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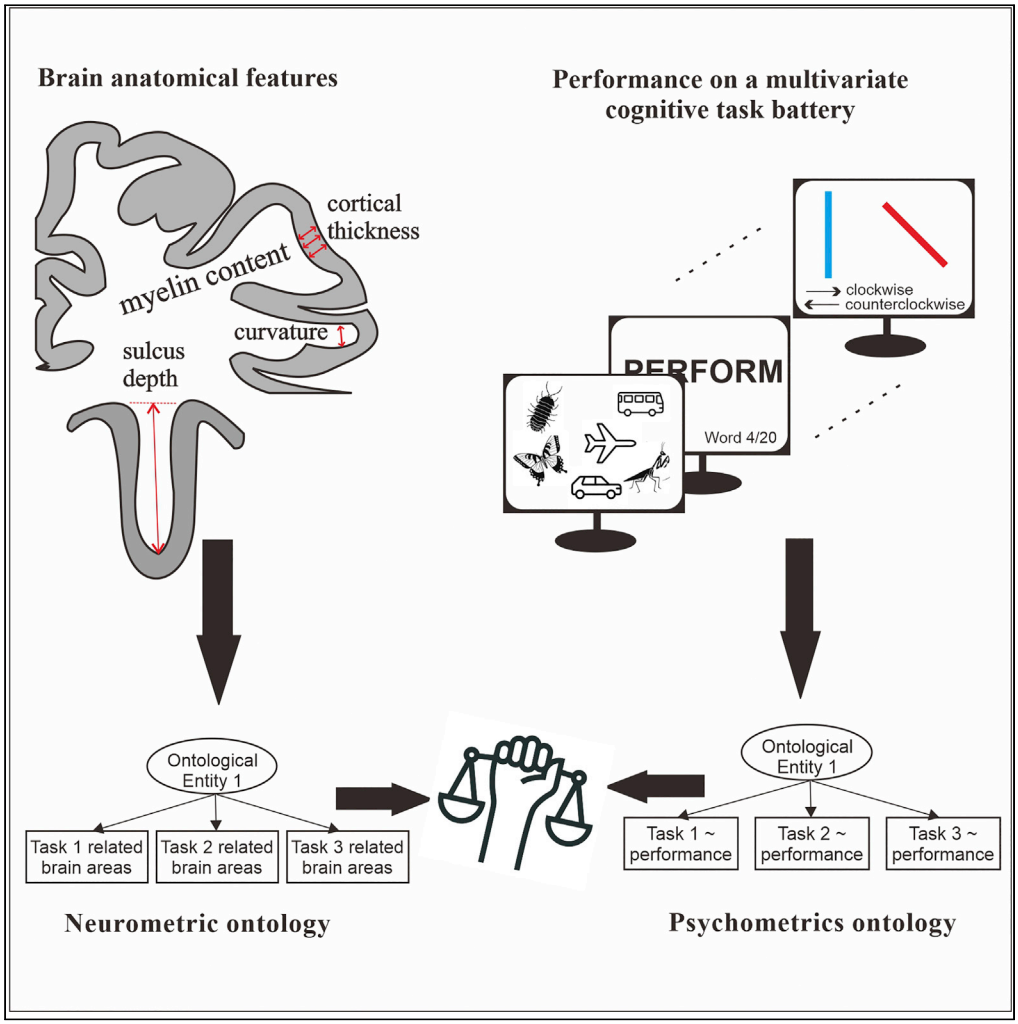

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Highlights

Psychometric and neurometric cognitive ontologies are partly equivalent

Ability-related brain areas are ontologically segregated with little to no overlap

However, ability-related brain areas are densely interconnected by fiber tracts

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What do neuroanatomical networks reveal about the ontology of human cognitive abilities?

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SUMMARY

Over the last decades, cognitive psychology has come to a fair consensus about the human intelligence ontological structure. However, it remains an open question whether anatomical properties of the brain support the same ontology. The present study explored the ontological structure derived from neuroanatomical networks associated with performance on 15 cognitive tasks indicating various abilities. Results suggest that the brain-derived (neurometric) ontology partly agrees with the cognitive performance-derived (psychometric) ontology complemented with interpretable differences. Moreover, the cortical areas associated with different inferred abilities are segregated, with little or no overlap. Nevertheless, these spatially segregated cortical areas are integrated via denser white matter structural connections as compared with the general brain connectome. The integration of ability-related cortical networks constitutes a neural counterpart to the psychometric construct of general intelligence, while the consistency and difference between psychometric and neurometric ontologies represent crucial pieces of knowledge for theory building, clinical diagnostics, and treatment.

INTRODUCTION

Broadly accepted cognitive ontologies are crucial for unified neurocognitive theories, diagnostics, and the planning of mental health interventions. Over many decades, research on human cognition and intelligence, which aims at describing, measuring, and classifying abilities and unveiling their ontological structure, has been exclusively based on covariations of inter-individual performance differences across multiple tasks. Since the unified theory of cognitive abilities, known as the Cattell–Horn–Carroll (CHC) model, was compiled and disseminated (McGrew, 2009), there has been widespread consensus on the psychometric ontology of intelligence, notwithstanding some caveats (Schulze, 2005). According to the CHC model, stratum I comprises individual differences in a large number of cognitive tasks that require maximal performance in terms of speed or/and accuracy. Stratum II incorporates broad latent abilities that are not directly observable but derived from multiple tasks, for example, fluid reasoning (*Gf*), comprehension knowledge (*Gc*, also called crystallized intelligence), short-term memory (*Gsm*), long-term storage and retrieval (*Glr*), and cognitive processing speed (*Gs*). These broad but domain-specific abilities are nevertheless positively associated with one another. This positive manifold is accounted for in the CHC model by a general factor of intelligence (*G*) at stratum III. A somewhat separate literature on ontological entities of human intelligence concerns executive functions (*EF*). The most widely accepted suggestions about the ontological entities of *EF* encompass the abilities of working memory, shifting, and inhibition (e.g., Miyake et al., 2000).

Cognitive neuroscience – a much younger discipline than the psychometrics of intelligence – investigates, among others, the anatomical and functional properties and neural mechanisms underlying the ontological entities of human cognition. Early studies focused on stratum I abilities, aiming to understand the neuroanatomical basis and neurofunctional mechanisms underpinning mastery on specific cognitive tasks. In this line of research, studies adopted connectome-based predictive modeling (e.g., Finn et al., 2015; Shen et al., 2017), and mapped brain properties and performance scores in specific cognitive tasks (e.g., Beaty et al., 2014; Cui et al., 2018; deMooij et al., 2018; Kristanto et al., 2020). As a further step toward generalization, latent cognitive abilities at stratum II of the CHC model were mapped onto brain structure and function (e.g., Barbey, 2018; Colom et al., 2006; Dubois et al., 2018; Jung and Haier, 2007; Kovacs and Conway, 2016; M. Liu et al., 2020). The latter studies generated neuroanatomical and neurofunctional explanations of the psychometric ontological entities of cognition beyond specific tasks. In a further step, the quest for

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brain-derived ontological entities of cognition has recently gained traction. In this perspective, the psychometric entities are not taken for granted but explored in a bottom-up fashion (Poldrack et al., 2011).

In an attempt to derive a brain-based ontology in addition to the established psychometric ontology, the cognitive neuroscience community has insufficiently appreciated the psychometric desiderata of distinguishing between constructs and their operational measures (Cronbach and Meehl, 1955). That is, a single task, brain measure, or indicator contains idiosyncratic, specific characteristics, whereas generalizable ontological entities of cognition must be determined by multivariate analyses going beyond single tasks, measures, or indicators (Cocchi et al., 2013). Consequently, modern cognitive neuroscientific approaches to derive ontological entities must use multiple tasks to explore distinct indicators of anatomical and functional properties of the brain to support the existence of stratum II ontological entities of cognition (the top-down approach), and mine the brain to derive ontological entities that do not take psychometric entities for granted (the bottom-up approach, Lenartowicz et al., 2010).

The recent availability of large-scale, cognitive neuroscientific databases enables a bottom-up approach, allowing one to explore ontological entities of human cognition on the basis of brain properties (King et al., 2019; Poldrack and Yarkoni, 2016). For example, Bolt et al. investigated which cognitive entities are revealed by brain activation patterns when participants perform a battery of cognitive tasks (Bolt et al., 2017). Unfortunately, the authors did not systematically explore the consistency and disparity between their derived neurometric ontology and the ontology as established in psychometrics. We argue that such descriptive comparison is necessary in order to substantiate the ontology of human cognition, which should accommodate the covariance structures of both task performance and the brain systems supporting these abilities (Anderson, 2015; Jonikaitis and Moore, 2019; Lenartowicz et al., 2010).

The present study contributes to establishing a formal cognitive ontology for psychology, cognitive neuroscience, and their applied disciplines by adopting a bottom-up approach (see Lenartowicz et al., 2010). We explored the cognitive ontology as derived from anatomical cortical properties frequently employed in brain behavior studies (Bayard et al., 2020; Reese McKay et al., 2013; Tadayon et al., 2020; Williamson and Lyons, 2018). We refer to this as neurometric ontology. The brain properties analyzed in relation with performance in 15 psychometric tasks were cortical thickness, myelination, curvature, and sulcus depth. Importantly, we performed the analyses on a large dataset with resampling realizations to explore the robustness of the derived neurometric ontology. Going beyond existing approaches, we compared the neurometric ontology with the psychometric one revealed by covariances of performance measures in the same tasks. Specifically, we investigated the extent to which the derived neurometric ontology is consistent with or distinguishable from the established psychometric ontology at stratum II of the CHC model. We expected that the ability-related cortical areas are segregated, supporting the differentiation between the inferred cognitive ontological entities. Finally, we investigated how ability-related cortical areas are coupled via fiber connections to possibly substantiate the positive manifold of domain-specific psychometric entities underlying general intelligence at stratum III of the CHC model.

RESULTS

Our methodological approach is illustrated in Figure 1, consisting of the exploration of neurometric ontology in several resampling realizations and the comparison of the neurometric ontology with the psychometric one. We also performed further analyses on cortical areas related to the neurometric ontological entities to investigate the underlying anatomical network. The STAR Methods section provides a detailed description of the applied analyses.

Neurometric versus psychometric ontological entities

The psychometric ontology for descriptive reference was obtained by submitting the correlation matrix of task performance scores (Figure 2A) to confirmatory factor analysis (CFA). For deriving the neurometric ontology, we applied exploratory factor analysis (EFA) on the task-related cortical areas shared by each pairwise tasks. Shared cortical areas were quantified by the Intersection OverUnion (IOU) index (Figures 2B and 2C).

The psychometric ontology was obtained by a confirmatory model in line with the CHC theory. Following previous analyses of the HCP data for the same 15 tasks (Dubois et al., 2018; M. Liu et al., 2020), we estimated five domain-specific abilities as psychometric ontological entities—namely, *reasoning*,

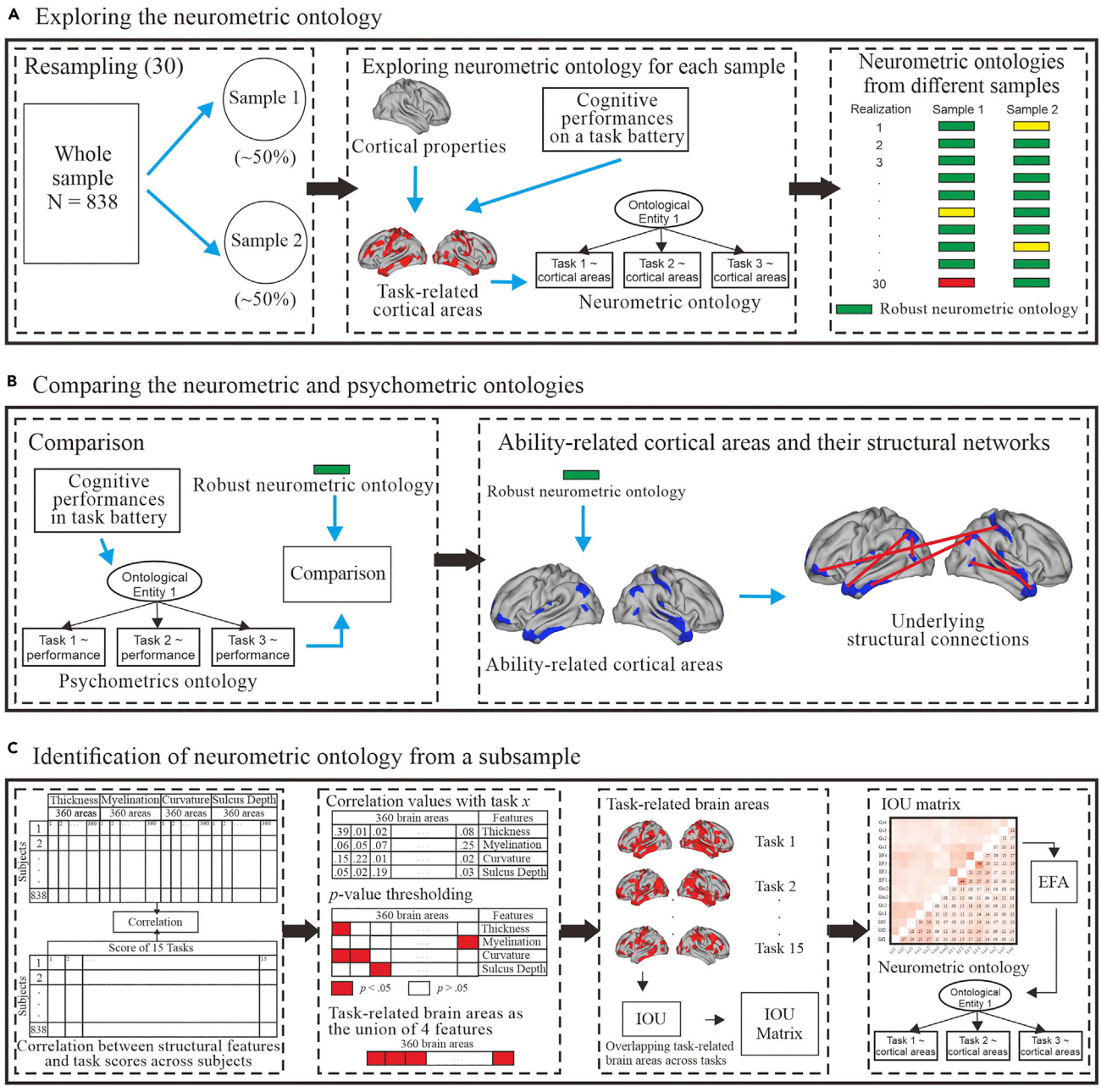

Figure 1. Methodological approach of the study. Summary of our methodological framework illustrating the systematic procedures

(A) To explore the neurometric ontology, we resampled the whole dataset to obtain several realizations, where each realization consisted of two independent samples. We identified task-related brain areas based on linear associations between brain properties (thickness, myelination, curvature, and sulcus depth) and task performance across individuals. Next, we quantified the overlap between task-related brain areas with these different anatomical properties by creating matrices of the Intersection OverUnion (IOU) index. These matrices were then subjected to exploratory factor analysis (EFA; used here as a descriptive method and not for inferential purpose) to obtain a neurometric ontology. Across samples and iterations, we selected the most robust, that is, most frequently replicated neurometric ontology across samples.

(B) The concluded neurometric ontology was descriptively compared with the psychometric ontology derived from covariances across the same cognitive tasks estimated in the whole sample. To this aim, we applied confirmatory factor analysis (CFA) on the correlation matrix of task performance scores following the propositions of the CHC structure (Table 1). Next, we identified overlapping brain areas associated with the different entities of the neurometric ontology (henceforth referred to as ability-related brain areas) and investigated the underlying anatomical network connections between those areas.

(C) The approach of identifying the neurometric ontology on every subsample consisted of several steps: Identify task-related brain areas, compute IOU matrices, and apply EFA on the IOU matrix to explore its structure.

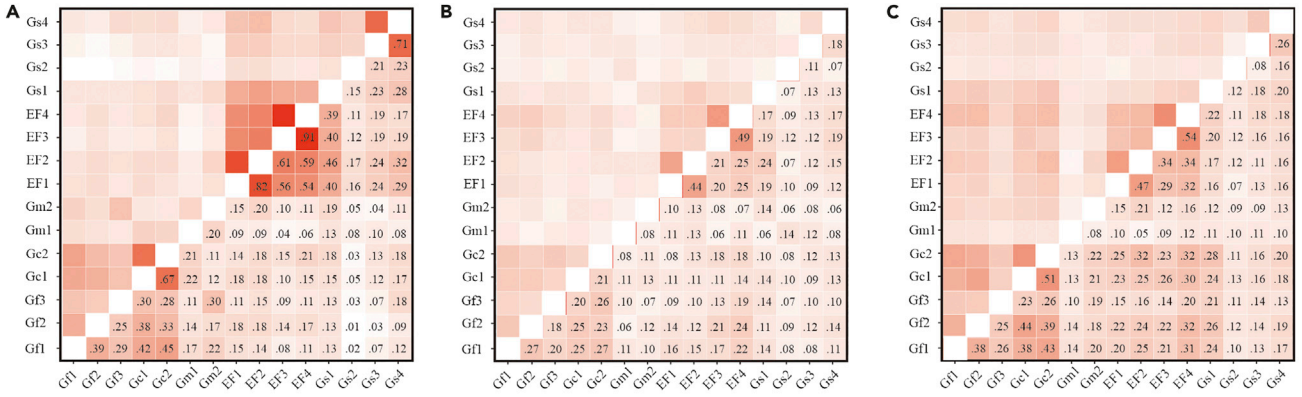

Figure 2. Correlation and IOU matrices

(A) Correlation matrix of task performance scores in the whole sample.

(B) IOU matrix from one random sample obtained by the resampling procedure.

(C) IOU matrix obtained for the whole sample.

comprehension knowledge, *memory*, *executive functions*, and *mental speed*—corresponding to those listed in Table 1 (see *SI Appendix* Table S1 for the detailed task description), and depicted in Figure 3A. Domain-specific ability factors were allowed to correlate with each other. To account for task specificity, three residual correlations between two pairs of *EF* tasks and one pair of *Gs* tasks were required. These indicators reflect two different conditions of the same tasks, implicating task specificity by design. The five correlated factors model fitted the matrix of task performance associations well (see *SI Appendix* Table S2, providing the statistical evaluation of model fit). The standardized factor loadings for all domain-specific abilities were significant, but their magnitude varied across ontological entities (see *SI Appendix* Table S3). The correlations between domain-specific abilities ranged from 0.26 to 0.79, with the smallest correlation observed between *EF* and *Gc* and the largest between *Gf* and *Gc* and between *EF* and *Gs*. This pattern of correlations between psychometric ontological entities is consistent with the vast literature on human intelligence (Carroll, 1993). Moreover, we computed individuals' scores on the psychometric factors estimated in the bifactor model minus 1 as depicted in Figure S1. The frequency distributions of these factor scores are provided in Figure S2.

Aiming to derive a robust neurometric ontology, the analyses were repeated on 60 subsamples originating from 30 resampling realizations of two subsamples obtained from the whole dataset by random allocation. The results of the neurometric ontology across subsamples are listed in *SI Appendix* Table S4. Most frequently we observed a 3-factorial structure (47 out of 60 subsamples). In 19 out of 30 resampling realizations this structure was obtained in both samples. Importantly, the most frequently observed neurometric ontology was consistent with the one derived from the whole sample which reflected a 3-factorial structure (see *SI Appendix* Table S2 for evaluation of the model fit and Figure S3 for the scree plot analysis to determine the number of factors).

Figure 3B illustrates a simplified representation of the neurometric ontology obtained by resampling. We only depict loadings which were consistent across samples; *Gf1, Gf2, Gf3, Gc1, Gc2* were consistently assigned to factor 1; *EF1, EF2, EF3, EF4* were consistently assigned to factor 2; and *Gs1, Gs2, Gs3, Gs4* were consistently assigned to factor 3. However, because *Gm1* and *Gm2* were associated with different factors across samples, we did not assign them to any of the factors in the simplified structure. In addition, the factor loadings of *Gm1* and *Gm2* were smaller as compared to the other tasks within the same factor (refer to *SI Appendix* Table S4 for details and Table S5 for an example of the loadings in one of the samples). Figure 3C illustrates the simplified neurometric ontology derived from the whole sample. The entire factor loading matrix estimated by the EFA on the whole sample IOU matrix is displayed in *SI Appendix* Table S6. Not obviously interpretable loadings are shown as broken lines in Figure 3C. As indicated in *SI Appendix* Table S6, these loadings are much weaker than those indicated by solid lines. Overall, both loading patterns obtained by resampling and in the whole sample suggest a first factor which is interpretable as *reasoning and comprehension knowledge* (*G*). This reflects shared brain properties associated with rather difficult tasks, scored by performance accuracy (covering *Gf1*, *Gf2*, *Gf3*, *Gc1*, and *Gc2*). A second factor (*EF*)

Table 1. Cognitive tasks and associated domain-specific abilities included in the present study

Domain-specific abilities	Tasks
Reasoning *(Gf)*	Raven's Progressive Matrices *(Gf1)*
	Spatial Orientation Processing *(Gf2)*
	List-Sorting Working Memory *(Gf3)*
Comprehension Knowledge *(Gc)*	Oral Reading Recognition Test *(Gc1)*
	Vocabulary Comprehension *(Gc2)*
Memory *(Gm)*	Verbal Episodic Memory *(Gm1)*
	Picture Sequence Memory *(Gm2)*
Executive Function *(EF)*	Dimensional Change Card Sort – Color *(EF1)*
	Dimensional Change Card Sort – Shape *(EF1)*
	Flanker Inhibitory Control and Attention Task – Congruent *(EF3)*
	Flanker Inhibitory Control and Attention Task – Incongruent *(EF4)*
Mental Speed *(Gs)*	Pattern Comparison Processing Speed *(Gs1)*
	Sustained Attention *(Gs2)*
	Relational Processing 1 *(Gs3)*[a]
	Relational Processing 2 *(Gs4)*[a]

For a detailed description of these tasks see Table S1 and in the HCP manual (Van Essen et al., 2013).
[a]Tasks were performed during the fMRI scanning (in-scanner tasks).

reflects shared brain properties relevant for executive functions covering *EF1*, *EF2*, *EF3*, and *EF4*. Finally, a third factor (*Gs*) comprises mental speed-related brain areas shared across easy cognitive tasks scored by the swiftness of responses, covering *Gs1*, *Gs2*, *Gs3*, and *Gs4*.

To further assess the robustness of the concluded neurometric ontology, we performed additional analyses using a different approach. Specifically, we performed a multi-parameter-correlation approach by regressing the task scores onto the four different brain propertied measured in a given brain area simultaneously. The regression model was repeated on 10 subsamples ($n \sim 419$). Next, for each brain area, we quantified the correlation between estimated task score from the multiple regression and the actual values of the task scores. We thus obtained the correlation of estimated and actual values of the task scores for all 360 brain areas. Finally, we concluded on the brain areas related with a given tasks by thresholding the pvalue of the multiple correlations ($p< 0.05$). The task-related brain areas were then submitted to the next step of the analysis pipeline (i.e., quantification of the overlap in terms of IOUs for every task pair and factor analysis) to obtain the neurometric ontology. In eight out of ten subsamples, we found equivalent results as in the previous analyses using single-feature correlations as shown in *SI Appendix* Table S7. Moreover, in most of the repetitions, the identified neurometric ontology was three-factorial, including *G*, *EF*, and *Gs*.

By comparison, the neurometric ontology derived from the IOU matrices of task-related brain areas (both from resampling and the whole sample) revealed a partly consistent, but less differentiated ontological structure as compared with the established psychometric ontology. To further explore, we fitted a model mimicking the cognitive ontological entities to the whole sample's IOU matrix using CFA. As summarized in *SI Appendix* Table S2, the fit of this model was poor. Furthermore, the model parameter estimates indicated that the IOU matrix did not reflect a 5-factor structure. This was mainly because in the IOUs, *Gf*, *Gc*, and *Gm* were highly correlated and not differentiable. Thus, these analyses further confirmed that task-related cortical areas reveal substantially different ontological entities as compared to those derived from associations of task performance scores across individuals.

Cortical areas corresponding to the neurometric ontological entities

We further identified the cortical areas corresponding to the neurometric entities. These areas were defined as the overlapping task-related cortical areas subsumed under a given entity in the EFA. For instance, the entity *Gs* derived from the IOU matrix (Figure 3B) is reflected by cortical properties associated

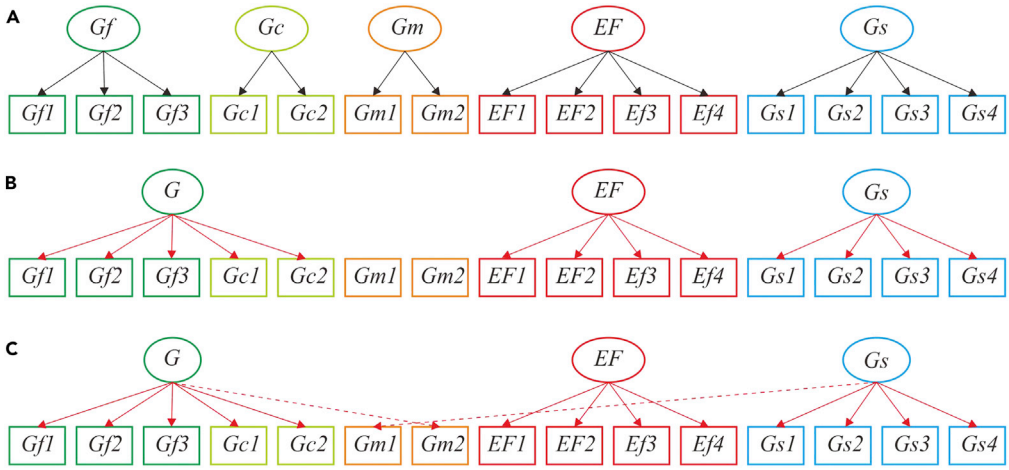

Figure 3. Schematic representation of the neurometric and psychometric ontology

Descriptive comparison of the psychometric and neurometric cognitive ontology.

(A) Psychometric ontology obtained by modeling the covariance structure of performance scores in 15 tasks.

(B) The most frequently replicated neurometric ontology obtained by resampling.

(C) Neurometric ontology derived from the IOU matrix of task-related brain areas in the whole sample. Note: In all analyses the factors were correlated but the correlations are not displayed here for simplicity. Details on model fit and loading estimates are provided in *SI Appendix* Tables S2, S3, S4, S5, and S6. The solid lines indicate the ontological structure used for further analysis, whereas the broken lines indicate non-interpretable, weak loadings.

with tasks *Gs1*, *Gs2*, *Gs3*, and *Gs4*. Thus, the cortical areas corresponding to *Gs* are those that are shared by the tasks *Gs1*, *Gs2*, *Gs3*, and *Gs4*. Note that in the following, the 3-factorial structure supported by the whole sample's data will serve as reference neurometric ontology. Thus, ability-related cortical areas used task-related cortical areas as the basis, which were identified from the correlation between anatomical brain properties and performance scores from all participants (Figure S4).

Figure 4A illustrates the ability-related cortical areas for the three neurometric ontological entities. In details, *G*, *EF*, and *Gs* respectively involved 26, 32, and two cortical areas, respectively. The areas associated with the *G* factor were dominated by frontal, lateral temporal and auditory association cortex. *EF* was neuro-anatomically represented by more widely distributed cortical networks from both hemispheres, covering the prefrontal, motor, parietal, and the visual cortex. Finally, there were only two areas identified for *Gs*: area four in the motor cortex and area 7m in the cingulate cortex.

As the ability domain specific areas seem to be segregated across ontological entities, we quantified their exclusiveness by computing their pairwise overlap using the IOU index (see STAR Methods), as shown in Figure 4B. We found little to no overlap between the ability-related cortical areas. Specifically, the overlap was small between *G* and *EF* (0.07), and between *EF* and *Gs* (0.03). For reference, the overlaps of task-related cortical areas between tasks *EF1-EF2* and *EF3-EF4*, which were corresponding to the same ability (*EF*), were 0.47 and 0.54, respectively (see Figure 2A). Interestingly, *G* and *Gs* did not share any brain areas. These results show that the ability-related cortical areas were well segregated among the entities of the neurometric ontology.

Anatomical connectivity between ability-related cortical areas

In the ontology of human intelligence, the positive manifold among abilities is accounted for by general intelligence at stratum III. Hence we asked how the segregated ability-related cortical areas might support such a positive manifold. Thus, we analyzed the network connectivity underlying the segregated ability-related cortical areas. Structural connectivity was obtained by probabilistic tractography averaged across individuals (see STAR Methods). The ability-related cortical areas as defined above for each ontological entity were set as core areas whereas the union of all task-related cortical areas of the corresponding ontological entity, excluding the core, was considered as extended areas. We examined (1) the connections between the core areas and (2) the connections between the extended areas. Both connectivity levels can be applied within areas of the same ontological entity and between entities.

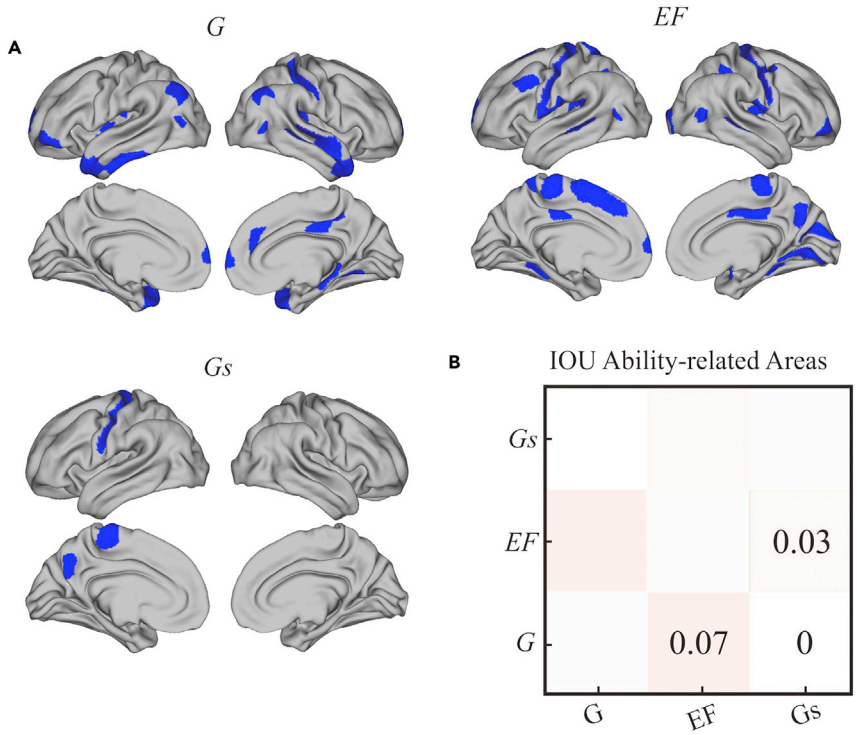

Figure 4. Inferred ability-related cortical areas

(A) Brain areas corresponding to the neurometric ontological entities.

(B) Pairwise overlaps computed from the IOU index of the ontological-entity-related brain areas reflecting domain specific abilities. All maps were visualized using Connectome Workbench (https://www.humanconnectome.org/software/connectome-workbench).

We applied network density thresholds of 10%, 20%, and 50% of the strongest connections in the weighted group-averaged connectivity matrix to identify existing connections (binary 0 or 1). For each level of connections (core and extended areas), we obtained the connection density as the ratio between the number of existing connections and the number of possible connections. Under all thresholds, the connection density of the core areas was clearly larger and that of extended areas was clearly smaller than the average connection density of the whole brain network (Figure 5B). This finding indicates that although the ability-related cortical areas were segregated in their regional anatomical properties, they were nevertheless densely connected by subcortical white matter projections, such that their average connection density is greater than that of the brain connectome. An exception holds for *Gs* at connectivity thresholds 10 and 20%, where the core areas were not connected (Figure 5A). This might be because of the fact that there were only two brain areas related to *Gs*, considerably fewer than for the other abilities. However, at the 50% connectivity threshold (see *SI Appendix* Figure S5), the areas related to *Gs* were structurally connected. It indicated that the areas for Gs were indeed connected by white matter fibers.

DISCUSSION

We explored the ontology reflected in the task-related anatomical properties of the cortex (neurometric ontology) and compared it with the widely established psychometric ontology based on correlations between task performance scores alone as reflected in the CHC model. Macroscale anatomical brain features (i.e., thickness, myelination, curvature, and sulcus depth) have been widely used in the previous literature for understanding the association between brain properties and psycho-behavioral outcomes, such as mental disorder (Bayard et al., 2020; C. Li et al., 2017), psychological tasks (Cui et al., 2018; Kristanto et al., 2020; Masouleh et al., 2019), drug abuse (Hamidullah et al., 2020; Y. Li et al., 2015; Wade et al., 2019), and development (Cheng et al., 2020; Hall et al., 2021). All these brain anatomical measures have been validated by showing that they were behaviorally relevant, at least to some extent. Prior literature also demonstrated that these anatomical features as measured by MRI are associated with microscopic or cytoarchitecture, as well as functional brain properties. For example, cortical thickness is a distance measure between the pial surface and the gray-white matter border

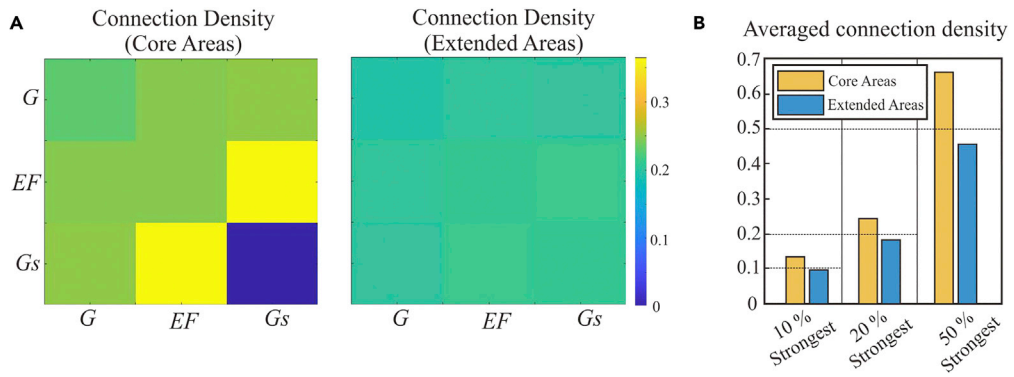

Figure 5. Comparison of the anatomical connection density between the ability-related cortical areas (core areas) and the other task-related areas (extended areas)

(A) Connection density within and between cognitive entities included in the neurometric ontology at network density threshold of 20%.

(B) The average connection density of core areas across different entities and all extended areas at different network density thresholds (10%, 20%, and 50%, horizontal dotted lines) in the whole structural connectivity network.

and was found to correlate with the number of neurons within a voxel. Thus, the measure is taken to inform about neuron distribution in the gray matter (Alvarez et al., 2019; Herculano-Houzel et al., 2013). Furthermore, higher myelination – determined as the ratio of T1 and T2 weights – indicates higher abundance of myelin sheaths in a given voxel (Glasser and van Essen, 2011). Notably, myelin content was found to influence neural circuit dynamics by modulating transmission speed of axonal action potentials and thus, it is considered an indicator of neuron type (Call and Bergles, 2021; Yalçın and Monje, 2020). Finally, curvature and sulcus depth are measures of sulcal morphology. The sulcal folding has previously been found to reflect neuronal connections and other cytoarchitectonic properties (Mangin et al., 2010). Those regional features coupled with anatomical connectivity have been shown to predict functional connectivity (Deco et al., 2014; Demirtaş et al., 2019; Shine et al., 2021; P. Wang et al., 2019a). Moreover, combined measures of different anatomical brain features have been found to correlate more strongly with psychological variables. For example, merging several anatomical features improve the prediction of behavioral tasks (Kristanto et al., 2020; Valizadeh et al., 2017), enhance the classification performance of Alzheimer's disease (deVos et al., 2016) and Schizophrenia onset (Skudlarski et al., 2010), and better predict antidepressant treatment outcomes (Korgaonkar et al., 2015). More recently, the combination of regional and connection measures of brain anatomy has been reported to better explain brain dynamics and more strongly correlate with functional brain connections (Deco et al., 2014; Demirtaş et al., 2019; Shine et al., 2021; P. Wang et al., 2019). Overall, we expected that MRI-derived brain structural properties showing reliable association with a multitude of cognitive tasks would help to elucidate the neurometric ontology of human cognition. Hence, aiming to represent brain anatomy in a comprehensive fashion, we explored the ontology derived from a combination of anatomical features (i.e., thickness, myelination, curvature, and sulcus depth).

In order to cross-validate the neurometric ontology, we used a resampling approach to create 60 samples and explored the neurometric ontology based on each sample (see STAR Methods). We found that the most frequently observed ontological structure implies three entities: *G*, *EF*, and *Gs*. The neurometric ontology was partly consistent with the psychometric ontology, but it was less differentiated. Interestingly, the ability-related brain areas demonstrated competing features: On the one hand, the cortical areas associated with different abilities were spatially segregated, as there was little overlap. On the other hand, they were also integrated via structural fiber connections that were denser than the average brain connectome. Next, we discuss the three main findings of the current study.

Consistencies and differences between the psychometric and neurometric cognitive ontology

The neurometric ontology was derived from the IOU matrix quantifying overlapping task-related cortical areas identified from correlations between anatomical brain properties and task performance. The psychometric ontology was derived from correlations of task performance scores. Here, the question may arise whether the IOU and task performance correlation matrices are similar in structure just because they both involve task performance and hence are redundant. We argue that correlation between cognitive task performance

scores may be observed even for tasks instantiated by distinct brain networks (Oberauer et al., 2005). Thus, correlations between task performances are not necessarily because of a greater neuroanatomical overlap between task associated brain areas and hence higher values in the IOU index. For example, the tasks *Gf3* and *Gm2* were correlated in performance 0.3, but their IOU index was 0.1 (Figure 2). In contrast, *EF4* and *Gc1* showed a small correlation (0.15), but the corresponding brain area overlap in the IOU index was 0.3. Hence, the neurometric and psychometric ontology might in principle converge or dissociate.

Indeed, we found that the neurometric ontology aligns with the psychometric ontology to some extent, but that they also dissociate in other respect. The most evident consistency is that the *Gs* and *EF* entities were found in both. These similarities are remarkable because the dependent measures subjected to factor analyses (performance speed and accuracy versus anatomical properties of the brain) are very different in nature. It can thus be concluded that there is a partially robust isomorphy between cognitive ontological entities derived from cognitive behavior and their associated neuroanatomical properties. This validates important aspects of the CHC structure of human cognition from a neurometric point of view.

In contrast to these consistencies, we also observed interesting and interpretable differences between the psychometric and neurometric ontology. First, the IOU matrix did not show a separation between *Gf* and *Gc*. We thus termed the overarching ontological entity as *reasoning and comprehension knowledge* (*G*). This unified *Gf* and *Gc* is in line with Cattell's view on general intelligence, encompassing these two facets of cognition (Cattell, 1943). A strong relationship between *Gf* and *Gc* was also suggested in terms of skill acquisition (Wenger et al., 2017) and emotional intelligence (Olderbak et al., 2019).

Moreover, taking a closer look at the ontological entities derived from resampling, the second-most frequently obtained neurometric ontology was a 4-factorial structure, in which the separation of *EF* was evident (i.e., *EF1* and *EF2* were assigned to a single factor whereas *EF3* and *EF4* were assigned to another factor). This observation can be explained by referring to Table S1: *EF1* and *EF2* tapped into *switching* whereas *EF3* and *EF4* are measuring *inhibition*. It is interesting that switching and inhibition, which are often treated as one overarching entity (*EF*) in psychometrics (for an exception see Miyake et al., 2000), can be distinguished when analyzing the structure of overlapping cortical areas.

Another difference between the psychometric and neurometric ontology revealed that *Gm* could not be identified as an independent cognitive entity based on task-related cortical areas. Note that cortical areas related to memory tasks were scattered into several neurometric ontological entities (i.e., *G* and *Gs* in case of the IOU matrix from the whole sample, see Figure 3C). This may indicate that cortical areas associated with *Gm* are complex and widely distributed, such that they may not be quantifiable by neuroanatomical properties of cortical regions alone (Nadel and Hardt, 2011; Squire, 2009). This is illustrated by Figure S4, where the areas related to *Gm1* and *Gm2* were, although fewer compared to other tasks, distributed across the cortex. However, detailed analyses of task-related cortical areas in terms of these properties may facilitate the understanding of brain networks underlying *Gm* in the future. Here we observed overlaps with the brain networks associated with *G* and *Gs*. In addition, *Gm* was also found to be associated with anatomical properties of subcortical areas, which were not well captured by the MMP atlas (Koshiyama et al., 2018; Lee et al., 2019) applied in this study.

We argue that the results above, indicating similarity and explainable dissimilarity between psychometric and neurometric cognitive ontologies are compelling, considering that we explored only a limited number of anatomical properties of cortical regions. These findings have the potential to prompt further psycho-neuro-informatics studies to explore the neurometric ontology using a broader range of anatomical, biochemical, genomic and functional properties of the brain supported by different computational modeling approaches (Guest and Martin, 2021). From a more general perspective, we emphasize that the present comparative approach, focusing on similarities and dissimilarities, is highly valuable for exploring whether ontological entities derived from psychometrics (stratum II in the CHC model) translate into brain anatomy and function (Anderson, 2015). The potential translation is not only of theoretical importance, but also relevant for neuropsychological diagnostics and therapy.

Segregation of ability-related cortical areas in the neurometric ontology

After analyzing similarities of and differences between the psychometric and neurometric ontologies, we investigated whether the entities of the neurometric ontology are built upon distinct neural networks. This approach was inspired by a study on cognitive control (i.e., executive functions) by Lenartowicz

et al. (Lenartowicz et al., 2010). The authors applied a machine learning approach to classify data from more than one hundred neuroimaging studies, aiming to isolate component operations with similar and dissimilar brain-activation patterns across experiments (Lenartowicz et al., 2010). They found that ontological entities described in the psychometric literature of cognitive control were generally also differentiable on the basis of brain activation patterns. However, while *shifting* was consistently identified as a specific ontological entity in psychometrics, in the brain-activity covariance structure it could not be discriminated from *response selection* or *response inhibition* (Miyake et al., 2000).

Here we compare the cortical areas corresponding to the entities in the neurometric ontology with the results of other studies on ability-related anatomical brain networks. First, *G* was dominated by frontal, medial temporal, and auditory association cortices. This agrees with a previous study claiming that the cortical thickness of frontal and parietal cortex is related to intelligence in general (IQ; Bajaj et al., 2018). In addition, the association between temporal and auditory cortex with fluid and crystallized intelligence, as part of *G* in the present study, has been studied using structural MRI (Kristanto et al., 2020; Phinney et al., 2007). Areas related to *EF* were widely distributed across the cortical surface, suggesting that *EF* is a complex ability that requires integration of different brain networks, in line with previous studies on *EF* (Niendam et al., 2012; Zink et al., 2021). For *Gs*, our results indicate that motor cortex is relevant to *mental speed*. Considering that the present study exclusively considered anatomical properties, our finding complements previous research on the association between the motor cortex and mental speed, mostly found in functional properties. For example, beta-band oscillations in the motor cortex have been related to movement speed in human and macaque (Khanna and Carmena, 2017; Zhang et al., 2020). Another study showed that the functional connection between motor and visual areas were predictive for processing speed (Gao et al., 2020). Moreover, aside from their consistency with some previous studies, we found that the areas corresponding to each entity had little overlap with other entities or even showed complete exclusiveness. Although there are some small overlaps of *EF* and other entities, *G* and *Gs* do not share any cortical areas. This is in line with research on speed and accuracy, suggesting that these performance outcomes are substantiated by independent brain networks. For example, using EEG, Perri et al. (2014) found that accuracy tasks trigger activity in the frontal cortex, while speed tasks rely on activity in the motor cortex.

The present findings about the neurometric ontology, namely (1) its consistency with and interpretable dissimilarities to the psychometric ontology, in terms of inferred cognitive entities, and (2) the exclusive and functionally relevant brain areas corresponding to the inferred entities (see previous sections) suggest that the neurometric ontology may be an important complement for psychometric entities of human cognition. There are at least three main reasons for this claim. First, convergence or divergence between the psychometric and neurometric cognitive ontology helps to identify and resolve weaknesses reflected in psychological terminology and theory building (Anderson, 2015; Poldrack and Yarkoni, 2016). Second, it will elevate the quest for brain behavior relationships from the task-specific level to the theoretically more interesting level of domain-specific abilities. Third, the juxtaposition of the psychometric and neurometric ontology is relevant from an applied clinical perspective, for which the mapping of psychological functions to their corresponding brain systems is essential (Fornito et al., 2017).

Dense fiber connections between segregated ability-related cortical areas

The segregated core areas for different neurometric entities, especially at 50% connectivity thresholds (see Figure 5 and *SI Appendix* Figure S5), were found to be more densely connected, whereas the extended areas of different entities were more sparsely connected than the average whole brain connectome. Studies of segregated modules or communities in structural or functional brain networks typically find inter-module connectivity to be sparser than intra-module connectivity (Meunier et al., 2009, 2010). Thus, our finding of denser connections between segregated core areas of different abilities is unexpected, and to the best of our knowledge unparalleled in the literature. Our findings indicate that segregated ability-related cortical areas are actually integrated in terms of structural connections.

We therefore want to emphasize two important but at first sight contradictory features of the inferred ability-related brain areas: On the one hand, they are exclusive (segregated), but on the other hand more densely connected (integrated by fiber tracts) than the average of the brain. We interpret the "segregation" feature to reflect the partial independence of stratum II entities in the psychometric structure of cognition. Furthermore, the relatively dense connections of the ability-related brain areas across ontological entities, i.e., the "integration" feature, appear to support the positive manifold of the abilities that produces general intelligence at stratum III in the CHC ontology. This interpretation offers a new perspective on how the structure of human

intelligence can be understood in terms of underlying neural clusters in the regional neuroanatomical properties and fiber network projections in the brain to support both segregation and integration. The segregation and integration configuration of brain networks have been studied to achieve a better understanding of cognitive abilities, including their relationships with general intelligence (Bassett and Bullmore, 2017; Deco et al., 2015; Fair et al., 2007; Oldham and Fornito, 2019; Sporns, 2013; R. Wang et al., 2019a, 2021). However, these previous studies focused on functional properties of the brain, prompting our question whether also neuroanatomical properties reveal similar segregation and integration organizational features. The results of the present study provide an affirmative answer to this question. Future studies may specifically investigate the association between the structural connections and the inter-individual variability between segregated ability-related cortical areas and general intelligence.

Moreover, we emphasize that segregation and integration are interpreted from an anatomical perspective here. This interpretation implies that abilities are independent in terms of ability-related local anatomical brain features, but integrated as reflected by anatomical connections in the brain. Segregation and integration concepts are also applied from a functional perspective on the brain. In this framework, they indicate whether abilities recruit different functional subsystems, such as perception, categorization, memory encoding, memory retrieval, decision making networks (Bolt et al., 2017; Shafiei et al., 2020; Thomas Yeo et al., 2011), etc. These subsystems are partially independent from each other (segregated), but also have functional links which connect different subsystems (integrated). For example, from a functional perspective, *Gf* and *Gc* (Figure 3A) may recruit different subsystems of perception and memory, while *switching* and *inhibition* (measured by *EF1-EF2* and *EF3-EF4*, respectively), may appear more push-pull as segregated functional subsystems. However, in our study, those abilities are lumped or integrated into the abilities *G* and *EF*, respectively, based on the anatomical features of brain areas associated with them. Thus, we found that abilities can be segregated at the functional level, even if relying on integrated anatomical networks. Taking together, the interpretation of segregation and integration needs both perspectives, the structural and the functional ones. Future studies on the neurometric ontology may systematically compare and investigate the relation between functional and anatomical subsystems to derive ontological conclusions. Such an approach will provide a deeper understanding on how abilities are manifested in the brain.

Conclusion

We applied a novel approach to derive a neurometric cognitive ontology from anatomical properties of the brain, and compared this ontology with a largely standard psychometric ontology derived from task performance. The results revealed that the entities of the neurometric ontology partly reflect the current psychometric view. In important respects, the brain areas related to the neurometric ontologies correspond to findings from previous imaging studies of cognitive abilities. We also found sparse (or even no) overlap between brain areas related to different neurometric ontological entities, reflecting the neural reality of separable psychometric cognitive entities. Although the cognitive entities were segregated, the structural connections between their core brain areas were relatively dense. These findings seem to explain the moderate correlations of psychometric abilities at stratum II by the result of segregated ability-related cortical areas, and the positive manifold captured at stratum III by the revealed dense fiber connections between cortical core areas.

Limitations of the study

The present study has some limitations. First, it relies on 15 cognitive tasks and four anatomical properties of the brain only. Applying a larger number of cognitive tasks and measuring more brain properties, such as cytoarchitecture, connectivity, biochemistry, GABA concentration, and gene expression, which were found to be correlated with general intelligence (Beaty et al., 2018; Schmidt-Wilcke et al., 2017; Zimmerman et al., 2020), will be a promising direction toward a more comprehensive view on the neurometric ontology of human cognition. In addition, behavioral outcomes may not rely only on regional properties, as studied here, but also on connection properties. By including the connection properties (which may change the modularity and integration), the brain areas which were not well separable in term of anatomical properties could become more differentiated. Recent network neuroscience investigates how cognitive functions are reflected in brain networks. However, most of these studies have only considered connection properties. Future studies should consider both regional and connection properties to explain the segregation and integration of task-related brain areas (e.g., Wang et al., 2019b, 2021).

Moreover, we derived the ability-related brain areas by overlapping task-related brain areas across corresponding tasks of a given cognitive entity. Therefore, employing a larger number of tasks which

are representative for the targeted abilities and providing more indicators should result in a more robust determination of the psychometric ontology. Furthermore, a particular cognitive task may not be sufficiently pure to measure a specific cognitive function (see Poldrack and Yarkoni, 2016). For example, the *Gs1* task challenges visual and semantic processing in addition to mental speed. Therefore, future work should rely on cognitive tasks that are as pure as possible to capture specific cognitive functions.

In addition, referring to the frequency distribution of the general intelligence scores (Figure S2) and applying the criterion of more than two *SD*s above the mean to classify exceptionally intelligent individuals, we only found very few individuals (n = 10) in this range. Therefore, we claim that the present findings are valid for the average intelligence range, but not for gifted (exceptionally intelligent) individuals (We performed additional analyses to explore and compare the neurometric ontologies of low versus high ability individuals. We used several criteria to define the low versus high ability range. However, the usual criterion of two*SD*s above the population mean to classify exceptionally intelligent (gifted) individuals was not applicable, because the sample was not covering this high ability range. The neurometric ontologies for low vs. high individuals are equivalent. Given larger sample size of the low versus high ability groups, the concluded neurometric ontology overlaps with the one obtained on the basis of the entire sample. These results are summarized in Table S8). The analyzed database aimed to capture the general population but did not oversample gifted individuals. For understanding whether gifted individuals have potentially less differentiated neurometric ontology, future studies on such special samples are to come.

Finally, the task-related cortical areas were identified by linear associations. As suggested in the literature (Kriegeskorte, 2015), a non-linear approach using, for instance, artificial neural networks could be applied, to afford a more precise mapping of anatomical properties of the brain and cognitive behavior.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2022.104706.

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AUTHOR CONTRIBUTIONS

DK: Conceptualization, methodology, software, formal analysis, writing-original draft, visualization. XL: resources, methodology, software, formal analysis. WS: Conceptualization, writing-review and editing,

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

Alvarez, I., Parker, A.J., and Bridge, H. (2019). Normative cerebral cortical thickness for human visual areas. Neuroimage *201*, 116057. https://doi.org/10.1016/j.neuroimage.2019.116057.

Anderson, M.L. (2015). Mining the brain for a new taxonomy of the mind. Philos. Compass *10*, 68–77. https://doi.org/10.1111/phc3.12155.

Bajaj, S., Raikes, A., Smith, R., Dailey, N.S., Alkozei, A., Vanuk, J.R., and Killgore, W.D. (2018). The relationship between general intelligence and cortical structure in healthy individuals. Neuroscience *388*, 36–44. https://doi.org/10.1016/j.neuroscience.2018.07.008.

Barbey, A.K. (2018). Network neuroscience theory of human intelligence. Trends Cognit. Sci. *22*, 8–20. https://doi.org/10.1016/j.tics.2017.10.001.

Barch, D.M., Burgess, G.C., Harms, M.P., Petersen, S.E., Schlaggar, B.L., Corbetta, M., Glasser, M.F., Curtiss, S., Dixit, S., Feldt, C., et al. (2013). Function in the human connectome: task-fMRI and individual differences in behavior. Neuroimage *80*, 169–189. https://doi.org/10.1016/j.neuroimage.2013.05.033.

Bassett, D.S., and Bullmore, E.T. (2017). Small-world brain networks revisited. Neuroscientist *23*, 499–516. https://doi.org/10.1177/1073858416667720.

Bayard, F., Nymberg Thunell, C., Abé, C., Almeida, R., Banaschewski, T., Barker, G., Bokde, A.L.W., Bromberg, U., Büchel, C., Quinlan, E.B., et al. (2020). Distinct brain structure and behavior related to ADHD and conduct disorder traits. Mol. Psychiatr. *25*, 3020–3033. https://doi.org/10.1038/s41380-018-0202-6.

Beaty, R.E., Benedek, M., Wilkins, R.W., Jauk, E., Fink, A., Silvia, P.J., Hodges, D.A., Koschutnig, K., and Neubauer, A.C. (2014). Creativity and the default network: a functional connectivity analysis of the creative brain at rest. Neuropsychologia *64*, 92–98. https://doi.org/10.1016/j.neuropsychologia.2014.09.019.

Beaty, R.E., Kenett, Y.N., Christensen, A.P., Rosenberg, M.D., Benedek, M., Chen, Q., Fink, A., Qiu, J., Kwapil, T.R., Kane, M.J., and Silvia, P.J. (2018). Robust prediction of individual creative ability from brain functional connectivity. Proc. Natl. Acad. Sci. USA *115*, 1087–1092. https://doi.org/10.1073/pnas.1713532115.

Bolt, T., Nomi, J.S., Yeo, B.T., and Uddin, L.Q. (2017). Data-driven extraction of a nested model of human brain function. J. Neurosci. *37*, 7263–7277. https://doi.org/10.1523/JNEUROSCI.0323-17.2017.

Call, C.L., and Bergles, D.E. (2021). Cortical neurons exhibit diverse myelination patterns that scale between mouse brain regions and regenerate after demyelination. Nat. Commun. *12*, 4767. https://doi.org/10.1038/s41467-021-25035-2.

Carroll, J.B. (1993). Human Cognitive Abilities: A Survey of Factor-Analytic Studies (Cambridge University Press).

Cattell, R.B. (1943). The measurement of adult intelligence. Psychol. Bull. *40*, 153–193. https://doi.org/10.1037/h0059973.

Chen, P.-Y., Yang, C.-M., and Morin, C.M. (2015). Validating the cross-cultural factor structure and invariance property of the Insomnia Severity Index: evidence based on ordinal EFA and CFA. Sleep Med. *16*, 598–603. https://doi.org/10.1016/j.sleep.2014.11.016.

Cheng, W., Rolls, E., Gong, W., Du, J., Zhang, J., Zhang, X.Y., Li, F., and Feng, J. (2020). Sleep duration, brain structure, and psychiatric and cognitive problems in children. Mol. Psychiatry *26*, 3992–4003. https://doi.org/10.1038/s41380-020-0663-2.

Cocchi, L., Zalesky, A., Fornito, A., and Mattingley, J.B. (2013). Dynamic cooperation and competition between brain systems during cognitive control. Trends Cognit. Sci. *17*, 493–501. https://doi.org/10.1016/j.tics.2013.08.006.

Colom, R., Jung, R.E., and Haier, R.J. (2006). Distributed brain sites for the g-factor of intelligence. Neuroimage *31*, 1359–1365. https://doi.org/10.1016/j.neuroimage.2006.01.006.

Cronbach, L.J., and Meehl, P.E. (1955). Construct validity in psychological tests. Psychol. Bull. *52*, 281–302. https://doi.org/10.1037/h0040957.

Cui, Z., Su, M., Li, L., Shu, H., and Gong, G. (2018). Individualized prediction of reading comprehension ability using gray matter volume. Cereb. Cortex *28*, 1656–1672. https://doi.org/10.1093/cercor/bhx061.

de Mooij, S.M., Henson, R.N., Waldorp, L.J., and Kievit, R.A. (2018). Age differentiation within gray matter, white matter, and between memory and white matter in an adult life span cohort. J. Neurosci. *38*, 5826–5836. https://doi.org/10.1523/JNEUROSCI.1627-17.2018.

de Vos, F., Schouten, T.M., Hafkemeijer, A., Dopper, E.G.P., van Swieten, J.C., de Rooij, M., van der Grond, J., and Rombouts, S.A.R.B. (2016). Combining multiple anatomical MRI measures improves Alzheimer's disease classification. Hum. Brain Mapp. *37*, 1920–1929. https://doi.org/10.1002/hbm.23147.

Deco, G., Ponce-Alvarez, A., Hagmann, P., Romani, G.L., Mantini, D., and Corbetta, M. (2014). How local excitation-inhibition ratio impacts the whole brain dynamics. J. Neurosci. *34*, 7886–7898. https://doi.org/10.1523/JNEUROSCI.5068-13.2014.

Deco, G., Tononi, G., Boly, M., and Kringelbach, M.L. (2015). Rethinking segregation and integration: contributions of whole-brain modelling. Nat. Rev. Neurosci. *16*, 430–439. https://doi.org/10.1038/nrn3963.

Demirtaş, M., Burt, J.B., Helmer, M., Ji, J.L., Adkinson, B.D., Glasser, M.F., Van Essen, D.C., Sotiropoulos, S.N., Anticevic, A., and Murray, J.D. (2019). Hierarchical heterogeneity across human cortex shapes large-scale neural dynamics. Neuron *101*, 1181–1194.e13. https://doi.org/10.1016/j.neuron.2019.01.017.

Dubois, J., Galdi, P., Paul, L.K., and Adolphs, R. (2018). A distributed brain network predicts general intelligence from resting-state human neuroimaging data. Phil. Trans. Biol. Sci. *373*, 20170284. https://doi.org/10.1098/rstb.2017.0284.

Fair, D.A., Dosenbach, N.U.F., Church, J.A., Cohen, A.L., Brahmbhatt, S., Miezin, F.M., Barch, D.M., Raichle, M.E., Petersen, S.E., and Schlaggar, B.L. (2007). Development of distinct control networks through segregation and integration. Proc. Natl. Acad. Sci. USA *104*, 13507–13512. https://doi.org/10.1073/pnas.0705843104.

Finn, E.S., Shen, X., Scheinost, D., Rosenberg, M.D., Huang, J., Chun, M.M., Papademetris, X., and Constable, R.T. (2015). Functional connectome fingerprinting: identifying individuals using patterns of brain connectivity. Nat. Neurosci. *18*, 1664–1671. https://doi.org/10.1038/nn.4135.

Fornito, A., Bullmore, E.T., and Zalesky, A. (2017). Opportunities and challenges for psychiatry in the connectomic era. Biol. Psychiatr. Cogn. Neurosci. Neuroimaging *2*, 9–19. https://doi.org/10.1016/j.bpsc.2016.08.003.

Gao, M., Wong, C.H., Huang, H., Shao, R., Huang, R., Chan, C.C., and Lee, T.M. (2020). Connectome-based models can predict processing speed in older adults. Neuroimage *223*, 117290. https://doi.org/10.1016/j.neuroimage.2020.117290.

Glasser, M.F., Coalson, T.S., Robinson, E.C., Hacker, C.D., Harwell, J., Yacoub, E., Ugurbil, K., Andersson, J., Beckmann, C.F., Jenkinson, M., et al. (2016). A multi-modal parcellation of human cerebral cortex. Nature *536*, 171–178. https://doi.org/10.1038/nature18933.

Glasser, M.F., Sotiropoulos, S.N., Wilson, J.A., Coalson, T.S., Fischl, B., Andersson, J.L., Xu, J., Jbabdi, S., Webster, M., Polimeni, J.R., et al. (2013). The minimal preprocessing pipelines for the Human Connectome Project. Neuroimage *80*, 105–124. https://doi.org/10.1016/J.NEUROIMAGE.2013.04.127.

Glasser, M.F., and van Essen, D.C. (2011). Mapping human cortical areas in vivo based on myelin content as revealed by T1- and T2-weighted MRI. J. Neurosci. *31*, 11597–11616. https://doi.org/10.1523/JNEUROSCI.2180-11.2011.

Guest, O., and Martin, A.E. (2021). How computational modeling can force theory building in psychological science. Perspect. Psychol. Sci. *16*, 789–802. https://doi.org/10.1177/1745691620970585.

Hall, P.A., Best, J.R., Danckert, J., Beaton, E.A., and Lee, J.A. (2021). Morphometry of the lateral orbitofrontal cortex is associated with eating dispositions in early adolescence: findings from a large population-based study. Soc. Cogn. Affect. Neurosci. nsab084. https://doi.org/10.1093/scan/nsab084.

Hamidullah, S., Thorpe, H.H.A., Frie, J.A., Mccurdy, R.D., and Khokhar, J.Y. (2020). Adolescent substance use and the brain: behavioral, cognitive and neuroimaging correlates. Front. Hum. Neurosci. *14*, 298. https://doi.org/10.3389/fnhum.2020.00298.

Herculano-Houzel, S., Watson, C., and Paxinos, G. (2013). Distribution of neurons in functional areas of the mouse cerebral cortex reveals quantitatively different cortical zones. Front. Neuroanat. *7*, 35. https://doi.org/10.3389/fnana.2013.00035.

Hu, L., and Bentler, P.M. (1999). Cutoff criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives. Struct. Equ. Model. *6*, 1–55. https://doi.org/10.1080/10705519909540118.

Jaccard, P. (1912). The distribution of the flora in the alpine zone. New Phytol. *11*, 37–50. https://doi.org/10.1111/j.1469-8137.1912.tb05611.x.

Jonikaitis, D., and Moore, T. (2019). The interdependence of attention, working memory and gaze control: behavior and neural circuitry. Curr. Opin. Psychol. *29*, 126–134. https://doi.org/10.1016/j.copsyc.2019.01.012.

Jung, R.E., and Haier, R.J. (2007). The parieto-frontal integration theory (P-FIT) of intelligence: converging neuroimaging evidence. Behav. Brain Sci. *30*, 135–154. https://doi.org/10.1017/S0140525X07001185.

Khanna, P., and Carmena, J.M. (2017). Beta band oscillations in motor cortex reflect neural population signals that delay movement onset. Elife *6*, e24573. https://doi.org/10.7554/eLife.24573.

King, M., Hernandez-Castillo, C.R., Poldrack, R.A., Ivry, R.B., and Diedrichsen, J. (2019). Functional boundaries in the human cerebellum revealed by a multi-domain task battery. Nat. Neurosci. *22*, 1371–1378. https://doi.org/10.1038/s41593-019-0436-x.

Korgaonkar, M.S., Rekshan, W., Gordon, E., Rush, A.J., Williams, L.M., Blasey, C., and Grieve, S.M. (2015). Magnetic resonance imaging measures of brain structure to predict antidepressant treatment outcome in major depressive disorder. EBioMedicine *2*, 37–45. https://doi.org/10.1016/j.ebiom.2014.12.002.

Koshiyama, D., Fukunaga, M., Okada, N., Yamashita, F., Yamamori, H., Yasuda, Y., Fujimoto, M., Ohi, K., Fujino, H., Watanabe, Y., et al. (2018). Subcortical association with memory performance in schizophrenia: a structural magnetic resonance imaging study. Transl. Psychiatry *8*, 20. https://doi.org/10.1038/s41398-017-0069-3.

Kovacs, K., and Conway, A.R.A. (2016). Process overlap theory: a unified account of the general factor of intelligence. Psychol. Inq. *27*, 151–177. https://doi.org/10.1080/1047840X.2016.1153946.

Kriegeskorte, N. (2015). Deep neural networks: a new framework for modeling biological vision and brain information processing. Annu. Rev. Vis. Sci. *1*, 417–446. https://doi.org/10.1146/annurev-vision-082114-035447.

Kristanto, D., Liu, M., Liu, X., Sommer, W., and Zhou, C. (2020). Predicting reading ability from brain anatomy and function: from areas to connections. Neuroimage *218*, 116966. https://doi.org/10.1016/j.neuroimage.2020.116966.

Lee, S.-H., Kravitz, D.J., and Baker, C.I. (2019). Differential representations of perceived and retrieved visual information in Hippocampus and cortex. Cerebr. Cortex *29*, 4452–4461. https://doi.org/10.1093/cercor/bhy325.

Lenartowicz, A., Kalar, D.J., Congdon, E., and Poldrack, R.A. (2010). Towards an ontology of cognitive control. Top. Cogn. Sci. *2*, 678–692. https://doi.org/10.1111/j.1756-8765.2010.01100.x.

Li, C., Huang, B., Zhang, R., Ma, Q., Yang, W., Wang, L., Wang, L., Xu, Q., Feng, J., Liu, L., et al. (2017). Impaired topological architecture of brain structural networks in idiopathic Parkinson's disease: a DTI study. Brain Imaging Behav. *11*, 113–128. https://doi.org/10.1007/s11682-015-9501-6.

Li, Y., Yuan, K., Cai, C., Feng, D., Yin, J., Bi, Y., Shi, S., Yu, D., Jin, C., von Deneen, K.M., et al. (2015). Reduced frontal cortical thickness and increased caudate volume within fronto-striatal circuits in young adult smokers. Drug Alcohol Depend. *151*, 211–219. https://doi.org/10.1016/j.drugalcdep.2015.03.023.

Liu, M., Liu, X., Hildebrandt, A., and Zhou, C. (2020). Individual cortical entropy profile: test–retest reliability, predictive power for cognitive ability, and neuroanatomical foundation. Cereb. Cortex Commun. *1*, tgaa015. https://doi.org/10.1093/texcom/tgaa015.

Liu, X., Hildebrandt, A., Meyer, K., Sommer, W., and Zhou, C. (2019). Patterns of individual differences in fiber tract integrity of the face processing brain network support neurofunctional models. Neuroimage *204*, 116229. https://doi.org/10.1016/j.neuroimage.2019.116229.

Mangin, J.-F., Jouvent, E., and Cachia, A. (2010). In-vivo measurement of cortical morphology: means and meanings. Curr. Opin. Neurol. *23*, 359–367. https://doi.org/10.1097/wco.0b013e32833a0afc.

Masouleh, S.K., Eickhoff, S.B., Hoffstaedter, F., and Genon, S.; Alzheimer's Disease Neuroimaging Initiative (2019). Empirical examination of the replicability of associations between brain structure and psychological variables. Elife *8*, e43464. https://doi.org/10.7554/eLife.43464.

McGrew, K.S. (2009). CHC theory and the human cognitive abilities project: standing on the shoulders of the giants of psychometric intelligence research. Intelligence *37*, 1–10. https://doi.org/10.1016/j.intell.2008.08.004.

Meunier, D., Lambiotte, R., and Bullmore, E.T. (2010). Modular and hierarchically modular organization of brain networks. Front. Neurosci. *4*, 200. https://doi.org/10.3389/fnins.2010.00200.

Meunier, D., Lambiotte, R., Fornito, A., Ersche, K.D., and Bullmore, E.T. (2009). Hierarchical modularity in human brain functional networks. Front. Neuroinf. *3*, 37. https://doi.org/10.3389/neuro.11.037.2009.

Mian, N.D., Godoy, L., Briggs-Gowan, M.J., and Carter, A.S. (2012). Patterns of anxiety symptoms in toddlers and preschool-age children: evidence of early differentiation. J. Anxiety Disord. *26*, 102–110. https://doi.org/10.1016/j.janxdis.2011.09.006.

Miyake, A., Friedman, N.P., Emerson, M.J., Witzki, A.H., Howerter, A., and Wager, T.D. (2000). The unity and diversity of executive functions and their contributions to complex "frontal lobe" tasks: a latent variable analysis. Cognit. Psychol. *41*, 49–100. https://doi.org/10.1006/cogp.1999.0734.

Müllner, J., Delmaire, C., Valabrégue, R., Schüpbach, M., Mangin, J.-F., Vidailhet, M., Lehéricy, S., Hartmann, A., and Worbe, Y. (2015). Altered structure of cortical sulci in gilles de la Tourette syndrome: further support for abnormal brain development: sulcal Structure in GTS. Mov. Disord. *30*, 655–661. https://doi.org/10.1002/mds.26207.

Murray, A.L., Booth, T., Eisner, M., Obsuth, I., and Ribeaud, D. (2019). Quantifying the strength of general factors in psychopathology: a comparison of CFA with maximum likelihood estimation, BSEM, and ESEM/EFA bifactor approaches. J. Pers. Assess. *101*, 631–643. https://doi.org/10.1080/00223891.2018.1468338.

Nadel, L., and Hardt, O. (2011). Update on memory systems and processes. Neuropsychopharmacology *36*, 251–273. https://doi.org/10.1038/npp.2010.169.

Niendam, T.A., Laird, A.R., Ray, K.L., Dean, Y.M., Glahn, D.C., and Carter, C.S. (2012). Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. Cognit. Affect Behav. Neurosci. *12*, 241–268. https://doi.org/10.3758/s13415-011-0083-5.

Oberauer, K., Wilhelm, O., and Schmiedek, F. (2005). Experimental strategies in multivariate research. In Multivariate Research Strategies: Festschrift in honor of Werner W (Shaker Verlag), pp. 119–149.

Olderbak, S., Semmler, M., and Doebler, P. (2019). Four-branch model of ability emotional intelligence with fluid and crystallized intelligence: a meta-analysis of relations. Emotion Rev. *11*, 166–183. https://doi.org/10.1177/1754073918776776.

Oldham, S., and Fornito, A. (2019). The development of brain network hubs. Dev. Cogn. Neurosci. *36*, 100607. https://doi.org/10.1016/j.dcn.2018.12.005.

Perri, R.L., Berchicci, M., Spinelli, D., and Di Russo, F. (2014). Individual differences in response speed and accuracy are associated to specific brain activities of two interacting systems. Front. Behav. Neurosci. *8*, 251. https://doi.org/10.3389/fnbeh.2014.00251.

Phinney, E., Pennington, B., Olson, R., Filley, C., and Filipek, P. (2007). Brain structure correlates of component reading processes: implications for reading disability. Cortex *43*, 777–791. https://doi.org/10.1016/S0010-9452(08)70506-9.

Poldrack, R.A., Kittur, A., Kalar, D., Miller, E., Seppa, C., Gil, Y., Parker, D.S., Sabb, F.W., and Bilder, R.M. (2011). The cognitive atlas: toward a knowledge foundation for cognitive neuroscience. Front. Neuroinf. *5*, 17. https://doi.org/10.3389/fninf.2011.00017.

Poldrack, R.A., and Yarkoni, T. (2016). From brain maps to cognitive ontologies: informatics and the search for mental structure. Annu. Rev. Psychol. *67*, 587–612. https://doi.org/10.1146/annurev-psych-122414-033729.

Reese McKay, D., Kochunov, P., Cykowski, M.D., Kent, J.W., Laird, A.R., Lancaster, J.L., Blangero, J., Glahn, D.C., and Fox, P.T. (2013). Sulcal depth-position profile is a genetically mediated neuroscientific trait: description and characterization in the central sulcus. J. Neurosci. *33*, 15618–15625. https://doi.org/10.1523/JNEUROSCI.1616-13.2013.

Rezatofighi, H., Tsoi, N., Gwak, J., Sadeghian, A., Reid, I., and Savarese, S. (2019, June). Generalized intersection over union: a metric and a loss for bounding box regression. In Proceedings of the IEEE/CVF Conference on Computer Vision and Pattern Recognition (CVPR) (IEEE).

Schmidt-Wilcke, T., Fuchs, E., Funke, K., Vlachos, A., Müller-Dahlhaus, F., Puts, N.A.J., Harris, R.E., and Edden, R.A.E. (2017). GABA—from inhibition to cognition: emerging concepts. Neuroscientist *24*, 501–515. https://doi.org/10.1177/1073858417734530.

Schulze, R. (2005). Modeling structures of intelligence. In Handbook of understanding and measuring intelligence, pp. 241–263.

Shafiei, G., Markello, R.D., Vos de Wael, R., Bernhardt, B.C., Fulcher, B.D., and Misic, B. (2020). Topographic gradients of intrinsic dynamics across neocortex. Elife *9*, e62116. https://doi.org/10.7554/eLife.62116.

Shen, X., Finn, E.S., Scheinost, D., Rosenberg, M.D., Chun, M.M., Papademetris, X., and Constable, R.T. (2017). Using connectome-based predictive modeling to predict individual behavior from brain connectivity. Nat. Protoc. *12*, 506–518. https://doi.org/10.1038/nprot.2016.178.

Shimony, J.S., Smyser, C.D., Wideman, G., Alexopoulos, D., Hill, J., Harwell, J., Dierker, D., Van Essen, D.C., Inder, T.E., and Neil, J.J. (2016). Comparison of cortical folding measures for evaluation of developing human brain. Neuroimage *125*, 780–790. https://doi.org/10.1016/j.neuroimage.2015.11.001.

Shine, J.M., Müller, E.J., Munn, B., Cabral, J., Moran, R.J., and Breakspear, M. (2021). Computational models link cellular mechanisms of neuromodulation to large-scale neural dynamics. Nat. Neurosci. *24*, 765–776. https://doi.org/10.1038/s41593-021-00824-6.

Skudlarski, P., Jagannathan, K., Anderson, K., Stevens, M.C., Calhoun, V.D., Skudlarska, B.A., and Pearlson, G. (2010). Brain connectivity is not only lower but different in schizophrenia: a combined anatomical and functional approach. Biol. Psychiatry *68*, 61–69. https://doi.org/10.1016/j.biopsych.2010.03.035.

Sporns, O. (2013). Network attributes for segregation and integration in the human brain. Curr. Opin. Neurobiol. *23*, 162–171. https://doi.org/10.1016/j.conb.2012.11.015.

Squire, L.R. (2009). Memory and brain systems: 1969-2009. J. Neurosci. *29*, 12711–12716. https://doi.org/10.1523/JNEUROSCI.3575-09.2009.

Tadayon, E., Pascual-Leone, A., and Santarnecchi, E. (2020). Differential contribution of cortical thickness, surface area, and gyrification to fluid and crystallized intelligence. Cerebr. Cortex *30*, 215–225. https://doi.org/10.1093/cercor/bhz082.

Thomas Yeo, B.T., Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, D., Hollinshead, M., Roffman, J.L., Smoller, J.W., Zöllei, L., Polimeni, J.R., et al. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. J. Neurophysiol. *106*, 1125–1165. https://doi.org/10.1152/jn.00338.2011.

Valizadeh, S.A., Hänggi, J., Mérillat, S., and Jäncke, L. (2017). Age prediction on the basis of brain anatomical measures. Hum. Brain Mapp. *38*, 997–1008. https://doi.org/10.1002/hbm.23434.

Van Essen, D.C., Smith, S.M., Barch, D.M., Behrens, T.E., Yacoub, E., and Ugurbil, K. (2013). The WU-minn human connectome project: an overview. Neuroimage *80*, 62–79. https://doi.org/10.1016/J.NEUROIMAGE.2013.05.041.

Wade, N.E., Bagot, K.S., Cota, C.I., Fotros, A., Squeglia, L.M., Meredith, L.R., and Jacobus, J. (2019). Orbitofrontal cortex volume prospectively predicts cannabis and other substance use onset in adolescents. J. Psychopharmacol. *33*, 1124–1131. https://doi.org/10.1177/0269881119855971.

Wang, P., Kong, R., Kong, X., Liégeois, R., Orban, C., Deco, G., Van Den Heuvel, M.P., and Thomas Yeo, B.T. (2019a). Inversion of a large-scale circuit model reveals a cortical hierarchy in the dynamic resting human brain. Sci. Adv. *5*, eaat7854. https://doi.org/10.1126/sciadv.aat7854.

Wang, R., Lin, P., Liu, M., Wu, Y., Zhou, T., and Zhou, C. (2019b). Hierarchical connectome modes and critical state jointly maximize human brain functional diversity. Phys. Rev. Lett. *123*, 038301. https://doi.org/10.1103/PhysRevLett.123.038301.

Wang, R., Liu, M., Cheng, X., Wu, Y., Hildebrandt, A., and Zhou, C. (2021). Segregation, integration, and balance of large-scale resting brain networks configure different cognitive abilities. Proc. Natl. Acad. Sci. USA *118*, e2022288118. https://doi.org/10.1073/pnas.2022288118.

Weintraub, S., Dikmen, S.S., Heaton, R.K., Tulsky, D.S., Zelazo, P.D., Bauer, P.J., Carlozzi, N.E., Slotkin, J., Blitz, D., Wallner-Allen, K., et al. (2013). Cognition assessment using the NIH Toolbox. Neurology *80*, S54–S64. https://doi.org/10.1212/WNL.0b013e3182872ded.

Wenger, E., Brozzoli, C., Lindenberger, U., and Lövdén, M. (2017). Expansion and renormalization of human brain structure during skill acquisition. Trends Cognit. Sci. *21*, 930–939. https://doi.org/10.1016/j.tics.2017.09.008.

Williamson, J.M., and Lyons, D.A. (2018). Myelin dynamics throughout life: an ever-changing landscape? Front. Cell. Neurosci. *12*, 424. https://doi.org/10.3389/fncel.2018.00424.

Yalçın, B., and Monje, M. (2020). Bespoke myelin tailored to neuron type. Science *370*, 1414–1415. https://doi.org/10.1126/science.abf4646.

Zhang, X., Li, H., Xie, T., Liu, Y., Chen, J., and Long, J. (2020). Movement speed effects on beta-band oscillations in sensorimotor cortex during voluntary activity. J. Neurophysiol. *124*, 352–359. https://doi.org/10.1152/jn.00238.2020.

Zimmerman, A.J., Hafez, A.K., Amoah, S.K., Rodriguez, B.A., Dell'Orco, M., Lozano, E., Hartley, B.J., Alural, B., Lalonde, J., Chander, P., et al. (2020). A psychiatric disease-related circular RNA controls synaptic gene expression and cognition. Mol. Psychiatr. *25*, 2712–2727. https://doi.org/10.1038/s41380-020-0653-4.

Zink, N., Lenartowicz, A., and Markett, S. (2021). A new era for executive function research: on the transition from centralized to distributed executive functioning. Neurosci. Biobehav. Rev. *124*, 235–244. https://doi.org/10.1016/j.neubiorev.2021.02.011.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Participants	Human Connectome Project	https://www.humanconnectome.org/
Software and algorithms		
Confirmatory analysis	Confirmatory Factor Analysis (CFA) in R LAVAAN package	https://lavaan.ugent.be
Exploratory analysis	Exploratory Factor Analysis (EFA) in R PSYCH package	https://cran.r-project.org/web/packages/psych/index.html
Brain visualization	Connectome Workbench	https://www.humanconnectome.org/software/connectome-workbench
MATLAB R2020a	MathWorks	https://github.com/kristantodan12/Mining-the-brain

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and fulfilled by lead contact: Changsong Zhou.

Materials availability

This study did not generate new unique reagents.

Data and code availability

- The datasets that support the findings of this study are available at http://www.humanconnectome.org/study/hcp-young-adult.
- The codes used in this study are available at https://github.com/kristantodan12/Mining-the-brain.
- Any additional information required to reanalyze the data reported in this study is available upon request from the lead contact.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Participants

This study used the publicly available data from the WU-Minn Young Adult Human Connectome Project (HCP), covering several magnetic resonance imaging (MRI) modalities, including resting-state functional MRI, diffusion MRI, and structural MRI (Van Essen et al., 2013). The HCP database also provides demographic data and performance measures for a number of cognitive tasks. Of the 1,206 data sets in the HCP database at the time of study, those with incomplete information were excluded, yielding a final sample of $N = 838$ (449 females, 760 right-handed, and three ambidextrous) individuals. Age ranged from 22 to 35 years. Across all subjects, there were 401 different families identified by the ID of the mother and father of the participants. For more detailed information on data acquisition protocols of the HCP please refer to the project's website (https://www.humanconnectome.org/). The local ethics committee of Washington University approved the HCP study.

Anatomical measures

We considered four properties of the cortex, derived from structural MRI: *thickness*, *myelination*, *curvature*, and *sulcus depth*. The T1-weighted and T2-weighted images (see (Glasser and van Essen, 2011) for the details of the scanning processes) in the database have been pre-processed to correct distortions and align the images to the Montreal Neurological Institute space template (Glasser et al., 2013). Using the

pre-processed images, gray and white matter of the cortical surface was reconstructed. All anatomical properties of the cortex used in the present study were estimated from the surface reconstruction. Cortical thickness was measured as distance between the pial surface and the gray–white matter border (Alvarez et al., 2019). The thickness of the cortex correlates with the number of neurons (Herculano-Houzel et al., 2013). Myelination, that is, myelin content of a given voxel, was determined as the ratio of T1 and T2 weights (Glasser and van Essen, 2011), with a higher ratios indicating the higher abundance of myelin in a given voxel. Curvature indicates the bending of each vertex of the cortical surface, and a higher curvature indicates sharper bending, with positive values corresponding to convex bending (Shimony et al., 2016). Lastly, sulcus depth was calculated as the distance between mid-surface gyri and sulci (Müllner et al., 2015). Curvature and sulcus depth contribute to determining the sulcal patterns predicting the acquisition of cognitive skills (Mangin et al., 2010). All voxel-wise data, including both individual and group averages, were taken from the HCP website. We used the Multi-Modal Parcellation (MMP) atlas (Glasser et al., 2016), which divides each hemisphere of the brain into 180 areas. We averaged the voxel-wise property measures within a given brain area to obtain an area-specific measure of the respective property. Thus, for each participant, four brain properties were featured in each brain area.

For the analysis of connections among brain areas, we measured structural connectivity based on white matter projections between brain areas in the MMP atlas. We applied probabilistic tractography to the diffusion MRI data to trace white matter connections. Briefly, we set seed and target areas for a pair of brain areas. From each vertex of the seed area, we generated 5,000 streamlines and counted how many reached the target area. When the streamlines met with a voxel whose fractional anisotropy was less than 0.1, the propagation was stopped. There were two streamline directions, given that an area can serve as both, seed and target. Thus, the final structural connectivity between two areas was the average of two directional connectivity probabilities (see Liu et al., 2019 for details).

Cognitive tasks

Performance in 15 cognitive tasks was used for the present analyses. The tasks were adopted from the task-evoked fMRI measurement (in-scanner test), NIH Toolbox, and Penn Computerized Cognitive Battery (Barch et al., 2013; Dubois et al., 2018; Van Essen et al., 2013), and were selected by the HCP as a representative set of tasks covering most of the domain-specific abilities at stratum II, according to the CHC model (see above). Table 1 provides a summary of the tasks grouped into different stratum II abilities. We also included executive function (*EF*) as a domain-specific ability (Zink et al., 2021) because it plays a crucial role in human cognition and has pivotal diagnostic relevance in many mental conditions.

The indicators obtained in the tasks *Gf1*, *Gf2*, *Gf3*, *Gc1*, *Gc2*, *Gm1*, and *Gm2* were performance accuracies (Weintraub et al., 2013), whereas in the tasks *EF1*, *EF2*, *EF3*, *EF4*, *Gs1*, *Gs2*, *Gs3*, and *Gs4* we used inverted reaction times of correct responses, indicating the number of trials correctly solved per second. All performance indicators were standardized prior to statistical analyses. In all tasks, higher values correspond to better performance.

METHOD DETAILS

As illustrated in Figure 1, we explore the neurometric ontology (Figure 1A) to descriptively compare it with the well-established psychometric ontology (Figure 1B). We derive the neurometric ontology by several analytic steps. These include (1) the identification of the brain areas linearly associated with the psychometric tasks, (2) quantification of the overlap of task-related brain areas across pairs of tasks (IOU), and (3) factor analysis of pairwise overlap matrices between brain areas related with different tasks to obtain a neurometric ontological structure. Each of these steps is illustrated in Figure 1C and explained below in more detail. For a valid comparison between psychometric and neurometric ontologies, the psychometric one also needs confirmation in the present sample as well. The procedure of deriving the psychometric ontology is described below.

Identifying task-related cortical areas

We identified task-related cortical areas for each of the 15 tasks by correlating anatomical properties of the 360 brain areas with task performance across individuals (Figure 1A, middle panel). The CORR function in MATLAB (https://www.mathworks.com/help/stats/corr.html) was applied to determine the Pearson's correlation coefficients. This analysis resulted in a single correlation value for each cortical area for a given

brain property and task. Thus, for all tasks and the four cortical properties together, there were 15 × 4 correlation values in each cortical area. The CORR function additionally provides *p*-values; thresholding at $p < 0.05$ was applied to select relevant cortical areas associated with a given task. Thus, cortical areas that were significantly correlated with performance were regarded as task-related. The selection of the *p*-value threshold ($p < 0.05$) was based on a previous study (Kristanto et al., 2020) where a smaller *p*-value threshold ($p < 0.01$ or $p < 0.005$) had resulted in the identification of cortical areas specific for a particular cognitive task. In the present study, we explored the relationships among cognitive tasks in terms of shared cortical areas. Thus, we selected a more liberal *p*-value threshold ($p < 0.05$) which captured not only the cortical areas specific for a particular task, but also cortical areas shared between tasks.

As data mining was applied to four anatomical properties of the brain, four sets of task-related cortical areas were obtained for each task. For a multimodal representation, we determined the union of these sets of task-related cortical areas across the four anatomical properties. Thus, to qualify as task-related, a given cortical area had to be significantly correlated with the task score ($p < 0.05$) in at least one of the four properties. The obtained cortical networks for each of the 15 tasks from all samples were subjected to further analysis.

Note that we performed the identification of task-related cortical areas in each sample and in the whole sample. Figure S4 depicts the cortical areas related to each task identified from the whole sample, together with their hemisphere-specific distributions. The masks of the task-related cortical areas are also provided as supplementary materials in form of *.gii* files (gifti) by using the MMP atlas. Figure S4 additionally illustrates the contributions of different cortical properties to the task-related cortical areas. Importantly, taken together, the task-related cortical areas covered approximately 80% of the entire cortex.

Quantifying the overlap of task-related cortical areas

The task-related cortical areas were not exclusive to individual tasks, and therefore overlapped across some tasks. Therefore we quantified the overlap for every pair of tasks by using the well-known index of Intersection OverUnion (IOU) (Jaccard, 1912; Rezatofighi et al., 2019). The IOU index is widely used in measuring the similarity between sample sets. In our case, the IOU index of two tasks was calculated as the ratio between the number of common brain areas related to both tasks and the total number of distinct brain areas in each of the two tasks, and expressed as follows:

$$IOU = \frac{|A \cap B|}{|A \cup B|}.$$

where A and B are sets of related cortical areas for Task 1 and Task 2, respectively. The computation of IOU indices of all 15 task pairs resulted in a 15 × 15 IOU matrix. As the task-related cortical areas were based on the correlations between performance and brain properties, we emphasize that the IOU matrices reflect the covariance structure of task pairs across the participants in terms of neuroanatomical properties. Figures 2B and 2C visualized the IOU matrices of task-related cortical areas identified from one of the samples and the whole sample. respectively.

Exploring the structure of IOU matrices

We derived the neurometric ontology from the IOU matrix of task-related cortical areas for each of the 60 participant samples. The factorial structure was assessed by exploratory factor analysis (EFA), using the psych package (https://cran.r-project.org/web/packages/psych/index.html) in R. EFA is a data-driven approach that allows determining the number of factors needed to explain the structure of an association matrix, and the pattern of factor loadings. As different ontological entities indicated by factors in EFA are expected to be correlated, oblique (promax) rotation was applied to achieve a simple structure with interpretable factors. The number of required factors was found by scree plots, based on eigenvalues of a principal components and comparison with random eigenvalues (Figure S3).

For EFAs, model fit was evaluated with the χ^2 test statistic and RMSEA. In large samples, the χ^2 test statistic is highly sensitive. Thus, alternative fit indices play an important role in model fit evaluation. The acceptable value for the RMSEA is < 0.08 (Hu and Bentler, 1999).

Comparison with the psychometric ontology

We compared the most frequently observed neurometric ontology derived from the structure of IOU matrices with the psychometric ontology established by covariance analyses of task performance scores as a reference model. First, we performed a confirmatory factor analysis (CFA) of the correlation matrix of task performance scores of the 15 tasks to provide a baseline model of cognitive ontological entities. For CFA we used the lavaan package (https://lavaan.ugent.be) in R Software for Statistical Computing (https://www.r-project.org/). The CFA model included the domain-specific cognitive ontological entities listed in Table 1. Factors were standardized for identification purposes, such that all factor loadings could be freely estimated. Model fit of CFA was quantified by the χ^2 goodness-of-fit index (χ^2), the comparative fit index (CFI), the root-mean-squared error of approximation (RMSEA), and the standardized root-mean-squared residual (SRMR). Acceptable values for these indices are $> .95$ for the CFI and < 0.08 for both the RMSEA and SRMR (Hu and Bentler, 1999).

CFA and EFA rely on different assumptions, but may lead to consistent factorial structures when applied to the same data (Chen et al., 2015; Mian et al., 2012; Murray et al., 2019). The methodological choices above reflect the assumptions made. There is vast knowledge on which tasks are loaded onto which cognitive entity in the psychometric ontological structure. Furthermore, previous studies of the HCP data (e.g., Dubois et al., 2018; M. Liu et al., 2020) have confirmed the domain-specific cognitive entities considered in the current study. Thus, the factorial structure provided by the CFA of the covariance matrix of performance scores is not specific for the present analyses; rather, it is a descriptive reference for interpreting the ontological entities derived from brain properties. Furthermore, there is no prior knowledge on how the IOU matrices of brain areas related to the 15 specific cognitive tasks are clustered. Thus, by applying a CFA to the IOU matrices mimicking the psychometric ontological structure, we investigated whether task-related brain areas reveal exactly the same entities as obtained from performance. Hence, exploring the structure of the IOU matrices and identify potential differences between psychometric and neurometric ontological entities, an EFA approach appears to be reasonable.

QUANTIFICATION AND STATISTICAL ANALYSES

Aiming to obtain robust and reliable results, we analyzed subsets of data from several resampling realizations. As depicted in Figure 1A (left panel), we first resampled the dataset to obtain 30 realizations, where each realization consisted of two different subsamples while assigning siblings in the dataset to different subsamples. Therefore, in total, we obtained 60 samples. Each sample was used separately in the analysis of the neurometric ontology.