019), permitting alternative levels of resolution when parcellating the functional connectome and allowing slightly different sets of regions and edges to be considered. Fourth, there is necessarily an imperfect fit between Schaefer et al. (2018) cortical parcellations and the ground truth clusters observed in task-based and activation-based studies of localist network connectivity, inducing small amounts of measurement error when calculating regional overlap. Fifth, due to feature-selection without control for Type II error, CPM may be prone to overfitting (O'Connor et al., 2021), motivating the replication of these results in additional datasets.

Our results suggest that localist profiles of functional connectivity may fail to fully capture important aspects of global network architecture and topology that predict individual differences in intelligence. This study focused on measures of resting-state functional connectivity given their established role in shaping brain network dynamics and accounting for individual differences in cognitive ability (Bolt et al., 2017; Dehaene et al., 1998; Kitzbichler et al., 2011; Schultz & Cole, 2016; Thiele et al., 2022). However, our study did not permit a direct examination of brain network dynamics, which remains an important area for future investigation.

## 5 | CONCLUSIONS

Emerging research in network neuroscience suggests that the standard appeal to spatially localized regions or networks in accounting for human intelligence may be incomplete, providing evidence that intelligence may instead reflect global, system-wide network mechanisms. In this article, we deployed CPM to predict individual differences in intelligence based on local and global profiles of functional connectivity. Using a large sample of resting-state imaging data ( $N = 297$ ) and a diverse battery of well-validated intelligence tasks, we demonstrate that while general intelligence can be predicted from spatially localized patterns of functional connectivity, intelligence is best modeled and most accurately and reliably predicted based on global profiles of whole-brain functional connectivity, as predicted by the NNT. Our results suggest that there is an important need for future neuroscientific theories of intelligence to reconcile neuroanatomically localized regions and networks with global topological properties and dynamics of network organization across the human connectome. These findings highlight the importance of global profiles of functional connectivity for producing reliable and generalizable predictions of  $g$  from resting-state fMRI data, furthering our

understanding of the neurobiological substrates that give rise to intelligence, and emphasizing the importance of considering localized neural representations in the context of a large-scale, global information-processing architecture.

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## DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available from the corresponding author upon reasonable request.

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