Received: 4 December 2020 | Revised: 3 March 2021 | Accepted: 10 March 2021

DOI: 10.1002/hbm.25420

RESEARCH ARTICLE

WILEY

Distinct functional and structural connections predict crystallised and fluid cognition in healthy adults

Elvisha Dhamala[1,2] | Keith W. Jamison[1] | Abhishek Jaywant[3,4,5] | Sarah Dennis[6] | Amy Kuceyeski[1,2]

[1]Department of Radiology, Weill Cornell Medicine, New York, New York

[2]Brain and Mind Research Institute, Weill Cornell Medicine, New York, New York

[3]Department of Psychiatry, Weill Cornell Medicine, New York, New York

[4]Department of Rehabilitation Medicine, Weill Cornell Medicine, New York, New York

[5]NewYork-Presbyterian Hospital/Weill Cornell Medical Center, New York, New York

[6]Sarah Lawrence College, Bronxville, New York

Correspondence
Elvisha Dhamala and Amy Kuceyeski, Department of Radiology, Weill Cornell Medicine, New York, NY 10065.
Email: elvisha@gmail.com (E. D.) and amk2012@med.cornell.edu (A. K.)

Present address
Sarah Dennis, Department of Mathematics, Brandeis University, Waltham, Massachusetts,

Funding information
National Institutes of Health, Grant/Award Numbers: R01NS102646-01A1, R21NS104634-01; National Center of Medical Rehabilitation Research/ Eunice Kennedy Shriver National Institute of Child Health and Human Development, Grant/Award Number: 1K12-HD093427-04

Abstract

White matter pathways between neurons facilitate neuronal coactivation patterns in the brain. Insight into how these structural and functional connections underlie complex cognitive functions provides an important foundation with which to delineate disease-related changes in cognitive functioning. Here, we integrate neuroimaging, connectomics, and machine learning approaches to explore how functional and structural brain connectivity relate to cognition. Specifically, we evaluate the extent to which functional and structural connectivity predict individual crystallised and fluid cognitive abilities in 415 unrelated healthy young adults (202 females) from the Human Connectome Project. We report three main findings. First, we demonstrate functional connectivity is more predictive of cognitive scores than structural connectivity, and, furthermore, integrating the two modalities does not increase explained variance. Second, we show the quality of cognitive prediction from connectome measures is influenced by the choice of grey matter parcellation, and, possibly, how that parcellation is derived. Third, we find that distinct functional and structural connections predict crystallised and fluid abilities. Taken together, our results suggest that functional and structural connectivity have unique relationships with crystallised and fluid cognition and, furthermore, studying both modalities provides a more comprehensive insight into the neural correlates of cognition.

KEYWORDS
cognition, connectomics, functional connectivity, machine learning, neuroimaging, prediction, structural connectivity

1 | INTRODUCTION

Tens of billions of neurons interconnect in the human brain. Direct and indirect structural white matter connections between these neurons facilitate the flow of functional activation between distinct brain regions. Together, these functional and structural connections give rise to human behaviour and cognition. Insight into multimodal neural correlates of cognitive abilities in the healthy brain provides an important foundation with which to delineate the mechanisms underlying age-, injury-, and disease-related changes in cognitive functioning. Furthermore, a thorough understanding of specific functional and structural connections that are associated with cognition can guide the investigation of causality, can inform interventions to maintain and optimise cognitive health for specific cognitive abilities at distinct stages of the ageing/injury process, and can guide the development of targeted neuromodulatory treatments for cognitive dysfunction.

Functional connectivity (FC) represents temporal dependency patterns between regional blood-oxygenation-level dependent signals as measured via functional magnetic resonance imaging (fMRI), and structural connectivity (SC) represents the integrity of inter-regional white matter pathways estimated from diffusion MRI (dMRI). FC and SC have individually been linked to cognitive functioning and used to predict cognitive measures in healthy individuals (Bassett et al., 2011; He et al., 2020; Kelly, Uddin, Biswal, Castellanos, & Milham, 2008; Klein et al., 2016; Kong et al., 2018; Li et al., 2019; Liégeois et al., 2019; Matejko, Price, Mazzocco, & Ansari, 2013; Menon & Uddin, 2010; Moeller, Willmes, & Klein, 2015; Pamplona, Santos Neto, Rosset, Rogers, & Salmon, 2015; Seeley et al., 2007; M. Song et al., 2009; M. Song et al., 2008; Uddin, Supekar, Ryali, & Menon, 2011; Willmes, Moeller, & Klein, 2014; Zimmermann, Griffiths, & McIntosh, 2018). Although neural function and structure are inexorably linked, most studies analyse their contribution to behaviour independently.

Most studies to date have focused on using resting-state FC to study relationships between connectivity and cognition. FC is associated with performance variability in executive control (Seeley et al., 2007) and intellectual functioning (van den Heuvel, Stam, Kahn, & Hulshoff Pol, 2009), and can successfully predict a range of cognitive measures: Kong et al. (2018) used spatial topography of cortical functional networks to predict behaviour; Li et al. (2019) found global signal regressed resting-state FC improves behavioural prediction; and He et al. (2020) showed that machine learning and deep learning methods are equally effective in predicting behavioural, cognitive, and demographic measures from resting-state FC.

While less studied, the mapping between SC and cognition has also been examined. Morphometric similarity networks capturing neuroanatomical properties from structural and diffusion images (e.g., fractional anisotropy, grey matter volume, surface area, cortical thickness, intrinsic curvature, and folding index) can explain up to 40% of the variability in general intellectual function using a partial least squares approach (Seidlitz et al., 2018), and SC is associated with cognitive abilities (Zimmermann et al., 2018).

In the most similar study to date, Zimmermann et al. (2018) investigated connectome-cognition relationships in 609 genetically unrelated subjects from the Human Connectome Project (van Essen et al., 2013). They generated three main components from 11 cognitive measures, including working memory, cognitive flexibility, processing speed, fluid intelligence, episodic memory, and attention/inhibitory control, and used partial least squares analyses to identify four latent variables that describe the connectome-cognition relationships: two captured FC-cognition associations and two captured SC-cognition associations. They found FC and SC uniquely map onto cognitive functions: a large set of corticocortical and corticosubcortical functional connections, and a limited set of short-range structural connections distinctively map onto cognitive function. While this study addressed the relationship between both connectivity modalities and cognition, it did not compare whether one modality explained more variance than the other or integrate the two modalities into a single predictive model.

To this end, Amico and Goñi (2018) combined FC and SC into a single "hybrid" connectome that allowed extraction of patterns from both task-based and task-free fMRI data. They showed this "hybrid" connectome's fingerprint captures individual differences, that is, they were individually identifiable; however, its relationship with cognitive function has not yet been explored. Here, we sought to determine if FC, SC, or integration of the two (Amico & Goñi, 2018) into hybrid connectivity (HC) best predicts cognition in order to compare connectome-cognition mapping across modalities. Given that functional and structural connections, and the relationship between them, can be altered by ageing, injury, and illness (Jaywant, DelPonte, Kanellopoulos, O'Dell, & Gunning, 2020; Pievani, Filippini, van den Heuvel, Cappa, & Frisoni, 2014; Ramanoël et al., 2019; J. Song et al., 2014), insight into the shared and distinct functional and structural connections that underlie individual differences in cognitive abilities, and the strength of those relationships, will advance our understanding of the baseline neuroanatomical and neurophysiological bases of cognition. Quantifying the importance of distinct functional and structural connections as they relate to cognition can pave the way for the development of personalised tools to predict changes in cognitive abilities as a result of age-, injury-, or illness- related connectomic alterations along with targeted and efficacious interventions to optimise healthy cognitive function and to prevent or minimise cognitive dysfunction.

Here, we study the extent to which FC, SC, and HC can predict individual crystallised and fluid cognitive abilities in 415 healthy young adults from the Human Connectome Project (van Essen et al., 2013) dataset. First, we evaluate whether FC or SC can better predict individual cognitive abilities, and whether integrating connectivity modalities can improve predictions. Second, we quantify the unique functional and structural connections that predict crystallised and fluid abilities.

2 | METHODS

Our experimental workflow is shown in Figure 1 (van Essen et al., 2013). Codes used to generate the results presented here are available on GitHub (https://github.com/elvisha/CognitivePredictions).

2.1 | Dataset

We used publicly available high resolution, preprocessed MRI data from the Human Connectome Project – Young Adult S1200 (van Essen et al., 2013) in this study. HCP MRI data were acquired on a Siemens Skyra 3 T scanner at Washington University in St. Louis. HCP scanning included T1-weighted and T2-weighted anatomical images (0.7 mm isotropic), functional MRI (2.0 mm isotropic, TR/TE = 720/33.1 ms, 8x multiband acceleration), and diffusion MRI (1.25 mm isotropic, TR/TE = 5520/89.5 ms, 3x multiband acceleration, b = 1,000; 2,000; 3,000 with 90 directions/shell).

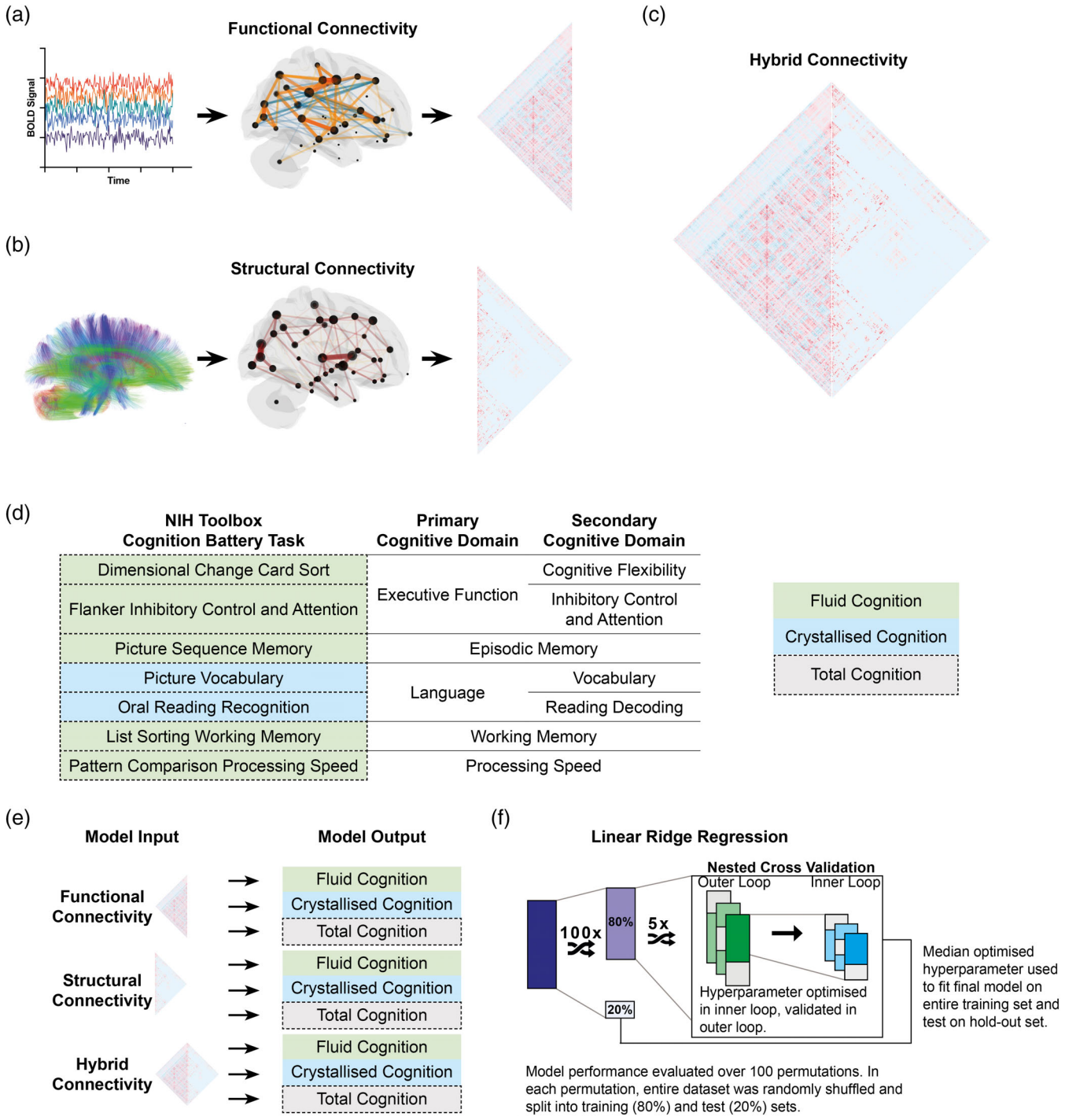

FIGURE 1 Experimental workflow. First, we generated functional, structural, and hybrid connectivity (a–c). We derived functional connectivity using Pearson correlation of regional global signal regressed blood-oxygen-level-dependent (BOLD) functional magnetic resonance imaging (MRI) time series (a) and Fisher's z-transformed the upper triangular part of the matrix. We derived structural connectivity using probabilistic tractography from diffusion weighted MRI (b). We concatenated the upper triangular functional and lower triangular structural connectivity to generate hybrid connectivity (c). Second, we compiled cognitive scores for all subjects (d). The National Institutes of Health (NIH) Toolbox Cognition Battery assesses five cognitive domains using seven tests. The crystallised cognition composite (blue) reflects language (vocabulary, reading decoding). The fluid cognition composite (green) reflects executive function (cognitive flexibility, inhibitory control, and attention), episodic memory, working memory, and processing speed. The total cognition composite (dotted) combines the crystallised and fluid composite scores. Third, we predicted each cognitive score from each of the connectivity matrices (e) using linear ridge regression (f). We randomly shuffled and split the data into train (80%) and test (20%) subsets. For each training subset, we performed five shuffled iterations of nested cross validation with threefold inner and outer loops. The model hyperparameter was optimised in the inner loop and validated in the outer loop. The median optimised hyperparameter from five iterations of nested cross validation was used to train the final model on the entire training set and evaluated on the test hold-out set. This was repeated for 100 unique train/test splits

Functional and diffusion MRI were collected with both left–right and right–left phase encoding. We examined resting-state functional MRI (rfMRI) time series and dMRI from 415 unrelated healthy adults (213 males; ages 22–37). The subset of the HCP dataset used in this analysis were those subjects that had four complete rfMRI runs, a dMRI scan, and crystallised and fluid cognitive scores.

2.2 | Parcellation

We performed all analyses using two separate parcellations. We parcellated the brain using (a) an 86 region atlas derived from FreeSurfer (FS 86), and (b) an in-house 439 region atlas (CoCo 439). FC and SC were extracted using both of these atlases to allow comparisons.

2.2.1 | *FS 86*

As part of the HCP preprocessing workflow (M. F. Glasser et al., 2013), FreeSurfer's recon-all pipeline (Dale, Fischl, & Sereno, 1999; Fischl et al., 2002; Fischl et al., 2008; Fischl, Liu, & Dale, 2001; Fischl, Sereno, & Dale, 1999; Fischl, Sereno, Tootell, & Dale, 1999; Segonne, Grimson, & Fischl, 2005) was optimised for the high-resolution HCP anatomical data. The 68 region Desikan-Killiany gyral atlas (aparc.annot, 34 cortical regions per hemisphere) was combined with the 16 bilateral subcortical structures (aseg.mgz, excluding brainstem) and 2 cerebellar structures to produce an 86 region whole brain anatomically defined parcellation for each subject (Desikan et al., 2006; Fischl et al., 2002).

2.2.2 | *CoCo 439*

This parcellation was developed in-house by combining parts of several atlases. The parcellation includes 358 (of 360) functionally derived cortical regions from HCP multimodal parcellation (Glasser et al., 2016) (two regions were excluded as they were identified as parts of the hippocampus and included in separate subcortical ROIs); 12 anatomically defined subcortical regions derived from FreeSurfer's aseg.mgz, adjusted by FSL's FIRST tool (Patenaude, Smith, Kennedy, & Jenkinson, 2011); 12 anatomically defined subcortical nuclei from AAL3v1 (Rolls, Huang, Lin, Feng, & Joliot, 2020); 30 anatomically defined subcortical nuclei from FreeSurfer 7 (Iglesias et al., 2018) (50 nuclei were merged down to 30 to remove the smallest nuclei, as with AAL3v1); and 27 anatomically defined cerebellar regions from the SUIT atlas (Diedrichsen, Balsters, Flavell, Cussans, & Ramnani, 2009). Similar to FS 86, this 439-region atlas is a subject-specific parcellation. Additional details and corresponding files for this parcellation are available on GitHub (https://github.com/kjamison/nemo#parcellations).

2.3 | FC extraction

Each subject underwent four gradient-echo EPI rfMRI runs of ~15 min each over two sessions. The data consisted of 1,200 volumes per rfMRI for a total of 4,800 volumes for each subject over the four runs. The minimal preprocessing pipeline performed by the HCP consortium included motion and distortion correction, registration to subject anatomy and standard MNI space, and automated removal of noise artefacts by independent components analysis (M. F. Glasser et al., 2013; Griffanti et al., 2014; Salimi-Khorshidi et al., 2014). We regressed the global signal and its temporal derivative from each rfMRI time series and concatenated the four scans. We then computed the zero lag Pearson correlation to derive the FC from the concatenated time series, which we then Fisher's z-transformed. We used the vectorised upper triangular of this FC to predict cognition.

2.4 | SC extraction

The HCP minimally preprocessed diffusion data have been processed to correct for motion, EPI and eddy-current distortion, and registered to subject T1 anatomy (M. F. Glasser et al., 2013). We then used MRtrix3 to estimate a voxel-wise multi-shell, multi-tissue constrained spherical deconvolution model and then compute whole brain tractography for each HCP subject (Jeurissen, Tournier, Dhollander, Connelly, & Sijbers, 2014). We computed separate whole-brain tractograms using both probabilistic (iFOD2 (Tournier, Calamante, & Connelly, 2010) with anatomically constrained tractography (Smith, Tournier, Calamante, & Connelly, 2012)) and deterministic (SD_STREAM (Tournier, Calamante, & Connelly, 2012)) tractography algorithms. Each method produced 5 million streamlines per subject, using dynamic seeding, and computed streamline weights to reduce known biases in tractography algorithms and better match the whole brain weighted tractogram to diffusion properties of the observed data (SIFT2, (Smith, Tournier, Calamante, & Connelly, 2015)). We parcellated the tractograms to produce ROI-volume normalised pairwise SC matrices, where each pairwise connection is the sum of the SIFT2 weights of streamlines connecting those regions, divided by the sum of the grey matter volume of those regions. We generated two SC matrices for each subject: one using deterministic tractography and another using probabilistic tractography. We used the vectorised lower triangular portion of the SC matrices to predict cognition. To quantify the effect of tractography algorithm type on the accuracy of cognitive prediction, we evaluated the difference in model performance metrics for all three cognitive scores using SC derived from deterministic versus probabilistic tractography for the FS 86 parcellation. Specifically, we performed two-tailed *t* tests for each cognitive metric and corrected for multiple comparisons using Bonferroni correction. SC derived from probabilistic tractography significantly outperformed SC derived from deterministic tractography in the prediction of crystallised, fluid, and total cognitive abilities (Figure S1), see Supplementary Materials for a detailed discussion of

these results. All results presented in the main paper use SC derived from probabilistic tractography.

2.5 | Hybrid connectome

We concatenated the upper triangular of the FC and the lower triangular of the SC matrices to generate HC (Amico & Goñi, 2018). We used the vectorised HC to predict cognition.

2.6 | Cognition

The NIH Toolbox Cognition Battery is an extensively validated battery of neuropsychological tasks (Carlozzi et al., 2017; Gershon et al., 2013; Heaton et al., 2014; Mungas et al., 2014; Tulsky et al., 2017; Weintraub et al., 2013; Weintraub et al., 2014; Zelazo et al., 2014) that assesses five cognitive domains: language, executive function, episodic memory, processing speed, and working memory through seven individual test instruments (Heaton et al., 2014). The specific tasks include Dimensional Change Card Sort Test (executive function – cognitive flexibility), Flanker Inhibitory Control and Attention Test (executive function – inhibitory control and attention), Picture Sequence Memory Test (episodic memory), Picture Vocabulary Test (language – vocabulary), Oral Reading Recognition Test (language – reading decoding), List Sorting Working Memory Test (working memory), and Pattern Comparison Processing Speed Test (processing speed) (Heaton et al., 2014). Three composite scores were derived from participants' scores on the NIH Toolbox Cognitive Battery tasks: crystallised cognition composite, fluid cognition composite, and total cognition composite (Heaton et al., 2014). The crystallised cognition composite comprises the picture vocabulary and oral reading recognition tests and assesses language and verbal skills. The fluid cognition composite comprises scores on the dimensional change card sort, flanker inhibitory control and attention, picture sequence memory, list sorting working memory, and pattern comparison processing speed tests. It is a composite that broadly assesses processing speed, memory, and executive functioning. The total cognition composite combines the crystallised and fluid cognition composites. We used the crystallised, fluid, and total cognition composites in this study, rather than the individual scores from the tasks, because they are likely to have a higher signal-to-noise ratio. Composite scores also tend to be more reliable/stable and are less susceptible to variability in individual tasks (Heaton et al., 2014). Finally, by using the composite scores, we greatly reduce the number of models that need to be trained, thus reducing the number of multiple comparisons.

2.7 | Prediction of cognitive performance

We used three distinct inputs (FC, SC, and HC) to predict three distinct outputs (crystallised, fluid, and total cognition): a separate linear ridge regression model was trained for each input/output combination. For each model, we randomly shuffled and split the data into 100 distinct training (80%) and testing (20%) splits. We fit a linear ridge regression model on Scikit-learn (Pedregosa et al., 2011) using the training subset and tuned the regularisation parameter with five iterations of nested cross validation with threefold inner and outer loops. We optimised the regularisation parameter in the inner loop and validated it in the outer loop. We took the median optimised hyperparameters from the five iterations to generate a single final model. We trained this model on the entire training set, extracted feature weights, and evaluated the model's explained variance and prediction accuracy on the hold-out test set. We quantify prediction accuracy as the Pearson correlation between the true and predicted values (Li et al., 2019). A shared set of 100 distinct, random train/test splits were used to generate a distribution of performance metrics for each predictive model.

2.8 | Model significance and comparisons

For each predictive model, we generated a corresponding null distribution for assessing model significance in the following way. We permuted the predicted variables (cognitive score) 25,000 times and then randomly split the data into train and test sets. For each of these 25,000 permutations, we trained and tested the model on the permuted data to obtain a null distribution of model performance.

We assessed whether the original model's performance was significantly non-zero by comparing the prediction accuracy from each of the original model's 100 train/test splits to the median prediction accuracy from the null distribution. Specifically, the *p*-value for the model's significance is the proportion of 100 original models that had prediction accuracies less than or equal to the median performance of the null model. We then corrected the *p*-values for multiple comparisons over all models using the Benjamini–Hochberg false discovery rate ($q = 0.05$) procedure (Benjamini & Hochberg, 1995). We used an exact test of differences to evaluate prediction performance differences across the models (MacKinnon, 2009).

2.9 | Feature importance

We averaged feature weights obtained over the 100 linear ridge regression models to get a mean feature weight for each model. We then reconstructed activation patterns from mean feature weights to increase their interpretability as described in Haufe et al. (2014). Briefly, for each iteration of a model, we used the feature weights, W, the covariance of the connectivity for the training set, Σ_x, and the covariance of the output variable (cognitive score), Σ_y, for the training set to extract the activation patterns, A, as follows: $A = \Sigma_x W \Sigma_y^{-1}$. We then averaged the activation patterns over the 100 shuffled iterations of each model to get the mean feature importance from each model. We summarised each region's importance in the prediction models by taking the sum of their positive and negative pairwise regional feature importances separately. In addition, pairwise regional feature importance matrices

were mapped to a network level by averaging the positive and negative pairwise regional feature importances separately across functionally defined networks. Each cortical region from the two parcellations was assigned to one of seven networks from the Yeo seven-network parcellation (Yeo et al., 2011). Subcortical regions were assigned to a subcortical network, and cerebellar regions to a cerebellar network. We evaluated the Pearson correlation between feature importances, at a regional and a network level, obtained from FC and SC models to predict crystallised, fluid, and total cognitive scores. Regional assignments from the FS 86 and CoCo 439 atlas to the Yeo network are shown in the Supplemental Materials (Figures S2 and S3).

3 | RESULTS

3.1 | Prediction of cognitive performance

Explained variance from models using FC, SC, and HC predicting crystallised, fluid, and total cognition are shown in Table 1 and Figure 2. Prediction accuracy for all models is shown in Figure S4. All models predicting total cognition performed significantly better than chance ($p < .05$ after corrections for multiple comparisons). Models using FC and HC to predict crystallised cognition performed significantly better than chance for both parcellations, but the model using SC performed better than chance only for the FS 86 parcellation. Models using FC and HC to predict fluid cognition, but not SC, performed significantly better than chance for both parcellations. We evaluated differences in model performance (as measured by explained variance) using exact tests for differences between all 18 models, as shown in Figure 3.

3.2 | Feature importance

Correlations between pairwise regional and network-level feature importance maps for the prediction of cognitive metrics using FC and SC were assessed for both parcellations (Figure 4). Within the FC and SC modalities, pairwise regional feature importances are strongly

TABLE 1 Model performance results. Model performance using FC, SC, and HC to predict crystallised, fluid, and total cognition. Median explained variance (%) (interquartile range) are shown for the FS 86 atlas and the CoCo 439 atlas.

Connectivity type		FS 86			CoCo 439		
Cognition		FC	SC	HC	FC	SC	HC
Explained variance (%)	Crystallised	**10.2 (6.7)**	**8.1 (5.9)**	**12.8 (7.4)**	**22.8 (8.6)**	5.3 (5.1)	**19.8 (7.2)**
	Fluid	**6.2 (5.2)**	3.6 (3.3)	**7.9 (6.2)**	**9.8 (6.7)**	5.3 (3.1)	**10.5 (7.2)**
	Total	**11.2 (9.1)**	**8.2 (6.7)**	**13.9 (7.6)**	**20.7 (9.3)**	**8.3 (5.6)**	**20.9 (8.5)**

Note: Bold values denote that the model performed better than chance.
Abbreviations: FC, functional connectivity; HC, hybrid connectivity; SC, structural connectivity.

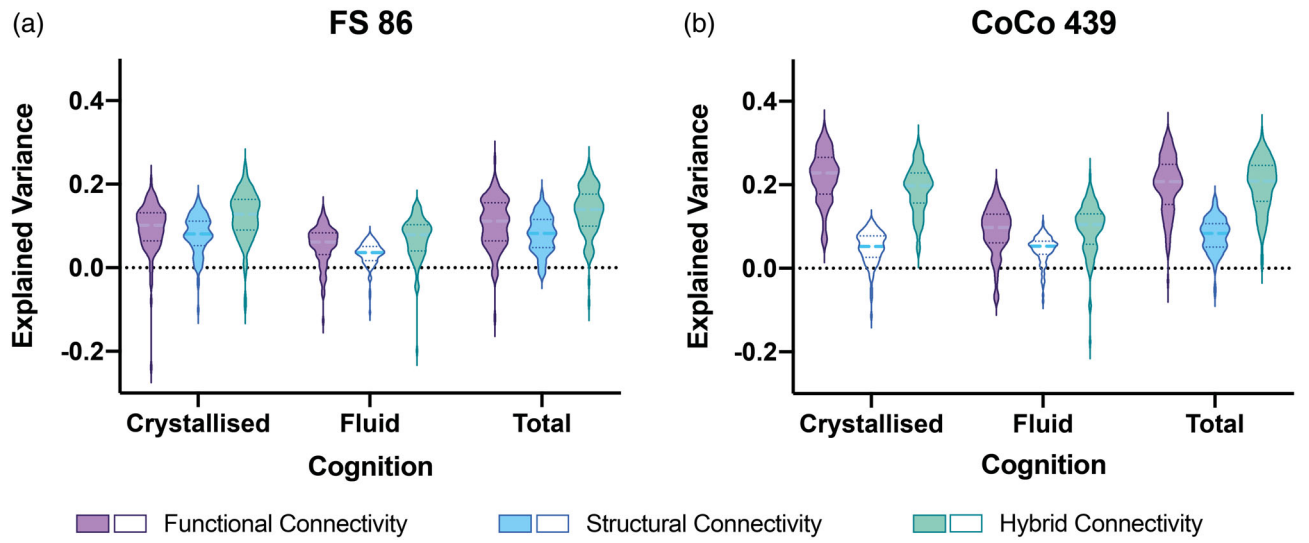

FIGURE 2 Model performance for prediction of cognitive metrics. Explained variance (a,b) violin plots for models using functional (purple), structural (blue), and hybrid (green) connectivity to predict crystallised, fluid, and total cognition. Results using the FreeSurfer 86 (FS 86) parcellation are shown on the left (a) and the CoCo 439 parcellation are shown on the right (b). Solid lines indicate the distribution of values, dashed lines indicate the median, and dotted lines indicate the interquartile range. Solid coloured violin plots indicate model performance that is better than chance (corrected $p < .05$)

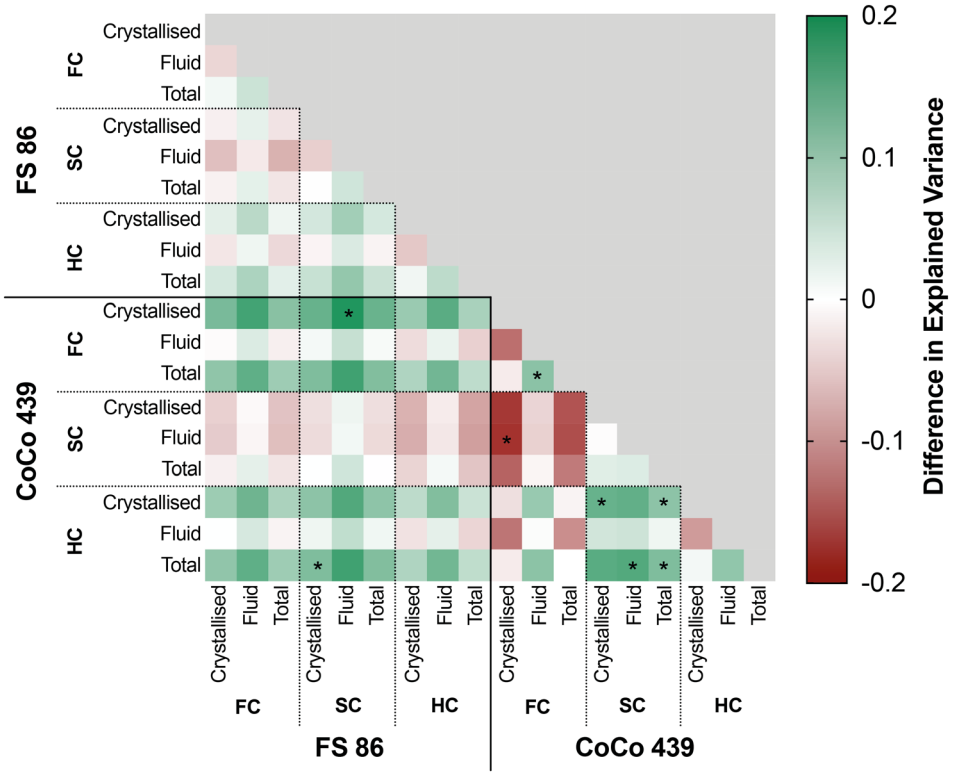

FIGURE 3 Differences in model performance for prediction of cognitive metrics. Difference in explained variance between pairs of models using functional connectivity (FC), structural connectivity (SC), and hybrid connectivity (HC) to predict crystallised, fluid, and total cognition. Model differences were calculated by averaging the difference in explained variance for each of the 100 train/test splits. Both the FreeSurfer 86 (FS 86) atlas and the CoCo 439 atlas are shown here. Significance of differences in explained variance were evaluated using exact tests for differences. * denotes corrected $p < .05$. A positive difference value indicates that the model on the y-axis has a greater explained variance than the model on the x-axis

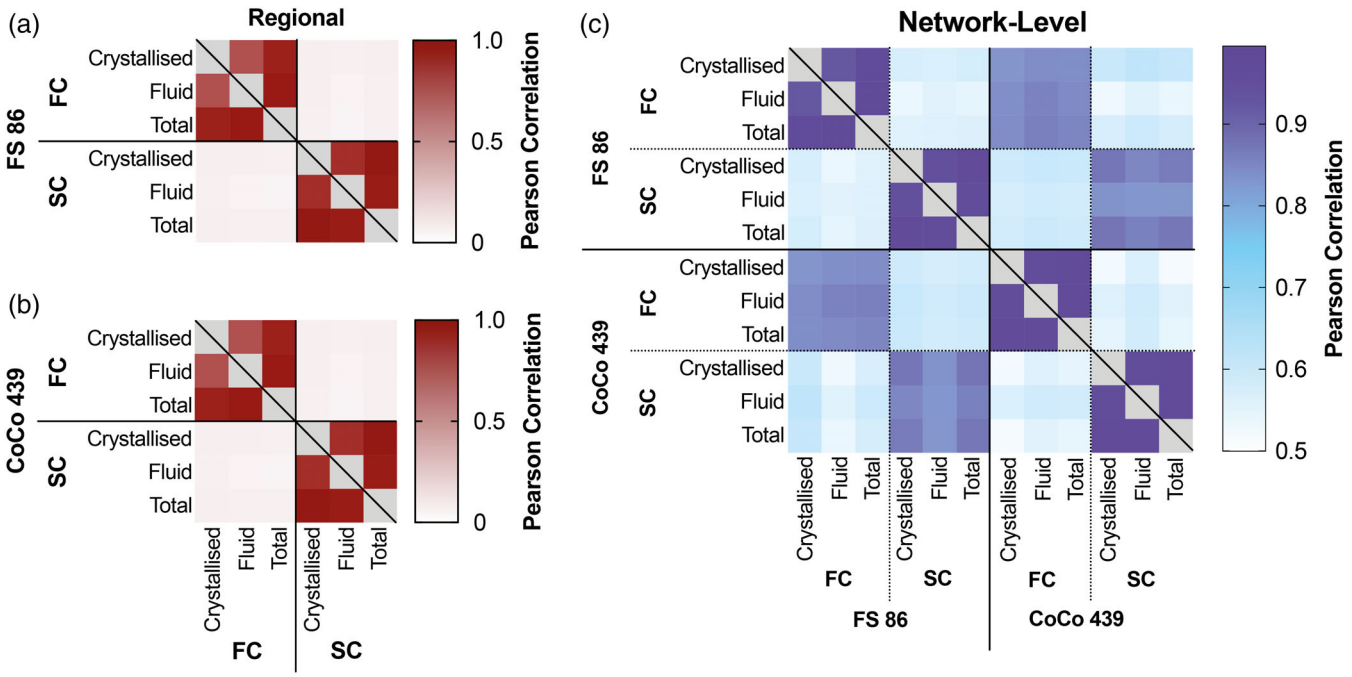

FIGURE 4 Correlation between pairwise regional feature importance for models predicting cognitive metrics. Pearson correlation between pairwise regional feature importance (a,b) from models using functional connectivity (FC) and structural connectivity (SC) to predict crystallised, fluid, and total cognition using the FS 86 (a) and the CoCo 439 atlas (b). Pearson correlation between pairwise network-level feature importance (c). Positive and negative network-level feature importances were computed by taking the positive and negative sums of the regional feature importance. Correlations were evaluated between the concatenated positive and negative network-level feature importances

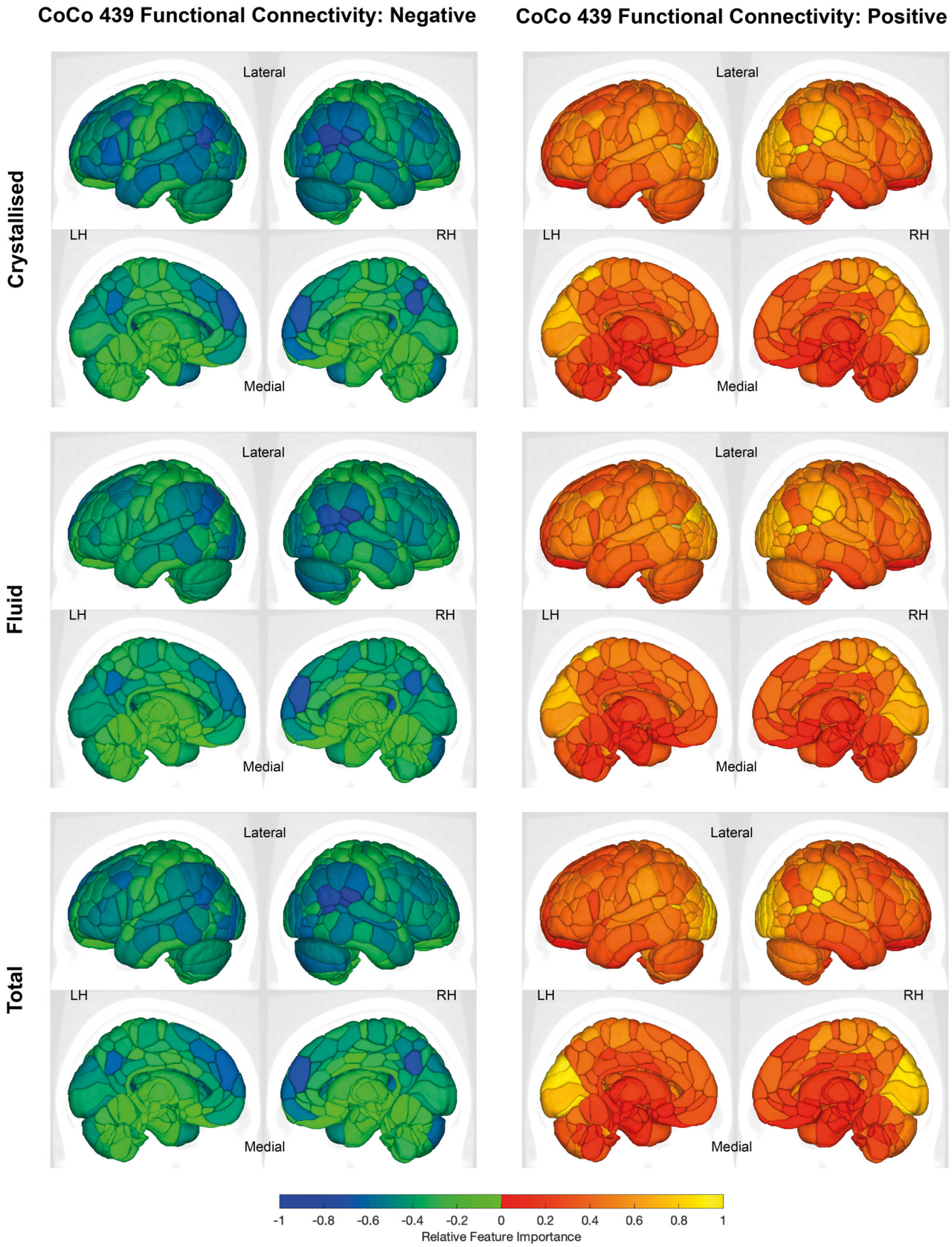

FIGURE 5 Regional importance for CoCo 439 functional connectivity models predicting cognitive metrics. Positive and negative regional feature importances from the CoCo 439 atlas functional connectivity models were computed by taking the sum of all positive and negative pairwise connections for each region, respectively. Relative regional feature importance measures for predicting crystallised (top), fluid (middle), and total (bottom) cognition using functional connectivity are shown here. Lateral and medial views of the right (RH) and left (LH) hemispheres are shown. Warmer colours are used for positive feature importance, and cooler colours for negative feature importance

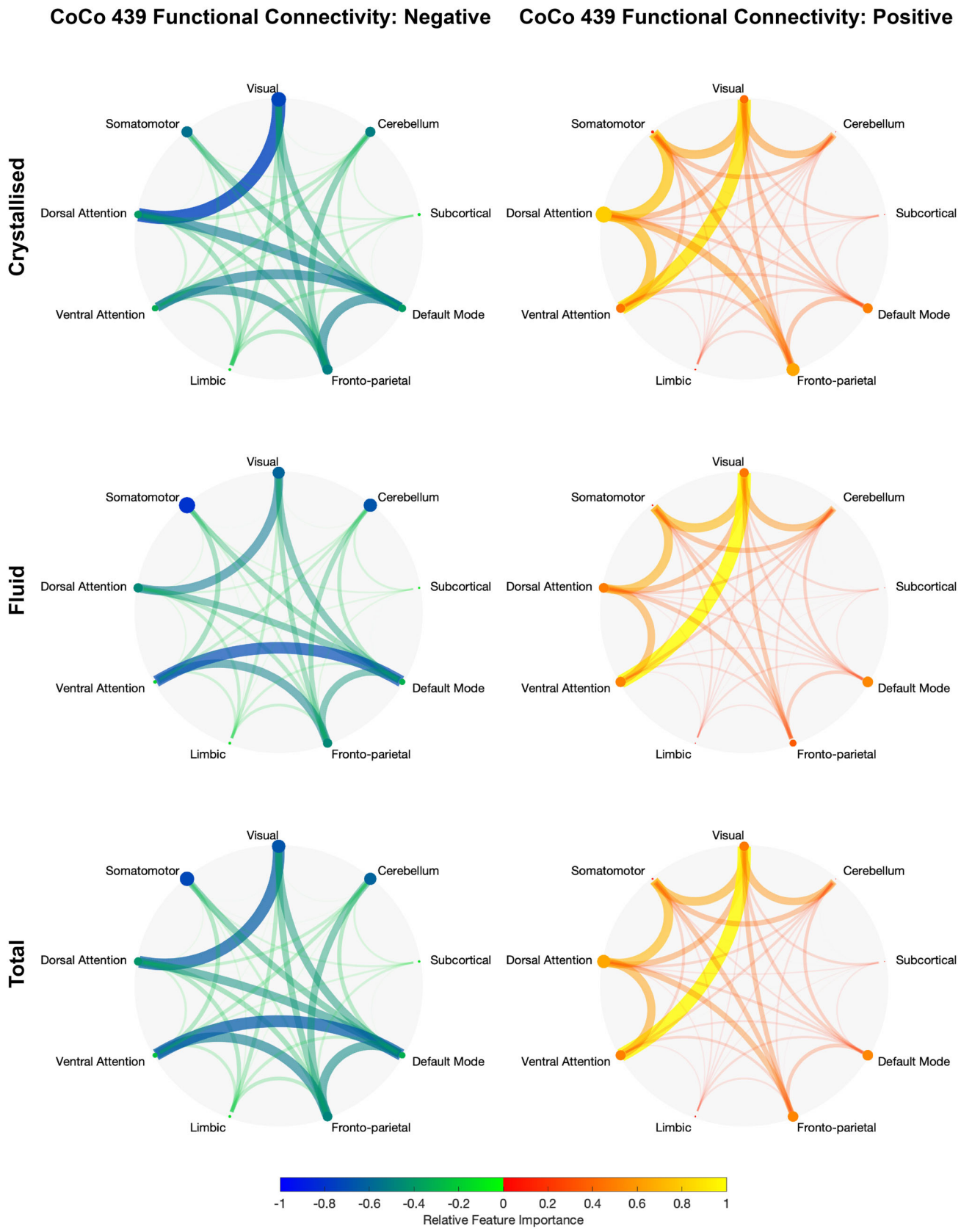

FIGURE 6 Network-level feature importance for functional connectivity predicting cognitive metrics. Network-level positive and negative feature importance for functional connectivity to predict crystallised (top), fluid (middle), and total (bottom) cognition, based on the pair-wise feature importance matrix from the CoCo 439 atlas. Node radii and colour denote strength of intra-network positive and negative feature importance. Edge weight and colour denote strength of inter-network positive and negative feature importance. Warmer colours are used for positive feature importance, and cooler colours for negative feature importance

correlated across cognitive domains, but across the FC and SC modalities, feature importances are not correlated. Pairwise network-level features are strongly correlated across cognitive domains and parcellations within the FC and SC modalities, but not across the modalities. At a regional level, functional connections involving the temporal–parietal–occipital junction and the visual cortex are most important for predicting crystallised and fluid abilities (Figure 5). At a pairwise network-level, functional and structural connections within and between cortical, subcortical, and cerebellar networks to predictions of crystallised and fluid abilities to varying extents (Figure 6, Figures S5–S7). More specifically, functional connections between visual, somatomotor, dorsal attention, ventral attention, and cerebellar networks and within dorsal attention and frontoparietal networks are positively associated with crystallised and fluid abilities. Conversely, functional connections within visual, somatomotor, and cerebellar networks and between visual-dorsal attention, and ventral attention-default mode networks are negatively associated with crystallised and fluid abilities. Structural dorsal attention-frontoparietal, dorsal attention-visual, and limbic-subcortical networks are positively associated with crystallised and fluid abilities, while structural connections within cerebellum, visual, and frontoparietal networks are negatively associated with crystallised and fluid abilities.

4 | DISCUSSION

In this study, we evaluated the brain–behaviour relationships between multimodal connectivity and cognition in 415 healthy, unrelated young adults. Using whole brain resting-state FC, SC, and hybrid function–structure connectivity (HC), we predicted individual crystallised, fluid, and total cognition abilities. First, we demonstrate FC is generally more predictive of cognitive scores than SC and, furthermore, integrating the two modalities does not always increase explained variance. Second, we show the accuracy of cognitive prediction from connectome measures is influenced by the choice of grey matter parcellation, and, possibly, how that parcellation is derived. Third, we find that distinct functional and structural connections contribute to the prediction of individual crystallised and fluid abilities.

Prior studies have implemented machine (He et al., 2020; Kong et al., 2018; Li et al., 2019) and deep learning (He et al., 2020) algorithms to predict behaviour and cognition using the Human Connectome Project's FC data. Li et al. reported cross-validated prediction accuracies ranging from approximately 0.1 to 0.4 to predict Dimensional Change Card Sort, Flanker Inhibitory Control and Attention, Picture Sequence Memory, Picture Vocabulary, Oral Reading Recognition, List Sorting Working Memory, and Pattern Comparison Processing Speed tasks using FC (Li et al., 2019). He et al. demonstrated that kernel regression, fully connected neural networks, and BrainNetCNN (Kawahara et al., 2017) achieve comparable prediction accuracies when used to predict behavioural and cognitive measures using FC (He et al., 2020). In this study, we predict cognition composite scores (which are derived from the individual task scores) as they may be less noisy and more reliable than the individual scores. Our results, in which we achieve prediction accuracies ranging from 0.25 to 0.47 for the composite scores, support this idea.

White matter pathways and neural coactivation patterns in the brain produce complex cognitive functions. While brain functional and structural connections are undeniably related, most studies analyse their independent contributions to behaviour. Previously, Zimmerman et al. examined how FC and SC profiles map to cognition (Zimmermann et al., 2018); however, they did not compare the strength of the connectivity-cognition mapping between the two modalities to quantify whether one modality is more predictive of cognition than the other. Although our exact tests for differences do not find that models using FC or HC significantly outperform models using SC, our permutations tests suggest there might be some differences in how predictive FC, SC, and HC are of individual cognitive abilities. Models using FC and HC perform above chance levels to predict all three cognitive scores for both parcellations, while models using SC only perform above chance levels to predict crystallised and total cognition for the FS 86 parcellation, and to predict total cognition for the CoCo 439 parcellation. Hence, we demonstrate, for the first time, that FC is typically more predictive of individual cognitive abilities than SC. Additionally, we show that integrating the two modalities into a single model does not always enhance the predictability of cognitive measures. A technical reason why the FC matrices may outperform the SC matrices pertains to their sparsity. FC matrices used in our analyses are dense, while SC matrices are sparse—the FS 86 matrices are approximately 15% sparse within individuals while the CoCo 439 matrices are approximately 55% sparse within individuals. The sparsity of the SC matrices means a large proportion of the information the model is using to predict individual abilities at a subject-level is useless (i.e., zeros) and thus there is less information available for the SC models to map to cognition. The FC matrices do not suffer from the same issue and thus might be capturing more relevant information for use in the FC-cognition mapping.

The choice of parcellation when analysing neuroimaging data is a crucial one that can affect overall results (Lord et al., 2016; Zalesky et al., 2010). In this work, we use two different parcellations—the FS 86 and the CoCo 439. These two parcellations differ in their number, spatial distribution, size, and process of node creation. While our exact tests for differences do not clearly identify one parcellation as the superior one for predicting individual cognitive abilities, we do observe general trends in the explained variance suggesting the CoCo 439 parcellation might be better when using FC to predict crystallised and total cognition. This may be due to two different reasons. The CoCo atlas has much higher dimensionality (96,141 edges in CoCo 439 compared to 3,655 edges in FS 86) and might be capturing high-resolution edge-level information that is particularly important for individual-level cognitive abilities. Furthermore, the CoCo 439 atlas' cortical regions are functionally defined, compared to the FS 86 atlas regions that are anatomically defined. An atlas that has regions defined by grouping areas with similar functional activation patterns is likely to capture more functionally relevant signal within each region compared to a structurally defined one which may include regions with very different functional activation patterns in a single

anatomical region. Similarly, a functionally defined atlas may not be optimal for measuring SC. In fact, we observe that the FS 86 SC models generally perform better than CoCo 439 SC models for predictions of crystallised cognition. Together, this suggests the definition (functional vs. structural) of the atlases may play a critical role in determining how strongly the various connectivity modalities map to cognition. This is consistent with findings and recommendations from other work (Lord et al., 2016; Messé, 2020; Wu, Xu, Potter, Zhang, & Alzheimer's Disease Neuroimaging Initiative, 2019).

Interpretation of feature weights from supervised prediction models, even within a linear framework, can be challenging (Douglas & Anderson, 2019; Haufe et al., 2014). Here, we transform the feature weights obtained from our linear models into corresponding activation patterns, which are thought to more likely capture meaningful signals and resemble the true underlying relationships (Haufe et al., 2014). The raw feature weights emphasise regions in subcortical, cerebellar, and limbic networks, particularly ones with quite small volume that may be noisy (data not shown), whereas the activation patterns emphasise larger regions within the cortex. Extant literature has demonstrated that in many cases, noisy features may be assigned weights that are stronger than (or comparable to) those assigned to features capturing relevant information in order to maximise prediction performance (Haufe et al., 2014). The smaller regions strongly weighted by our feature weights likely represent a lot of noise as subcortical regions are typically more susceptible to physiological noise compared to cortical regions (Hutton et al., 2011; Kasper et al., 2017; Viviani, 2016). The transformation into activation vectors account for this by using information about the covariance of each feature. Hence, we focus our interpretations on the activation patterns and refer to those as our feature importances.

Our results demonstrate that distinct functional and structural connections predict individual cognitive abilities, and regional pairwise feature importance is not correlated between the two modalities. Our results support and build upon findings from prior work. In their study, Zimmerman et al. identified a large set of corticocortical and corticosubcortical functional connections and a smaller set of distributed structural connections that show relationships with cognition and conclude that functional and structural connections uniquely map onto cognition (Zimmermann et al., 2018). Here, we concur that distinct corticocortical functional and structural connections are important to predict cognitive abilities. We also replicate that there are strong relationships between connectivity and cognitive abilities for a large set of functional connections, and a smaller set of structural connections. However, we also observe that within modalities (functional or structural) overlapping connections predict distinct cognitive abilities, and functional and structural connections within the cerebellum are important for the predictions, which they do not report. These differences in results may be attributable to differences in statistical modelling choice and in parcellation. First, they used a partial least squares approach that maps SC or FC not to a single cognitive outcome but to a linear combination of the cognitive scores. This results in models that are a bit more difficult to interpret, as they represent mixtures of various cognitive domain scores. In addition, the previous work parcellated the brain into 34 cortical and 7 subcortical ROIs per hemisphere plus the brainstem—the cerebellum was not included in their analyses (Zimmermann et al., 2018). The contribution of cerebellar connections to our models, and the known role of cerebellum in cognitive function (Buckner, 2013; Schmahmann & Caplan, 2006), highlight the importance of studying whole-brain FC and SC when studying relationships with cognition. Overall, our results suggest that FC and SC capture unique and complementary information.

Cattell and Horn's two-component theory of intellectual development proposes a distinction between crystallised and fluid abilities in how they develop and transform throughout life (Cattell, 1967; Horn & Cattell, 1966, 1967). Crystallised intelligence is the ability to use learned knowledge, experience, and skills, and fluid intelligence is the ability to solve new problems using logic, encode new episodic memories, and adapt to novel situations in everyday life (Heaton et al., 2014). In the HCP dataset (van Essen et al., 2013), the NIH Toolbox Cognition Battery was used to assess crystallised and fluid abilities. Crystallised abilities are thought to be influenced by education and cultural factors, and fluid abilities, while also dependent on educational and cultural factors, are thought to be more dependent on biological processes within neural structures that enable brain function (Cattell, 1967; Heaton et al., 2014; Horn & Cattell, 1966, 1967). Interestingly, in our results, FC and SC patterns were less predictive of fluid abilities than of crystallised abilities. In the NIH Toolbox Cognition Battery, the crystallised cognition composite reflects scores from tasks measuring vocabulary and reading decoding, while the fluid cognition composite reflects scores from tasks measuring cognitive flexibility, inhibitory control and attention, episodic memory, working memory, and processing speed. The eloquent nature of the mapping between brain anatomy/physiology and language, including vocabulary and reading as measured by the crystallised cognition composite, may explain the higher explained variance of those scores when compared to the fluid cognition composite that may rely on several overlapping brain networks involved in several overlapping but distinct cognitive skills (e.g., inhibition, flexibility, working memory). Another possible explanation for the higher predictability of crystallised abilities (relative to fluid) lies in the impact of environment on the brain's connectomes. FC and SC have been shown to be related to learning and life experience (Johansen-Berg, Scholz, & Stagg, 2010; Peng et al., 2018; Tooley et al., 2019; Zatorre, Fields, & Johansen-Berg, 2012). Hence, it is possible that the joint impact of environment on connectivity networks and crystallised abilities means it is easier to predict one from the other. Finally, crystallised abilities are more stable across the lifespan and generally less susceptible to a multitude of factors such as mood, stress, and sleep, all of which influence executive functions and memory (Nilsson et al., 2005; O'Neill, Kamper-DeMarco, Chen, & Orom, 2020; Salthouse, 2010). This may also contribute to the higher predictability of crystallised abilities.

Crystallised cognition, as measured by the NIH Toolbox, mainly represents language (vocabulary and reading decoding) abilities. Fluid cognition represents a wide range of cognitive processes: executive

function (cognitive flexibility and inhibitory control and attention), episodic memory, working memory, and processing speed. Both crystallised and fluid cognition rely on a distributed network of connections throughout the brain (Brancucci, 2012). In this work, we find features underlying predictions for both cognitive domains overlap within the functional and structural modalities, but are unique across the modalities. Our predictions based on the functional modality generally outperform those from the structural modality, and thus we primarily focus our interpretation of feature importances for functional connections.

Stronger functional connections between visual, somatomotor, dorsal attention, ventral attention, and cerebellar networks, and within dorsal attention and frontoparietal networks are indicative of higher crystallised and fluid abilities. At the same time, stronger functional connections within visual, somatomotor, and cerebellar networks and between visual-dorsal attention, and ventral attention-default mode networks indicate lower crystallised and fluid abilities. The visual network is responsible for visual information processing and thus contributes to the perception and recognition of stimuli presented across different cognitive tasks (Gazzaniga, Ivry, & Mangun, 2014). The somatomotor (or sensorimotor) network is responsible for the dynamic and continuous coupling between sensory input, neural processing, and motor output and thus underlies biological information processing at a fundamental level (Lungarella & Sporns, 2006; Respino et al., 2019). The dorsal attention network modulates voluntary attention and exerts goal-driven attentional orientation, while the ventral attention network responds to stimulus novelty and exerts stimulus-driven attentional orientation (Gazzaniga et al., 2014); Both dorsal and ventral attention networks are involved in a wide of range cognitive processes (Bowren et al., 2020; Dixon et al., 2017; Majerus et al., 2012). The frontoparietal network is implicated in modulating executive function, cognitive flexibility, and working memory (Cole, Yarkoni, Repovs, Anticevic, & Braver, 2012; Iidaka, Matsumoto, Nogawa, Yamamoto, & Sadato, 2006; Marek & Dosenbach, 2018; Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015). The default mode network is active during passive rest and mind-wandering, and modulates self-referential thinking, theory of mind, working memory, and processing speed (Andrews-Hanna, 2012; Jaywant et al., 2020; Leech, Kamourieh, Beckmann, & Sharp, 2011; Sheline et al., 2009; M. Song et al., 2009; Spreng & Grady, 2010; Vatansever, Manktelow, Sahakian, Menon, & Stamatakis, 2018). The cerebellum, traditionally associated with planning and executing movements, is implicated in a wide range of cognitive functions such as working memory, linguistic processing, visual spatial organisation, memory, abstract reasoning, and cognitive planning (Buckner, 2013; Leiner, Leiner, & Dow, 1993; Schmahmann & Caplan, 2006).

Structural connections between dorsal attention and frontoparietal networks, and between limbic and subcortical networks are indicative of higher crystallised and fluid abilities, while structural connections within the visual, frontoparietal, and cerebellar networks predict lower crystallised and fluid abilities. The limbic network is involved in memory, language processing, decision-making, and reinforcement learning (Altmann, Bohrn, Lubrich, Menninghaus, & Jacobs, 2012; Howett et al., 2019; Pehrs et al., 2017; Wilson, Takahashi, Schoenbaum, & Niv, 2014). The subcortical network plays an important role in cognition, emotion, and social function (Berridge & Kringelbach, 2015; Bickart, Wright, Dautoff, Dickerson, & Barrett, 2011; Eichenbaum, 2004; Fischi-Gómez et al., 2015; Johnson, 2005; Koshiyama et al., 2018; Utter & Basso, 2008; van Schouwenburg, den Ouden, & Cools, 2010).

Taken together, these results emphasise that distinct functional and structural connections underlie cognitive abilities, and both modalities should be studied to understand the diverse neural correlates of cognition.

4.1 | Limitations

Machine learning algorithms using neuroimaging data are prone to the curse of dimensionality. Voxel-wise imaging data, on the order of hundreds of thousands of features, and regional data can have hundreds or thousands of features. Here, we parcellate the brain into 86 or 439 regions. When taking the upper or lower triangular of the pairwise FC and SC matrices, this leaves us with 3,655 or 96,141 features. Dimensionality reduction through parcellation decreases noise, reduces computational cost, and enables more interpretable models, but loses valuable information captured in the voxel-wise data. Future work performing voxel-wise analyses of very large sample data can address this issue.

Here, we compare whether integrating FC and SC into HC can improve predictions of individual cognitive abilities. To generate HC, we concatenate FC and SC. This results in the dimensionality of HC being twice as large as that of FC and SC and this may influence our predictive models. One potential approach to address this difference in dimensionality would be to implement dimensionality reduction through principal component analysis and keep the number of principal components consistent across the models. While this approach is ideal to optimise model performance, it presents additional limitations when interpreting the feature weights as it transforms the data into a different feature space. For the purposes of this study, we are equally interested in model performance and the functional and structural connections that drive the performance, so we chose to make predictions based on pairwise connectivity. However, future work can examine how additional dimensionality reduction approaches may improve model performance, especially when dealing with differences in dimensionality across the models.

In this study, we only used data from the Human Connectome Project. Although we exclusively evaluate our models on test hold-out sets and perform 100 iterations of each model with unique train/test splits, the results we report here may not be generalisable to other datasets. Future work performing out-of-dataset evaluations can address this limitation.

Age (Damoiseaux, 2017; J. Song et al., 2014), sex (Gong, He, & Evans, 2011; Gur & Gur, 2017; Ingalhalikar et al., 2014; Jacobs & Goldstein, 2018; Jacobs et al., 2016; Satterthwaite et al., 2015; Weis

et al., 2019), and environment/experience (Sripada, Swain, Evans, Welsh, & Liberzon, 2014; Tooley et al., 2019) influence connectivity. Hence, it is likely that they, along with other demographic variables such as gender and ethnicity, may influence the relationship between connectomics and cognition (Jiang et al., 2020). Future work should examine how the relationship between connectomics and cognition varies based on demographics.

5 | CONCLUSIONS

Having a comprehensive map of neural correlates underlying cognition in healthy individuals is a critical first step towards understanding changes in cognitive functioning as a result of age, injury, and disease. Here, we integrate neuroimaging, connectomics, and machine learning approaches to explore brain–behaviour relationships between functional and SC and crystallised and fluid cognition. We report three main findings. We demonstrate FC is more predictive of individual cognitive abilities than SC and integrating functional and structural modalities does not generally increase the variance explained. We show the accuracy of prediction of individual cognitive abilities from connectomes is influenced by the choice of parcellation, and, possibly, how the atlas is derived. Finally, we report that distinct functional and structural connections predict crystallised and fluid abilities. Specifically, stronger functional connections between visual, somatomotor, dorsal attention, ventral attention, frontoparietal, and cerebellar networks, and within dorsal attention and frontoparietal networks predict higher crystallised and fluid abilities, along with stronger structural connections between dorsal attention and frontoparietal networks, dorsal attention and visual networks, and limbic and subcortical networks. Conversely, stronger functional connections within visual, somatomotor, and cerebellar networks predict lower crystallised and fluid abilities, along with stronger structural connections within cerebellum, visual, and frontoparietal networks. Taken together, this suggests that functional and SC have unique relationships with individual abilities of crystallised and fluid cognition, and that both modalities should be studied to understand neuroanatomical and neurophysiological correlates of cognition.

6 | CITATION GENDER DIVERSITY STATEMENT

Recent work in neuroscience and other fields has identified a bias in citation practices such that papers from women and other minorities are under-cited relative to the number of such papers in the field (Caplar, Tacchella, & Birrer, 2017; Chakravartty, Kuo, Grubbs, & McIlwain, 2018; Dion, Sumner, & Mitchell, 2018; Dworkin et al., 2020; Maliniak, Powers, & Walter, 2013; Thiem, Sealey, Ferrer, Trott, & Kennison, 2018). Here, we sought to proactively consider choosing references that reflect the diversity of the field in thought, form of contribution, gender, and other factors. We used classification of gender based on the first names of the first and last authors (Dworkin et al., 2020), with possible combinations including male/male, male/female, female/male, and female/female. Excluding self-citations to the first and last authors of our current paper, the references contain 57.1% male/male, 17.7% male/female, 18.5% female/male, and 6.7% female/female. We look forward to future work that could help us to better understand how to support equitable practices in science.

ACKNOWLEDGMENTS

This work was supported by the following National Institutes of Health (NIH) grants awarded to A.K. R21 NS104634-01 and R01 NS102646-01A1. A. J. is funded through a K12 Career Development Award from the National Center of Medical Rehabilitation Research/Eunice Kennedy Shriver National Institute of Child Health and Human Development (1K12HD093427-04), via a subaward from Georgetown University. The sponsors did not have any role in the study design, the analysis, or interpretation of the data; the writing of the report; or the decision to submit the manuscript for publication. Data were provided and made available by the Human Connectome Project, WU-Minn Consortium (Principal Investigators: David Van Essen and Kamil Ugurbil; 1U54MH091657) funded by the 16 NIH Institutes and Centres that support the NIH Blueprint for Neuroscience Research; and by the McDonnell Centre for Systems Neuroscience at Washington University. The authors would like to acknowledge Dr Mallar Chakravarty and Raihaan Patel from McGill University for contributions to an earlier version of this work.

CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

Elvisha Dhamala and **Amy Kuceyeski**: Conceptualization. **Elvisha Dhamala**, **Keith W. Jamison**, and **Amy Kuceyeski**: Methodology. **Elvisha Dhamala** and **Sarah Dennis**: Software. **Elvisha Dhamala** and **Sarah Dennis**: Investigation. **Elvisha Dhamala**: Formal analysis. **Amy Kuceyeski**: Resources. **Elvisha Dhamala** and **Keith W. Jamison**: Data curation. **Elvisha Dhamala**: Writing – original draft. **Elvisha Dhamala**, **Keith W. Jamison**, **Abhishek Jaywant**, **Sarah Dennis**, and **Amy Kuceyeski**: Writing – review and editing. **Elvisha Dhamala**: Visualisation. **Amy Kuceyeski**: Supervision. **Amy Kuceyeski**: Funding acquisition.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available as part of the Human Connectome Project at https://www.humanconnectome.org/study/hcp-young-adult/document/1200-subjects-data-release.

ORCID

Elvisha Dhamala https://orcid.org/0000-0002-8253-6962
Keith W. Jamison https://orcid.org/0000-0001-7139-6661
Abhishek Jaywant https://orcid.org/0000-0003-4307-5742

Sarah Dennis https://orcid.org/0000-0003-0370-4284
Amy Kuceyeski https://orcid.org/0000-0002-5050-8342

REFERENCES

Altmann, U., Bohrn, I. C., Lubrich, O., Menninghaus, W., & Jacobs, A. M. (2012). The power of emotional valence—From cognitive to affective processes in reading. *Frontiers in Human Neuroscience*, *6*, 192.

Amico, E., & Goñi, J. (2018). Mapping hybrid functional-structural connectivity traits in the human connectome. *Network Neuroscience*, *2*(3), 306–322.

Andrews-Hanna, J. R. (2012). The brain's default network and its adaptive role in internal mentation. *The Neuroscientist*, *18*(3), 251–270.

Bassett, D. S., Wymbs, N. F., Porter, M. A., Mucha, P. J., Carlson, J. M., & Grafton, S. T. (2011). Dynamic reconfiguration of human brain networks during learning. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(18), 7641–7646.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate—A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, *57*(1), 289–300.

Berridge, K. C., & Kringelbach, M. L. (2015). Pleasure systems in the brain. *Neuron*, *86*(3), 646–664.

Bickart, K. C., Wright, C. I., Dautoff, R. J., Dickerson, B. C., & Barrett, L. F. (2011). Amygdala volume and social network size in humans. *Nature Neuroscience*, *14*(2), 163–164.

Bowren, M., Adolphs, R., Bruss, J., Manzel, K., Corbetta, M., Tranel, D., & Boes, A. D. (2020). Multivariate lesion-behavior mapping of general cognitive ability and its psychometric constituents. *Journal of Neuroscience*, *40*(46), 8924–8937.

Brancucci, A. (2012). Neural correlates of cognitive ability. *Journal of Neuroscience Research*, *90*(7), 1299–1309.

Buckner, R. L. (2013). The cerebellum and cognitive function: 25 years of insight from anatomy and neuroimaging. *Neuron*, *80*(3), 807–815.

Caplar, N., Tacchella, S., & Birrer, S. (2017). Quantitative evaluation of gender bias in astronomical publications from citation counts. *Nature Astronomy*, *1*(6), 1–5.

Carlozzi, N. E., Tulsky, D. S., Wolf, T. J., Goodnight, S., Heaton, R. K., Casaletto, K. B., … Heinemann, A. W. (2017). Construct validity of the NIH toolbox cognition battery in individuals with stroke. *Rehabilitation Psychology*, *62*(4), 443–454. https://doi.org/10.1037/rep0000195

Cattell, R. B. (1967). The theory of fluid and crystallized general intelligence checked at the 5-6 year-old level. *The British Journal of Educational Psychology*, *37*(2), 209–224. https://doi.org/10.1111/j.2044-8279.1967.tb01930.x

Chakravartty, P., Kuo, R., Grubbs, V., & McIlwain, C. (2018). #Communicationsowhite. *Journal of Communication*, *68*(2), 254–266.

Cole, M. W., Yarkoni, T., Repovs, G., Anticevic, A., & Braver, T. S. (2012). Global connectivity of prefrontal cortex predicts cognitive control and intelligence. *The Journal of Neuroscience*, *32*(26), 8988–8999. https://doi.org/10.1523/JNEUROSCI.0536-12.2012

Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis. I. Segmentation and surface reconstruction. *NeuroImage*, *9*(2), 179–194. https://doi.org/10.1006/nimg.1998.0395

Damoiseaux, J. S. (2017). Effects of aging on functional and structural brain connectivity. *NeuroImage*, *160*, 32–40.

Desikan, R. S., Segonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., … Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage*, *31*(3), 968–980. https://doi.org/10.1016/j.neuroimage.2006.01.021

Diedrichsen, J., Balsters, J. H., Flavell, J., Cussans, E., & Ramnani, N. (2009). A probabilistic mr atlas of the human cerebellum. *NeuroImage*, *46*(1), 39–46.

Dion, M. L., Sumner, J. L., & Mitchell, S. M. (2018). Gendered citation patterns across political science and social science methodology fields. *Political Analysis*, *26*(3), 312–327.

Dixon, M. L., Andrews-Hanna, J. R., Spreng, R. N., Irving, Z. C., Mills, C., Girn, M., & Christoff, K. (2017). Interactions between the default network and dorsal attention network vary across default subsystems, time, and cognitive states. *NeuroImage*, *147*, 632–649.

Douglas, P. K., & Anderson, A. (2019). Feature fallacy: Complications with interpreting linear decoding weights in fMRI. In *Explainable AI: Interpreting, explaining and visualizing deep learning* (pp. 363–378). Cham, Switzerland: Springer.

Dworkin, J. D., Linn, K. A., Teich, E. G., Zurn, P., Shinohara, R. T., & Bassett, D. S. (2020). The extent and drivers of gender imbalance in neuroscience reference lists. *Nature Neuroscience*, *23*, 918–926. https://doi.org/10.1038/s41593-020-0658-y

Eichenbaum, H. (2004). Hippocampus: Cognitive processes and neural representations that underlie declarative memory. *Neuron*, *44*(1), 109–120.

Fischi-Gómez, E., Vasung, L., Meskaldji, D.-E., Lazeyras, F., Borradori-Tolsa, C., Hagmann, P., … Hüppi, P. S. (2015). Structural brain connectivity in school-age preterm infants provides evidence for impaired networks relevant for higher order cognitive skills and social cognition. *Cerebral Cortex*, *25*(9), 2793–2805.

Fischl, B., Liu, A., & Dale, A. M. (2001). Automated manifold surgery: Constructing geometrically accurate and topologically correct models of the human cerebral cortex. *IEEE Transactions on Medical Imaging*, *20*(1), 70–80. https://doi.org/10.1109/42.906426

Fischl, B., Rajendran, N., Busa, E., Augustinack, J., Hinds, O., Yeo, B. T., … Zilles, K. (2008). Cortical folding patterns and predicting cytoarchitecture. *Cerebral Cortex*, *18*(8), 1973–1980. https://doi.org/10.1093/cercor/bhm225

Fischl, B., Salat, D. H., Busa, E., Albert, M., Dieterich, M., Haselgrove, C., … Dale, A. M. (2002). Whole brain segmentation: Automated labeling of neuroanatomical structures in the human brain. *Neuron*, *33*(3), 341–355.

Fischl, B., Sereno, M. I., & Dale, A. M. (1999). Cortical surface-based analysis. II: Inflation, flattening, and a surface-based coordinate system. *NeuroImage*, *9*(2), 195–207. https://doi.org/10.1006/nimg.1998.0396

Fischl, B., Sereno, M. I., Tootell, R. B., & Dale, A. M. (1999). High-resolution intersubject averaging and a coordinate system for the cortical surface. *Human Brain Mapping*, *8*(4), 272–284.

Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (2014). *Cognitive neuroscience: The biology of the mind* (4th ed.). New York, NY: W. W. Norton & Company.

Gershon, R. C., Wagster, M. V., Hendrie, H. C., Fox, N. A., Cook, K. F., & Nowinski, C. J. (2013). NIH toolbox for assessment of neurological and behavioral function. *Neurology*, *80*(11 Suppl 3), S2–S6. https://doi.org/10.1212/WNL.0b013e3182872e5f

Glasser, M. F., Coalson, T. S., Robinson, E. C., Hacker, C. D., Harwell, J., Yacoub, E., … Jenkinson, M. (2016). A multi-modal parcellation of human cerebral cortex. *Nature*, *536*(7615), 171–178.

Glasser, M. F., Sotiropoulos, S. N., Wilson, J. A., Coalson, T. S., Fischl, B., Andersson, J. L., … WU-Minn Human Connectome Project. (2013). The minimal preprocessing pipelines for the Human Connectome Project. *NeuroImage*, *80*, 105–124. https://doi.org/10.1016/j.neuroimage.2013.04.127

Gong, G., He, Y., & Evans, A. C. (2011). Brain connectivity: Gender makes a difference. *The Neuroscientist*, *17*(5), 575–591. https://doi.org/10.1177/1073858410386492

Griffanti, L., Salimi-Khorshidi, G., Beckmann, C. F., Auerbach, E. J., Douaud, G., Sexton, C. E., … Smith, S. M. (2014). Ica-based artefact removal and accelerated fMRI acquisition for improved resting state network imaging. *NeuroImage*, *95*, 232–247. https://doi.org/10.1016/j.neuroimage.2014.03.034

Gur, R. C., & Gur, R. E. (2017). Complementarity of sex differences in brain and behavior: From laterality to multimodal neuroimaging. *Journal of Neuroscience Research*, *95*(1–2), 189–199. https://doi.org/10.1002/jnr.23830

Haufe, S., Meinecke, F., Görgen, K., Dähne, S., Haynes, J.-D., Blankertz, B., & Bießmann, F. (2014). On the interpretation of weight vectors of linear models in multivariate neuroimaging. *NeuroImage*, *87*, 96–110.

He, T., Kong, R., Holmes, A. J., Nguyen, M., Sabuncu, M. R., Eickhoff, S. B., … Yeo, B. T. (2020). Deep neural networks and kernel regression achieve comparable accuracies for functional connectivity prediction of behavior and demographics. *NeuroImage*, *206*, 116276.

Heaton, R. K., Akshoomoff, N., Tulsky, D., Mungas, D., Weintraub, S., Dikmen, S., … Gershon, R. (2014). Reliability and validity of composite scores from the NIH toolbox cognition battery in adults. *Journal of the International Neuropsychological Society*, *20*(6), 588–598. https://doi.org/10.1017/S1355617714000241

Horn, J. L., & Cattell, R. B. (1966). Refinement and test of the theory of fluid and crystallized general intelligences. *Journal of Education & Psychology*, *57*(5), 253–270. https://doi.org/10.1037/h0023816

Horn, J. L., & Cattell, R. B. (1967). Age differences in fluid and crystallized intelligence. *Acta Psychologica*, *26*(2), 107–129. https://doi.org/10.1016/0001-6918(67)90011-x

Howett, D., Castegnaro, A., Krzywicka, K., Hagman, J., Marchment, D., Henson, R., … Chan, D. (2019). Differentiation of mild cognitive impairment using an entorhinal cortex-based test of virtual reality navigation. *Brain*, *142*(6), 1751–1766.

Hutton, C., Josephs, O., Stadler, J., Featherstone, E., Reid, A., Speck, O., … Weiskopf, N. (2011). The impact of physiological noise correction on fMRI at 7 t. *NeuroImage*, *57*(1), 101–112.

Iglesias, J. E., Insausti, R., Lerma-Usabiaga, G., Bocchetta, M., van Leemput, K., Greve, D. N., … Paz-Alonso, P. M. (2018). A probabilistic atlas of the human thalamic nuclei combining ex vivo MRI and histology. *NeuroImage*, *183*, 314–326.

Iidaka, T., Matsumoto, A., Nogawa, J., Yamamoto, Y., & Sadato, N. (2006). Frontoparietal network involved in successful retrieval from episodic memory. Spatial and temporal analyses using fMRI and ERP. *Cerebral Cortex*, *16*(9), 1349–1360.

Ingalhalikar, M., Smith, A., Parker, D., Satterthwaite, T. D., Elliott, M. A., Ruparel, K., … Verma, R. (2014). Sex differences in the structural connectome of the human brain. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(2), 823–828. https://doi.org/10.1073/pnas.1316909110

Jacobs, E. G., & Goldstein, J. M. (2018). The middle-aged brain: Biological sex and sex hormones shape memory circuitry. *Current Opinion in Behavioral Sciences*, *23*, 84–91. https://doi.org/10.1016/j.cobeha.2018.03.009

Jacobs, E. G., Weiss, B. K., Makris, N., Whitfield-Gabrieli, S., Buka, S. L., Klibanski, A., & Goldstein, J. M. (2016). Impact of sex and menopausal status on episodic memory circuitry in early midlife. *Journal of Neuroscience*, *36*(39), 10163–10173.

Jaywant, A., DelPonte, L., Kanellopoulos, D., O'Dell, M. W., & Gunning, F. M. (2020). The structural and functional neuroanatomy of post-stroke depression and executive dysfunction: A review of neuroimaging findings and implications for treatment. *Journal of Geriatric Psychiatry and Neurology*, 0891988720968270.

Jeurissen, B., Tournier, J. D., Dhollander, T., Connelly, A., & Sijbers, J. (2014). Multi-tissue constrained spherical deconvolution for improved analysis of multi-shell diffusion MRI data. *NeuroImage*, *103*, 411–426. https://doi.org/10.1016/j.neuroimage.2014.07.061

Jiang, R., Calhoun, V. D., Fan, L., Zuo, N., Jung, R., Qi, S., … Sui, J. (2020). Gender differences in connectome-based predictions of individualized intelligence quotient and sub-domain scores. *Cerebral Cortex*, *30*(3), 888–900.

Johansen-Berg, H., Scholz, J., & Stagg, C. J. (2010). Relevance of structural brain connectivity to learning and recovery from stroke. *Frontiers in Systems Neuroscience*, *4*, 146.

Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, *6*(10), 766–774.

Kasper, L., Bollmann, S., Diaconescu, A. O., Hutton, C., Heinzle, J., Iglesias, S., … Pruessmann, K. P. (2017). The physio toolbox for modeling physiological noise in fMRI data. *Journal of Neuroscience Methods*, *276*, 56–72.

Kawahara, J., Brown, C. J., Miller, S. P., Booth, B. G., Chau, V., Grunau, R. E., … Hamarneh, G. (2017). Brainnetcnn: Convolutional neural networks for brain networks; towards predicting neurodevelopment. *NeuroImage*, *146*, 1038–1049. https://doi.org/10.1016/j.neuroimage.2016.09.046

Kelly, A. C., Uddin, L. Q., Biswal, B. B., Castellanos, F. X., & Milham, M. P. (2008). Competition between functional brain networks mediates behavioral variability. *NeuroImage*, *39*(1), 527–537.

Klein, E., Suchan, J., Moeller, K., Karnath, H. O., Knops, A., Wood, G., … Willmes, K. (2016). Considering structural connectivity in the triple code model of numerical cognition: Differential connectivity for magnitude processing and arithmetic facts. *Brain Structure & Function*, *221*(2), 979–995. https://doi.org/10.1007/s00429-014-0951-1

Kong, R., Li, J., Orban, C., Sabuncu, M. R., Liu, H., Schaefer, A., … Yeo, B. T. T. (2018). Spatial topography of individual-specific cortical networks predicts human cognition, personality, and emotion. *Cerebral Cortex*, *29*(6), 2533–2551. https://doi.org/10.1093/cercor/bhy123

Koshiyama, D., Fukunaga, M., Okada, N., Yamashita, F., Yamamori, H., Yasuda, Y., … Watanabe, Y. (2018). Role of subcortical structures on cognitive and social function in schizophrenia. *Scientific Reports*, *8*(1), 1–9.

Leech, R., Kamourieh, S., Beckmann, C. F., & Sharp, D. J. (2011). Fractionating the default mode network: Distinct contributions of the ventral and dorsal posterior cingulate cortex to cognitive control. *Journal of Neuroscience*, *31*(9), 3217–3224.

Leiner, H. C., Leiner, A. L., & Dow, R. S. (1993). Cognitive and language functions of the human cerebellum. *Trends in Neurosciences*, *16*(11), 444–447.

Li, J. W., Kong, R., Liegeois, R., Orban, C., Tan, Y. R., Sun, N. B., … Yeo, B. T. T. (2019). Global signal regression strengthens association between resting-state functional connectivity and behavior. *NeuroImage*, *196*, 126–141. https://doi.org/10.1016/j.neuroimage.2019.04.016

Liégeois, R., Li, J., Kong, R., Orban, C., van de Ville, D., Ge, T., … Yeo, B. T. (2019). Resting brain dynamics at different timescales capture distinct aspects of human behavior. *Nature Communications*, *10*(1), 1–9.

Lord, A., Ehrlich, S., Borchardt, V., Geisler, D., Seidel, M., Huber, S., … Walter, M. (2016). Brain parcellation choice affects disease-related topology differences increasingly from global to local network levels. *Psychiatry Research: Neuroimaging*, *249*, 12–19.

Lungarella, M., & Sporns, O. (2006). Mapping information flow in sensorimotor networks. *PLoS Computational Biology*, *2*(10), e144.

MacKinnon, J. G., & (2009). Bootstrap hypothesis testing. In D. Belsley & K. Erricos John (Eds.), *Handbook of computational econometrics* (Vol. 183, p. 213). Chichester, England: John Wiley & Sons, Ltd.

Majerus, S., Attout, L., D'Argembeau, A., Degueldre, C., Fias, W., Maquet, P., … van der Linden, M. (2012). Attention supports verbal short-term memory via competition between dorsal and ventral attention networks. *Cerebral Cortex*, *22*(5), 1086–1097.

Maliniak, D., Powers, R., & Walter, B. F. (2013). The gender citation gap in international relations. *International Organization*, *67*(4), 889–922.

Marek, S., & Dosenbach, N. U. (2018). The frontoparietal network: Function, electrophysiology, and importance of individual precision mapping. *Dialogues in Clinical Neuroscience*, *20*(2), 133–140.

Matejko, A. A., Price, G. R., Mazzocco, M. M., & Ansari, D. (2013). Individual differences in left parietal white matter predict math scores on the

preliminary scholastic aptitude test. *NeuroImage*, *66*, 604–610. https://doi.org/10.1016/j.neuroimage.2012.10.045

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain Structure and Function*, *214*(5–6), 655–667.

Messé, A. (2020). Parcellation influence on the connectivity-based structure–function relationship in the human brain. *Human Brain Mapping*, *41*(5), 1167–1180.

Moeller, K., Willmes, K., & Klein, E. (2015). A review on functional and structural brain connectivity in numerical cognition. *Frontiers in Human Neuroscience*, *9*, 227. https://doi.org/10.3389/fnhum.2015.00227

Mungas, D., Heaton, R., Tulsky, D., Zelazo, P. D., Slotkin, J., Blitz, D., … Gershon, R. (2014). Factor structure, convergent validity, and discriminant validity of the NIH toolbox cognitive health battery (NIHTB-CHB) in adults. *Journal of the International Neuropsychological Society*, *20*(6), 579–587. https://doi.org/10.1017/S1355617714000307

Nilsson, J. P., Söderström, M., Karlsson, A. U., Lekander, M., Åkerstedt, T., Lindroth, N. E., & Axelsson, J. (2005). Less effective executive functioning after one night's sleep deprivation. *Journal of Sleep Research*, *14*(1), 1–6.

O'Neill, J., Kamper-DeMarco, K., Chen, X., & Orom, H. (2020). Too stressed to self-regulate? Associations between stress, self-reported executive function, disinhibited eating, and BMI in women. *Eating Behaviors*, *39*, 101417.

Pamplona, G. S., Santos Neto, G. S., Rosset, S. R., Rogers, B. P., & Salmon, C. E. (2015). Analyzing the association between functional connectivity of the brain and intellectual performance. *Frontiers in Human Neuroscience*, *9*, 61. https://doi.org/10.3389/fnhum.2015.00061

Patenaude, B., Smith, S. M., Kennedy, D. N., & Jenkinson, M. (2011). A Bayesian model of shape and appearance for subcortical brain segmentation. *NeuroImage*, *56*(3), 907–922.

Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., … Duchesnay, E. (2011). Scikit-learn: Machine learning in python. *Journal of Machine Learning Research*, *12*, 2825–2830.

Pehrs, C., Zaki, J., Schlochtermeier, L. H., Jacobs, A. M., Kuchinke, L., & Koelsch, S. (2017). The temporal pole top-down modulates the ventral visual stream during social cognition. *Cerebral Cortex*, *27*(1), 777–792.

Peng, L., Zeng, L. L., Liu, Q., Wang, L., Qin, J., Xu, H., … Hu, D. (2018). Functional connectivity changes in the entorhinal cortex of taxi drivers. *Brain and Behavior*, *8*(9), e01022.

Pievani, M., Filippini, N., van den Heuvel, M. P., Cappa, S. F., & Frisoni, G. B. (2014). Brain connectivity in neurodegenerative diseases—From phenotype to proteinopathy. *Nature Reviews Neurology*, *10*(11), 620–633.

Ramanoël, S., York, E., le Petit, M., Lagrené, K., Habas, C., & Arleo, A. (2019). Age-related differences in functional and structural connectivity in the spatial navigation brain network. *Frontiers in Neural Circuits*, *13*, 69.

Respino, M., Jaywant, A., Kuceyeski, A., Victoria, L. W., Hoptman, M. J., Scult, M. A., … Murri, M. B. (2019). The impact of white matter hyperintensities on the structural connectome in late-life depression: Relationship to executive functions. *NeuroImage: Clinical*, *23*, 101852.

Rolls, E. T., Huang, C.-C., Lin, C.-P., Feng, J., & Joliot, M. (2020). Automated anatomical labelling atlas 3. *NeuroImage*, *206*, 116189.

Salimi-Khorshidi, G., Douaud, G., Beckmann, C. F., Glasser, M. F., Griffanti, L., & Smith, S. M. (2014). Automatic denoising of functional MRI data: Combining independent component analysis and hierarchical fusion of classifiers. *NeuroImage*, *90*, 449–468. https://doi.org/10.1016/j.neuroimage.2013.11.046

Salthouse, T. A. (2010). Selective review of cognitive aging. *Journal of the International Neuropsychological Society: JINS*, *16*(5), 754–760.

Satterthwaite, T. D., Wolf, D. H., Roalf, D. R., Ruparel, K., Erus, G., Vandekar, S., … Gur, R. C. (2015). Linked sex differences in cognition and functional connectivity in youth. *Cerebral Cortex*, *25*(9), 2383–2394. https://doi.org/10.1093/cercor/bhu036

Schmahmann, J. D., & Caplan, D. (2006). Cognition, emotion and the cerebellum. *Brain*, *129*(2), 290–292.

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., … Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *The Journal of Neuroscience*, *27*(9), 2349–2356. https://doi.org/10.1523/JNEUROSCI.5587-06.2007

Segonne, F., Grimson, E., & Fischl, B. (2005). A genetic algorithm for the topology correction of cortical surfaces. *Information Processing in Medical Imaging*, *19*, 393–405.

Seidlitz, J., Vasa, F., Shinn, M., Romero-Garcia, R., Whitaker, K. J., Vertes, P. E., … Bullmore, E. T. (2018). Morphometric similarity networks detect microscale cortical organization and predict inter-individual cognitive variation. *Neuron*, *97*(1), 231, e237–247. https://doi.org/10.1016/j.neuron.2017.11.039

Sheline, Y. I., Barch, D. M., Price, J. L., Rundle, M. M., Vaishnavi, S. N., Snyder, A. Z., … Raichle, M. E. (2009). The default mode network and self-referential processes in depression. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(6), 1942–1947.

Smith, R. E., Tournier, J.-D., Calamante, F., & Connelly, A. (2012). Anatomically-constrained tractography: Improved diffusion MRI streamlines tractography through effective use of anatomical information. *NeuroImage*, *62*(3), 1924–1938.

Smith, R. E., Tournier, J.-D., Calamante, F., & Connelly, A. (2015). Sift2: Enabling dense quantitative assessment of brain white matter connectivity using streamlines tractography. *NeuroImage*, *119*, 338–351.

Song, J., Birn, R. M., Boly, M., Meier, T. B., Nair, V. A., Meyerand, M. E., & Prabhakaran, V. (2014). Age-related reorganizational changes in modularity and functional connectivity of human brain networks. *Brain Connectivity*, *4*(9), 662–676.

Song, M., Liu, Y., Zhou, Y., Wang, K., Yu, C., & Jiang, T. (2009). Default network and intelligence difference. *Conference Proceedings: Annual International Conference of the IEEE Engineering in Medicine and Biology Society*, *2009*, 2212–2215. https://doi.org/10.1109/IEMBS.2009.5334874

Song, M., Zhou, Y., Li, J., Liu, Y., Tian, L., Yu, C., & Jiang, T. (2008). Brain spontaneous functional connectivity and intelligence. *NeuroImage*, *41*(3), 1168–1176. https://doi.org/10.1016/j.neuroimage.2008.02.036

Spreng, R. N., & Grady, C. L. (2010). Patterns of brain activity supporting autobiographical memory, prospection, and theory of mind, and their relationship to the default mode network. *Journal of Cognitive Neuroscience*, *22*(6), 1112–1123.

Sripada, R. K., Swain, J. E., Evans, G. W., Welsh, R. C., & Liberzon, I. (2014). Childhood poverty and stress reactivity are associated with aberrant functional connectivity in default mode network. *Neuropsychopharmacology*, *39*(9), 2244–2251.

Thiem, Y., Sealey, K. F., Ferrer, A. E., Trott, A. M., & Kennison, R. (2018). Just ideas? The status and future of publication ethics in philosophy: A white paper

Tooley, U. A., Mackey, A. P., Ciric, R., Ruparel, K., Moore, T. M., Gur, R. C., … Bassett, D. S. (2019). Associations between neighborhood SES and functional brain network development. *Cerebral Cortex*, *30*(1), 1–19. https://doi.org/10.1093/cercor/bhz066

Tournier, J. D., Calamante, F., & Connelly, A. (2010). Improved probabilistic streamlines tractography by 2nd order integration over fibre orientation distributions. Paper Presented at the Proceedings of the International Society for Magnetic Resonance in Medicine.

Tournier, J. D., Calamante, F., & Connelly, A. (2012). Mrtrix: Diffusion tractography in crossing fiber regions. *International Journal of Imaging Systems and Technology*, *22*(1), 53–66.

Tulsky, D. S., Holdnack, J. A., Cohen, M. L., Heaton, R. K., Carlozzi, N. E., Wong, A. W. K., … Heinemann, A. W. (2017). Factor structure of the NIH toolbox cognition battery in individuals with acquired brain injury.

Rehabilitation Psychology, *62*(4), 435–442. https://doi.org/10.1037/rep0000183

Uddin, L. Q., Supekar, K. S., Ryali, S., & Menon, V. (2011). Dynamic reconfiguration of structural and functional connectivity across core neurocognitive brain networks with development. *The Journal of Neuroscience*, *31*(50), 18578–18589. https://doi.org/10.1523/JNEUROSCI.4465-11.2011

Utter, A. A., & Basso, M. A. (2008). The basal ganglia: An overview of circuits and function. *Neuroscience & Biobehavioral Reviews*, *32*(3), 333–342.

van den Heuvel, M. P., Stam, C. J., Kahn, R. S., & Hulshoff Pol, H. E. (2009). Efficiency of functional brain networks and intellectual performance. *The Journal of Neuroscience*, *29*(23), 7619–7624. https://doi.org/10.1523/JNEUROSCI.1443-09.2009

van Essen, D. C., Smith, S. M., Barch, D. M., Behrens, T. E., Yacoub, E., Ugurbil, K., & WU-Minn Human Connectome Project. (2013). The WU-Minn Human Connectome Project: An overview. *NeuroImage*, *80*, 62–79. https://doi.org/10.1016/j.neuroimage.2013.05.041

van Schouwenburg, M. R., den Ouden, H. E., & Cools, R. (2010). The human basal ganglia modulate frontal-posterior connectivity during attention shifting. *Journal of Neuroscience*, *30*(29), 9910–9918.

Vatansever, D., Manktelow, A., Sahakian, B. J., Menon, D. K., & Stamatakis, E. A. (2018). Default mode network engagement beyond self-referential internal mentation. *Brain Connectivity*, *8*(4), 245–253.

Viviani, R. (2016). A digital atlas of middle to large brain vessels and their relation to cortical and subcortical structures. *Frontiers in Neuroanatomy*, *10*, 12.

Wallis, G., Stokes, M., Cousijn, H., Woolrich, M., & Nobre, A. C. (2015). Frontoparietal and cingulo-opercular networks play dissociable roles in control of working memory. *Journal of Cognitive Neuroscience*, *27*(10), 2019–2034.

Weintraub, S., Bauer, P. J., Zelazo, P. D., Wallner-Allen, K., Dikmen, S. S., Heaton, R. K., … Gershon, R. C. (2013). I. NIH toolbox cognition battery (CB): Introduction and pediatric data. *Monographs of the Society for Research in Child Development*, *78*(4), 1–15. https://doi.org/10.1111/mono.12031

Weintraub, S., Dikmen, S. S., Heaton, R. K., Tulsky, D. S., Zelazo, P. D., Slotkin, J., … Gershon, R. (2014). The cognition battery of the NIH toolbox for assessment of neurological and behavioral function: Validation in an adult sample. *Journal of the International Neuropsychological Society*, *20*(6), 567–578. https://doi.org/10.1017/S1355617714000320

Weis, S., Patil, K. R., Hoffstaedter, F., Nostro, A., Yeo, B. T. T., & Eickhoff, S. B. (2019). Sex classification by resting state brain connectivity. *Cerebral Cortex*, *30*, 824–835. https://doi.org/10.1093/cercor/bhz129

Willmes, K., Moeller, K., & Klein, E. (2014). Where numbers meet words: A common ventral network for semantic classification. *Scandinavian Journal of Psychology*, *55*(3), 202–211. https://doi.org/10.1111/sjop.12098

Wilson, R. C., Takahashi, Y. K., Schoenbaum, G., & Niv, Y. (2014). Orbitofrontal cortex as a cognitive map of task space. *Neuron*, *81*(2), 267–279.

Wu, Z., Xu, D., Potter, T., Zhang, Y., & Alzheimer's Disease Neuroimaging Initiative. (2019). Effects of brain parcellation on the characterization of topological deterioration in Alzheimer's disease. *Frontiers in Aging Neuroscience*, *11*, 113.

Yeo, B. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., … Polimeni, J. R. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*(3), 1125–1165.

Zalesky, A., Fornito, A., Harding, I. H., Cocchi, L., Yücel, M., Pantelis, C., & Bullmore, E. T. (2010). Whole-brain anatomical networks: Does the choice of nodes matter? *NeuroImage*, *50*(3), 970–983.

Zatorre, R. J., Fields, R. D., & Johansen-Berg, H. (2012). Plasticity in gray and white: Neuroimaging changes in brain structure during learning. *Nature Neuroscience*, *15*(4), 528–536.

Zelazo, P. D., Anderson, J. E., Richler, J., Wallner-Allen, K., Beaumont, J. L., Conway, K. P., … Weintraub, S. (2014). NIH toolbox cognition battery (CB): Validation of executive function measures in adults. *Journal of the International Neuropsychological Society*, *20*(6), 620–629. https://doi.org/10.1017/S1355617714000472

Zimmermann, J., Griffiths, J. D., & McIntosh, A. R. (2018). Unique mapping of structural and functional connectivity on cognition. *The Journal of Neuroscience*, *38*(45), 9658–9667. https://doi.org/10.1523/JNEUROSCI.0900-18.2018

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Dhamala E, Jamison KW, Jaywant A, Dennis S, Kuceyeski A. Distinct functional and structural connections predict crystallised and fluid cognition in healthy adults. *Hum Brain Mapp*. 2021;42:3102–3118. https://doi.org/10.1002/hbm.25420