

Review Paper: Linking Brain Biology to Intellectual Endowment: A Review on the Associations of Human Intelligence With Neuroimaging Data



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ABSTRACT

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Human intelligence has always been a fascinating subject for scientists. Since the inception of Spearman's general intelligence in the early 1900s, there has been significant progress towards characterizing different aspects of intelligence and its relationship with structural and functional features of the brain. In recent years, the invention of sophisticated brain imaging devices using Diffusion-Weighted Imaging (DWI) and functional Magnetic Resonance Imaging (fMRI) has allowed researchers to test hypotheses about neural correlates of intelligence in humans. This review summarizes recent findings on the associations of human intelligence with neuroimaging data. To this end, first, we review the literature that has related brain morphometry to intelligence. Next, we elaborate on the applications of DWI and resting-state fMRI on the investigation of intelligence. Then, we provide a survey of literature that has used multimodal DWI-fMRI to shed light on intelligence. Finally, we discuss the state-of-the-art of individualized prediction of intelligence from neuroimaging data and point out future strategies. Future studies hold promising outcomes for machine learning-based predictive frameworks using neuroimaging features to estimate human intelligence.

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Highlights

- Neuroimaging (NI) has been used to study neural correlates of intelligence in humans.
- Anatomical features of brain in T1-weighted MRI are related to human intelligence.
- Diffusion features of brain tissue in DWI are associated with human intelligence.
- Functional connectivity of brain extracted from fMRI may predict human intelligence.
- Integrated analysis of multiple NI modalities can improve prediction of intelligence.

Plain Language Summary

Everyone knows human intelligence and cares about it. Progress of institutions and societies depend on the intelligence of their human resources. Scientists have developed specific tests to evaluate and characterize different aspects of human intelligence. They have discovered the relationship between intelligence and structural and functional features of the brain. Recent development of sophisticated brain imaging (neuroimaging) using Diffusion Weighted Imaging (DWI) and functional Magnetic Resonance Imaging (fMRI) has allowed discovery of neural correlates of intelligence. This paper summarizes recent findings regarding the relationship between human intelligence and neuroimaging data. First, it surveys the literature that has related brain morphometry to intelligence. Next, it describes the applications of DWI and resting-state fMRI for the investigation of intelligence. Then, it presents literature that has discovered the relationship between multi-modal DWI-fMRI and intelligence. Finally, it explains the state-of-the-art of individualized prediction of intelligence from neuroimaging data and suggests future strategies. The future work will apply machine learning-based predictive frameworks to neuroimaging features to estimate human intelligence.

1. Introduction

Intelligence can be defined as “[...] the aggregate or global capacity of the individual to act purposefully, to think rationally and to deal effectively with his environment” (Wechsler, 1944) and comprises several distinct aptitudes. The introduction of intelligence tests in psychometrics allowed the quantification of intellectual aptitude. These measures are useful for a myriad of reasons. It allows studying how intellectual performance varies with respect to behavioral, environmental, and genetic factors. It constitutes a powerful tool for clinical screening purposes, as cognitive deficits are often associated with neurological disorders. In Autism Spectrum Disorder (ASD), for example, recent research shows that ASD children also tend to have some extent of intellectual disability (Charman et al., 2011).

One of the most influential intelligence tests is the Wechsler Adult Intelligence Score (WAIS) (Wechsler, 1944). Its third edition, the WAIS-III, is recommended for subjects aged 16 years or older. It includes 13 sub-tests and comprises 4 indices. It has been normalized for age, i.e. the average score is maintained across the lifespan, even though the test scores vary between ages. The Verbal Comprehension Index (VCI)

is obtained from the information, similarities, and vocabulary tests. The Working Memory Index (WMI) is obtained from the arithmetic and digit span tests. The Perceptual Organization Index (POI) is obtained from the block design, matrix reasoning, and picture completion sub-tests. The Processing Speed Index (PSI) is obtained from the digit symbol-coding and symbol search tests. In turn, these indices can be combined into Intelligence Quotients (IQ). The VCI and WMI sub-indices compose the Verbal Intelligence Quotient (VIQ), while POI and PSI compose the Performance Intelligence Quotient (PIQ). Finally, VIQ and PIQ together form the Full-Scale Intelligence Quotient (FSIQ).

Another commonly studied measurement of intelligence is the Raven's progressive matrices (Raven, 1941). This family of tests has been published in many forms in the literature. Their common feature is a sole presence test where a graphical matrix is visually shown, with a missing sector. The participant is instructed to select, among the alternatives presented later, the correct figure that completes the matrix shown initially. Its non-verbal character is especially useful for application in different sociodemographic contexts.

In general, intelligence tests demand new normative information and adaptations due to the evolving under-

standing of human cognition and clinical practice (Tulsky, Saklofske, & Zhu, 2003). For example, WAIS is revised every two decades, and we currently use its fourth edition (Wechsler, 2008). For an in-depth overview of several intelligence instruments and aptitude tests, see Gregory (2014) chapters 5–6.

It has been noted that there are substantial positive correlations among seemingly unrelated tests. In other words, individuals that score high in a specific sub-test tend to score high in other sub-tests as well. This evidence proves the existence of a general intelligence factor, or *g*, as Spearman termed it (Spearman, 1904). This general intelligence factor has been constructed to be a numeric score that summarizes the positive correlations among subtests and is therefore positively correlated with the generalized intellectual ability of individuals. However, the psychometric literature is not unanimous on the measurability of *g*. This score is often assessed by factor analysis or related techniques to summarize various intelligence tests. Some studies claim that specific tests, such as Raven's Progressive Matrices (RPM) (Raven, 1941), has very high loading on *g* such that they alone could provide sufficient information on the *g* factor (Jensen, 1980), prompting studies to employ these single tests as proxies for *g* (Jensen, 1973), but not without criticism (Gignac, 2015).

Not all intelligence measurements are equal. Differences in quality have been shown to have a moderating effect on the correlation between brain volume and intelligence (Gignac & Bates, 2017) and resting-state functional connectivity and intelligence (Dubois, Galdi, Paul, & Adolphs, 2018). In general, some measurements may lend themselves better to a single cognitive dimension, such as the RPM, not fulfilling criteria to be considered as a good measurement of intelligence. Gignac and Bates (2017) presented an essential guide relating the number of tests, its cognitive dimensions, testing time, and correlation with *g* to a 4-point quality scale.

Spearman also postulated that inter-individual differences in tests overlooked by the overall mental performance measured by *g* were due to *s*—a factor named after specific abilities. It is important to note that IQ is often termed "intelligence in general" in contraposition to general intelligence (Jensen, 1992) and is also influenced by *s* (Colom, Abad, García, & Juan-Espinosa, 2002).

The Spearman hypotheses were further developed by others. The general intelligence factor was separated into crystallized general ability, *gc*, and fluid general ability, *gf* (Cattell, 1963), which received ample support in the lit-

erature. Crystallized general ability is highlighted in tasks that make use of abilities previously acquired through learning. Fluid general ability is manifested in situations requiring adaptability, where no previously learned skill is useful. Competing theories of the estimation and hierarchy *g* have been created as well; for more details on factorial models that contain *g*, see Beaujean (2015).

As it turns out, intelligence is partially driven by genetics. Intelligence displays high heritability, as studies with twins and adopted children have shown, reaching up to 80% in late adulthood (Panizzon et al., 2014). The correlation between the intelligence estimated at 11 years of age and old age (65, 70 or 79 years) has been estimated at 0.62, with genomic information accounting for 0.24 of the variation in intelligence from childhood to old age (Deary et al., 2012). For an overview of genetic influence on intelligence differences, see Plomin and Deary (2015).

It has been noted that genetics does not directly cause variations in intelligence. Genetics influences phenotypes, which in turn influences general intelligence. For this reason, the neurobiological basis of intelligence composes an open and heavily explored scientific question. Variations in intellectual skills due to evolution (phylogeny) and development (ontogeny) make neuroimaging a fundamental tool to answer this question.

The drive to find neural substrates of intelligence started roughly with Chase et al. (1984) and Haier et al. (1988), first with Positron Emission Tomography (PET). It was the preferred imaging technique at the time, which allows one to study brain metabolism in vivo. These works established the feasibility of studying inter-individual variations of intelligence using neuroimaging. In a few years, Magnetic Resonance Imaging (MRI) took over PET for the in vivo, macroscopic studies of the brain and was applied to the study of intelligence (Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997; Kroger et al., 2002). Compared to other neuroimaging techniques, MRI generates good temporal or spatial resolution and displays optimal soft-tissue contrast. Due to magnetic resonance properties of the cerebral tissues and physiology, MRI contrast can be made sensible to the separation of gray and white matter, brain hemodynamic response, or water diffusion in nerve fibers.

Studies using MRI show a substantial correlation between intracranial volume and general indices of intelligence (Luders, Narr, Thompson, & Toga, 2009), reproducible across genders and age ranges (McDaniel, 2005). Several MRI studies show that other indices that touch upon connectivity, neuroanatomy, and brain microstruc-

ture, such as white matter volume, fractional anisotropy in several tracts, and cortical gray matter thickness, are also related to intelligence (Ritchie et al., 2015). Theories on the neural bases of human intelligence are often corroborated with evidence drawn from MRI studies (Barbey 2018; Duncan & Owen, 2000; Duncan 2010; Jung and Haier 2007; Kovacs and Conway 2016). Barbey exposed some of these theories and his Network Neuroscience Theory (NNT) in a recent article (Barbey 2018). They are the lateral prefrontal cortex theory (LPFCT) (Duncan & Owen, 2000), the Parieto-Frontal Integration theory (P-FIT) (Jung and Haier 2007), the Multiple-Demand Theory (M-DT) (Duncan, 2010), and process overlap theory (POT) (Kovacs & Conway, 2016).

The P-FIT, which is perhaps the most studied theory, proposes the existence of a network responsible, at least partially, for the sustenance of human intelligence (Haier, 2015). Substantial empirical evidence from PET and functional Magnetic Resonance Imaging (fMRI) studies (Jung and Haier 2007) verify that notion. This theory postulates that intelligence is associated with efficient connectivity between several cortical regions, located mostly across the dorsolateral prefrontal cortex (Brodmann areas 6, 9, 10, 45, 46, 47) and parietal lobe (Brodmann areas 39, 40) plus adjacent areas in the anterior cingulate cortex, temporal, and occipital lobes (Brodmann areas 32, 21, 37, 18 and 19, respectively). As the theory concerns the communication of distant areas, it also implicates some fasciculi. In this regard, there is the integrative theory of prefrontal cortex function, which considers this region as a flexible hub involved in executive control that can reconfigure its connectivity to better conform to cognitive task demands (Miller & Cohen, 2001). Mounting evidence shows that functional connectivity from this region is a predictor of intelligence (Song et al. 2008; Cole, Yarkoni, Repovš, Anticevic, & Braver, 2012; Cole, Ito, & Braver, 2015). Other neuroimaging studies not directly linked to previous theories showed morphometric indices of specific brain regions related to the neural substrate of intelligence. For example, Fjell et al. (2015) showed that heterogeneous cortical surface area expansion, both during evolution and development, is positively correlated with intellectual abilities.

Intelligence issues are not just a concern of neuroscientists. Based on its definition, individual intelligence has an enormous impact on the most diverse areas of society. General intelligence is, directly and indirectly, related to job performance (Hunter, 1986). Intelligence quotients from childhood predict adult morbidity and mortality (Gottfredson & Deary, 2004). These outcomes might be more subtle than a simple causal relationship (Byington

& Felps, 2010), but the fact remains that intelligence is fundamental to human life.

Snapshots of the literature at the time were presented by other studies in the past. Because of advances in recent years we consider that a new survey makes itself necessary. The fundamental work positing the P-FIT (Jung & Haier, 2007) integrates up to that point in time most neuroimaging-derived findings on intelligence. The relationships between neuroimaging and intelligence, including functional, anatomical and diffusion magnetic resonance imaging, are examined in Colom et al. (2010). However, they report a few predictive studies, that were not as common at the time as today. Recently, a survey on individualized prediction of cognition and behavior, both in pathology and health was published. Our research focuses solely on the associations (individual and populational) between neuroimaging and human intelligence. Our narrower scope allows an in-depth selection and discussion of findings.

In this article, we aim to provide a thorough review and unified reference of studies reporting findings on neuroimaging-based correlates of human intelligence. In the next four sections, we review papers dealing with MRI-based morphometry, diffusion MRI, functional MRI, and multimodal approaches fusing more than one modality. Having reported the main findings derived from populations, we also report on the state-of-the-art individualized prediction of intelligence, a flourishing field of study due to the growing popularity of machine learning-based predictive frameworks and individualized neuroimaging assessments.

2. Brain Morphometry and Human Intelligence

The speculation that brain volume might associate with intelligence has been one of the earliest hypotheses relating brain characteristics to intelligence. Many papers in the literature have established a positive correlation between total brain volume and intelligence. Recently, it has become feasible to investigate the relationship between the morphology of different brain tissues and anatomical regions with intelligence. In this section, we briefly summarize more recent findings on this subject.

One way of representing the relation between brain volume and intelligence is to consider the correlation between the volumes of different tissues or regions of the brain with particular components of Full-Scale IQ (FSIQ) (general intelligence), e.g. performance IQ (PIQ) or Verbal IQ (VIQ) (fluid intelligence or crystallized intelligence). Lange, Froimowitz, Bigler, and Lainhart

(2010) found positive correlations between temporal gray matter, temporal white matter, and frontal white matter volumes with FSIQ ($+0.14-0.27$) in children and adolescents are due in large part to their correlations with PIQ and not VIQ. In this regard, (Colom et al., 2013) showed that cortical gray matter volume and cortical surface area in the middle frontal gyrus were correlated with fluid intelligence while, in the inferior frontal gyrus, they were associated with crystallized intelligence. In another significant study, Ritchie et al. (2015) however, how much variance in intelligence other brain measurements would account for if included together with brain volume in a multivariable model. We examined a large sample of individuals in their seventies ($n=672$) used structural equation modeling to relate 6 common magnetic resonance imaging-derived brain variables, i.e. brain volume, cortical thickness, white matter structure, white matter hyperintensity load, iron deposits, and microbleeds, to general and fluid intelligence. The brain volume accounted for the largest portion of variance ($+12\%$). Although all neuroimaging variables together accounted for 18%–21% of the variance in intelligence, adding mainly cortical thickness ($+5\%$) and white matter hyperintensity load ($+2\%$) increased the predictive value of the model.

Regarding total brain volume, more recently, a preregistered study (Nave, Jung, Karlsson Linnér, Kable, & Koellinger, 2019) investigated the relationship between brain volume and cognitive ability using a sample of adults ($N=13608$) in the United Kingdom. The analysis was systematically controlled for sex, age, height, socioeconomic status, and population structure, and it was free of publication bias. A robust association between total brain volume and fluid intelligence ($r=0.19$) was found that was consistent with previous findings in the literature.

Other studies measure the relationship between volumes of subcortical brain regions with intelligence. Burgaleta et al. (2014) performed shape analyses to understand how individual differences in the local morphology of basal ganglia relate to variability in cognitive performance. To this end, structural MRI was acquired in 104 young adults, and the outer surfaces of striatal structures (caudate, nucleus accumbens, and putamen), globus pallidus, and thalamus were estimated for each subject and hemisphere. Moreover, 9 cognitive tests were used to measure fluid, crystallized, and spatial intelligence. Significant correlations were found for fluid and spatial but not crystallized intelligence for the right striatal structures and thalamus after controlling for age, sex, and adjusted for brain size.

Moreover, MacDonald, Ganjavi, Collins, Evans, and Karama (2014) showed that volume of left striatum, including caudate nucleus and putamen, was positively correlated with intelligence specifically for male children. Furthermore, Grazioplene et al. (2015) hypothesized that due to the central role of the caudate in learning, better attentional function, and verbal ability, there is a positive association between intelligence and caudate volume. Indeed, regression of IQ onto bilateral caudate volume controlling for age, sex, and total brain volume indicated a significant positive correlation between caudate volume and intelligence.

Additionally, the corpus callosum is another major anatomical part of the brain, widely explored for any possible correlation with intelligence. In a study, Luders et al. (2011) found mixed results after mapping the correlations between standardized intelligence measures and callosal thickness. Although the strongest correlations were negative and confined to the splenium, the strength and the direction of intelligence-callosal thickness associations vary considerably. While significant correlations in females were mainly positive, significant correlations in males were exclusively negative. However, only the negative correlations in the overall sample remained significant when controlling for multiple comparisons. In a recent study, Westerhausen et al. (2017) re-examined the association between the corpus callosum and intelligence measures in a large longitudinal sample using raw test scores for accounting for the ongoing cognitive development in young adults. Without considering the age effect, they found a positive association between the thickness of splenium of the corpus callosum with both verbal and performance raw test scores.

The correlation between cortical thickness and intelligence is another major issue that has been explored in the literature. Karama et al. (2011) cognitive ability domains, and specific test requirements and idiosyncrasies. Cortical thickness has been previously associated with *g*. In the present study, we systematically analyzed associations between cortical thickness and cognitive performance with and without adjusting for the effects of *g* in a representative sample of children and adolescents ($N=207$, Mean age=11.8; $SD=3.5$; Range=6 to 18.3. years systematically analyzed associations of cortical thickness with cognitive performance with and without adjusting for the effects of general intelligence in a representative sample of children and adolescents. Cognitive domain and individual test scores and residualized scores were regressed against cortical thickness. They found that general intelligence and cognitive domain scores were positively correlated with cortical thickness

in very similar areas across the brain. Furthermore, [Yang et al. \(2013\)](#) used the FSIQ and the cortical measurements to determine how much combining various cortical measures (cortical thickness, cortical surface area, sulcal depth, absolute mean curvature) explain human intelligence. They applied Partial Least Square (PLS) regression to overcome multicollinearity among cortical measures. They showed that 30% of FSIQ was explained by the first latent variable—mostly supported by cortical thickness—extracted from PLS regression analysis.

Moreover, [Menary et al. \(2013\)](#) performed a cortical thickness mapping analysis on data from 182 healthy, typically developing adults to identify correlates of general intelligence scores. They found a widely distributed pattern of positive associations between cortical thickness and general intelligence scores derived from the factor analysis of WASI subtest scores. Additionally, [Margolis et al. \(2013\)](#) investigated whether differences between abilities that affect performance on verbal and performance tasks correlate with cortical thickness. They found that a progressively thinner cortical mantle in anterior and posterior regions bilaterally was associated with more positive VIQ-regressed-on-PIQ scores, and a progressively thicker cortical mantle in anterior and posterior regions bilaterally was associated with more positive PIQ-regressed-on-VIQ scores. In another study, [Schnack et al. \(2015\)](#) examined the relationship between IQ and changes in cortical thickness over time in 504 healthy subjects. While at age 10, more intelligent children have a slightly thinner cortex than children with a lower IQ. By the age of 42, this relationship reverses so that a thicker cortex is associated with higher intelligence. Finally, [Bajaj et al. \(2018\)](#) examined the association between cortical thickness, cortical volume, cortical surface area, and cortical gyrification with PIQ, VIQ, and FSIQ in 56 healthy adults. They observed significant positive relationships between cortical thickness and all three IQ variables in regions within the posterior frontal and superior parietal lobes.

Overall, these findings show that brain morphology, or more specifically, brain volume, volumes of gray matter and white matter, the volume of subcortical anatomical features, and callosal and cortical thicknesses generally have positive correlations with intelligence. These findings are summarized in [Table 1](#). A possible future work could be finding the relation between the size of functional brain space and intelligence. The term functional space here refers to the space defined by sequential time-points of brain fMRI volumes comprised of high-dimensional signals of all voxels. To this end, topological data analysis can reduce the dimensionality of brain signals

and calculate the volume or area of the active region in a low-dimensional space ([Saggar et al., 2018](#)).

3. Diffusion Imaging and Human Intelligence

Via diffusion-weighted imaging (DWI), it is possible to non-invasively estimate the location and orientation of the brain's white matter tracts ([Douek, Turner, Pekar, Patronas, & Bihan, 1991](#)). Using this imaging method, microstructure properties of the brain like Fractional Anisotropy (FA), Mean Diffusivity (MD), and Radial Diffusivity (RD) can be measured. Additionally, brain structural connectivity properties can be extracted from the tractography technique based on DWI. Recent studies have focused on the relationship between cognitive performance and properties of the brain's white matter tracts, considering the effects of sex and age ([Pisner, Smith, Alkozei, Klimova, & Killgore, 2017](#); [Ohtani et al., 2017](#)).

Analyses on the white matter microstructure of a group of adolescents revealed positive correlations between FA and FSIQ in the right inferior fronto-occipital fasciculus ([Wang et al., 2012](#)). [Clayden et al. \(2012\)](#) showed that FA tends to increase or stay constant with age, while MD tends to decrease or remain constant in the whole brain. The highest variance in both FA and MD values has been found in the corpus callosum splenium ([Clayden et al., 2012](#)). Another research on subjects 18-50 years old shows a positive correlation of IQ scores with FA and their negative correlation with MD in the corpus callosum of men, without such correlations in women ([Dunst, Benedek, Koschutnig, Jauk, & Neubauer, 2014](#)). On the other hand, [Navas-Sánchez et al. \(2014\)](#) showed a positive correlation between IQ and FA, mainly in the corpus callosum of a group consisting of male and female subjects. Considering other tracts, a positive correlation between FA in the left corticospinal tract and superior longitudinal fasciculus and verbal IQ has also been observed in girls ([Wang et al., 2012](#)).

[Nusbaum et al. \(2017\)](#) studied the differences of WM regional differences in FA, MD, AD, and RD of two children's profiles with High IQ (HIQ). They divided the children into two groups of homogeneous HIQ and heterogeneous HIQ, defined by a significant difference between verbal comprehension index and perceptual reasoning index. They used 48 regions and 21 fiber-bundles of WM. Hom-HIQ children presented higher FA than Het-HIQ children in widespread WM regions. AD was also greater in numerous WM regions of the Total-HIQ, Hom-HIQ, and Het-HIQ groups when compared to the control group. Hom-HIQ and Het-HIQ groups also dif-

Table 1. Research studies showing relations between brain morphometries and intelligence

The First Author	Sample N (Sex)	Age Range, y Mean±SD	Intelligence Test	Main Results	Brain Parameter
Lange et al. (2010)	285 (130 M, 155 F)	4.83±18.33	WASI	Positive correlations between temporal gray matter, temporal white matter, and frontal white matter volumes with performance IQ	Total and regional brain volume
Luders et al. (2009)	200 (100 M, 100 F)	6-17 -	WASI	A negative association between callosal thickness and intelligence	Corpus callosum
Karama et al. (2011)	207 (92 M, 115 F)	6-18.3 11.8±3.5	WASI, WJPEB-III	Cortical thickness correlates of specific cognitive performance after accounting for the general factor of intelligence	Cortical thickness
Burgaleta et al. (2013)	104 (45 M, 59 F)	-19.83±1.6	APM, DAT-AR, DAT-NR, DAT-SR, DAT-VR, PMA-R, PMA-S, PMA-V	Correlation of local morphology of the right basal ganglia and right thalamus with fluid and spatial but not with crystallized intelligence	Striatal structures (caudate, nucleus accumbens, putamen), globus pallidus, thalamus
Colom et al. (2013)	104 (45 M, 59 F)	-19.9±1.6	DAT-AR, DAT-NR, PMA-R, RAPM	The relationship between structural features of gray matter in the frontal lobes with intelligence	Cortical gray matter volume, cortical surface area, cortical thickness
Margolis et al. (2013)	141 (79 M, 62 F)	5-57 -	WASI, WISC-III	Correlation of cortical thickness in anterior and posterior regions with the verbal and performance IQ discrepancy	Cortical thickness
Menary et al. (2013)	181 (81 M, 100 F)	9-24 16.31±3.99	WASI	Associations between cortical thickness and general intelligence in children, adolescents, and young adults	Cortical thickness
Yang et al. (2013)	78 (39 M, 39 F)	17-27 22.7±1.9	WAIS	Cortical thickness correlates with intelligence	Cortical thickness, cortical surface area, sulcal depth, absolute mean curvature
MacDonald et al. (2014)	303 (142 M, 161 F)	6-18.3 11.4±3.5	WASI	A positive correlation between intelligence and striatal volume	Striatal volume
Grazioplene et al. (2015)	285 (144 M, 141 F)	20-40 26.2±5.0	WASI, WAIS-III, WAIS-IV	A positive correlation between caudate volume and intelligence	Caudate volume
Ritchie et al. (2015)	672 (353 M, 319 F)	- 72.49±0.71	NART, WAIS-III, WMS-III, WTAR	A positive correlation of brain volume, cortical thickness, and white matter hyper-intensity load with intelligence	Brain volume, cortical thickness, white matter structure
Schnack et al. (2015)	504 (282 M, 222 F)	9-60 -	WAIS, WAIS-III, WISC-III	The relation between cortical thickness and cortical surface area with intelligence across development	Cortical thickness, cortical surface area

The First Author	Sample N (Sex)	Age Range, y Mean±SD	Intelligence Test	Main Results	Brain Parameter
Westerhausen et al. (2017)	495 (245 M, 250 F)	6.4–21.9 -	WASI	A positive correlation of corpus callosum morphology with intelligence	Corpus callosum
Bajaj et al. (2018)	56 (29 M, 27 F)	18-45 30.8±8.1	WASI-II	A positive correlation of cortical thickness and volume with intelligence	Cortical thickness, cortical volume, cortical surface area, cortical gyrification
Nave et al. (2019)	13608 (6425 M, 7183 F)	>40 -	Fluid intelligence test	A positive correlation between total brain volume and intelligence after controlling for sex, age, height, socioeconomic status, and population structure	Total brain volume

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APM: Advanced Progressive Matrices; DAT-AR: Differential Aptitude Tests - Abstract Reasoning; DAT-NR: Differential Aptitude Tests - Numerical Reasoning; DAT-SR: Differential Aptitude Tests - Space Relations; DAT-VR: Differential Aptitude Tests - Verbal Reasoning; NART: National Adult Reading Test; PMA-R: Primary Mental Abilities - Reasoning; PMA-S: Primary Mental Abilities - Spatial; PMA-V: Primary Mental Abilities - Verbal; RAPM: Raven Advanced Progressive Matrices Test; WAIS: Wechsler Adult Intelligence Scale; WASI: Wechsler abbreviated Scale of Intelligence; WISC: Wechsler Intelligence Scale for children; WJPEB-III: Woodcock-Johnson Psycho-Educational Battery-III; WMS: Wechsler Memory Scale; WTAR: Wechsler Test of Adult Reading.

ferred by their hemispheric lateralization in AD differences compared to controls.

Properties of the brain structural network have been shown to significantly correlate with age but not with IQ scores ([Fischer, Wolf, Scheurich, & Fellgiebel, 2014](#)). Moreover, [Koenis et al. \(2018\)](#) stated that a correlation between intelligence and global and local efficiency of the brain increases with age. Another study utilized a graph network approach to examine sex differences in the relationship between WM efficiency, frontoparietal GM volume, and General Cognitive Ability (GCA). The results indicated that in males, a latent factor of frontoparietal GM was significantly related to GCA, while in females, WM efficiency and total GM volume were significantly associated with GCA.

Recently, [Kocevar et al. \(2019\)](#) utilized graph measures to characterize the brain's structural connectivity and understand its relation with the neural substrate of intelligence in children. They revealed a strong relationship between high intelligence scores and the density of the network, mainly in the temporal and parietal lobes. Besides, WM of major fiber-bundle showed an increased axonal density associated with high intelligence.

[Pisner et al. \(2017\)](#) showed that cognitive performance was directly related to the structural connections in the brain. Moreover, [Ponsoda et al. \(2017\)](#) reported that the number of tracts between specific regions in the brain

plays an important role in explaining cognitive ability differences among individuals. To understand the relation between the brain tracts and different types of IQ, several research projects have been done. A study of math-gifted adolescents showed increased FA in white matter connections between frontal lobes, basal ganglia, and parietal regions increase relative to controls ([Navas-Sánchez et al., 2014](#)). Also, higher fluid reasoning, visuospatial working memory, and creative capabilities in these children are correlated with enhanced connections between the forceps minor and the splenium. Different types of intelligence have been related to different features of the white matter tracts. For example, fluid intelligence has shown a positive correlation with the FA value of all tracts ([Haász et al., 2013](#)).

Moreover, understanding emotions is related to FA in tracts between somatosensory and sensory-motor regions, particularly those of the left superior longitudinal fasciculus and corticospinal tract ([Pisner et al., 2017](#)). Also, managing emotions is related to FA in the tracts between the frontal-parietal cingulum and the interhemispheric corpus callosum ([Pisner et al., 2017](#)). The FA of the tracts between the left posterior Medial Frontal Cortex (pmFC) and the rostral Anterior Cingulate Cortex (rACC) is related to the executive functions of the attentional control and general intelligence ([Ohtani et al., 2017](#)). Moreover, [Nesstor et al. \(2015\)](#) utilized the Pearson correlation to investigate the relationship between

mOFC-rACC tracts with intelligence and memory. Results showed a significant correlation between these connections and IQ.

Penke et al. (2012) investigated the relationship between general intelligence and 12 major fiber pathways. The FA of the tracts was positively correlated with general intelligence. They provided evidence that lower brain-wide WM tract integrity exerts a substantial adverse effect on general intelligence through reduced information-processing speed. Another study (Ponsoda et al., 2017) investigated the relationship between the structural connectivity pattern of individuals and their cognitive differences for executive control, recognition, learning, language processing, and visuospatial processing. The researchers selected the connections that could better predict the individuals' cognitive scores. The selected connections are distributed across the entire brain, although their number is limited.

A novel computational approach—network control theory—was applied on DTI data by Kenett et al. (2018) to quantify the relation between the role of different brain regions in “driving” whole-brain neural dynamics related to creativity and intelligence. The strength of this approach is its ability to characterize the potential role of each brain region in regulating whole-brain network function based on its anatomical fingerprint and a simplified model of node dynamics. Results showed that intelligence is related to the ability to “drive” the brain system into easy to reach neural states by the right inferior parietal lobe and lower integration abilities in the left retrosplenial cortex.

More recently, Genç et al. (2018) have used advanced multi-shell diffusion tensor imaging combined with a culture-fair matrix-reasoning test to show that higher intelligence in healthy individuals is related to lower values of dendritic density and arborization.

According to the DTI studies reviewed and summarized in Table 2, there is no significant correlation between the global mean of diffusion indices and IQ, while local diffusion indices are correlated with verbal IQ in the left hemisphere and nonverbal IQ in the right hemisphere. Significant differences were found in network properties such as the total number of edges and global efficiency between people with high IQ and low IQ. Future studies may utilize a larger sample size to obtain a higher confidence level. They may also find robust diffusion indices and brain subnetworks predicting IQ.

4. fMRI and Human Intelligence

Functional connectivity can be assessed during task performance or resting-state fMRI. Task fMRI yields the functional architecture of the brain while performing a particular task. Functional connectivity analysis of resting-state fMRI data provides insight into the functional architecture of the brain unrelated to any particular task. In this section, we review the studies that focused on neural bases of intelligence using fMRI data obtained either at rest or with a task.

A newly published study, Li et al. (2018) investigated the relation between fluid intelligence (gf) and pattern of the functional characteristics in adults using images from 100 participants in the Human Connectome Project (HCP) database. This study used the amplitude of low-frequency BOLD fluctuations to find the regions that were related to gf. The most notable finding was that the left Anterior Cingulate Cortex (ACC) and right Middle Occipital Gyrus (MOG) could predict gf. Besides, to investigate whether the connectivity of these two regions was related to intelligence, FC maps of these regions with regions across the whole brain were computed. The connection of left ACC with other regions was correlated to gf. Most contributing regions were located in the right prefrontal cortex.

Based on previous studies (Koziol et al., 2014; Styliadis, Ioannides, Bamidis, & Papadelis, 2015), the lobes that are most related to intelligence including prefrontal and posterior parietal lobes have many connections to Cerebellum. In this regard, Pezoulas et al. (2017) compared the network of cerebellum in individuals with low and high IQ. This study used the resting-state fMRI data of 136 subjects who participated in HCP. A Minimum Spanning Tree (MST) is a spanning tree that preserves only the edges that minimize the sum of the weights of the edges. It compacts the graph representation to simplify the distinction of different populations by calculating different graph metrics, including degree, between centrality, and eccentricity. The statistical analysis of this paper (Pezoulas et al., 2017) revealed that local MST metrics did not have any significant differences between the low and high IQ groups. Moreover, no significant differences were exhibited on any global metrics between the low and high IQ males. Conversely, significant differences were found for 5 global metrics between females with low and high IQ.

Several studies investigated the relationship between intelligence and global efficiency for the various dataset and obtained contradictory results. To solve this

Table 2. Research studies showing relations between DWI features and intelligence.

The First Author	Sample N (Sex)	Age Range, y Mean±SD	Intelligence Test	Main Results	Brain Region
Clayden et al. (2012)	59 (25 M, 34 F)	8-16 11.5±2.1	WISC-IV UK	Secondary components of some parameters, such as age and gender, predict full-scale IQ	Whole-brain
Wang et al. (2012)	16 (8 M, 8 F)	3-18 15.3±1.24 16.26±1.3	WAIS	Significant positive correlations were found between FA and full-scale IQ in some regions.	Whole-brain
Penke et al. (2012)	420 (228 M, 192 F)	71-73 72.3±0.6	WAIS-III	Lower brain-wide WM integrity exerts a substantial negative effect on general intelligence.	Whole-brain
Haász et al. (2013)	100 (33 M, 67 F)	49-80 63.8±7.2	CVLT-II, WASI-Matrix Reasoning, CWIT	Higher gf score is related to a higher degree of WM integrity.	Whole-brain
Dunst et al. (2014)	63 (25 M, 38 F)	18-50 23.8± -	INSBAT	White matter microstructure differs between individuals as a function of intelligence and sex.	Whole-brain
Fischer et al. (2014)	43 (28 M, 15 F)	60-85 -	HAWIE-Revised	Network properties were correlated to intelligence scores within two age groups.	Whole-brain
Navas-sánchez et al. (2014)	36 Math-gifted group: (5/8) Control: (4/19)	11.8-15 Math-gifted Group: 13.8±4.2 Control: 13.4±4.23	WISC	IQ shows a significant positive correlation with FA, mainly in the corpus callosum.	Whole-brain
Nestor et al. (2015)	26 (26 M)	- 38.62±10.61	WAIS-III	FA of mOFC-rACC and cognition scores are highly correlated.	mOFC, rACC
Ohtani et al. (2017)	26 (26 M)	19-55 38.62±10.61	WAIS-III, TMT, WCST	Posterior mOFC-rACC connections may play a key structural role linking attentional control processes and intelligence.	mOFC, rACC
Pisner et al. (2017)	32 (16 M, 16 F)	18-45 29.25±7.3	MSCEIT, WASI	White matter integrity in key tracts is positively correlated with strategic area branches of understanding emotions and managing emotions.	Whole-brain
Ponsoda et al. (2017)	94 (41 M, 53 F)	- 20±1.7	RAPMT, DAT, PMA	Cognitive scores are related to connectivity distances.	Whole-brain
Nusbaum et al. (2017)	44 (36 M, 8 F)	8-12 10.4±1.3	CBCL	Both inter- and intra-hemispheric WM integrity are enhanced in HIQ children.	Whole-brain
Koenis et al. (2018)	330 (158 M, 172 F)	9-22.9 13.45± -	WAIS-III	The dependency of FA-weighted global efficiency on IQ increased during adolescence.	Whole-brain
Kenett et al. (2018)	416 (191 M, 225 F)	- 20±1.26	TTCT, CRT	Intelligence is related to the ability to “drive” the brain system into easy to reach neural state.	Whole-brain
Kocevar et al. (2019)	43 (32 M, 11 F)	8-12 9.82±1.06	WISC-IV	Intelligence neural substrate is based on a strong WM microstructure of the major fiber-bundles	-

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WAIS: Wechsler Adult Intelligence Scale; WISC: Wechsler Intelligence Scale for Children; WASI: Wechsler Abbreviated Scale of Intelligence; CVLT: California Verbal Learning Test; CWIT: Color-Word Interference Test; INSBAT: Intelligence-Structure-Battery; HAWIE: Hamburg Wechsler Intelligence Test; TMT: Trail Making Test; WCST: Wisconsin Card Sorting; MSCEIT: Mayer-Salovey-Caruso Emotional Intelligence Test; RAPMT: Raven Advanced Progressive Matrices Test; DAT: Differential Aptitude Test; PMA: Primary Mental Abilities; PCA: Principal Component Analysis; ANCOVA: Analysis of Covariance; GLM: Generalized Linear Model; MDMR: Multivariate Distance Matrix Regression; mOFC: Medial orbital Frontal Cortex; rACC: Rostral Anterior Cingulate Cortex; CBCL: Child Behavior Checklist; TTCT: Torrance Tests of Creativity Thinking; CRT: Combined Raven's Test; WISC: Wechsler Intelligence Scale for Children.

contradiction, [Kruschwitz, Waller, Daedelow, Walter, and Veer \(2018\)](#) performed a replication of the previously reported association between general intelligence and global functional network efficiency using large sample size and high-quality data of HCP. They tested for separate association of crystallized and fluid intelligence with graph metrics such as global efficiency, characteristic path length, and global clustering coefficient. They found no significant relationship between general intelligence and functional brain network efficiency. Moreover, [Hilger, Ekman, Fiebach, and Baßen, \(2017a\)](#) evaluated the relationship between nodal and global measures of efficient network organization (i.e. nodal efficiency and global efficiency) and IQ scores. The results indicated no significant relationship between worldwide efficiency and IQ. However, nodal efficiency was significantly associated with intelligence in 3 brain regions. In particular, individuals with higher IQ scores had higher nodal efficiency in the right Anterior Insula (AI) and the dorsal Anterior Cingulate Cortex (dACC). While in the left Temporoparietal Junction Area (TPJ), the association between IQ scores and nodal efficiency was negative. It is reasonable to consider heterogeneity in the distribution of functional connectivity across the brain network, clustered into subnetworks (modules, communities) that are densely connected internally and weakly coupled with the rest of the network. Within these modular brain networks, each node is characterized by a specific profile of within- and between-module connectivity, determining the node's functional role in neural processing within and across different modules. [Hilger, Ekman, Fiebach, and Baßen, \(2017b\)](#) explored the relation between IQ scores and modular structure of the brain. They showed that intelligence was not associated with the global modularity features (e.g. number or size of modules) or the whole-brain proportions of different node types (e.g. connector hubs or provincial hubs). In contrast, there was a significant relationship between intelligence and node-specific measures of within- and between-module connectivity in the frontal and parietal brain regions previously linked to intelligence.

[Malpas et al. \(2016\)](#) also explored the relationship between intelligence and functional connectivity across the whole brain. The results of this paper emphasized that a single functional sub-network was significantly associated with full-scale IQ. This sub-network contained 44 nodes, including 20 nodes in the frontal, 11 in the temporal, 9 in the parietal, and 4 in the occipital lobes. Furthermore, [Hearne, Mattingley, and Cocchi \(2016\)](#) evaluated the relationship between functional connectivity and individual IQ scores using Network-Based Statistics (NBS). Functional connectivity matrices were

used as input into NBS. The results showed that connections between prefrontal and frontal cortices comprising the dorsal attention network had significant correlations with intelligence. Significant associations were observed for the posterior cingulate/precuneus, the superior parietal cortex, and the occipital cortex. Resting-state functional connectivity between bilateral prefrontal cortices encompassing the dorsal attention network and the right insula was also associated with the intelligence scores. [Pamplona et al. \(2015\)](#) investigated the association between various graph metrics of functional network and intelligence calculated by the Portuguese language version of the WAIS. Some previous findings were extended to the Portuguese-speaking population, specifically the presence of small-world organization of the brain and the relationship of the intelligence with the connectivity of the frontal, pre-central, parietal, occipital, fusiform, supra-marginal gyrus, and the caudate nucleus. No significant correlation was found between intelligence, and characteristic path length, global efficiency, and local efficiency except that verbal comprehension were associated with global network efficiency.

[Finn et al. \(2015\)](#), using functional connectivity data and Connectome-based Predictive Modeling (CPM), showed that the characteristic connectivity patterns were distributed throughout the brain, but the frontoparietal network emerged as distinctive. Other studies have confirmed that the interaction between parietal and frontal brain regions can describe the individual differences in intelligence. [Langeslag et al. \(2013\)](#) investigated this relationship for young children. These authors applied ICA on resting-state fMRI data of 115 healthy young children. They found that nonverbal intelligence positively correlated with functional connectivity between right parietal and right frontal regions and between right parietal and dorsal anterior cingulate regions. They concluded that connectivity between the parietal and frontal lobes was involved in intelligence in young individuals too.

Until 2011, no study focused on the relationship between intelligence and local functional connectivity of the brain. [Wang et al. \(2012\)](#) investigated the correlation between intelligence and local connectivity using the regional homogeneity (ReHo) as an index for evaluating the local connectivity. They used the resting-state fMRI data of 59 healthy participants. They found a positive correlation between IQ scores and ReHo values of the bilateral inferior parietal lobules, middle frontal, parahippocampal and inferior temporal gyri, the right thalamus, superior frontal, and fusiform gyri, and the left superior parietal lobule. The authors concluded that their

findings are consistent with the Parieto-Frontal Integration Theory (P-FIT).

Several studies explored the neural basis of intelligence using task-based datasets. These studies used the data collected while participants were performing a set of tasks related to intelligence. These tasks were either IQ tests or cognitive tests. In the remaining of this section, these studies are reviewed.

A set of frontal and parietal brain regions—the Multiple-Demand (MD) network—has been linked to fluid intelligence. Besides, fluid intelligence is linked to task complexity. The joint influence of fluid intelligence and task complexity to neural activity of multiple demand network was investigated by (Tschemtscher, Mitchell, & Duncan, 2017). In this study, 38 subjects were divided into two groups, a high-IQ group, and a low-IQ group. The participants were asked to press a key with the right hand to the cued target and to ignore the images related to a different cue (lure) as well as images associated with no cue (fillers). ANOVA was applied to parameter estimates of targets and lures, with factors “complexity,” “IQ group,” “stimulus” (targets vs lure), “hemisphere” (left vs right), and ROI. The results of this paper indicated that for more complex tasks, low-IQ subjects showed high error rates, as well as weaker neural signals across all multiple-demand network regions.

A recent meta-analysis (Santarnecchi, Emmendorfer, & Pascual-Leone, 2017) investigated the 47 available fMRI and PET studies about gf in humans. The authors classified the studies based on the type of stimuli, the different problem-solving stages (rule inference and rule application), and task difficulty. They found spatially segregated networks of cortical and subcortical regions related to gf processing. Dorsal attention, anterior salience, and left frontoparietal networks mostly contributed to verbal and visuospatial abstract reasoning tasks. More difficult trials engaged in the additional contribution of language and left frontoparietal networks. In a subsequent study, Santarnecchi et al. (2017) suggested a quantitative validation for their previous meta-analysis study. They assessed their findings for two different datasets with 84 and 130 healthy subjects. The results indicated a strong similarity between the connectivity profile of the gf network and the dorsal attention network. Besides, there was an overlap between the gf network and left and right frontoparietal networks. Consistent with previous studies, a negative correlation was detected between gf regions and medial prefrontal structures of the DMN, a significant predictor of intelligence scores.

Multiple studies found that resting-state networks were present during a wide range of tasks and that functional connectivity patterns were minimally modified during tasks. Schultz and Cole (2016) tested the hypothesis that these small portion of task-evoked FC updates from rest were strongly associated with behavioral performance. They used the fMRI data of 100 unrelated subjects of HCP. They focused on the language, reasoning, and working memory tasks. Cole et al. (2012) found that similarity between rest and task FC configurations was positively correlated with performance in all three tasks. In other words, they defined the FC reconfiguration efficiency factor as the similarity between rest and task FC structure. Considering this definition, it was shown that fluid intelligence was positively correlated with FC reconfiguration efficiency.

Functional networks extracted during task engagement and resting state were compared by Vakhtin, et al. (2014) using fMRI data of 79 healthy subjects. For each subject, fMRI data were collected during resting state and engagement in Raven’s progressive matrices test. This study provided a network-wise insight into the P-FIT framework. In this regard, functional networks were derived using ICA for both resting state and RPM task data. Comparing these extracted networks indicated that the regions involved in task-related functional networks were consistent with P-FIT. Moreover, it was shown that general features of functional brain networks were constant across resting state and engagement in a complex cognitive task.

Unlike previous studies which focused on the relationship between intelligence and brain activation of Task-Positive Network (TPN), Baeten, Stelzel, and Fiebach (2013) additionally considered the Task-Negative Network (TNN). They investigated the effects of intelligence on neural activity in TPN and TNN using fMRI data of 52 healthy participants scanned while performing working memory tasks. The authors defined the neural effort as signal increase in TPN and signal decrease in TNN. While the neural effort in TPN and TNN increased with task difficulty, the neural effort of these networks related to intelligence was different. There was a positive association in TPN and a negative association in TNN.

Another task-based fMRI study (Ebisch et al., 2012) explored the neural basis of cognitive components underlying gf, including induction, visualization, and spatial relationship abilities. In this study, 22 healthy subjects performed a set of induction, visualization, and spatial relationship tasks while undergoing an fMRI scan. Ebisch et al. (2012) found that these different tasks revealed common activation patterns and concluded that

Table 3. Research studies showing relations between resting-state fMRI features and intelligence

The First Author	Sample N (Sex)	Age Range, y Mean±SD	Intelligence Test	Main Results	Brain Region
Graham et al. (2010)	28 (12 M, 16 F)	Average IQ 29.9±11.9 High IQ 26.3±12.2	WAIS	Greater activation in many regions associated with complex reasoning (parietal, caudate, fusiform and occipital) for high-IQ group	Whole-brain
Wang et al. (2011)	59 (29 M, 30 F)	18.5-33.3 26.4±3.5	WAIS-RC	A positive correlation between IQ scores and ReHo values of the bilateral inferior parietal, middle frontal, parahippocampal and inferior temporal gyri, the right thalamus, superior frontal and fusiform gyri, and the left superior parietal lobule	Whole-brain
Ebisch et al. (2012)	22 (22 F)	20-24	Fluid intelligence test (FIT) was	The Gf is associated with a common network, frontoparietal network	Whole-brain
Cole et al. (2012)	121 (70 M, 51 F)	18-40 23± -	Raven (RAPM)	LPFC is a global hub	Whole-brain
Langeslag et al. (2013)	115 (56 M, 59 F)	5.4-7 6.2± -	Snijders-Oomen Niet-verbale intelligent Test	Involvement of connectivity between the parietal and frontal lobes in intelligence in young individuals	Whole-brain
Basten et al. (2013)	52 (25 M, 27 F)	19-27 22.23±1.92	Raven (RAPM)	Lower neural efficiency in the TPN and higher neural efficiency in the TNN for more intelligent individuals	Whole-brain
Vakhtin et al. (2014)	79 (46 M, 33 F)	- 21.7±3.1	Raven(RAPM)	The similarity of general features of functional brain networks for resting state and task phases	Whole-brain
Pamplona et al. (2015)	29 (15 M, 14 F)	26.8±5.8	WAIS-III	No significant association between FSIQ and global graph metrics	Whole-brain
Finn et al. (2015)	HCP data: 126 (40 M, 86 F) Yale data: 45 (28 M, 17 F)	22-35 19-50 31±7.3	RPM	The frontoparietal network predicts levels of fluid intelligence.	Whole-brain
Cole et al. (2015)	121 (51 M, 70 F)	18-40 23± -	Raven (RAPM)	LPFC is a connector hub	Whole-brain
Malpas et al. (2016)	91 (56 M, 35 F)	18-55	WAIS	A significant association between functional sub-network containing frontal, temporal, parietal, and occipital lobes and IQ scores	Whole-brain
Hearne et al. (2016)	317 (144 M, 173 F)	22-36 28.43±3.77	RPM	Significant correlation of connections between prefrontal and frontal cortices with intelligence	Whole-brain
Schultz & Cole (2016)	100 (46 M, 56 F)	HCP age intervals	Raven (RAPM)	The positive correlation of intelligence and FC reconfiguration efficiency	Whole-brain
Hilger et al. (2017a)	54 (31 M, 23 F)	18-30 23.37±3.35	WAIS-III	No significant relation between global efficiency and IQ scores. A significant relation between nodal efficiency and intelligence in three brain regions	Whole-brain
Hilger et al. (2017b)	309 (110 M, 199 F)	18-60 38.93±13.94	WASI	No correlation between intelligence and global modularity features	Whole-brain
Santarnecchi et al. (2017)	84 130	21-49 29±12 19-32 7±25	Raven (RAPM)	The similarity between the connectivity profile of the gf network and dorsal attention network	Whole-brain

The First Author	Sample N (Sex)	Age Range, y Mean±SD	Intelligence Test	Main Results	Brain Region
Santarnechi et al. (2017)	----	-----	-----	Contribution of dorsal attention, anterior salience, and left frontoparietal networks to verbal and visuospatial abstract reasoning tasks	Whole-brain
Tschentscher et al. (2017)	38	29-65 44± -	Culture fair test	High error rates and weaker neural signal across all multiple-demand network regions for low-IQ subjects	Whole-brain
Kruschwitz et al. (2018)	1096 (500 M, 596 F)	28.8±3.7	NIH toolbox	No significant relation between general intelligence and functional brain network efficiency.	Whole-brain
Li et al. (2018)	100 (46 M, 54 F)	HCP age intervals	Raven (RAPM)	A positive correlation between gf and ACC A positive correlation between gf and connection between the right prefrontal cortex and the left ACC	Whole-brain
Pezoulas et al. (2017)	136 (54 M, 82 F)	HCP age intervals	Raven (RAPM)	Significant differences between low and high IQ for five global metrics for females	Cerebellum network

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HCP: Human Connectome Project; WAIS: Wechsler adult Intelligence Scale; RPM: Raven's Progressive Matrices; WASI: Wechsler Abbreviated Scale of Intelligence; EQI: Emotional Quotient Inventory; CPM: connectome-Based Predictive Modeling; ICA: Independent Component Analysis; DMN: Default Mode Network.

while gf comprises distinguishable cognitive abilities, it is associated with a common network, named frontoparietal network. [Graham et al. \(2010\)](#) compared the neural activity of 28 healthy subjects with different IQ scores. This study compared event-related fMRI activation during cognitive set-shifting tasks between two groups, average-IQ and high-IQ. They found that the prefrontal and anterior cingulate regions of the average-IQ group have more activity during the response selection phase, consistent with the neural efficiency hypothesis. Inversely, during the feedback phase, the high-IQ group revealed greater activation in many regions associated with complex reasoning, including parietal, caudate, fusiform, and occipital regions. Although this result may be considered inconsistent with neural efficiency, it was interpreted as follows: high-IQ individuals were more strategic in evaluating feedback about the next trial and thus executed their responses more quickly ([Table 3](#)).

5. Multimodal Imaging and Human Intelligence

Multimodal MRI has become a valuable tool for assessing brain organization. This technique provides an opportunity to investigate the brain from different structural and functional aspects. Multimodal studies are divided into three main groups. The first approach analyzes the two modalities separately and then compares the results. In the second approach, the data of one modality is used for a more accurate analysis of the

other modality. In the third approach, the data of the two modalities are fused before the analysis. Regardless of the approach, multi-modality analysis can provide deep insight regarding the relationship between structure and function of the brain with intelligence. Here, we summarize recent findings for the application of multimodal MRI to investigate human intelligence.

One of the first multimodal fMRI-DTI studies on IQ was performed by [Tang et al. \(2010\)](#). The authors investigated the relation of the brain and intelligence using fMRI and DTI techniques. Their main goal was to determine whether the parietofrontal network underlies the g-factor of intelligence or not. In their study, they assessed intelligence using the 8 tests in the Johnson O'Connor Research Foundation (JOORF) battery and estimated a general intelligence g-score for each subject. They investigated the relationship between the level of activation during a working memory task and intelligence using fMRI. Besides, they performed tractography to find the connection of the activated regions through the white matter fiber tracts. Finally, they investigated the integrity of the axonal connections using an ROI-based method. Their results were in line with the Parietofrontal Integration Theory (P-FIT) of intelligence. They stated that the brain activation level was negatively correlated with general intelligence, speed of reasoning, numerical ability, and spatial ability. For DTI, positive and negative correlations were reported respectively between men's

and women's axonal integrity and intelligence in some specific parts of the interhemispheric and intrahemispheric white matter connections. They concluded that the brain structure and function underlie individual differences in intelligence.

In another study, testing the P-FIT theory using a multimodal approach, [Başten, Hilger, and Fiebach \(2015\)](#) performed a voxel-based quantitative meta-analysis of 16 fMRI and 12 structural MRI studies to test whether there is spatial convergence across studies. Their focus was on two types of studies. First, the studies which reported a correlation between brain activation during a cognitive task and intelligence. Second, the studies reported a correlation between the gray matter density, estimated using VBM, and intelligence. For the functional meta-analysis, they only considered studies that used an Individual Differences (ID) approach. Unlike the task approach that investigates neural correlates of processing a particular task, the ID approach finds the area which shows the difference between individuals during a cognitive test. Although they failed to find an overlap between functional and structural results, each of their results had a good match with the P-FIT theory. Based on the differences between their results and those of the P-FIT theory, they proposed an updated account for the P-FIT theory. For the fMRI analysis, in contrast to the P-FIT theory, they did not find a relationship between intelligence and sensory regions in the temporal and occipital lobes. They concluded that the use of the task approach might result in finding activation in sensory cortical regions in addition to the cognitive control regions of the brain. In addition to the brain regions included in the P-FIT theory, from this meta-analysis, they found three new areas that correlate with intelligence, including the Posterior Cingulate Cortex (PCC), caudate, and midbrain. PCC plays an important role in DMN based on the previous studies. For the structural analysis, the frontopolar cortex was associated with intelligence, but unlike the P-FIT theory, the temporal and occipital cortices were also related to intelligence.

One of the most well-known hypotheses relates brain activation to intelligence, is the neural efficiency hypothesis ([Neubauer & Fink, 2009](#)). It states that people with higher intelligence need less neural effort during a cognitive task compared to normal people. [Başten, Hilger, and Fiebach \(2015\)](#) reported that people with higher intelligence do not generally show less activation. They stated that, first, for an accurate interpretation of individuals' differences in the brain activation related to cognitive performance, the behavioral performance must be equal across the subjects to compare activation (neural effort). Secondly, most of the older studies used PET and EEG

for finding the correlation between brain activation and intelligence, and they mostly reported negative correlation, which resulted in proposing the neural efficiency hypothesis of intelligence. On the other hand, more recent fMRI studies report a positive correlation between the level of activation and intelligence. In their meta-analysis, most of the correlations are also positive.

In contrast with the two mentioned studies, which used task-based fMRI, more recent studies tend to use resting-state fMRI and also utilize it in a multimodal study to investigate the functional network of the brain. [Malpas et al. \(2016\)](#) investigated the relationship between function and structure of the brain using DTI and resting-state fMRI. General intelligence was estimated using WASI. Network-Based Statistics (NBS) approach was performed on the fMRI data and Tract-Based Spatial Statistics (TBSS) on the DTI data. They reported a positive correlation between FSIQ and FA within the right anterior thalamic radiation, the left superior longitudinal fasciculus, the left inferior frontal-occipital fasciculus, and the left uncinate fasciculus. For the fMRI data, a single subnetwork, which is most dominant in the frontal and parietal regions, correlates with the full-scale IQ. They concluded that a positive correlation between FA across the entire white matter and intelligence shows that smarter individuals have a greater white matter organization. The fMRI findings are mostly in line with the DTI findings and the P-FIT theory.

Structural features of the brain play an essential role in the MRI multimodal studies of intelligence. There is still little evidence about the relationship between verbal intelligence and structural properties of the brain. [Konrad et al. \(2012\)](#) investigated the relationship between verbal intelligence and structural properties of the brain using structural and diffusion MRI. They assessed IQ using the Hamburg-Wechsler Intelligence Test (HAWIE-R), which includes measurement of verbal and performance IQ. Using diffusion MRI, they performed voxel-wise regression analysis to find a possible correlation between FA and MD with verbal IQ. Using T1-weighted MRI, they assessed the relationship between VIQ and brain volume. They found a negative correlation between VIQ and FA and a positive correlation between VIQ and MD in the left-hemispheric Broca's area. Although their VBM regression analysis did not show significant results, analysis of the FA correlated regions in the Broca's area showed a positive correlation between the gray matter thickness and VIQ.

In another study using VBM and DTI, [Kievit et al. \(2012\)](#) used Structural Equation Modeling (SEM) to model the

Table 4. Research studies showing relations of brain structure and function with intelligence using multimodal MRI

The First Author	Sample N (Sex)	Age Range, y Mean±SD	Intelligence Test	Main Results	Brain Region	Modality
Tang et al. (2010)	40 (21 M, 19 F)	(Male: 26.62±4.60) (Female: 26.63±4.90)	JOCRf Battery	A negative correlation between brain activation and intelligence. Correlation between FA of interhemispheric connection and intelligence. Overlap in part of functional and structural analysis results	Whole-brain	tfMRI, DTI
Konrad et al. (2012)	30 (16 M, 14 F)	18-26 22.8± 1.5	HAWIE-R	A negative correlation between FA of Broca's area and VIQ, Positive association between Broca's area cortical thickness and VIQ	Broca's Area	Structural MRI, DTI
Kievit et al. (2012)	80 (29 M, 51 F)	18 – 29 21.1±2.55	WAIS-III	Complex models are needed to model the association between IQ and brain structure.	Whole-brain	Structural MRI, DTI
Basten et al. (2015)	464	-	RAPM, WAIS, CFT, JOCRf Battery, IST-2000-R, NART, DAT-5	No overlap between structural analysis and functional analysis results. Good overlap of findings with P-FIT theory	Whole-brain	Structural MRI, tfMRI
Malpas et al. (2016)	91 (35 M, 56 F)	35±89	WASI	Correlation between FA of multiple WM regions and IQ, Correlation between a subnetwork including all GM lobes and IQ	Whole-brain	rsfMRI, DTI

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WASI: Wechsler Abbreviated Scale of Intelligence; RAPM: Raven's Advanced Progressive Matrices; CFT: Cattell Culture Fair Intelligence Test; JOCRf: Johnson O'Connor Research Foundation; IST: Intelligence Structure Test; NART: National Adult Reading; DAT: Differential Aptitude Test; HAWIE-R: Hamburg-Wechsler Intelligence Test; RPM: Raven's Progressive Matrices; gc: Crystallized intelligence; gf: Fluid intelligence; rsfMRI: Resting-state fMRI; tfMRI: Task-based fMRI.

association between intelligence measures used to obtain *g*, and brain features. Using VBM and TBSS, they extracted 8 regions that had a strong correlation with FSIQ. To perform structural equation modeling analysis, they modeled 12 variables: 4 measurements of intelligence (WAIS score) and 8 measurements of DTI and VBM regions. Next, a set of methods from simple to the complex were used for fitting the SEM model. From the 4 tested methods, the Multiple Indicator Multiple Cause Model (MIMIC), as the most complex method tested, showed the best fit and was not declined by the Chi-square test of model fit. In this method, the contribution of various brain ROIs to *g* is estimated separately. They concluded that complex models are needed to describe the association between brain structures and intelligence.

Based on the multimodal studies reviewed and summarized in Table 4, the results of the structural and functional studies of intelligence do not necessarily overlap even though similarity in findings in some parts of the parietofrontal region of the brain has been reported. Most multimodal studies used the first aforementioned approach in which different modalities were analyzed separately and the analysis results compared. Future studies might integrate different modalities in a unified

analysis protocol to explore all information embedded in the multimodal data. Moreover, it seems reasonable to integrate EEG with fMRI to further investigate possible bases of intelligence in the brain.

6. Predicting Intelligence From Neuroimaging Data, the State-of-the-Art of Individualized Prediction of Intelligence

The studies inferring how brain properties can be explained from intelligence through statistical methods, whether morphological, structural, physiological, or metabolic brain characteristics, have led to several discoveries towards the neurobiological basis of intelligence. However, they might miss higher complexity patterns. Shifting the goal from method-driven inference to prediction using statistical learning methods allows one to perform a data-driven search for generalizable patterns in populations (Bzdok, Altman, & Krzywinski, 2018). Not surprisingly, statistical learning has enjoyed growing popularity in the imaging neuroscience community (Amin et al., 2018; Bzdok, 2017; Meng et al., 2017). The machine-learning-based estimation of age from neuroimaging has proven to be a robust biomarker of brain health (Cole & Franke, 2017).

Table 5. The state-of-the-art of individualized prediction of intelligence from neuroimaging data

The First Author	Sample N (Sex)	Data-set	Age Range, y Mean±SD	Intel- ligence Test	Algorithm	Modal- ity	Brain Region	Perfor- mance
Choi et al. (2008)	Structural: 116+48 Functional: 61+48	-	20.9±2.9	WAIS-RK FSIQ	Regression	MRI and task-fMRI (fluid reasoning)	Task activation and cortical thickness defined for whole cortex plus brain volume (selected a priori)	R ² =0.449
Yang et al. (2013)	78 (39 F)	-	22.7±1.9	WAIS-RK FSIQ	PLS	MRI	Combination of pre-selected cortical thickness, surface area, sulcal depth, curvature	R ² =0.302
Wang et al. (2015)	164 (34 F)	ABIDE	6-15 11.1±2.1	FSIQ	Multi-kernel SVR	MRI	Cerebral grey and white matter regional volume	R ² =0.516
Wang et al. (2015)	164 (34 F)	ABIDE	6-15 11.1±2.1	FSIQ	Single-kernel SVR	MRI	Cerebral grey and white matter regional volume	R ² =0.468
Finn et al. (2015)	118	HCP	22-35	gf (PMAT24)	CPM	rsfMRI	Whole-brain (negative edges)	R ² =0.068
Finn et al. (2015)	118	HCP	22-35	gf (PMAT24)	CPM	rsfMRI	Frontoparietal networks	R ² =0.25
Finn et al. (2015)	118	HCP	22-35	gf (PMAT24)	CPM	rsfMRI	Whole-brain (positive edges)	R ² =0.25
Noble et al. (2017)	606+12	HCP		gf (PMAT24)	CPM	rsfMRI	Whole gray matter (including sub-cortex)	R ² =0.048
Jiang et al. (2017)	360 (174 F)	-	17-24 19.4±1.1	WAIS-RC FSIQ	Relief+LASSO	rsfMRI	Cortical and subcortical grey matter plus cerebellum	R ² =0.262 (0.219 M / 0.520 F)
Powell et al. (2017)	838 (468 F)	HCP	22-37 28.76±	gf (PMAT24)	LASSO-PCR	Voxel-wise local structural connectome	Cerebral gray matter	R= 0.0849
Greene et al. (2018)	571 (320 F)	PNC	8-21	gf (PMAT18 + PMAT24)	CPM	Task fMRI (2 tasks)	Cortical and subcortical grey matter plus cerebellum	SR ² =0.123 (0.099)
Greene et al. (2018)	571 (320 F)	PNC	8-21	gf (PMAT18 + PMAT24)	CPM	rsfMRI	Cortical and subcortical grey matter plus cerebellum	SR ² =0.039
Greene et al. (2018)	515 (274 F)	HCP	22-36	gf (PMAT24)	CPM	Task fMRI (7 tasks)	Cortical and subcortical grey matter plus cerebellum	SR ² =0.128
Greene et al. (2018)	515 (274 F)	HCP	22-36	gf (PMAT24)	CPM	rsfMRI	Cortical and subcortical grey matter plus cerebellum	SR ² =0.029
Duboisb et al. (2018)	884 (475 F)	HCP	22-36 28.6±3.7	gf (PMAT24)	Univariate correlation filtering + Elastic net regression	rsfMRI	Cortical and subcortical grey matter	R ² =0.044
Duboisb et al. (2018)	884 (475 F)	HCP	22-36 28.6±3.7	g (derived from 10 cognitive tasks in the NIHTB-ANB and PCNB)	Univariate correlation filtering + Elastic net Regression	rsfMRI	ROIs in the whole cortex	R ² =0.206
He et al. (2018)	8868	UK Bio-bank	-	gf (distributed by the UK Biobank)	Kernel regression	rsfMRI	Whole-brain spatial ICA components	R=0.239
He et al. (2018)	8868	UK Bio-bank	-	gf (distributed by the UK Biobank)	Feed-forward neural network	rsfMRI	Whole-brain spatial ICA components	R=0.239

The First Author	Sample N (Sex)	Data-set	Age Range, y Mean±SD	Intelligence Test	Algorithm	Modality	Brain Region	Performance
He et al. (2018)	8868	UK Bio-bank	-	gf (distributed by the UK Biobank)	BrainNetCNN	rsfMRI	Whole-brain spatial ICA components	R=0.236
He et al. (2018)	8868	The UK Bio-bank	-	gf (distributed by the UK Biobank)	GCNN	rsfMRI	Whole-brain spatial ICA components	R=0.155
Li et al. (2018)	100 (54 F)	HCP	-	gf (PMAT24)	L2-SVR on ALFF	rsfMRI	Cortical and subcortical grey matter plus cerebellum	R=0.325
Li et al. (2018)	100 (54 F)	HCP	-	gf (PMAT24)	L2-SVR on seed connectivity maps from the left ACC	rsfMRI	Cortical and subcortical grey matter plus cerebellum	R=0.319
Zhang et al. (2019)	1065	HCP	-	gf (PMAT24)	TN-PCA	rsfMRI	ROIs in the whole cortex	R=0.240
Zhang et al. (2019)	1065	HCP	-	gf (PMAT24)	TN-PCA	Global structural connectome	ROIs in the whole cortex	R=0.2411
Yoo et al. (2019)	316	HCP	-	gf (PMAT24)	CPM on multivariate distance correlation	rsfMRI	Whole-brain	R=0.19 (inferred from the figure)
Elliott et al. (2019)	298	HCP	-	gf (PMAT24)	CPM	rsfMRI	Whole-brain	R ² =0.042
Elliott et al. (2019)	298	HCP	-	gf (PMAT24)	CPM on general functional connectivity	rsfMRI+ Task fMRI (7 tasks)	Whole-brain	R ² =0.076
Elliott et al. (2019)	591	Dunedin study	-	WAIS-IV	CPM	rsfMRI	Whole-brain	R ² =0.068
Elliott et al. (2019)	591	Dunedin study	-	WAIS-IV	CPM on general functional connectivity	rsfMRI+ Task fMRI (4 tasks)	Whole-brain	R ² =0.102

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ABIDE: Autism Brain Imaging Data Exchange; ACC: Anterior Cingulate Cortex; ALFF: Amplitude of Low-Frequency Fluctuation; CPM: Connectome-Based Predictive Modeling; FSIQ: Full-Scale Intelligence Quotient; g: General intelligence; gf: Fluid intelligence; GCNN: Graph-Convolutional Neural Network; HCP: Human Connectome Project; LASSO-PCR: LASSO Principal Components Regression; NIHTB-ANB: NIH toolbox for assessment of neurological and behavioral function; PCNB: Penn computerized neurocognitive battery; PLS: Partial-least squares multiple regression; PMAT18: 18-item version of the Penn progressive matrices test; PMAT24: 24-item version of the Penn progressive matrices test; SR²: Squared Spearman correlation; SVR: Support Vector Regression; TN-PCA: Tensor network PCA; WAIS-RC, Chinese revised Wechsler adult intelligence scale; WAIS-RK, Korean revised Wechsler adult intelligence scale.

Indeed, following that trend, using machine learning to estimate the individualized intelligence from neuroimaging data is in practice already, including brain surface neuroanatomical features (Yang et al., 2013), connectivity matrices (Finn et al., 2015), and functional activation patterns (Choi et al., 2008). This research area is still developing—the earliest work being only a decade old—and most of the literature has been published in the last three years.

Predictive modeling of intellectual scores from neuroimaging lends itself naturally to regression, as scores are defined on a dense numerical scale. For this reason, the most often employed evaluation metric is the explained variance, defined as one minus the ratio of the variance of the residuals and the variance of the observations. Discrimination between groups of performance levels could also be modeled, but some information is lost in the discretization of scores.

Choi et al. (2008) were the first to build a predictive model of intelligence from neuroimaging data, termed the Neurometric IQ model. They showed that morphometry, specifically cortical thickness, influences *g_c* the most, while *g_f* is mostly associated with the spatial patterns of functional activation of a demanding fluid reasoning task. The authors retrieved a series of functional and anatomical features from these findings, including brain volume as an a priori informative feature. They built a linear model predicting FSIQ, explaining one-half of the variance on the unseen data. Indeed, brain volume is the single most predictive feature for estimating intelligence, as highlighted before in this paper.

Yang et al. (2013) used Partial-Least Squares (PLS) regression on morphometric characteristics of the brain surface, explaining over 30% of the variance in IQ from the first latent variable alone. The authors demonstrated that regional cortical thickness had stronger explanatory importance than local surface area, sulcal depth, or absolute mean curvature. Among all regions, the morphometry of parahippocampal gyri was more correlated to IQ.

Finn et al. (2015) also established the relevance of the connectivity profiles to behavior by demonstrating, in a leave-one-subject-out cross-validation analysis, that functional connectivity profiles can be used to predict the fundamental cognitive trait of fluid intelligence across subjects. It shows that the characteristic connectivity patterns are distributed throughout the brain, but the frontoparietal network emerges as distinctive. Furthermore, connectivity profiles predict levels of fluid intelligence. The networks that are most discriminating of individuals are also most predictive of cognitive behavior. Their results indicate the potential to draw inferences about a single subject based on functional connectivity.

Wang et al. (2015) employed multi- and single-kernel Support Vector Regression (SVR) to predict FSIQ from gray and white matter regional volumetry in typical children and adolescents. The authors report an optimal R^2 of 0.516, remarkably higher than that of the total brain volume. This result suggests that local morphometric estimates are more specific to the problem of intelligence estimation.

CPM was first introduced with an application to the prediction of *g_f*, explaining 25% of the variance of this factor of intelligence from resting-state fMRI (Finn et al., 2015). They demonstrate that the CPM protocol performs as well as or better than many of the existing approaches for brain-behavior prediction. Its findings were tested by other authors but not fully corroborated (Dubois, Galdi, Han, Paul, & Adolphs, 2018; Nielsen et al., 2018; Noble et al., 2017;

Yoo et al., 2019). CPM is easily implemented and performed (Shen et al., 2017). It consists of filtering edges in a univariate fashion based on their correlation to the behavior variable of interest, summing the edges above the threshold, and building a linear regression model predicting the behavior of interest from this sum. The developers of CPM recommend treating negative and positive edges separately, resulting in two sums of edges per subject. A limitation of CPM is that it arbitrarily assumes that edges contribute equally to prediction, a decision based on the necessity of simpler models due to scarcity of data (Dubois et al., 2018).

Dubois et al. (2018) demonstrated that 20% of the inter-subject variability of general intelligence could be explained from resting-state functional connectivity matrices alone, an effect at the same level of magnitude as brain volume. They also showed that no single anatomical region or brain network was substantially more important for this prediction task. This suggests that general intelligence information is spread across the brain in a redundant fashion. When looking at predictions from single networks, though, it becomes evident that the DMN, FPN, CON, and VIS networks achieve better performance than the AUD, SMN, and DAN networks, mostly in agreement with the P-FIT theory. Their work is also important because it showed, accounting for several confounding factors, resting-state functional connectivity might be just as informative as brain volume, with added discriminability of function.

The predictability of intelligence from resting-state functional connectivity is still debated. Through the use of CPM, Greene, Gao, Scheinost, and Constable (2018) could explain around 20% of the variance of fluid intelligence with task fMRI in contrast to only 6% with resting-state fMRI, with data from the HCP and PNC (Philadelphia Neurodevelopmental Cohort) (Satterthwaite et al., 2016, 2014) cohorts. This result could be explained by the perturbations in brain activity elicited by the tasks being related to individual traits. They also showed that predictive performance varies per task for each sex, which must be explored further. Jiang et al. (2017) obtained a similar result with resting-state fMRI, where intelligence from females can be more reliably estimated than males. These researchers tested different regression models and found ReliefF + LASSO as the best predictor. In Greene et al. (2018), the resting-state lend itself better to predicting intelligence for males but with trivial performance.

On the other hand, Elliott et al. (2019) used CPM to predict cognitive ability by both resting-state functional connectivity and general functional connectivity, a new mea-

sure that combines both task and resting-state functional connectivity information. In the HCP dataset, resting-state functional connectivity predicted 4.2%, while general functional connectivity explained 7.6% of cognitive ability, obtained from the Penn progressive matrices test. Results were reproduced in the Dunedin study dataset. Even though adding task connectivity information improves the reliability of functional connectivity estimates, performance in cognitive ability estimation is substantially small.

Yoo et al. (2019) compared univariate and multivariate functional connectivity estimates and how multivariate approaches based on multivariate distance correlation improve the prediction of individual behavior. Using CPM, their work showed that distance correlation explains no less variation than the Pearson correlation-based connectivity requiring less acquisition time. With just 160 time-points, they obtained a correlation of circa 0.19 between predictions and estimates of fluid intelligence received from the Penn progressive matrices test.

Comparing kernel regression and artificial neural networks in the prediction of behavior from functional connectivity from almost 10000 subjects in the UK Biobank and HCP, He et al. (2018) demonstrated that a relatively simple kernel regression, with the kernel defined as the Pearson correlation between subjects' functional connectivity matrices, does not underperform compared to sophisticated models based on artificial neural networks. A correlation of circa 0.27 between predictions and fluid intelligence, defined as the Penn progressive matrices test results, was found for the HCP data, for kernel regression, a feed-forward neural network, and the BrainNetCNN, which is an architecture tailored to work on functional connectivity matrices (Kawahara et al., 2017). The correlation between predictions and fluid intelligence estimates in the UK Biobank dataset was estimated as 0.239 for both kernel regression and the feed-forward neural network, with the BrainNetCNN achieving a correlation of 0.236. In both datasets, the Graph-convolutional neural network (Parisot et al., 2018) underperformed. These experiments raise the possibility that fluid intelligence information lies in a linear manifold contained in resting-state functional connectivity matrices.

Li et al. (2018) employed L2-SVR to predict gf from regional estimates of the Amplitude of Low-Frequency Fluctuations (ALFF) and, separately, seed-based connectivity maps, including univariate filtering in the modeling procedures, from resting-state fMRI. They observed a correlation of $R=0.325$ between predictions and gf estimates when using ALFF as the input variable and identified clusters in the left Anterior Cingulate Cor-

tex (ACC) and right Middle Occipital Gyrus (MOG) as mostly responsible for differences captured in the model. When predicting gf from seed-based connectivity maps from these clusters, though, only the connectivity from the ACC could predict gf significantly better than chance. The connectivity between the left ACC and the right prefrontal cortex was the most discriminative for the model performance.

Few articles approached the problem of predicting intellectual abilities from structural connectivity and diffusion-weighted imaging features in general. Powell, Garcia, Yeh, Vettel, and Verstynen (2017) provided results on the predictability of fluid intelligence from structural connectivity, among other traits. They investigated the local structural connectome, derived from measures particular to diffusion MRI in a voxelwise fashion. Using principal components regression with LASSO, they achieved a correlation of $R=0.0849$ between predictions and actual estimates of fluid intelligence. Zhang et al. (2019) investigated the global structural connectome properties, estimated in a region-to-region approach. They achieved $R=0.240$, employing the Tensor network PCA method over features extracted from the streamlines, such as fractional anisotropy, mean diffusivity, fiber count, and connected surface area. In comparison, using the same parcellation and resting-state fMRI data, they achieved $R=0.2411$ to predict fluid intelligence from functional connectivity.

Albeit correlational studies often provide a measure of predictability of intelligence from neuroimaging, such as the percentage of the variance explained, this measure does not necessarily generalize to unseen subjects, mostly when the subjects were used to derive the features used to explain their variability, since the procedure maximizes performance for the data it has seen. A more accurate estimate should be obtained with proper validation. For this reason, in Table 5, we only included studies reporting the prediction of intellectual scores from neuroimaging with proper generalized performance estimation. We omit studies, such as Song et al. (2008), that asserts that functional connectivity estimates from the Dorsolateral Prefrontal Cortices (DLPFC) to other brain regions are strong predictors of FSIQ for a Chinese population, achieving $R^2=0.473$ and $R^2=0.730$ for two sets of 3 and 6 edges respectively, obtained with an a priori search heuristic.

The literature suggests that intelligence can be predicted from neuroimaging data alone to some degree. According to previous theories of the neural bases of intelligence that accommodated single or multiple networks, such as the P-FIT (Jung & Haier, 2007) and NNT (Barbey, 2018), the most recent works imply that predictive

information is dispersed across the brain. Accordingly, theories focusing on the high importance of a single cortex region, such as the LPFCT (Duncan & Owen, 2000), are not supported by these findings, which suggest redundancy, not dependency on single regions.

Some methodological issues must be considered in this specific prediction problem. Proper validation is required for the initial results obtained for the predictive modeling. For example, kinship must be considered in the HCP datasets (Dubois et al., 2018), something not common to other forms of analysis of neuroimaging data. Appropriate treatment of covariates is also necessary. It is required to account for differences in intracranial or brain volume, although subtler relations also exist. Sex, for example, is correlated with intracranial volume (Barnes et al., 2010) which is a strong predictor of intelligence. Movement is negatively correlated with intelligence (Dubois et al., 2018) and leaves a footprint in functional connectivity (van Dijk, Sabuncu, & Buckner, 2012) and morphometric estimates (Reuter et al., 2015). Development and aging cause phenotypical alterations associated with changes in measures obtained in neuroimaging. Development is also prominently associated with changes in intellectual scores. By lack of consensus and its complexity, special care must be taken with the metric of intelligence to be predicted.

Some new avenues can be explored in intelligence prediction from neuroimaging data. Dubois et al. (2018) suggest that naturalistic movie-watching fMRI might be an alternative to improve the Signal-to-Noise Ratio (SNR) by increasing variation in brain activity and retrieve more discriminative information. No study has yet been performed on this front. The use of diffusion-based MRI and dynamic functional connectivity to predict intelligence has also been neglected, with few studies reporting on the use of machine learning techniques to the estimation of intelligence from diffusion-tensor-based metrics or the structural connectome, which are the anatomical backbones that allow communication of distant regions of the brain. Dynamic functional connectivity relates to alternating brain states in short timespans (Calhoun, Miller, Pearlson, & Adali, 2014) and has been contemplated by a theory of intelligence (Barbey, 2018).

New datasets and computational tools from the whole scientific community should influence future steps to link brain biology and intellectual endowment. The advent of large-scale datasets on neuroimaging has furthered the search for the neural loci of intelligence. Examples include the Human Connectome Project (HCP) (Van Essen et al., 2013; Glasser et al., 2016), UK Biobank (Miller et

al., 2016; Sudlow et al., 2015), Cambridge Centre for Aging and Neuroscience (Cam-CAN) (Shafto et al., 2014; Taylor et al., 2017), and Nathan Kline Institute's Rockland Sample (NKI-RS) (Nooner et al., 2012). We expect future works use these datasets even more. In the spirit of CPM, the appearance of other toolboxes will also accelerate the widespread usage of machine learning in the study of human intelligence and other traits. Examples include the GraphVar (Brovkin et al., 2018) and PRoNTo (Schrouff et al., 2013; Schrouff et al., 2018) toolboxes.

The intelligence research area could also benefit from community challenges that proved productive to other fields of study in neuroscience and neuroimaging. Successful examples include the ADHD-200 Global Competition, Brain Tumor Segmentation, Radiomics Survival Prediction (BRATS) Challenges, and The Alzheimer's Disease Prediction Longitudinal Evolution (TADPOLE) Challenge. The ABCD Neurocognitive Prediction Challenge 2019, offered in conjugation with the 22nd International Conference on Medical Image Computing and Computer-Assisted Intervention, was a first and welcome competition aimed at deriving predictive models for fluid intelligence based on neuroimaging, and we expect the community to multiply these initiatives. With the increasing size of open neuroimaging databases, we believe it is time to employ more complex, possibly non-linear approaches. Even with the substantial negative results in He et al. (2018), deep learning and convolutional neural networks (LeCun, Bengio, & Hinton, 2015) have made inroads into neuroimaging with the increases in computational power and robustness of optimization methods and are a framework to be considered by any future studies. News venues of research are open to augment previous architectures with regularization specially tailored to the problem or create and deploy new less data-hungry architectures and training modalities.

Ethical Considerations

Compliance with ethical guidelines

The authors have no competing interests to declare.

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Authors' contributions

Equal contributions of the first authors: Aslan Satary Dizaji and Bruno Hebling Vieira; Conceptualization and supervision: Carlos Ernesto Garrido Salmon, Gholam Ali Hossein-Zadeh, Hamid Soltanianzadeh; Methodology, investigation and writing – original draft: Aslan Dizaji, Bruno Hebling Vieira, Mohammad Reza Khodaei, Mahnaz Ashrafi; Writing – review & editing: All authors; Funding acquisition and resources: Carlos Ernesto Garrido Salmon, Hamid Soltanianzadeh.

Conflict of interest

The authors declared no conflict of interest.

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