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Author contributions

B.L.M. and M.E.R. designed and conceived the study. M.J.W., P.M.T. and N.G.M. were responsible for the QTIM cohort design and genotyping. L.T.S., G.C.P., A.I.C. were involved in the data processing, quality control and preparation while B.L.M, M.E.R. and G.C.P. were responsible for the data analysis. A.O. provided the EA3 'leave-one-out' summary statistics. K.L.G, M.E.R. and S.E.M. provided guidance and aided in interpreting the data. B.L.M. wrote the manuscript. All authors assisted in the preparation and editing of the manuscript.



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24

1 Abstract

2 It is well established that higher cognitive ability is associated with larger brain size. 3 However, individual variation in intelligence exists despite brain size and recent studies have shown that a simple unifactorial view of the neurobiology underpinning cognitive ability is 4 probably unrealistic. Educational attainment (EA) is often used as a proxy for cognitive 5 6 ability since it is easily measured, resulting in large sample sizes and, consequently, sufficient 7 statistical power to detect small associations. This study investigates the association between three global (total surface area (TSA), intra-cranial volume (ICV) and average cortical 8 9 thickness) and 34 regional cortical measures with educational attainment using a polygenic scoring (PGS) approach. Analyses were conducted on two independent target samples of 10 young twin adults with neuroimaging data, from Australia (N=1,097) and the USA (N=723), 11 and found that higher EA-PGS were significantly associated with larger global brain size 12 measures, ICV and TSA (R^2 =0.006 and 0.016 respectively, p<0.001) but not average 13 thickness. At the regional level, we identified seven cortical regions-in the frontal and 14 temporal lobes-that showed variation in surface area and average cortical thickness over-15 and-above the global effect. These regions have been robustly implicated in language, 16 memory, visual recognition and cognitive processing. Additionally, we demonstrate that 17 these identified brain regions partly mediate the association between EA-PGS and cognitive 18 test performance. Altogether, these findings advance our understanding of the neurobiology 19 20 that underpins educational attainment and cognitive ability, providing focus points for future 21 research.

22

Keywords: educational attainment, brain structure, polygenic scores, intelligence, Broca'sarea

1 Introduction

It's widely understood that significant differences in cognitive ability exist between human
beings. However, the biological aetiology behind this variation remains somewhat elusive.
The advent of brain imaging has enabled the investigation of neural substrates for human
cognitive ability *in vivo*, leading to the identification of several anatomical and functional
correlates of cognitive ability (Jansen et al., 2019; Knol et al., 2019; Schmitt et al., 2019).

7

Previous evidence has suggested that healthy individuals with higher intelligence tend to have 8 9 larger brains. The first published study examining intelligence and brain size reported a correlation of 0.5 in a group of college students (Willerman, Schultz, Rutledge, & Bigler, 10 1991). However, these estimates lessened as sample sizes grew and associated variables, such 11 as height and socio-economic status (SES) were included in analyses. Several recent studies 12 have estimated the correlation between intelligence and intra-cranial volume (ICV) to be 13 between 0.2 and 0.4 (S. Cox, Ritchie, Fawns-Ritchie, Tucker-Drob, & Deary, 2019; 14 MacLullich et al., 2002; McDaniel, 2005; Pietschnig, Penke, Wicherts, Zeiler, & Voracek, 15 2015; Rushton & Ankney, 2009), with the two largest studies to date (N=13,600 and 16 N=8,000) reporting a correlation of 0.19 (Nave, Jung, Karlsson Linnér, Kable, & Koellinger, 17 2019) and 0.24 (Pietschnig et al., 2015) respectively. Although these correlation estimates are 18 modest, the association between brain size and intelligence appears to be almost entirely due 19 20 to genetics (Koenis et al., 2018; Posthuma et al., 2002).

21

22 Twin studies leverage the shared genes between twin siblings to disentangle the genetic and environmental influences behind phenotypic variability, and have contributed substantially to 23 24 the current understanding of cognitive neurobiology. Twin analyses have found that general cognitive ability positively correlated both phenotypically and genetically with total surface 25 26 area (TSA) however, no correlation was observed with average cortical thickness (Vuoksimaa et al., 2014; Walhovd et al., 2016). Additionally, the positive association 27 28 between cognitive ability and TSA remained significant throughout the lifespan (Walhovd et al., 2016). Though reportedly uncorrelated at a global level, some studies have found regional 29 30 variability in the correlations between average cortical thickness and cognitive ability, reporting both positive and negative correlations (Panizzon et al., 2009; Winkler et al., 2010). 31 32

1 Several neuroimaging studies suggest that general intelligence, termed 'g', is most strongly associated with grey matter volume measures from the pre-frontal cortex, language centres in 2 the fronto-parietal network and specific regions in the temporal and occipital lobes (Basten, 3 Hilger, & Fiebach, 2015; Gläscher et al., 2010; Jung & Haier, 2007). The morphometry of 4 these regions is also highly heritable in both children (Lenroot et al., 2009) and adults (Rimol 5 et al., 2010; Thompson et al., 2001). In addition, twin studies have reported that a high-6 7 expanded surface area (SA) in prefrontal, lateral temporal and inferior parietal regions was positively associated with general cognitive ability (Vuoksimaa et al., 2016; Walhovd et al., 8 2016) and that these regions exhibit cortical stretching, where increased SA is accompanied 9 by a thinner cortex. Other cerebral features, such as structural and resting-state connectivity 10 (Dubois, Galdi, Paul, & Adolphs, 2018), white matter microstructure (Chiang et al., 2009), 11 the magnitude of local coherence (synchronized functional activity between regions) (Fjell et 12 al., 2015; Wang, Song, Jiang, Zhang, & Yu, 2011) and neural network efficiency (Neubauer 13 & Fink, 2009; Santarnecchi, Galli, Polizzotto, Rossi, & Rossi, 2014; Van Den Heuvel, Stam, 14 Kahn, & Pol, 2009) have also been associated with general intelligence, highlighting 15 potential functional mechanisms underlying individual variability in intelligence 16 (Santarnecchi & Rossi, 2016). To add further complexity, the regional association of brain 17 18 structure with intelligence may change across the lifespan (Fjell et al., 2015). For instance, cortical surface area, the prefrontal cortex and anterior cingulate cortex are most strongly 19 20 associated with intelligence in children (Reiss, Abrams, Singer, Ross, & Denckla, 1996; Schnack et al., 2014; Wilke, Sohn, Byars, & Holland, 2003), while the orbitofrontal and 21 22 middle frontal cortices are most strongly associated with intelligence in adolescents (Frangou, Chitins, & Williams, 2004). For cortical thickness, the association with intelligence changes 23 24 with age, with the strength of these associations appearing to peak around age 12 (Schmitt et al., 2019; Shaw et al., 2006). These findings point to specific age-mediated structural and 25 26 functional anatomical events associated with cognitive ability (Fjell et al., 2015). Together 27 these findings indicate that a simple unifactorial view of the neurobiology underpinning cognitive ability is unrealistic, and that the relationship is far more dynamic and nuanced. 28

29

Intelligence is somewhat malleable through interventional strategies that include education,
improved diet and positive home environments (Brinch & Galloway, 2012; Protzko, 2016).
These correlates may be important mediators of the association between cognitive ability and
neurobiology. For example, children from lower income families showed greater variation in
cortical surface area and thickness than those from higher income families in the U.S. (Noble

et al., 2015). These relationships were most prominent in regions supporting language,
reading, executive functions and spatial skills. Environmental variables such as these, which
are themselves influenced by genetics (Lee et al., 2018; Lemery-Chalfant, Kao, Swann, &
Goldsmith, 2013; Liu, 2019), add to the complexity of unravelling observed relationships
between cognition and brain phenotypes.

6

7 Due to the recent availability of large genome-wide association studies (GWAS) of cognitiverelated phenotypes, the relationship between intelligence and its neurobiological correlates 8 can now be examined at the molecular level. Recent studies have given weight to previous 9 twin research and found shared genetic factors between cognitive traits and brain imaging 10 phenotypes, such as total brain size and cortical thickness (Elliott et al., 2018; Ge et al., 2018; 11 Schmitt et al., 2019). In fact, post-GWA studies of intelligence and brain volume found a 12 genetic correlation (r_g) of 0.23, which mapped to 67 shared genes (Jansen et al., 2019), and 13 indicated that brain volume accounted for approximately 2% of the variance observed in IQ 14 and 1% in educational attainment (Nave et al., 2019). These studies have predominantly 15 examined this relationship with global anatomical measures yielding insights into the shared 16 genetic aetiology between neuroanatomy and cognitive ability (Santarnecchi & Rossi, 2016). 17 18 Even so, the phenotypic and genetic correlations between regional cortical areas and cognitive ability have not been thoroughly explored (Grasby et al., 2018). Thus, further fine-19 20 scale analysis is required to ascertain the extent to which the genetics influencing cognitive ability affects the structure of individual cortical regions. 21

22

Educational attainment (EA), defined as the number of full-time years of education an 23 24 individual receives, is a useful proxy trait for cognitive ability and is associated with important health-related and life outcomes such as occupational success, social and 25 26 geographic mobility, mate choice and even the age an individual acquires reading and writing (Belsky et al., 2016; Plomin & von Stumm, 2018). EA is correlated both 27 skills phenotypically (0.50) and genetically (0.65) with intelligence (Plomin & von Stumm, 2018; 28 Rietveld et al., 2014) but is regarded as a combination of both cognitive and non-cognitive 29 skills, and is influenced by both genes and the environment (Belsky et al., 2018; Krapohl & 30 Plomin, 2016). For instance, parents' polygenic scores for educational attainment (EA-PGS)¹ 31 32 were shown to still predict their children's EA even after adjusting for the child's own EA-

¹ A polygenic score (PGS) is an individual's cumulative genetic score for a complex trait. PGS are derived from aggregating the contributions of all known trait-associated genetic variants (Sugrue & Desikan, 2019).

PGS, substantiating an effect of parental environment on children's EA (Belsky et al., 2018).
Additionally, children with higher EA-PGS often display more social mobility and surpass
their parents' occupational success (Belsky et al., 2018). As 'years of education' is a
commonly obtained demographic marker collected in almost every population or clinical
GWAS study, a recent educational attainment meta-analysis (termed EA3) was able to
aggregate a sample size of 1.1 million people, giving unparalleled statistical power (Cesarini
& Visscher, 2017; Lee et al., 2018).

8

While the current literature suggests that genetics, neuroanatomic specificity, and age are all 9 critical to understanding the neural substrates of intelligence, few studies have addressed this 10 using large-scale genetic data. Studies of the shared genetic aetiology between neuroanatomy 11 and intelligence have predominantly focused on global measures, perhaps due to the limited 12 statistical power of the GWAS of intelligence-related phenotypes available at the time. 13 Although this is one of the first studies investigating the associations between the genes for 14 education and brain anatomy using a polygenic scoring approach, a few recent studies have 15 used a similar approach of examining the association between PGS for behavioural/cognitive 16 traits and neuroanatomy (Aydogan et al., 2019; Foley et al., 2017; French et al., 2015; 17 Matloff, Zhao, Ning, Conti, & Toga, 2019). This study aimed to assess the association 18 between the genes related to education (as a proxy for general cognitive ability) and the 19 20 morphometry of specific cortical regions (3 global and 34 regional). Secondly, we assessed whether the established association between an EA-PGS and IQ scores is mediated by 21 22 identified brain structures.

1 Materials and Methods

2 **Participants**

Two cohorts were examined in this study. The first cohort was the Queensland Twin Imaging 3 Study (QTIM) (Blokland et al., 2014) consisting of 1165 Australian twins and siblings. As it 4 has previously been shown that the EA-PGS (calculated from European ancestry GWAS), 5 has poor predictive ability in non-European samples (Lee et al., 2018), the cohort was filtered 6 7 by genetic ancestry, determined using principal component analysis, resulting in a final sample of 1097 participants included in this study. Principal component analysis was 8 performed to identify ancestry outliers² using SmartPCA 1600 in EIGENSOFT 7.2.1 9 (https://www.hsph.harvard.edu/alkes-price/software/). This ensured that individuals in the 10 analysis were of European descent by excluding those individuals who were more than 6 s.d. 11 from the principal component 1 and 2 centroid from the 1000 Genomes European population 12 (68 individuals excluded). Thus, the final sample included 176 MZ pairs, 228 DZ pairs, 212 13 unpaired twins and 77 siblings, with a mean age of 22.3 years (s.d.=3.3, range 16-30). 14 Written informed consent was obtained from each participant and from a parent or legal 15 guardian for participants under the age of 18. All of these individuals had previously 16 participated in the Brisbane Twin Memory and Cognition study at age 16 (Wright & Martin, 17 2004). Thus, additional information was available on general cognitive ability (full-scale 18 intelligence quotient; FIQ), as well as Verbal and Performance IQ (VIQ and PIQ). The mean 19 interval between cognitive testing and magnetic resonance imaging (MRI) scanning was 4.4 20 years (range 0-14 years). Gestational duration, birth weight, and parental socioeconomic 21 status were also obtained from parental reports. Individuals with significant medical, 22 psychiatric, or neurological conditions—including head injuries, a current or past diagnosis 23 24 of substance abuse, or current use of medication that could affect cognition-were excluded from participating in the study. Zygosity was determined using genome-wide single 25 nucleotide polymorphism (SNP) genotyping chips (Illumina 610K). 26

27

The second cohort was from the *Human Connectome Project* (HCP) (Van Essen et al., 2013),
which consists of 1,113 ethnically-diverse adults primarily from Missouri, USA (mean age

30 28.8, s.d.=3.7, range 22–37 years) with imaging data available. Individuals of non-European

² Systematic differences in genetic variant frequencies can occur in samples that contain individuals from different ancestry populations, which can confound results of GWAS. Genetic principal component analysis (PCA) can be used to identify individuals in different ancestry groups so they can be excluded from analyses. For more information see: (Abegaz et al., 2019; Price et al., 2006; Price, Zaitlen, Reich, & Patterson, 2010)

ancestry were filtered according to i) their self-reported race (white) and ethnicity (not 1 Hispanic/Latino) and ii) genetic ancestry determined using principal components analysis (as 2 3 described for the QTIM cohort). Thus, the final HCP sample analysed in this study consisted of 723 white, non-Hispanic/Latino individuals, mean age 29.1 s.d.=3.5, range 22-36 years, 4 consisting of 119 MZ and 64 DZ pairs, 96 singletons, and 261 siblings (390 individuals 5 excluded). All subjects were scanned on a customized 3 T scanner at Washington University 6 7 in St Louis (WashU). Genotyping was performed on the Illumina Infinium HD beadchip. Demographic and behavioural information, including fluid and crystallized IQ scores, was 8 also collected. Demographic information for both QTIM and HCP cohorts are shown in Table 9 1. 10

Table 1: Demographic information for QTIM and HCP samples						
		QTIM Sam	ple		HCP Samp	le
	Females	Males	Total	Females	Males	Total
Full sample (N)	683	414	1097	384	339	723
Twins (N)	631	389	1020	234	228	462
MZ pairs (N)	106	70	176	62	57	119

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DZ pairs (N)	125	103	228	35	29	64
Age (s.d.)	22.2 (3.3)	22.4 (3.4)	22.3 (3.3)	29.9 (3.3)	28.1 (3.5)	29.1 (3.5)
FIQ/Fluid	111.8 (12.1)	116.8 (13.1)	113.6 (12.7)	115.2 (10.6)	117.1 (11.3)	116.0 (11)
Intelligence ^a						
Height (cm)	166 (6.9)	180.7 (7.3)	171.5 (10)	167 (6.6)	181.5 (7.4)	173.7 (10.1)
BMI (kg/m ²)	22.8 (3.9)	23.9 (3.7)	23.2 (3.9)	25.6 (5.4)	27.0 (4.3)	26.8 (5.6)
Socio-Economic	53.3 (20.9)	56.6 (21.2)	54.6 (21.1)	5.3 (2.1)	5.5 (1.9)	5.4 (2.0)
Status ^b						
Total Surface Area	164049	184379	171229	165203	187667	175736
(mm²)	(13046)	(14713)	(16759)	(12741)	(14511)	(17622)
Average Thickness	2.5 (0.09)	2.5 (0.08)	2.5 (0.09)	2.7 (0.07)	2.7 (0.09)	2.7 (0.08)
(mm)						

1 Parentheses indicate standard deviation

^{a:} Full-Scale Intelligence quotient (FIQ) measured in QTIM sample an average of 4 years prior to scanning;

3 Fluid Intelligence measured in HCP sample at time of scanning.

^b Socioeconomic status (SES) is calculated on the Australian Socioeconomic Index occupational status scale in
 QTIM (scale 0-100) while SES in HCP was computed using income-to-poverty ratio based on self-reported

6 family income relative to poverty thresholds in the United States (scale 0-10).

8 Ethics Statement

7

9 The QTIM study was approved by the Human Research Ethics Committees of the QIMR
10 Berghofer Medical Research Institute, the University of Queensland, and Uniting Health Care
11 at Wesley Hospital. The HCP study was approved by the internal review board of
12 Washington University (IRB # 201204036).

13 MRI acquisition and processing

14 *QTIM cohort:*

Imaging was conducted on a 4 Tesla Bruker Medspec whole body scanner (Bruker, 15 Germany) with a transverse electromagnetic (TEM) head coil in Brisbane, Australia. 16 Structural T1-weighted 3D images were acquired (TR=1500 ms, TE=3.35 ms, TI=700 ms, 17 230 mm FOV, 0.9 mm slice thickness, 256 or 240 slices depending on acquisition orientation 18 (86% coronal [256 slices], 14% sagittal [240 slices]). Surface area and cortical thickness were 19 20 measured using FreeSurfer (v5.3; http://surfer.nmr.mgh.harvard.edu/) as previously described 21 (Fischl & Dale, 2000). Prior to FreeSurfer analysis, the raw T1-weighted images were corrected for intensity inhomogeneity with SPM12 (Wellcome Trust Centre for 22 Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm). Total surface area and 23 average cortical thickness were extracted for 34 regions of interest (ROI) per hemisphere 24 from the Desikan-Killiany atlas (Desikan et al., 2006) contained within FreeSurfer. Three 25

global measures, intra-cranial volume, total surface area, average cortical thickness, were also
extracted. Cortical reconstructions and ROI labelling were checked using the standardised
procedures of the ENIGMA consortium (enigma.ini.usc.edu) (Thompson et al., 2014), with
any incorrectly delineated cortical structures also being excluded from the analysis.

5

6 *HCP Cohort:*

7 Details of the specific processing procedures used for the HCP dataset can be found in previous articles (Glasser et al., 2013; Van Essen et al., 2013). Briefly, for each subject in the 8 HCP a pair of T1-weighted scans and a pair of T2-weighted (T2w) scans were acquired, both 9 with a spatial resolution of 0.7 mm (isotropic voxels). All scans were quality-rated based on 10 visual inspection before processing, and only those of excellent quality in both categories 11 entered the processing pipeline. The HCP structural pipelines used a specialized version of 12 FreeSurfer 'FreeSurfer 5.3-HCP' software. Registration to atlas space included an initial 13 volumetric registration to MNI152 space using FreeSurfer's linear FLIRT tool, followed by 14 the nonlinear FNIRT algorithm to align subcortical structures. Cortical surfaces were aligned 15 further to population-average surfaces using FreeSurfer to register each hemisphere to a 16 separate left and right hemisphere surfaces based on the matching of cortical folding patterns 17 18 (Fischl et al., 1999) and landmark assisted registration using the Conte69 atlas (Van Essen et al., 2012). 19

20

Left and right hemispheres were averaged for each of the 68 regions of the Desikan-Killiany 21 22 atlas (Desikan et al., 2006) in both cohorts resulting in a final 34 cortical ROI. This atlas was chosen as it is a common output from Freesurfer and yields larger regions based on common 23 24 cortical folding patterns resulting in regions that have clear boundaries and are largely 25 consistent between cohorts (Grasby et al., 2018). Averaging the ROIs across hemispheres 26 was done primarily due to the high genetic correlation between corresponding ROI in each 27 hemisphere (Strike et al., 2018; Wen et al., 2016), indicating that variation between corresponding ROI may be more environmental in nature and thus, not within the scope of 28 this study. Additionally, averaging across hemispheres effectively halves the multiple testing 29 burden, an important consideration in genetic studies with relatively small associations -30 especially in cohorts with smaller sample sizes. Lastly, averaging regions combats laterality 31 issues such as possible switching of left and right MRI scans and the need to account for 32 33 other confounding variables such as handedness.

34

1 Computation of polygenic scores for educational attainment (EA-PGS)

Standard genotyping, imputation and quality control procedures for the QTIM sample have 2 been described previously (Colodro-Conde et al., 2018). Briefly, quality-control, conducted 3 using PLINK 1.9 (Hwang et al., 2019), included removing minor allele frequency 4 (MAF<0.005), SNP call rate (>95%), ancestral outliers and Hardy-Weinberg equilibrium 5 deviation $(p < 1x10^{-6})$ before imputation using the Haplotype Reference Consortium 1.1 6 reference panel. After imputation, prior to EA-PGS calculation, insertions and deletions, 7 ambiguous strands, and low-quality imputation variants ($R^2 < 0.6$) were excluded. For the 8 HCP cohort, imputed genotypes in dosage format from the HCP (dbgap: phg000988.v1) were 9 transformed best 10 to guess using gtool (https://www.well.ox.ac.uk/~cfreeman/software/gwas/gtool.html). QC procedures 11 were conducted as described for QTIM. 12

13

Summary statistics from the most recent EA GWAS (EA3) (Lee et al., 2018) were used to 14 calculate the EA-PGS for all individuals in the QTIM (N=1,097) and HCP (N=723) cohorts. 15 The EA3 GWAS comprised data from over a million individuals (N=1,131,881) of European 16 ancestry from 71 independent cohorts across the world. As the QTIM cohort was included in 17 the EA GWAS, 'leave-one-out' summary statistics for EA were required to avoid sample 18 overlap. Leave-one-out summary statistics were generated by removing all individuals from 19 20 the Queensland Twin Registry (which includes the QTIM cohort) from the original dataset and re-conducting the GWAS. 21

22

Using the leave-one-out summary statistics, EA-PGS were calculated using PLINK 1.9. SNPs were clumped according to Purcell *et. al.* 2007 guidelines ($r^2 < 0.1$, kb=10000) to account for linkage disequilibrium (Purcell et al., 2007). Eight EA-PGSs were calculated using different SNP *p*-value significance thresholds: $p < 5x10^{-8}$, $p < 1x10^{-5}$, p < 0.001, p < 0.01, p < 0.05, p < 0.1, p < 0.5, p < 1. For each individual, at each threshold, EA-PGS was calculated by multiplying the dosage and effect size for each SNP, and then these values were summed across all loci. For the number of SNPs included at each *p*-value threshold, see Supplementary Table 1.

30

31 Correlations between EA-PGS and examined phenotypes

Partial correlations between all EA-PGS thresholds, the three global brain measures, IQ, and
educational attainment (available only in HCP cohort) were assessed in SPSS 22.0 (SPSS
Inc., Chicago, IL, USA). One member from each family was selected to ensure individuals

were unrelated to avoid dependency among residuals within family. Significance values were calculated using a two-tailed Students *t*-test (DF=979 in QTIM and DF=718 in HCP). All correlations were corrected for sex and age and significance values were Bonferroni corrected for multiple testing (p<0.05/ effective number of independent observations).

5 Polygenic score association analysis

The association between the genetic influences on educational attainment and neuroimaging 6 7 phenotypes was assessed by estimating how much of the variance in brain phenotypes was accounted for by the EA-PGS in each cohort. The initial neuroimaging phenotypes of interest 8 were ICV, TSA and average cortical thickness. This was done using a linear mixed model 9 regression with the EA-PGS as a predictor variable while accounting for sex, age, age^2 , 10 sex*age, sex*age², the first ten genetic principal components (to account for residual 11 population stratification), and imputation run as fixed effects; relatedness among individuals 12 was accounted for as a random effect with a genetic relatedness matrix, implemented in 13 GCTA 1.91.7 (Yang, Lee, Goddard, & Visscher, 2011; Yang, Zaitlen, Goddard, Visscher, & 14 Price, 2014). A partial R^2 was used to estimate the variance explained by the polygenic risk 15 score. Significance values were calculated using a two-tailed Student's t test. To correct for 16 17 multiple testing error, the effective number of independent observations (calculated from a correlation matrix of 8 PGS thresholds x 3 ROIs) was estimated using Matrix Spectral 18 Decomposition (MatSpD) (Nyholt, 2004) before undergoing Bonferroni correction. 19

20

After assessing the association with global brain measures, EA-PGS were then tested for 21 association with surface area and average cortical thickness for each of the 34 cortical regions 22 of interest. For these analyses, TSA or average thickness were added as covariates to the 23 linear mixed model regression in GCTA to test whether the EA-PGS predicted variance that 24 was specific to the cortical region. Resulting p-values were corrected for multiple testing 25 26 error as described above. The ROI analyses were conducted separately from those of the global measures as they included either TSA or average thickness as covariates. Thus, 27 multiple testing correction was conducted separately for the global measure analysis and the 28 regional analyses. 29

30

We next tested the robustness of observed associations between EA-PGS and cortical measures when controlling for height, body mass index (BMI) and socio-economic (SES). In both cohorts, both height and body weight were collected at the time of MRI scanning. The

1 closest available approximation for family SES was calculated as a product of parental income and occupation status at the time of IQ testing (an average of 4 years prior to 2 scanning) using the Australian Socioeconomic Index 2006 (AUSEI06) occupational status 3 scale for the QTIM cohort as previously described (McMillan, Beavis, & Jones, 2009) (scale 4 0-100). For the HCP cohort, SES was computed using income-to-poverty ratio based on 5 self-reported family income relative to poverty thresholds in the United States and is adjusted 6 7 by family size (Diemer, Mistry, Wadsworth, López, & Reimers, 2013; Somerville et al., 2018) (scale 0–10). 8

9

10 Testing the association between EA-PGS and cognitive ability

Similar to the analyses described above, the proportion of individual variance in general 11 cognitive ability that could be predicted by the EA-PGS was examined. Three measures of IQ 12 were used in the QTIM cohort: Full IQ, Performance IQ and Verbal IQ (FIQ, PIQ and VIQ) 13 (Jackson, 1998) and two in the HCP cohort (Crystallized and Fluid IQ) (Weintraub et al., 14 2014). The GCTA analysis was conducted using the same covariates as above. Next, PGS-15 based regressions were conducted to assess the association between EA-PGS, 16 neuroanatomical correlates and IQ scores. TSA and the identified cortical regions of interest 17 18 were used as covariates (both independently and simultaneously) to ascertain the amount of variance in the association between EA-PGS and IQ scores that these regions account for. To 19 20 test the significance of each regional cortical measure as a covariate on the EA-PGS association with FIQ score, the standardized fixed effect (β) and s.e. for each covariate were 21 22 used in a Wald test to calculate their associated *p*-value.

23

24 Mediation analysis

A mediation analysis was conducted to test if the regional cortical ROIs mediated the 25 26 relationship between EA-PGS and FIQ (using the EA-PGS calculated at p < 1 threshold). FIQ 27 was chosen as the best representative of general cognitive ability (as it is calculated as a function of both PIQ and VIQ) (Jackson, 1998). A series of linear mixed models were fitted 28 in GCTA using sex, age, height, 10 PCs as covariates and the genetic relationship matrix as a 29 random effect. First, EA-PGS was used as a predictor of FIQ (path C). Secondly, EA-PGS 30 was used as a predictor of the mediator variable (the relevant ROI) (path A). Thirdly, both 31 EA-PGS (path C') and the moderator ROI (path B) were included as predictors of FIQ (see 32 Figure 1). Ideally a bias-corrected bootstrap CI would be used to assess the significance of 33 the indirect path (Hayes & Scharkow, 2013); however, this was not a computation option 34

1 using GCTA. A Sobel test was conducted to test the significance of the indirect path (AB) so as to establish whether mediation was occurring (Sobel, 1982). Although the Sobel test is 2 considered conservative, given that our sample size was > 500 this ought not to impede the 3 decision accuracy in these data (Hayes & Scharkow, 2013). In addition to testing the regional 4 5 ROIs independently, all ROIs, as well as a model with all ROIs and TSA were included in multiple mediation models. The effective number of independent observations was calculated 6 7 between all ROI and TSA using MatSpD as described for previous analysis. All comparisons were corrected for multiple testing using the Bonferroni multiple testing correction as 8 9 described.



16

Figure 1. Schematic of mediation model (based on Hayes 2017) (Hayes, 2017) where EA-PGS represents the independent variable, FIQ the dependent variable and ROI the mediator.

17

18 **Results**

19 Correlation between EA-PGS, IQ and brain measures

All EA-PGS thresholds had a significant, positive correlation with TSA in both samples after 20 correcting for the effects of age and sex (See Figure 2). ICV was also significantly correlated 21 with EA-PGSs at most *p*-value thresholds in QTIM; however, the association did not survive 22 multiple testing correction in the HCP sample. Average cortical thickness was negatively 23 24 correlated with TSA in both samples. Full-Scale IQ and Fluid IQ showed significantly positive correlations with TSA, ICV and all EA-PGS thresholds in both the QTIM and HCP 25 cohorts respectively. Similarly, educational attainment was significantly correlated with all 26 measures except average thickness in the HCP cohort (EA data not collected in QTIM) (see 27 28 Figure 2). Notably, given the age range in the HCP cohort, it is possible that individuals are still studying and that this measure of EA may not reflect their final education level. Further, 29

1 the EA-PGS explains a maximum of 1.6% of variance in TSA in the QTIM cohort and 1.2% 2 of the variance in the HCP cohort (*p*<0.005) (Figure 3, Supplementary Figure 1). Similarly, EA-PGS explains up to 0.5% of the variance in ICV in both cohorts (p < 0.005). The amount 3 of variance explained in cortical thickness by the EA-PGS did not reach statistical 4 significance at any EA-PGS threshold in either cohort. 5 6 7 8 9 10 11 12 13 14 15 16 17 **Thickness** p < 5e-8 0 < 1e - 5p < 0.00 Fluid IQ p < 0.01 p < 0.05 p < 0.5 p < 0.1 18 p < 1 TSA 20 19 FIQ 0.257 0.253 0.234 0.229 0.238 0.236 -0.061 0.134 0.145 0.208 0.228 20 TSA 0.089 0.876 -0.244 0.08 0.086 0.089 0.106 0.107 0.113 0.123 0.123 0.75 21 ICV 0.699 -0.064 0.096 0.053 0.122 0.121 0.121 0.066 0.08 0.104 0.11 22 0.5 Thickness -0.039 0.07 -0.022 -0.01 0.015 0.021 0.018 0.017 -0.165 0.007 0.004 23 0.486 p < 5e-8 0.097 0.048 0.016 -0.079 0.799 0.609 0.404 0.39 0.366 0.361 Magnitude of correlation 0.25 24 0.76 0.797 p < 1e-5 0.092 0.07 0.032 -0.073 0.677 0.582 0.559 0.516 0.512 25 p < 0.001 0.145 0.49 0.68 0.875 0.787 0.761 0.714 0 0.046 0.04 0.014 0.709 26 p < 0.01 0.125 0.554 0.812 0.923 0.837 0.054 0.036 0.003 0.404 0.891 27 -0.25 p < 0.05 0.128 0.07 0.064 0.019 0.357 0.504 0.724 0.87 0.92 0.916 28 0.947 p < 0.1 0.121 0.063 0.062 0.025 0.339 0.477 0.678 0.826 29 -0.5 p < 0.5 0.142 0.087 0.052 0.001 0.92 0.99 0.316 0.434 0.644 0.76 0.861 30 -0.75 31 0.76 0.858 p < 1 0.144 0.086 0.05 0.001 0.313 0.434 0.64

- 32
- 33 34

Figure 2. Partial correlations between global cortical measures, IQ, educational attainment and EA-PGS *p*-value thresholds in both the QTIM and HCP cohorts. Correlations control for sex and age using only unrelated individuals. Correlations above the diagonal are for the QTIM cohort and below the diagonal are for the HCP cohort. Magnitude of correlations are colour coded as indicated by colour bar. White squares indicate correlations that did not meet significance after correction for multiple testing (p<0.05). Educational attainment (Years of Edu) was only available for HCP cohort.

0.2

Years of Edu 0.147 0.133 0.125 -0.002 0.103 0.173 0.223 0.177 0.227 0.205 0.203

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Total variance explained in global measures by EA-PGS at p<1 threshold

Figure 3. EA-PGS (p<1) predicts a maximum of 1.6% of variance in total surface area and 0.5% of variance in ICV but does not predict average cortical thickness in both cohorts of young adults. Results presented are from p<1 EA-PGS threshold as it generally represented the greatest amount of variance explained in global brain measures. Error bars represent 95% confidence intervals, Significance is indicated by *; calculated as p < 0.05 (after Bonferroni correction for multiple testing).

3 Secondary analysis controlling for height, BMI and SES

Further examinations were made to assess whether the associations between EA-PGS and the three global measures were influenced by height, BMI and SES; all of which have been associated with differences in both EA and brain structure. The only variable with a significant effect on all three global measures in both samples was height (see Table 2), which was negatively associated with average thickness, though the association was small.

9 Socio-economic status had a small but nominally significant (p<0.05) effect on TSA (std β : 10 0.04 [0.00 -0.08]) and ICV (std β : 0.05 [0.01-0.09]) but not average thickness in the HCP 11 cohort. The effect of SES was not significant for all three variables in the QTIM cohort. 12 Adjusting for all three covariates produced very similar results in the variance explained of 13 global measures and had no significant effect on regional analysis. Nonetheless, height was 14 included as a covariate in all subsequent analyses. It is important to note that height, BMI and

- 1 SES all share a substantial genetic correlation with EA (see Lee *et. al.* 2019) so adding these
- 2 as covariates may diminish legitimate effects produced from pleiotropic genes.
- 3 Table 2: Standardized effect sizes, 95% Confidence Intervals (CI) and *p*-values of height, BMI
- 4 and SES on the association between EA-PGS (p<1 threshold) and global brain measures.

			QTIM			НСР	
		Std β	95% CI	Pval	Std β	95% CI	Pval
	EA-PGS	0.231	0.13 – 0.33	1.08E-05	0.393	0.191 - 0.582	1.05E-04
	Height	0.120	0.077 – 0.163	2.05E-08	0.308	0.224 - 0.392	6.21E-13
TSA	BMI	0.021	-0.008 - 0.049	0.153	0.017	-0.031 - 0.064	0.489
	SES	0.033	-0.005 - 0.070	0.875	0.044	0.003 - 0.086	0.035
	EA-PGS	0.143	0.074 - 0.203	7.06E-06	0.203	0.07 4- 0.321	3.94E-06
	Height	0.090	0.051 - 0.129	2.58E-06	0.167	0.084 - 0.249	4.29E-10
ICV	BMI	0.003	-0.024 - 0.030	0.883	0.060	0.012-0.108	0.015
	SES	0.015	-0.017 - 0.047	0.349	0.051	0.006 - 0.095	0.026
	EA-PGS	1.34E-03	-1.23E-03-0.001	0.614	-0.024	-0.094 - 0.042	0.50
			-0.0070.001	8.20E-04		-0.072	
	Height	-0.004			-0.060	0.048	1.83E-14
Av.	BMI	-0.003	-0.0040.001	0.799	0.034	-0.038 - 0.105	0.348
Thickness	SES	9.60E-05	-0.002 - 0.002	0.924	-0.014	-0.082 - 0.054	0.687

5 6 7 Note: Standardized betas for EA-PGS (*p*<1) are for the association with the three global measures after accounting for the effects of height, BMI and SES (as well as other standard covariates).

8 Cortical surface area ROI analysis

9

Further analysis of the association between regional surface area and EA-PGS was 10 conducted. Cortical regions were divided into 5 groups based on their anatomical location 11 (frontal, parietal, temporal and occipital lobes and the cingulate) and averaged across 12 hemispheres. The regions that comprise each area were designated according to the Desikan-13 Killiany atlas (Desikan et al., 2006). In the QTIM sample, the EA-PGS explained some of the 14 variance in seven cortical regions, three in the temporal lobes and four in the frontal lobes 15 over and above the effect of TSA - an effect that remained significant after Bonferroni 16 multiple testing correction (Figure 3). EA-PGS significantly predicted up to 0.6% of variance 17 18 in the surface area of these cortical structures at most *p*-value thresholds. These regions were the fusiform gyrus, entorhinal cortex, banks of the superior temporal sulcus (bankssts) in the 19 20 temporal lobes, all three parts of the inferior frontal gyrus (pars orbitalis, pars opercularis 21 and *pars triangularis*) and the *medial orbital frontal gyrus* (Figure 4). In the HCP replication 22 sample, five of the same regions (up to 0.6% of variance explained) were also significantly predicted by the EA-PGS, with the exception of *bankssts* and *medial orbital frontal gyrus* 23 24 (that did not survive multiple testing correction) (Figure 4). Most regions were positively

1

associated with EA-PGS, indicating that higher EA genetic scores were correlated with larger

SA, except for the *medial orbital frontal gyrus* that was in the opposite direction (higher 2 genetic scores associated with smaller SA). No regions were significantly predicted in either 3 cohort in any of the remaining lobes or the cingulate after multiple testing correction 4 (Supplementary Figure 2). Supplementary table 2 contains the standardized effect sizes of all 5 34 examined ROI SA and EA-PGS associations. 6 7 8 9 10 11 12 13 14 Lateral View Medial View 15 16 0.8 1.6 2.4 3.2 -3.2 -2.4 -1.6 -0.8 0 4 z-score Temporal Frontal p<5x10-8 p<1x10-5 0.6 p<0.001 p<0.01 НСР p<0.05 ** p<0.1 p<0.5 0.4 lained p<1 0.3 p<5x10-8 p<1x10-5 0.2 p<0.001 QTIM p<0.01 p<0.05 0.1 p<0.1 p<0.5 - 0.0 p<1 medialorbitofrontal_SA parstriangularis_SA parahippocampal_SA parsoorbitalis_SA parsopercularis_SA caudalmiddlefrontal_SA ateralorbitofrontal SA temporalpole_SA fusiform SA superiortemporal_SA paracentral_SA rostralmiddlefrontal_SA precentral_SA superiorfrontal_SA transversetemporal_SA inferiortemporal_SA entorhinal_SA bankssts_SA insula_SA middletemporal_SA S frontalpole_

Figure 4: Surface area: PGS for educational attainment (EA3) predict four **frontal** cortical surface areas (left) and three **temporal** (right) in both the QTIM (lower) and HCP (upper) cohorts. Brain plots show the location, as well as direction of association (z-scores), for identified regions with blue regions depicting negative associations and red scores depicting positive associations. The *y*-axes of the heatmaps represent the *p*-value cut-off thresholds for EA-associated SNPs used to calculate the PGS. The heatmap colour shading represents the amount of variance explained by the PGS. The double asterisk represents significant predictions after Bonferroni correction for multiple testing. ** p<0.0001, * indicates associations that did not survive multiple testing correction. Only the medial orbitofrontal gyrus showed a negative association with EA-PGS

1 Cortical thickness ROI analysis

Based on the findings of SA ROIs that covary with EA-PGS over-and-above the effect of 2 TSA, and the knowledge that cortical thickness varies substantially between brain regions 3 (Jha et al., 2018; Schmitt et al., 2019; Shaw et al., 2006), the associations between EA-PGS 4 5 and the average thickness of all 34 cortical ROIs were examined, despite the lack of a global association. Thickness ROIs showed substantially more differentiation between cohorts than 6 7 was observed in SA ROIs (Figure 5, Supplementary Figure 3). Most of the identified ROIs from the SA analysis were also significantly associated with EA-PGS (explaining up to 1.5% 8 9 of variance), with the exception of *bankssts*. The pars triangularis association did not survive multiple testing correction in the HCP cohort (Figure 5). Several novel ROIs were also 10 identified. These included the cuneus, supramarginal, post central and inferior parietal 11 thickness. Most of these associations did not survive multiple testing correction or were only 12 observed in one cohort with the exception of *inferior parietal* thickness which remained 13 significant in both cohorts (Supplementary Figure 3). Most thickness associations with EA-14 PGS were negative, indicating that individuals with higher EA-PGS have thinner cortices in 15 these regions. Supplementary Table 3 contains the standardized effect sizes of all examined 16 ROI thickness and EA-PGS associations. 17



1

2 Figure 5: Thickness: PGS for educational attainment (EA3) significantly associate with the cortical thickness 3 in four frontal regions (left) in at least one cohort and two temporal (right). Brain plots show the location, as 4 well as direction of association (z-scores), for identified regions with blue regions depicting negative 5 associations and red scores depicting positive associations. The y-axes of the heat maps represent the p-value 6 cut-off thresholds for EA-associated SNPs used to calculate the PGS. The heatmap colour shading represents the 7 amount of variance explained by the PGS. The double asterisk represents significant predictions after 8 Bonferroni correction for multiple testing. ** p<0.0001, * indicates associations that did not survive multiple 9 testing correction. All regions showed a negative association with EA-PGS

10

11 Estimating the effects of cortical surface area on cognitive ability

12 EA-PGS (at p < 1 threshold) was significantly positively correlated with IQ scores (r=0.23,

13 p < 0.001) and TSA (r=0.13, p < 0.001) (Figure 6) in the QTIM cohort. This threshold for the

14 EA-PGS was chosen as it generally accounted for the most variance explained in previous

- 15 global brain measures and it predicted the largest amount of variance in the original EA3
- 16 GWAS (Lee et al., 2018). Additionally, EA-PGS explained approximately ~5.7% percent of

- 1 variance (std β =0.2, *p*<0.001) in FIQ scores in the QTIM cohort (**Figure 7**). When examining
- 2 IQ sub-types, EA-PGS accounted for significantly greater variance in VIQ (~7.2%, std
- 3 $\beta=0.23$, p<0.001) than PIQ (~3.6%, std $\beta=0.15$, p<0.001) (difference=p=0.006, two-tailed
- 4 Students *t*-test, DF=979). In the HCP cohort, EA-PGS predicted up to 2.5% of the variance in
- 5 crystallized IQ (std β =0.10, p<0.001) but did not significantly predict fluid IQ
- 6 (Supplementary Figure 4).
- 7



Figure 6: EA-PGS (p < 1 threshold) is positively correlated with FIQ (blue; r=0.23) and TSA (green; r=0.13) in QTIM. The *x*-axis represents the deciles of EA-PGS scores, *y*-axis represents the mean \pm standard deviation of TSA and FIQ by decile.



When accounting for the effect of TSA, the EA-PGS explained ~4.5% of variance in FIQ 2 scores (a 25% reduction) and a maximum of 5.8% and 2.9% in VIQ and PIQ respectively (a 3 20% reduction; p=0.25, p=0.28 and p=0.6 respectively; Figure 7). The reduction in variance 4 explained is attributable to the effect of TSA on the association between EA-PGS and the IQ 5 measures. Next, we tested both the individual and combined effect of the ROI identified from 6 the EA-PGS prediction in the QTIM cohort by adding them as covariates (without TSA) to 7 the analysis. The significance of adding each cortical region as a covariate (over and above 8 9 the effect of TSA) was tested using a two-tailed Student's t-test. All ROIs in the QTIM sample had a significant effect on the association, except for the entorhinal region that was 10 only nominally so. Additionally, the *fusiform* and *pars orbitalis* had the greatest effect on the 11 association with FIQ (Supplementary Table 4). When examining the effect of all ROI as a 12 group, the percentage of variance in FIQ explained by the PGS scores dropped even further to 13 ~3.8% (p=0.12; Figure 7). A similar decrease in variance explained for VIQ and PIQ (~4.8% 14 and 2.5%; p=0.06 and p=0.8) was observed. When assessing the six ROIs and TSA 15 simultaneously as covariates, the variance explained was significantly different from the 16 original analysis, indicating that these regions capture a significant amount of the variance in 17 18 IQ measures that is explained by the EA-PGS (Figure 7). Similar results were seen in the crystallized IQ measures from the HCP cohort (Supplementary Figure 5). 19



1



Figure 7: EA-PGS predicts up to 7.5% of variance in VIQ, 5.8% FIQ and 3.6% in PIQ scores in the QTIM cohort. This decreases to approximately 5.8%, 4.5% and 2.9% when TSA is added as an additional covariate for VIQ, FIQ and PIQ respectively. A further reduction (approximately 15%) is observed in all three IQ scores when all ROIs are added as covariates simultaneously (4.8%, 3.8% and 2.5% respectively). Only the ROI and TSA analysis was significantly different from the original analysis. Error bars represent 95% confidence intervals

1 Mediation Analysis

- 2 As established, FIQ is significantly predicted by EA-PGS (β [95% CI] =0.25 [0.192–0.310], p<0.001) (path C). All paths and indirect paths were significant for all ROI associations 3 4 remained significant after Bonferroni multiple testing correction (α =0.013). The Sobel test established partial but significant mediation by all ROI, with *fusiform* having the largest 5 6 mediation effect (percentage mediation) and the medial oribtofrontal gyrus having the smallest mediatory effect (See Table 3). As a group, all ROIs were still significant mediators 7 as well as when all ROIs and TSA were added simultaneously as multilevel mediators. The 8 combination of all ROI as multiple mediators had the largest mediatory effect (3.2%) (see 9 Table 3). 10 11 12
- 13 14 15
- 16 Table 3: Mediation model testing the significance of identified ROIs SA as mediators of the EA-
- 17 **PGS and FIQ association.**

ROI	Model	Std β	95% CI	P-value	% Mediation	Sobel	P sobel
	С	0.251	0.192 - 0.310	<2e-16			
	А	0.113	0.050 - 0.176	5.54E-04			
Fusiform	В	0.197	0.140 - 0.254	9.29E-12			
	C'	0.225	0.168 - 0.282	3.29E-14	2.6%	3.100	0.002
	А	0.121	0.056 - 0.186	2.15E-04			
Bankssts	В	0.151	0.098 - 0.204	5.49E-08			
	C'	0.228	0.169 - 0.287	2.86E-14	2.3%	3.089	0.002
	А	0.113	0.048 - 0.178	5.87E-04			
Entorhinal	В	0.100	0.047 - 0.153	2.28E-04			
	C'	0.240	0.181 - 0.299	2.12E-15	1.1%	2.423	0.015
	А	0.126	0.061 -0.191	1.49E-04			
Pars Opercularis	В	0.156	0.101 - 0.211	3.97E-08			
	C'	0.230	0.171 - 0.289	1.60E-14	2.1%	3.276	0.001
	А	0.080	0.017 - 0.143	1.23E-02			
Pars Orbitalis	В	0.130	0.077 - 0.183	1.88E-06			
	C'	0.236	0.177 - 0.295	3.49E-15	1.3%	2.360	0.018
	А	0.088	0.023 - 0.153	8.06E-03			
Pars Triangularis	В	0.165	0.112 - 0.218	1.00E-09			

			ournal Pre-pro	of			
	C'	0.238	0.181 - 0.295	1.04E-15	1.3%	2.432	0.015
	А	0.068	-0.016 -0.152	1.06E-03			
Medial Orbitofrontal	В	0.123	0.072 - 0.174	1.00E-09			
	C'	0.243	0.200 - 0.286	1.04E-15	0.8%	3.240	0.012
	А	0.110	0.049 -0.171	4.58E-04			
TSA	В	0.257	0.198 - 0.316	<2e-16			
	C'	0.226	0.169 - 0.283	1.66E-14	2.5%	3.252	0.001
All ROI	C'	0.217	0.160 - 0.274	3.26E-13	3.4%		
All ROI + TSA	C'	0.219	0.162 - 0.276	1.90E-13	3.2%		

1 * Mediation models including sex, age, height, 10 PCs and a genetic relationship matrix as covariates.

2 Note: β = Beta, CI = Confidence Intervals, %= percentage

3

4 Discussion

5 In this study, the association between the genetic influences on educational attainment and cortical morphology was examined. Using two large twin cohorts, robust, positive association 6 7 was established between EA-PGS, total surface area and intra-cranial volume but not average 8 cortical thickness - lending weight to similar results from previous twin studies (Brouwer et 9 al., 2014; Vuoksimaa et al., 2014; Vuoksimaa et al., 2016). These results also suggest that cortical surface area and average thickness share a small correlation (r=0.08) at both global 10 and regional levels, despite both phenotypes being significantly heritable (h^2 =0.8 and above; 11 narrow sense) (Panizzon et al., 2009; Reiss et al., 1996; Schnack et al., 2014; Wilke et al., 12 2003; Winkler et al., 2010). These results also support recent studies utilizing large-cohort 13 GWAS. For example, a strong (~0.8), positive genetic correlation (r_g) between TSA and ICV, 14 while a negative r_g between TSA and average cortical thickness was seen in a recent, 15 exceptionally large (35k individuals), neuroimaging meta-analysis (Grasby et al., 2018), as 16 well as smaller studies (Strike et al., 2018). Significant, positive $r_{\rm g}$ between TSA and EA 17 (~0.2) and general cognitive ability (~0.2) has also been reported in the ENGIMA consortium 18 study (Grasby et al., 2018). Similarly, a GWAS of brain volume (N=54,407) reported a r_g of 19 0.23 between brain volume and intelligence (Jansen et al., 2019). The authors were able to 20 21 identify 67 overlapping genes, which are predominantly involved in cell growth pathways 22 (Jansen et al., 2019). This is in line with other studies that suggest that the phenotypic relationship between brain size and intelligence may be driven by TSA rather than cortical 23 24 thickness (Brouwer et al., 2014; S. Cox et al., 2019; S. R. Cox et al., 2018; Nave et al., 2019; Panizzon et al., 2009; Vuoksimaa et al., 2014; Vuoksimaa et al., 2016). Additionally, a study 25 26 by Cox et. al. (2019) found that global measures account for double the variation in general

cognitive ability in older adults compared to middle-aged adults (S. Cox et al., 2019),
 suggesting that age may moderate this relationship.

3

This study found a significant effect of height on our associations, but not of BMI (Pietschnig 4 5 et al., 2015; Vuoksimaa et al., 2018). However, our associations still held even when correcting for all three covariates, as was also seen in other studies (Pietschnig et al., 2015; 6 7 Rushton & Ankney, 2009). SES was a nominally significant covariate only in the HCP cohort, possibly due to the active recruitment of individuals from diverse social backgrounds 8 in this study. Studies have shown that both genes and environment play substantial roles in 9 the EA phenotype. In fact, individuals with higher EA-PGS have been shown to be born in to 10 homes of higher socio-economic standing and be both socially and geographically mobile 11 (Belsky et al., 2018; Belsky et al., 2016; Walhovd et al., 2016). Additionally, the association 12 between EA-PGS and educational attainment has been shown to be mediated through 13 personality traits such as self-control and neuroticism (Belsky et al., 2016). It is thus 14 understandable that both cognitive and non-cognitive domains may play a role in the 15 association between EA and brain morphology. Despite these associations, it is important to 16 note that EA shares substantial genetic correlation with all three examined variables and thus, 17 18 by adding them as covariates, it may diminish legitimate associations that are driven by pleiotropic genes (Vuoksimaa et al., 2018). 19

20

Significant regional heterogeneity and individual variation exist in the associations among 21 22 cortical ROI and cognitive phenotypes (Panizzon et al., 2009; Vuoksimaa et al., 2016; Winkler et al., 2010). This study identified seven specific cortical regions associated with 23 24 EA-PGS over-and-above the effect of global surface area, four in the frontal lobe and three in the temporal lobe, which showed replicable association with EA-PGS in both independent 25 26 samples. These regions were the *medial orbitofrontal gyrus* (part of the prefrontal cortex, responsible for cognitive process and decision-making) and all three parts of the inferior 27 frontal gyrus (Broca's area). Broca's area is responsible for speech production (Flinker et al., 28 2015), perception (Imada et al., 2006; Watkins & Paus, 2004) and language 29 comprehension(Musso et al., 2003) and has been linked to semantic processing (Belyk, 30 Brown, Lim, & Kotz, 2017; Sabb, Bilder, Chou, & Bookheimer, 2007) and working memory 31 (Sabb et al., 2007). The surface area of three regions in the temporal lobe were significantly 32 predicted by EA-PGS, including the fusiform gyrus implicated in semantic processing 33 (Balsamo, Xu, & Gaillard, 2006), reading (McCandliss, Cohen, & Dehaene, 2003), face 34

perception (Kanwisher & Yovel, 2006) and the learning of languages (Mei et al., 2015; Tan 1 et al., 2011); the entorhinal cortex involved in memory, navigation, and perception, and the 2 banks of the superior temporal sulcus which has been linked to multisensory processing 3 (Hein & Knight, 2008). EA-PGS also showed a significant negative association with the 4 thickness of several of these regions, which aligns with previous twin studies that identified 5 cortical stretching in regions associated with cognitive ability (Vuoksimaa et al., 2016). In 6 7 addition, EA-PGS was negatively associated with the thickness of the cuneus and the inferior parietal cortex. Our findings substantiate previous studies that show an expanded SA (and 8 9 cortical thinning) in prefrontal, lateral temporal and inferior parietal regions was positively associated with general cognitive ability (Nave et al., 2019; Vuoksimaa et al., 2014; 10 Vuoksimaa et al., 2016). 11

12

We hence examined if the surface area of the identified regions mediated the relationship 13 between EA-PGS and IQ scores. EA-PGS explained a significantly greater amount of 14 variance in VIQ than in QTIM. Verbal IQ is a measure of acquired knowledge and verbal 15 reasoning (Kaufman, 1976), while PIQ assesses non-verbal cognitive ability such as 16 perceptual organization and processing speed. Previous studies have found a phenotypic 17 correlation of 0.16 with Fluid IQ (Ritchie et al., 2018) while another study reported a similar 18 correlation of 0.19 with VIQ on a large sample of over 13,000 individuals (Nave et al., 2019). 19 The increased prediction of EA-PGS into VIQ indicates that the variants captured by the EA-20 PGS probably relate more strongly to verbal cognitive processing, which also supports the 21 finding that the EA-PGS were associated with cerebral regions important for memory and 22 language. In addition, using a Sobel test we also found significant evidence that all identified 23 ROIs partially mediate the relationship between EA-PGS and FIQ. 24

Although the results of this study provide evidence of the association between EA-PGS and 25 cortical brain regions, there is debate behind the meaning of cognitive neuroanatomical 26 correlations and how well results would generalize across populations or individuals at either 27 end of the cognitive ability spectrum. For example, Pietschnig et. al. (2015) and Richie et. al. 28 (2018) discuss whether brain size is a proxy for neuron number and what compensatory 29 30 mechanisms may be responsible for individual differences in intellectual ability (S. Cox et al., 2019; Deary, Irwing, Der, & Bates, 2007). The identification of regional heterogeneity 31 associated with EA in this study adds weight to the hypothesis of compensatory mechanisms 32 accounting for individual variation in intellectual ability over-and-above the effect of total 33

1 brain size. Another consideration regarding the generalizability of our findings is the demographics represented in our cohorts. The cohorts in this study were filtered to represent 2 homogenous European populations due to the poor predictive power of current PGSs in non-3 European populations. These samples were also over-representative of people of higher SES 4 and educational attainment and therefore our results may not extend to individuals of 5 different ethnic backgrounds, as well as in population with increased rates of inequality. 6 7 Lastly, as discussed by Nave et. al. (2019), the positive relationship between brain size and intelligence becomes substantially weaker when examining individuals at either end of the 8 cognitive ability spectrum. Thus, the results found in this study reflect associations for 9 individuals within the normal range of cognitive ability and may not generalize to individuals 10 with cognitive impairment or neurodegenerative diseases or those of extremely high-11 functioning cognitive ability. 12

13 Together, these findings expand on several previous twin and genomic studies that have identified a significant association between general cognitive ability and increased TSA. 14 Additionally, these findings robustly replicate the positive association between EA-PGS and 15 increased surface area, and a negative association with average thickness, in cortical regions 16 related to memory and language in two independent cohorts. However, some limitations must 17 be acknowledged. First, these results do not give any indication of the causality of the 18 relationship. Individuals with a genetic predisposition for higher cognitive ability may have 19 larger cortical regions; however, the causal direction may operate in reverse—whereby the 20 (genetically influenced) larger brain regions may allow individuals to achieve higher 21 educational attainment. Secondly, the use of two geographically diverse cohorts provides 22 confidence in the robustness of the observed associations, but also resulted in some measures 23 24 being either quantified or temporally assessed differently between cohorts. For instance, in the QTIM cohort, the IQ and SES scores were obtained from an earlier wave of data 25 collection that was conducted 0-14 (mean 4.4) years prior to MRI scanning. Although IQ is a 26 relatively stable measure from the age of 16 onwards, giving the growth trajectories during 27 28 this age period, it is possible that these measures may not be entirely representative of an individual's current cognitive ability at the time of MRI. Additionally, the measures of SES 29 between cohorts were calculated according to different indices that may also contribute to 30 additional variation between cohorts. Thirdly, in this study regions were averaged across 31 32 hemispheres using the Desikan-Killiany atlas for ROI delineation because it results in large regions with consistent borders between studies. Thus we are unable to test for differences in 33

1 laterality between hemispheres (specifically in the language regions). It would be interesting to conduct similar analyses using vertex-wide measures or genetically informative 2 parcellations examining differences in laterality with larger cohorts that can handle the 3 increase in testing burden. Another important factor to be cognisant of is that EA has a 4 correlation of 0.6 with IQ, and that as a proxy measure this indicates a portion of variance in 5 this phenotype that is also distinct from intelligence. Given the small effect sizes of genetic 6 7 variants known to influence IQ (Savage et al., 2018), we need much larger sample sizes to be have comparable power to the EA results in order to conduct a reliable comparison between 8 EA-PRS and IQ-PRS. Future studies would benefit from the comparison of the prediction 9 between EA- and IQ- PGS as sample sizes grow. Lastly, further statistical, molecular and 10 functional studies are needed to uncover the specific genes and pathways that underlie both 11 these traits and dissect the observed genetic overlap. 12

13 Conclusions

14

In this study, a significant, positive association was identified between the genetic 15 influences on educational attainment and total cortical surface area. Additionally, this 16 study is the first to extend the focus beyond the established proxy of global brain volume to 17 regional-specific associations with the genetics of general cognitive ability. Several 18 identified regions showed a positive association between EA-PGS and SA, while average 19 thickness was negatively associated in these areas. These regions, which include Broca's 20 area, have been implicated in language, memory, visual recognition and cognitive 21 processing. We also provide evidence that these brain regions may partially mediate the 22 association between the genetic predisposition to educational attainment and IQ scores. 23 However, much research is still required to understand the combined relationship between 24 structure and function. This study provides focus points for future research to examine causal 25 links between brain characteristics and cognitive performance. 26

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13 Author contributions

B.L.M. and M.E.R. designed and conceived the study. M.J.W., P.M.T. and N.G.M. were
responsible for the QTIM cohort design and genotyping. L.T.S., G.C.P., A.I.C. were involved
in the data processing, quality control and preparation while B.L.M, M.E.R. and G.C.P. were
responsible for the data analysis. A.O. provided the EA3 'leave-one-out' summary statistics.
K.L.G, M.E.R. and S.E.M. provided guidance and aided in interpreting the data. B.L.M.
wrote the manuscript. All authors assisted in the preparation and editing of the manuscript.

20 Competing interests

- 21
- 22 All authors report no conflicts of interest in relation with this study.
- 23

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