

# Connectome-based predictive modeling of fluid intelligence: evidence for a global system of functionally integrated brain networks

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Cognitive neuroscience continues to advance our understanding of the neural foundations of human intelligence, with significant progress elucidating the role of the frontoparietal network in cognitive control mechanisms for flexible, intelligent behavior. Recent evidence in network neuroscience further suggests that this finding may represent the tip of the iceberg and that fluid intelligence may depend on the collective interaction of multiple brain networks. However, the global brain mechanisms underlying fluid intelligence and the nature of multi-network interactions remain to be well established. We therefore conducted a large-scale Connectome-based Predictive Modeling study, administering resting-state fMRI to 159 healthy college students and examining the contributions of seven intrinsic connectivity networks to the prediction of fluid intelligence, as measured by a state-of-the-art cognitive task (the Bochum Matrices Test). Specifically, we aimed to: (i) identify whether fluid intelligence relies on a primary brain network or instead engages multiple brain networks; and (ii) elucidate the nature of brain network interactions by assessing network allegiance (within- versus between-network connections) and network topology (strong versus weak connections) in the prediction of fluid intelligence. Our results demonstrate that whole-brain predictive models account for a large and significant proportion of variance in fluid intelligence (18%) and illustrate that the contribution of individual networks is relatively modest by comparison. In addition, we provide novel evidence that the global architecture of fluid intelligence prioritizes between-network connections and flexibility through weak ties. Our findings support a network neuroscience approach to understanding the collective role of brain networks in fluid intelligence and elucidate the system-wide network mechanisms from which flexible, adaptive behavior is constructed.

**Key words:** human intelligence; fluid intelligence; connectome-based predictive modeling; network neuroscience theory; computational cognitive; neuroscience.

## Introduction

Research in the psychological and brain sciences has long sought to understand the nature and mechanisms of human intelligence (for a recent review, see Barbey et al. 2021). The foundations of modern research in this effort were established in the early twentieth century by Charles Spearman, who found that performance across a wide range of academic achievement measures were positively correlated and proposed a general factor,  $g$ , to account for the component of individual differences variance that is common across all tests of mental ability (Spearman 1904). Within factor analytic studies of intelligence, the best measures of  $g$  involve fluid intelligence ( $G_f$ ; Horn and Cattell 1966; Carroll 1993). Fluid intelligence represents the ability to solve novel problems and to reason adaptively in the face of limited knowledge and experience. The capacity to perform well on tests of  $G_f$  is known to predict professional and educational success (Jaeggi et al. 2008). Additionally,  $G_f$  is closely tied to general intelligence (Gray and Thompson 2004), which is predictive of success across a wide spectrum of cognitive domains, from educational and career achievements to social

well-being and mental health (Jensen 1998). Although research in psychometrics has enabled the precise measurement and modeling of  $G_f$ , uncovering the information processing architecture of intelligence requires multidisciplinary studies that incorporate evidence from cognitive neuroscience.

Early research in the neuroscientific study of intelligence established the importance of the prefrontal cortex (PFC) in general intelligence (Duncan et al. 2000), with a focus on the involvement of the dorsolateral PFC in cognitive control (Barbey et al. 2013). The later emergence of network-based theories reflected an effort to examine the neurobiology of intelligence through a wider lens, accounting for individual differences in  $G_f$  by appealing to distributed brain networks. The influential Parietal-Frontal Integration Theory (P-FIT) was the first to propose that “a discrete parieto-frontal network underlies intelligence” (Jung and Haier 2007) and that  $G_f$  reflects the capacity of this network to evaluate and test hypotheses for problem-solving (Gläscher et al. 2009; Barbey et al. 2012). A central feature of the P-FIT model is the integration of knowledge between

frontal and parietal cortex, afforded by white-matter fiber tracks that enable efficient communication among cortical regions. Evidence to support the frontoparietal network's role in a wide range of problem-solving tasks later motivated the Multiple-Demand (MD) Theory, which appeals to an even broader network of frontoparietal and cinguloopercular regions to account for cognitive control functions underlying  $G_f$  (Duncan 2010). Finally, the Process Overlap Theory (POT) represents a recent network-based approach that accounts for individual differences in  $G_f$  by appealing to the spatial overlap among specific cortical networks, reflecting the shared cognitive processes underlying task performance (Kovacs and Conway 2016). Given the focus of this theory on spatial overlap, this view emphasizes the role of strong connections that integrate and bind neural representations (in contrast to weak connections that reflect less spatial overlap; for evidence on the role of weak connections in general intelligence, see Anderson and Barbey 2023). Thus, contemporary theories suggest that individual differences in  $G_f$  originate from functionally localized processes within a specific cortical region, primary brain network, or the spatial overlap among networks.

Although theories of fluid intelligence have historically endorsed a localizationist perspective (for a recent review, see Barbey et al. 2021), accumulating evidence indicates that flexible behavior emerges from the dynamic recruitment and orchestration of multiple brain networks, reflecting a collective synthesis of functions within the human connectome. Indeed, a classic measure of fluid intelligence, the Matrix Reasoning Task, is known to engage cognitive operations for executive (Barbey et al. 2014), attentional (Petersen and Posner 2012), and perceptual processing (Shipstead and Yonehiro 2016). The rapidly developing field of network neuroscience further suggests that these functions recruit a highly distributed and interactive set of networks that collectively enable adaptive behavior (for a review, see Bassett and Sporns 2017).

Motivated by this emergent perspective, the Network Neuroscience Theory (NNT) proposes that  $G_f$  originates from individual differences in the system-wide topology and dynamics of the human brain (Barbey 2018). In the context of Matrix Reasoning, this framework predicts that multiple networks are engaged to support the executive, attentional, and perceptual processing underlying task performance (see also Duncan et al. 2020). Thus, rather than originate from a fixed set of cortical regions, a primary brain network, or the spatial overlap among networks, this theory emphasizes the need for dynamic information processing and the capacity to flexibly engage multiple brain networks in the service of task demands (Desimone et al. 1990; Desimone and Duncan 1995; Miller and Cohen 2001; Cole et al. 2013). Research in network neuroscience further suggests that fluid intelligence may rely on weak connections that enable the system to function within many difficult-to-reach network states (Barbey 2018), reflecting the capacity to adapt to novel situations by engaging mechanisms for flexible, goal-directed behavior (Gu et al. 2015; Anderson and Barbey 2023). The NNT framework therefore: (i) predicts that fluid cognition will engage between-network connections that integrate executive, attentional, and perceptual processes; and (ii) emphasizes the importance of weak connections in the formation of globally coordinated neural representations.

To investigate the predictions of this framework, the present study sought to: (i) examine whether the profile of functional connections that predict individual differences in  $G_f$  reside within a specific brain network or are distributed across multiple networks; and (ii) further characterize the network architecture of

fluid intelligence by investigating network allegiance (examining within- versus between-network connections) and network topology in the prediction of  $G_f$  (investigating the contribution of strong versus weak connections). We assessed these predictions by employing Connectome-based Predictive Modeling (CPM; Shen et al. 2017), a rigorous, cross-validation framework to establish predictive models of fluid intelligence from functional connectivity data.

Building upon recent predictive modeling studies of general intelligence (Anderson and Barbey 2023), the present research applied CPM methods to the novel context of fluid intelligence. Our study sought to incorporate methodological advances in the assessment of  $G_f$  and to conduct the highest fidelity CPM study of fluid intelligence reported to date. Prior CPM studies (Finn et al. 2015; Noble et al. 2017) have employed the Penn Matrix Reasoning Task (Gur et al. 2001, 2010, 2012), which exhibits important methodological limitations (Sefcek et al. 2016; Pahor et al. 2019). Although this task provides a time-efficient estimate of fluid intelligence, it is very brief, with an average administration time of less than 5 minutes (mean = 4.6 minutes; standard deviation = 3 minutes; Gur et al. 2012) and presents relatively simple problems of a small matrix size (i.e.  $2 \times 2$ ,  $3 \times 3$ , or  $5 \times 1$  matrices). These factors are known to: (i) reduce problem difficulty, (ii) decrease discriminability at high levels of performance (due to ceiling effects), and (iii) limit test reliability (Sefcek et al. 2016; Pahor et al. 2019). Indeed, testing guidelines for the assessment of fluid intelligence classify this measure as of "fair" quality (Gignac and Bates 2017; see also Dubois et al. 2018). Taken together, these methodological factors may limit the precision and generalizability of conclusions drawn about  $G_f$  from this task.

The present study sought to address this concern by administering a high-fidelity measure of fluid intelligence, the Bochum Matrices Test (BOMAT; Hossiep et al. 2001). In contrast to traditional tests of  $G_f$ , the BOMAT: (i) is completed in approximately 60 minutes (rather than 5 minutes); (ii) employs a larger matrix size (i.e. presenting  $5 \times 3$  matrices); and (iii) introduces a time limit of 1 hour to emphasize task efficiency. These changes to the matrix reasoning materials and experimental protocol together serve to increase task difficulty, reduce ceiling effects, and enable a high-fidelity assessment of fluid intelligence (Hossiep et al. 2001).

Thus, we aimed to advance prior research by employing the highest fidelity measure of fluid intelligence in a CPM study to date. By administering a rigorous test of  $G_f$  and applying contemporary CPM methods, the present study sought to elucidate the network architecture of fluid intelligence and to support theory-driven research on the neural mechanisms that give rise to flexible, adaptive behavior.

## Methods

### Participants

One hundred and fifty-nine healthy young adults were enrolled in the study (41% female, ages 18–44 years, mean  $25 \pm 6.08$  years) as part of a larger intervention trial (INSIGHT Phase 1a; for further detail, see Ward et al. 2017). This cohort is separate from the INSIGHT Phase 1b investigation of general intelligence reported by Anderson and Barbey 2023. The data in the present study are from the pre-intervention assessment and are therefore unaffected by the larger project. All subjects gave written informed consent in accordance with the Declaration of Helsinki. Study inclusion criteria recruited adults: (i) aged 18–44 years; (ii) fluent in English; (iii) possessing at least a high-school diploma; (iv) with normal or

corrected to normal vision and hearing; (v) free of any psychoactive medication; (vi) without history of neurological, psychological, or endocrine disease; (vii) without history of concussion for the past 2 years; (viii) not having learning disorders; (ix) not smoking > 10 cigarettes a day; (x) with a body mass index < 35; and (xi) with at least one positive response on the revised Physical Activity Readiness Questionnaire (Thomas et al. 1992). Additionally, to reduce the presence of motion artifacts in the fMRI analysis, we removed participants with a mean framewise displacement of more than 0.20 mm. All subjects reported in the present analysis were randomly assigned to brain imaging data collection and were right-handed.

### Cognitive assessment of fluid intelligence

The BOMAT Advanced Short Version is a well-validated Matrix Reasoning Task that assesses the adaptive problem-solving skills underlying fluid intelligence (Hossiep et al. 2001). Each trial consists of a  $5 \times 3$  matrix of abstract visuospatial figures whose shapes are governed by an unknown rule. The participant's task is to discover this rule and to select the figure that completes the pattern in the final empty cell of the matrix, choosing among 6 response options. The test consists of 10 practice items followed by 29 test questions arranged in ascending order of difficulty. In the present study, participants were randomly selected to receive either Version A or Version B and given 60 minutes to complete as many questions as possible. The large matrix size, progressive task difficulty, and time limit of the BOMAT serve to reduce ceiling effects and enable a high-fidelity assessment of task performance. In the context of the present brain imaging study, these properties help to ensure that individual differences in brain networks underlying fluid intelligence can be identified. Following standard procedures, performance on the BOMAT was analyzed according to normative (standard ten) scores based on a German population of 668 graduate and undergraduate students 18–35 years of age. All tests were completed through an online portal administered by Hogrefe Publishing Group (<https://www.hogrefe.com/uk/>).

### MRI data acquisition and preprocessing

All data were collected on a Siemens Magnetom 3 Tesla Trio scanner using a 32-channel head coil in the Beckman Institute Biomedical Imaging Center at the University of Illinois. A high-resolution multi-echo T1-weighted magnetization prepared gradient-echo structural image was acquired for each participant (0.9 mm isotropic; TR: 1,900 ms; TI: 900 ms; TE 2.32 ms, with GRAPPA and an acceleration factor of 2). The functional neuroimaging data were acquired using an accelerated gradient-echo echoplanar imaging (EPI) sequence (Auerbach et al. 2013), sensitive to blood oxygenation level dependent (BOLD) contrast ( $1.9 \times 1.9 \times 2.0$  mm<sup>3</sup> voxel size; 56 slices with 10% slice gap; TR: 2,000 ms; TE: 30 ms; FOV: 240 mm; 90° flip angle; 10-minute acquisition or 300 volumes). During the resting-state fMRI scan, participants were shown a white crosshair on a black background viewed on an LCD monitor through a head coil-mounted mirror. Participants were instructed to lie still, focus on the visually presented crosshair, and keep their eyes open (Van Dijk et al. 2010).

All MRI data processing was conducted using FSL (Version 5.0; <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>), Freesurfer (Version 7.1.1; <https://surfer.nmr.mgh.harvard.edu/fswiki/FreeSurferWiki/>), and AFNI (Version 20.2.05; <https://afni.nimh.nih.gov/>). The high-resolution T1 MPRAGE was brain-extracted using Freesurfer (Fischl 2012). Freesurfer segmentation was performed to delineate gray matter, white matter, and CSF voxels. Resting-state fMRI

data were preprocessed using FSL and AFNI analysis tools (Cox 1996). We applied conventional methods for resting-state fMRI data preprocessing, which entailed: (i) motion correction; (ii) distortion correction and registration to T1 space (2-mm isotropic voxel resolution); (iii) intensity normalization; (iv) non-aggressive ICA-AROMA denoising; (v) nuisance signal regression, temporal band-pass filtering (0.01–0.08 Hz), and linear detrending; and (vi) nonlinear registration of images to the FsAverage brain template (2-mm isotropic voxel resolution).

Given the importance of accounting for motion-related noise components, signal and noise variables were first modeled using ICA-AROMA. This method is known to outperform other more traditional motion denoising procedures (Parkes et al. 2018). The intensity normalized functional images were smoothed using a 6-mm full width at half-max kernel implemented with FSL's SUSAN (Pruim et al. 2015). Noise components were then non-aggressively removed from the non-smoothed functional images using FSL's Regfilt function. After removal of motion-related noise components, white matter and cerebrospinal fluid signals were averaged across all voxels identified from the Freesurfer segmentation of the high-resolution MPRAGE. The physical regressors were removed from the functional images using AFNI's 3dtProject while simultaneously performing bandpass filtering and linear detrending (Lindquist et al. 2019).

### Potential confounds

To examine whether brain size and head motion constitute confounding variables in the present study, we performed two follow up analyses. Here, brain volumetrics were extracted from Freesurfer's total gray matter volume output, and head motion metrics were generated as mean framewise displacement. The results of this analysis show that the relationship between brain size ( $\beta = 1.08e-6$ ;  $P = 0.24$ ) and head motion ( $\beta = -7.53$ ;  $P = 0.08$ ) with intelligence are both null and therefore do not constitute confounding variables in need of removal.

### Connectome-based predictive modeling of fluid intelligence

To generate functional connectomes, cortical regions were defined using the Human Connectome Project's Multi-modal Parcellation (Glasser et al. 2016). This parcellation was chosen to remain consistent with prior literature examining the neural bases of intelligence (Dubois et al. 2018). A template in Freesurfer's FsAverage space for the Glasser parcellation was applied (created by Dr Kathryn Mills from data supplied by the HCP group and available here: [https://figshare.com/articles/dataset/HCP-MMP1\\_0\\_projected\\_on\\_fsaverage/3498446](https://figshare.com/articles/dataset/HCP-MMP1_0_projected_on_fsaverage/3498446)). The generation of functional connectomes was performed using NiLearn (Version 0.6.2; <https://nilearn.github.io/stable/index.html>). Cortical regions were then assigned to one of seven intrinsic connectivity networks (ICNs) to be used in network specific predictive models (described below). To define the seven ICNs, we adopted the community assignment protocol originally generated by Ito and colleagues (Ito et al. 2017) using the Generalized Louvain method with resting-state fMRI data from the HCP data set and the Glasser parcellation (for further validation, see Dubois et al. 2018).

The present study employed an established CPM framework to examine the relationship between resting-state functional connectivity and fluid intelligence as measured by the BOMAT (Finn et al. 2015; Shen et al. 2017; Dubois et al. 2018). CPM is a data-driven method to establish and validate functional connectivity profiles that predict fluid intelligence through cross-validation.

In this approach, a univariate feature selection method is first applied to reduce the number of features in each prediction model by retaining only the connections that are reliably associated with  $G_f$  in the training dataset (size= $n - 1$ ). This feature selection process correlates all edges with fluid intelligence scores and discards edges whose  $P$ -value is above 0.01. Although the feature selection process reduces the number of edges, thousands of edges still remain, motivating the need to further reduce the number of features through the use of a regularization procedure. We therefore employed an elastic net model with regularization, implemented via the *Caret* package in R. Following Dubois et al. (2018), we fit the functional connectivity features to the observed  $G_f$  scores using a three-fold cross-validation procedure on the inner loop and selected the best alpha parameter from 50 different values. Each fold is created using an equal distribution based on partitioning the behavioral scores into quartiles. The best-performing model in the inner loop is then used to make a prediction on the held-out test subject.

Our application of CPM incorporates methodological refinements that enable a novel investigation of network allegiance and network topology in the prediction of fluid intelligence. With respect to network allegiance, we investigated the predictive success of models derived from including only connections: (i) within each network versus (ii) between pairwise networks.

With respect to the network topology, we investigated the strength of between-network connections that survived feature selection to determine whether  $G_f$  relies primarily on strong versus weak functional connections. Thus, the present study provides a novel lens for investigating the contributions of network allegiance and network topology to the prediction of fluid intelligence.

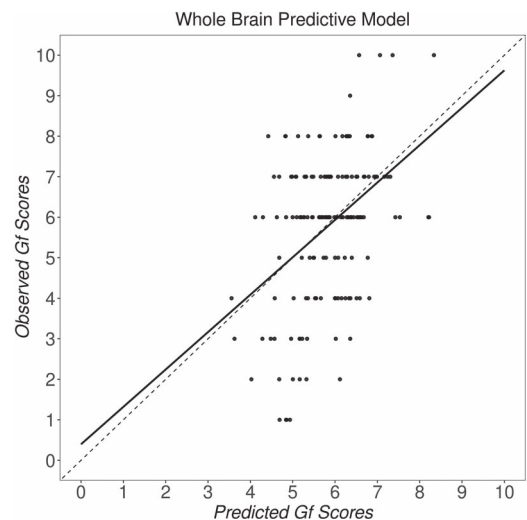
## Statistical analysis

We report multiple metrics to quantify the predictive success of functional connectivity profiles derived from CPM, including a Pearson correlation coefficient ( $R$ ), a coefficient of determination ( $R^2$ ), and a normalized root mean square deviation ( $nRMSD$ ) between the observed and predicted scores. To assess the statistical significance of CPM results we conducted a permutation test with 1000 random permutations, following established conventions (Finn et al. 2015; Shen et al. 2017; Dubois et al. 2018). This method creates a null distribution by randomly shuffling scores between subjects and running the predictive model in exactly the same manner. Permutation testing is necessary to establish statistical significance in cross-validation because folds are not independent from one another (and therefore standard parametric statistical tests are not warranted).

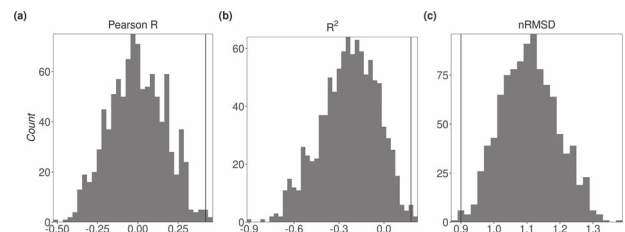
## Results

### Investigating the role of whole-brain functional connectivity in the prediction of fluid intelligence

We conducted nested leave-one-out cross-validation to train an elastic net model to predict out-of-sample  $G_f$  scores from whole-brain functional connectomes. Consistent with the predicted role of large-scale network mechanisms in fluid intelligence, we found that whole-brain resting-state functional connectivity accounted for a large proportion of variance in  $G_f$  (18%), yielding a significant correlation between observed and predicted  $G_f$  scores ( $R=0.42$ ;  $P_{1000}=0.004$ ; Fig. 1). In addition, we observed a significant coefficient of determination ( $R^2=0.18$ ;  $P_{1000}=0.004$ ) and an  $nRMSD$  that was significantly lower than the  $nRMSD$  from the null distribution ( $nRMSD=0.90$ ;  $P_{1000}=0.004$ ; Fig. 2).



**Fig. 1.** Whole-brain resting-state functional connectivity reliably predicts fluid intelligence ( $R=0.42$ ;  $R^2=0.18$ ;  $nRMSD=0.90$ ). The regression line is illustrated in black with the dashed black line providing a reference regression line with a slope of 1.

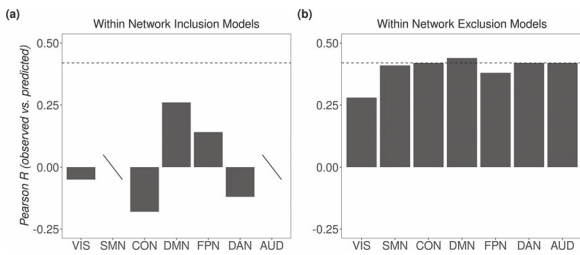


**Fig. 2.** Permutation test of performance metrics (with 1,000 shuffled datasets) to establish statistical significance with respect to an empirically derived null distribution. Black lines represent statistical values from the whole-brain model. (a) The correlation between predicted and observed values. (b) The coefficient of determination describing the proportion of variance explained. (c) The normalized root mean squared deviation conveying the average differences between predicted and observed scores.

### Investigating the contribution of specific brain networks to the prediction of fluid intelligence

A central question raised by the observed role of whole-brain functional connectivity in the prediction of  $G_f$  is whether this finding is driven by a specific set of brain networks. We therefore examined connections residing within each of the seven ICNs, systematically investigating the inclusion versus exclusion of each ICN in the prediction of  $G_f$ . This approach implements the same analysis pipeline described previously for the whole-brain model but either: (i) only includes connections within a specific ICN (i.e. the inclusion model); or (ii) excludes connections within a specific ICN from the whole-brain model (i.e. the exclusion model; cf., Dubois et al. 2018).

As Fig. 3(a) illustrates, the capacity to predict fluid intelligence from each of the seven networks was significantly lower than the whole-brain model (i.e. each bar of the histogram lies below the black-dashed line). Among the examined networks, the default mode (DMN) and frontoparietal (FPN) networks performed moderately well, suggesting that connections within each network carry information that is important for the prediction of  $G_f$  (relative to connections within other brain networks; Fig. 3a). Critically, however, the contribution of these networks in isolation is modest compared with the whole-brain model and therefore represents a narrow window for: (i) defining the network architecture of fluid intelligence, which appears to depend more heavily on global



**Fig. 3.** Prediction models derived from either (a) including versus (b) excluding connections within a specific ICN in the prediction of fluid intelligence. VIS=visual network, SMN=somatomotor network, CON=cinguloopercular network, DMN=default mode network, FPN=frontoparietal network, DAN=dorsal attention network, AUD=auditory network. The black-dashed line represents the performance of the whole-brain model. Black strikes indicate networks whose connections did not survive feature selection.

information processing (Figs. 1 and Fig. 3a); and (ii) explaining the functional role of these networks, which may reflect interactions with other ICNs. Indeed, a growing literature suggests that high-level cognition depends on the FPN's capacity to flexibly encode task-relevant information and orchestrate the recruitment and coordination of multiple brain networks in the service of goal-directed behavior (Desimone et al. 1990; Desimone and Duncan 1995; Miller and Cohen 2001; Cole et al. 2013).

In addition, we observed networks that resulted in modest negative prediction accuracy, including the cinguloopercular network (CON) and the dorsal attention network (DAN; Fig. 3a). These findings suggest that each network may: (i) compete with or inhibit the functions underlying fluid intelligence; and/or (ii) interact with other ICNs to produce a net positive contribution to  $G_f$  (rather than operating in isolation). We examine the latter possibility in the between-network models investigated below. Finally, we observed that connections within the somatomotor network (SMN) and the auditory network (AUD) did not survive the feature selection process, suggesting that these networks do not advance the prediction of fluid intelligence in isolation (Fig. 3a).

When removing within-network edges, we observed a reduction in performance for the visual network (VIS), whereas performance changed only minimally when removing connections within the other networks (Fig. 3b). Thus, our findings implicate the VIS network in the representation of visuospatial figures of the BOMAT (Fig. 3a). Finally, it should be noted that although the DMN inclusion model performed moderately well, the removal of these connections in the exclusion model increased predictive accuracy by a correlation of 0.03. These subtle differences in the performance of inclusion versus exclusion models have been observed in prior studies (Dubois et al. 2018) and are likely due to differences in the tuning of hyperparameters between models and/or sources of error in the prediction. Overall, our findings support the predictions of the NNT framework, demonstrating that fluid intelligence emerges from global, system-wide network mechanisms, with whole-brain models significantly outperforming those derived from specific networks (Fig. 3a) and relatively modest changes when an individual ICN is removed (Fig. 3b).

### Investigating the contribution of pairwise network interactions to the prediction of fluid intelligence

To further investigate how the observed global representations are constructed from network interactions, we conducted an analysis of between-network connections for each pair of ICNs in the prediction of  $G_f$ . This was accomplished by applying

the previously described inclusion versus exclusion modeling approach but in the context of between- (rather than within-) network connections.

Among the network interactions examined, we found the best performance for the between-network inclusion model of the FPN and DAN ( $R=0.37$ ; Fig. 4a). This finding accords with recent evidence to suggest that interactions between these networks enable the regulation and control of perceptual attention (Dixon et al. 2018), processes that are important for visuospatial reasoning in the BOMAT. In addition, we identified several other between-network inclusion models that performed moderately well, including the FPN-SMN ( $R=0.23$ ), FPN-CON ( $R=0.22$ ), CON-DAN ( $R=0.22$ ), and DAN-AUD ( $R=0.20$ ; Fig. 4a). As we discuss in greater detail below, the observed pattern of between-network connections reflects the interaction between cognitive control (FPN, CON), attentional (DAN), and/or perceptual networks (SMN, AUD), consistent with prior research implicating these operations in fluid intelligence (e.g. Petersen and Posner 2012; Barbey et al. 2014; Shipstead and Yonehiro 2016).

Finally, when removing specific between-network connections, predictive performance did not significantly decline, remaining similar to the whole-brain model (Fig. 4b). Thus, this finding suggests that the prediction of fluid intelligence does not heavily rely on or originate from connections between a specific pair of networks but rather from connections between several different networks. Taken together, our results highlight the importance of large-scale network interactions for  $G_f$  and identify a specific collection of cognitive control, attentional, and perceptual networks whose interactions support fluid intelligence.

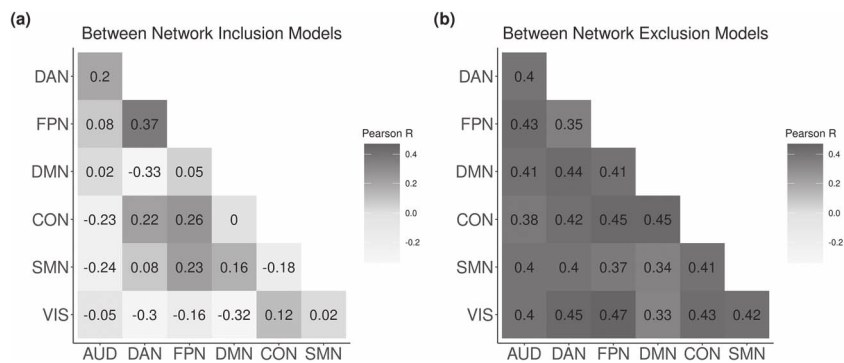
### Investigating within- versus between-network connections in the prediction of fluid intelligence

Although prior research on fluid intelligence has emphasized the importance of connections within specific brain networks (for a review, see Barbey et al. 2021), our findings suggest that between-network connections play an important role (i.e. enabling the integration of cognitive control, attentional, and perceptual processes underlying  $G_f$ ). To investigate this issue directly, we conducted an analysis to examine the proportion of variance in fluid intelligence explained by a whole-brain model comprised of within-versus between-network connections.

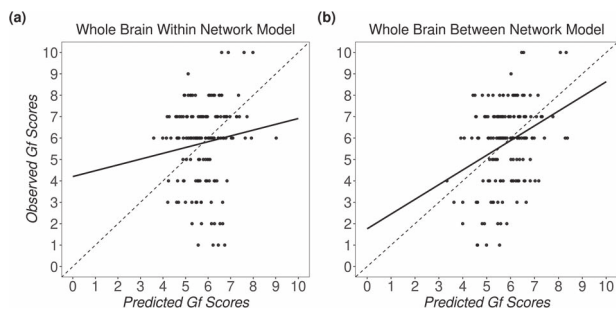
As Fig. 5(a) illustrates, the within-network model performed poorly, leading to a low correlation between observed and predicted values ( $R=0.13$ ), a negative proportion of variance explained ( $R^2=-0.09$ ), and a high level of error ( $n\text{RMSD}=1.04$ ). In contrast, the between-network model demonstrated superior performance (Fig. 5b), with a moderate correlation between observed and predicted values ( $R=0.33$ ), explaining 9% of the variance ( $R^2=0.09$ ), and a low level of error ( $n\text{RMSD}=0.95$ ). This pattern of findings highlights the importance of between-network connections in the prediction of  $G_f$  and further suggests that fluid intelligence depends on the recruitment and coordination of multiple ICNs enabled by between-network connectivity.

### Investigating the strength of between-network connections in the prediction of fluid intelligence

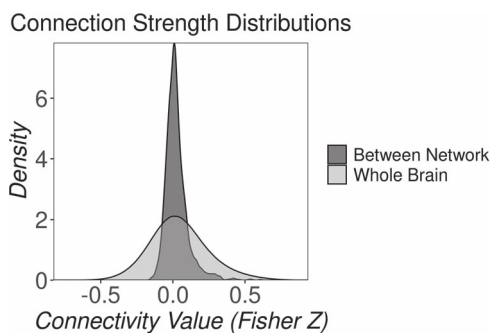
To further investigate the nature of between-network connections underlying fluid intelligence, we examined the distribution of all between-network connectivity values in the prediction of  $G_f$ . As Fig. 6 illustrates, the majority of between-network connections predictive of fluid intelligence represent weak ties—connections of relatively low strength but that provide important communication pathways that link multiple networks and serve to facilitate



**Fig. 4.** Prediction models derived from either (a) including versus (b) excluding connections between a specific pair of ICNs in the prediction of fluid intelligence. VIS=visual network, SMN=somatomotor network, CON=cinguloopercular network, DMN=default mode network, FPN=frontoparietal network, DAN=dorsal attention network, AUD=auditory network.



**Fig. 5.** Whole-brain prediction models including only (a) within- versus (b) between-network connections in the prediction of fluid intelligence. The between-network model performed better across all performance statistics ( $R=0.33$ ;  $R^2=0.09$ ;  $n\text{RMSD}=0.95$ ) compared with the within-network model ( $R=0.13$ ;  $R^2=-0.09$ ;  $n\text{RMSD}=1.04$ ).

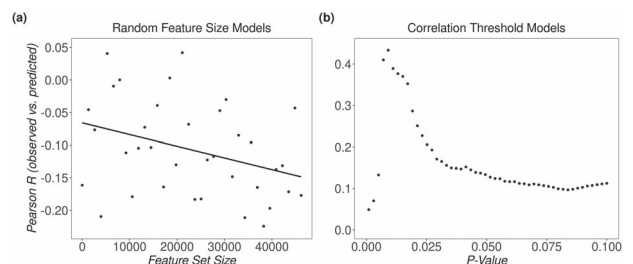


**Fig. 6.** Distributions of functional connectivity strength. The light-gray shaded area represents functional connectivity values across the whole brain concatenated across subjects. The dark-gray shaded area represents between-network connections that significantly correlated with  $G_f$  scores and averaged across all subjects. The distribution of significant between-network values is centered on weak connections, suggesting that weak ties are critical to the prediction of fluid intelligence.

efficient global information processing (Granovetter 1973; Bassett and Bullmore 2006, 2017). These findings highlight the importance of weak connections in the prediction of  $G_f$  and further suggest that between-network connections enable adaptive behavior through mechanisms for coordinated, system-wide information processing, as predicted by the NNT framework (Barbey 2018).

### Assessing feature set size bias

To investigate possible bias in model performance due to the size of the input feature space, we carried out two additional analyses. First, we performed a grid search across increasing feature set



**Fig. 7.** Models examining the accuracy bias of different feature set sizes based on (a) randomly selected edges and (b) behaviorally relevant edges. The random feature size model resulted in decreased performance with increasing set size. The correlation threshold model also resulted in decreased performance with increasing set size with maximum performance when the P-value threshold is set to 0.009.

sizes of randomly selected edges ( $n_{\text{edges}} = 3 - n_{\text{edges}} = 64,620$ , 50 values) to assess whether model accuracy is affected by the size of the input feature set, regardless of whether edges are correlated with behavior. Models with feature sets exceeding  $n_{\text{edges}} = 47,477$  did not converge, resulting in 37 separate set sizes. Second, we performed a grid search across increasing P-value thresholds ( $P < 0.001 - P < 0.1$ , 50 values) to assess whether large input feature sets of behaviorally correlated edges are more predictive compared with models with smaller behaviorally relevant input feature sets. Both analyses demonstrate that an increase in the size of the input feature space did not improve model performance, and thus did not serve to bias the reported findings (Fig. 7).

### Discussion

An extensive neuroscience literature has established the importance of the frontoparietal network in flexible behavior and adaptive problem solving (for a review, see Barbey et al. 2021). Recent evidence in network neuroscience, however, suggests that this finding may represent the tip of the iceberg and that fluid intelligence may depend on the collective interaction of multiple brain networks (Anderson and Barbey 2023). The present study therefore sought to elucidate the network architecture of fluid intelligence and to characterize the nature of within- and between-network interactions. We employed a CPM framework, administering resting-state fMRI to 159 healthy college students and examining the contributions of seven ICNs to the prediction of fluid intelligence, as measured by a state-of-the-art assessment tool (i.e. the BOMAT; Hossiep et al. 2001). Specifically, we sought to: (i) identify whether fluid intelligence relies on a primary brain network or instead engages multiple brain networks; and

(ii) elucidate the nature of brain network interactions by assessing network allegiance (within- versus between-network connections) and network topology (strong versus weak connections) in the prediction of fluid intelligence. We now review the primary findings and conclusions drawn from this research program.

### Whole-brain functional connectivity reliably predicts fluid intelligence

The present study demonstrates that individual differences in whole-brain functional connectivity reliably predict fluid intelligence, applying state-of-the-art CPM methods in the context of the highest fidelity assessment of fluid intelligence conducted to date (cf., Finn et al. 2015; Noble et al. 2017). Building on traditional tests of fluid cognition, the BOMAT employs a larger matrix size, progressive task difficulty, and a time limit that serve to reduce ceiling effects and enable a high-fidelity assessment of fluid intelligence (Hossiep et al. 2001). Our results demonstrate that whole-brain predictive models account for a large and significant proportion of variance in fluid intelligence (18%) and further illustrate that the contribution of individual networks is relatively modest by comparison. These findings are consistent with prior research illustrating the importance of whole brain models when predicting individual differences in high-level cognition (Finn et al. 2015; Noble et al. 2017; Dubois et al. 2018; He et al. 2020; Dhamala et al. 2021; Chen et al. 2022; Dhamala et al. 2022). Notably, the predictive performance of our whole brain model largely outperformed prior studies (Noble et al. 2017; He et al. 2020; Dhamala et al. 2021; Chen et al. 2022), illustrating the importance of employing a high-fidelity measure of fluid intelligence (i.e. the BOMAT).

The observed role of whole-brain functional connectivity in the prediction of fluid intelligence supports a network neuroscience perspective (Barbey 2018), which emphasizes the importance of global network mechanisms in  $G_f$  rather than engaging a specific brain region or cortical network. Accumulating evidence in network neuroscience supports this framework, emphasizing the need for dynamic information processing and the capacity to flexibly recruit multiple brain networks in the service of task demands (Cole et al. 2013; Miller and Cohen 2001; Desimone and Duncan 1995; Desimone et al. 1990). To further elucidate the network architecture of fluid intelligence, we examined the specific within- and between-network connections that figure most prominently in the prediction of  $G_f$ .

### Connections between cognitive control, attentional, and perceptual networks enable fluid intelligence

We conducted a comprehensive series of modeling analyses to uncover the functional connections that contribute significantly to the prediction of fluid intelligence by either sub-setting or lesioning specific within- versus between-network connections. Our results provide novel evidence that fluid intelligence depends on multiple networks that collectively support cognitive control, attentional, and perceptual processes.

Among the network interactions examined, we found the best performance for prediction models that included between-network connections of the FPN and DAN ( $R=0.37$ ; Fig. 4a). Accumulating evidence indicates that connections between these networks are critical for the regulation and control of perceptual attention, given the well-established control functions of the FPN (Desimone et al. 1990; Desimone and Duncan 1995; Miller and Cohen 2001; Cole et al. 2013) and the extensive connectivity of the

DAN with perceptual, visuospatial, and sensorimotor circuits (Corbetta and Shulman 2002; Ptak 2012; Buschman and Kastner 2015; Dixon et al. 2018). Thus, our findings provide novel evidence for the predictive role of FPN-DAN connections in  $G_f$  and suggest that cognitive control functions for the representation and processing of perceptual representations are central to fluid cognition.

More broadly, we observed a wide range of between-network connections whose CPM models performed moderately well, including the FPN-SMN ( $R=0.23$ ), FPN-CON ( $R=0.22$ ), CON-DAN ( $R=0.22$ ), and DAN-AUD ( $R=0.20$ ; Fig. 4a). Notably, in all cases, network interactions between cognitive control (FPN, CON), attentional (DAN), and/or perceptual (SMN, AUD) networks were implicated, providing further evidence to suggest that although fluid intelligence relies on global network mechanisms, processes for the regulation and control of perceptual representations are critical. Our findings align with prior research demonstrating that global network topology and connections between multiple brain networks are important for predicting high-level cognition (Dhamala et al. 2021; Chen et al. 2022; Dhamala et al. 2022). Indeed, recent advances in network neuroscience have begun to uncover the nature of network interactions underlying cognitive flexibility, suggesting that adaptive behavior may depend on multiple control networks that serve to flexibly coordinate task performance (i.e. the FPN) and to enable goal-directed attentional shifting (i.e. functions of the CON and DAN; Cocuzza et al. 2020; see also Dosenbach et al. 2007; Power and Petersen 2013; Sadaghiani and D'Esposito 2015). Thus, our results support a multi-network perspective and emphasize the need for future research to further characterize the large-scale network interactions underlying fluid intelligence.

### The importance of weak connections for the prediction of fluid intelligence

Accumulating evidence in network neuroscience suggests that fluid intelligence may rely on weak connections that enable the system to function within many difficult-to-reach network states, reflecting the capacity to adapt to novel situations by engaging mechanisms for flexible, goal-directed behavior (Barbey 2018). Network flexibility is particularly important for fluid intelligence given  $G_f$  requires adaptive solutions that cannot be solved purely from prior knowledge and experience. Thus, the NNT framework predicts that fluid intelligence will engage between-network connections that integrate cognitive control, attentional, and perceptual processes, and emphasizes the importance of weak connections in the formation of globally coordinated neural representations.

These predictions distinguish the NNT framework from standard theories of fluid intelligence, which emphasize the importance of a specific brain region (Duncan et al. 2000), primary brain network (Jung and Haier 2007), or the spatial overlap among networks (Kovacs and Conway 2016). Our findings provide novel support for the NNT theory, demonstrating that: (i) fluid intelligence is reliably predicted by whole-brain network connectivity (Fig. 1); (ii) relies primarily on between-network connections (rather than connections within a specific network; Fig. 5b); and (iii) engages weak connections that are known to facilitate system-wide network interactions and globally efficient information processing (Fig. 6; see also Granovetter 1973; Bassett and Bullmore 2006, 2017; Santarnecchi et al. 2014).

### Limitations

Although our findings suggest that whole-brain prediction models account for a large and significant proportion of variance in

fluid intelligence, we recognize several limitations and challenges that remain for future research in network neuroscience. First, although CPM has been widely used and validated in network neuroscience, it is not the only available predictive modeling approach (e.g., Feilong et al. 2021), nor would we expect this method to capture all forms of statistical regularities (e.g., it would not account for nonlinear relationships). Second, resting-state fMRI data is not the only neuroimaging modality that can be examined in such an analysis. For example, the present study neglects structural network topology and task-based functional dynamics. Third, although the present study employed a state-of-the-art areal map to define brain networks based on a multi-modal parcellation of the human cerebral cortex (Glasser et al. 2016), other network parcellations exist (e.g., Uddin et al. 2019), permitting differences in the regional and network definitions applied and therefore possible differences in the observed results. Fourth, 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. Fifth, further research is needed to increase the sample size of CPM studies and replicate the current findings using a high-fidelity measure of fluid intelligence (e.g. the BOMAT). Sixth, timed tests of cognition, such as the BOMAT, are known to increase task difficulty and cognitive load compared with untimed tests. Although an untimed version of the BOMAT is currently unavailable, it is important for future research to assess how timed tests of fluid intelligence compare to untimed tests with respect to reliability and predictive accuracy within the CPM framework.

## Conclusions

Rather than originate from a fixed set of cortical regions or a primary brain network, recent discoveries in network neuroscience suggest that fluid intelligence emerges from a rich constellation of networks whose functions are orchestrated in a flexible, goal-directed manner. Consistent with this perspective, the results of the present study demonstrate that whole-brain prediction models account for a large and significant proportion of variance in fluid intelligence (18%) and illustrate that the contribution of individual networks is relatively modest by comparison. In addition, we show that the global architecture of fluid intelligence largely reflects between-network connections and the formation of weak ties. Our findings support a network neuroscience approach to understanding the collective role of brain networks in fluid intelligence and elucidate the system-wide network mechanisms from which flexible, adaptive behavior is constructed.

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## Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

## CRedit author statement

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## Data availability

Restrictions made during informed consent by study participants on the distribution or future research uses of their deidentified data prevent open distribution of the dataset used in this paper. Code required to reproduce the following analyses may be made available from the authors on request.

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