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1 **Title: Genome-wide association study identifies 74 loci**
2 **associated with educational attainment**

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5
6 **Summary:** Educational attainment (EA) is strongly influenced by social and other
7 environmental factors, but genetic factors are also estimated to account for at least 20% of the
8 variation across individuals¹. We report the results of a genome-wide association study
9 (GWAS) for EA that extends our earlier discovery sample^{1,2} of 101,069 individuals to 293,723
10 individuals, and a replication in an independent sample of 111,349 individuals from the UK
11 Biobank. We now identify 74 genome-wide significant loci associated with number of years of
12 schooling completed. Single-nucleotide polymorphisms (SNPs) associated with educational
13 attainment are disproportionately found in genomic regions regulating gene expression in the
14 fetal brain. Candidate genes are preferentially expressed in neural tissue, especially during the
15 prenatal period, and enriched for biological pathways involved in neural development. Our
16 findings demonstrate that, even for a behavioral phenotype that is mostly environmentally
17 determined, a well-powered GWAS identifies replicable associated genetic variants that
18 suggest biologically relevant pathways. Because EA is measured in large numbers of
19 individuals, it will continue to be useful as a proxy phenotype in efforts to characterize the
20 genetic influences of related phenotypes, including cognition and neuropsychiatric disease.

21
22 **Main Text:**

23 We study educational attainment (EA), which is measured in all main analyses as the number
24 of years of schooling completed (*EduYears*, $N = 293,723$, mean = 14.33, SD = 3.61;
25 Supplementary Information sections 1.1-1.2). All genome-wide association studies (GWAS)
26 were performed at the cohort level in samples restricted to individuals of European descent
27 whose EA was assessed at or above age 30. A uniform set of quality-control (QC) procedures

1 was applied to the cohort-level summary statistics. In our GWAS meta-analysis of ~9.3M SNPs
2 from the 1000 Genomes Project, we used sample-size weighting and applied a single round of
3 genomic control at the cohort level.

4 Our meta-analysis identified 74 approximately independent genome-wide significant loci. For
5 each locus, we define the “lead SNP” as the SNP in the genomic region that has the smallest
6 P -value (Supplementary Information section 1.6.1). Fig. 1 shows a Manhattan plot with the
7 lead SNPs highlighted. The three SNPs that reached genome-wide significance in the discovery
8 stage of our previous GWAS meta-analysis of EA¹ are also highlighted. The quantile-quantile
9 (Q-Q) plot of the meta-analysis (Extended Data Fig. 1) exhibits inflation ($\lambda_{GC} = 1.28$), as
10 expected under polygenicity³.

11 Extended Data Fig. 2 shows the estimated effect sizes of the lead SNPs. The estimates range
12 from 0.014 to 0.048 standard deviations per allele (2.7 to 9.0 weeks of schooling), with
13 incremental R^2 in the range 0.01% to 0.035%.

14 To quantify the amount of population stratification in the GWAS estimates that remains even
15 after the stringent controls used by the cohorts (Supplementary Information section 1.4), we
16 used LD Score regression⁴. The regression results indicate that ~8% of the observed inflation
17 in the mean χ^2 is due to bias rather than polygenic signal (Extended Data Fig. 3a), suggesting
18 that stratification effects are small in magnitude. We also found evidence that the genetic
19 association signals taken as a whole replicate reliably in several within-family analyses
20 (Supplementary Information section 2 and Extended Data Fig. 3b).

21 To further test the robustness of our findings, we examined the within-sample and out-of-
22 sample replicability of SNPs reaching genome-wide significance (Supplementary
23 Information sections 1.7-1.8). We found that SNPs identified in the previous EA meta-analysis
24 replicated in the new cohorts included here, and conversely, that SNPs reaching genome-wide

1 significance in the new cohorts replicated in the old cohorts. For the out-of-sample replication
2 analyses of our 74 lead SNPs, we used the interim release of the U.K. Biobank⁵ (UKB) ($N =$
3 111,349). As shown in Extended Data Fig. 4, 72 out of the 74 lead SNPs have a consistent sign
4 ($P = 1.47 \times 10^{-19}$), 52 are significant at the 5% level ($P = 2.68 \times 10^{-50}$), and 7 reach genome-wide
5 significance in the U.K. Biobank dataset ($P = 1.41 \times 10^{-42}$). For comparison, the corresponding
6 expected numbers, assuming each SNP's true effect size is its estimated effect adjusted for the
7 winner's curse, are 71.4, 40.3, and 0.6. (Supplementary Information section 1.8.2). We also
8 find out-of-sample replicability of our overall GWAS results: the genetic correlation between
9 *EduYears* in our meta-analysis sample and in the UKB data is 0.95 (s.e. = 0.021; Supplementary
10 Table 1.14).

11 It is known that EA, cognitive performance, and many neuropsychiatric phenotypes are
12 phenotypically correlated, and several studies of twins find that the phenotypic correlations
13 partly reflect genetic overlap⁶⁻⁸ (Supplementary Information section 3.3.4). Here, we
14 investigate genetic correlation using our GWAS results for *EduYears* and published GWAS
15 results for 14 other phenotypes, using bivariate Linkage-Disequilibrium (LD) Score
16 regression⁹. First, we estimated genetic correlations with *EduYears*. As shown in Fig. 2, on
17 average, alleles associated with greater EA are also associated with increased cognitive
18 performance ($P = 9.9 \times 10^{-50}$) and intracranial volume ($P = 1.2 \times 10^{-6}$), increased risk of bipolar
19 disorder ($P = 7 \times 10^{-13}$), decreased risk of Alzheimer's ($P = 4 \times 10^{-4}$), and lower neuroticism (P
20 = 2.8×10^{-8}). We also found positive, statistically significant, but very small, genetic
21 correlations with height ($P = 5.2 \times 10^{-15}$) and risk of schizophrenia ($P = 3.2 \times 10^{-4}$).

22 Second, we examined whether our 74 lead SNPs are jointly associated with each phenotype
23 (Extended Data Fig. 5 and Supplementary Information section 3.3.1). We reject the null
24 hypothesis of no enrichment at $P < 0.05$ for 10 of the 14 phenotypes (all the exceptions are
25 subcortical brain structures).

1 Third, for each phenotype, we tested (in the published GWAS results) each of our 74 lead SNPs
2 or proxy for association at a significance threshold of 0.05/74. We found a total of 25 SNPs
3 meeting this threshold for any of these phenotypes (but only one reaching genome-wide
4 significance). While these results provide suggestive evidence that some of these SNPs may be
5 associated with other phenotypes, further testing of these associations in independent cohorts
6 is required (Supplementary Tables 3.2-3.4, Extended Data Fig. 6).

7 To consider potential biological pathways, we first tested whether SNPs in particular regions
8 of the genome are implicated by our GWAS results. Unlike what has been found for other
9 phenotypes, SNPs in regions that are DNase I hypersensitive in the fetal brain are more likely
10 to be associated with *EduYears* by a factor of ~ 5 (95% confidence interval 2.89–7.07; Extended
11 Data Fig. 7). Moreover, the 15% of SNPs residing in regions associated with histones marked
12 in the central nervous system (CNS) explain 44% of the heritable variation (Extended Data Fig.
13 8a and Supplementary Table 4.4.2). This enrichment factor of ~ 3 for CNS ($P = 2.48 \times 10^{-16}$) is
14 greater than that of any of the other nine tissue categories in this analysis.

15 Given that our findings disproportionately implicate SNPs in regions regulating brain-specific
16 gene expression, we examined whether genes located near *EduYears*-associated SNPs show
17 elevated expression in neural tissue. We tested this hypothesis using data on mRNA transcript
18 levels in the 37 adult tissues assayed by the Genotype-Tissue Expression Project (GTEx)¹⁰.
19 Remarkably, the 13 GTEx tissues that are components of the CNS—and only those 13
20 tissues—show significantly elevated expression levels of genes near *EduYears*-associated
21 SNPs (FDR < 0.05; Extended Data Fig. 8b and Supplementary Table 4.5.2).

22 To investigate possible functions of the candidate genes from the GWAS associated loci, we
23 examined the extent of their overlap with groups of genes (“gene sets”) whose products are
24 known or predicted to participate in a common biological process¹¹. We found 283 gene sets
25 significantly enriched by the candidate genes identified in our GWAS (FDR < 0.05;

1 Supplementary Table 4.5.1). To facilitate interpretation, we used a standard procedure¹¹ to
2 group the 283 gene sets into “clusters” defined by degree of gene overlap. The resulting 34
3 clusters, shown in Fig. 3, paint a coherent picture, with many clusters corresponding to stages
4 of neural development: the proliferation of neural progenitor cells and their specialization (the
5 *cluster npBAF complex*), the migration of new neurons to the different layers of the cortex
6 (*forebrain development, abnormal cerebral cortex morphology*), the projection of axons from
7 neurons to their signaling targets (*axonogenesis, signaling by Robo receptor*), the sprouting of
8 dendrites and their spines (*dendrite, dendritic spine organization*), and neuronal signaling
9 and synaptic plasticity throughout the lifespan (*voltage-gated calcium channel complex,*
10 *synapse part, synapse organization*).

11 Many of our results implicate candidate genes and biological pathways that are active during
12 distinct stages of prenatal brain development. To directly examine how the expression levels
13 of candidate genes identified in our GWAS vary over the course of development, we used gene
14 expression data from the BrainSpan Developmental Transcriptome¹². As shown in Extended
15 Data Fig. 9, these candidate genes exhibit above-baseline expression in the brain throughout
16 life but especially higher expression levels in the brain during prenatal development (1.36 times
17 higher prenatally than postnatally, $P = 6.02 \times 10^{-8}$).

18 A summary overview of some promising candidate genes for follow-up work is provided in
19 Table 1.

20 We constructed polygenic scores¹³ to assess the joint predictive power afforded by the GWAS
21 results (Supplementary Information section 5.2). Across our two holdout samples, the mean
22 predictive power of a polygenic score constructed from all measured SNPs is 3.2% ($P =$
23 1.18×10^{-39} ; Supplementary Table 5.2 and Supplementary Information section 5).

24 Studies of genetic analyses of behavioral phenotypes have been prone to misinterpretation,
25 such as characterizing identified associated variants as “genes for education.” Such

1 characterization is not correct for many reasons: EA is primarily determined by environmental
2 factors, the explanatory power of the individual SNPs is small, the candidate genes may not be
3 causal, and the genetic associations with EA are mediated by multiple intermediate
4 phenotypes¹⁴. To illustrate this last point, we studied mediation of the association between the
5 all-SNPs polygenic score and *EduYears* in two of our cohorts. We found that cognitive
6 performance can statistically account for 23-42% of the association ($P < 0.001$) and the
7 personality trait “openness to experience” for approximately 7% ($P < 0.001$; Supplementary
8 Information section 6).

9 It would also be a mistake to infer from our findings that the genetic effects operate
10 independently of environmental factors. Indeed, a recent meta-analysis of twin studies found
11 that genetic influences on EA are heterogeneous across countries and birth cohorts¹⁵. We
12 conducted exploratory analyses in the Swedish Twin Registry to illustrate how environmental
13 factors may amplify or dampen the impact of genetic influences (Supplementary Information
14 section 7). We found that the predictive power of the all-SNPs polygenic score is heterogeneous
15 by birth cohort, with smaller explanatory power in younger cohorts (Extended Data Fig. 10;
16 see also Supplementary Information section 7.4 for discussion of the contrast between these
17 results and findings from a seminal twin study that estimated EA heritability by birth cohort¹⁶).

18

19 **Methods:** All methods are described in the Supplementary Information.

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37

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2 Supplementary Information section 8.

3

4 **Author Information** Results can be downloaded from the SSGAC website
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11

1 **Table 1 | Selected candidate genes implicated by bioinformatics analyses.** Fifteen
2 candidate genes implicated most consistently across various analyses. To assemble this list,
3 each gene in a DEPICT-defined locus (Supplementary Information section 4.5) was assigned
4 a score equal to the number of criteria it satisfies out of ten (see Supplementary Table 4.1 for
5 details). The DEPICT prioritization *P*-value was used as the tiebreaker. “SNP”: the SNP in
6 the gene’s locus with the lowest *P*-value in the *EduYears* meta-analysis. “Syndromic”: which,
7 if any, of three neuropsychiatric disorders have been linked to *de novo* mutations in the gene
8 (Supplementary Information section 4.6). “Top-ranking gene sets”: DEPICT reconstituted
9 gene sets of which the gene is a top-20 member (Supplementary Table 4.5.1). The three most
10 significant gene sets are shown if more than three are available. ID, intellectual disability;
11 ASD, autism spectrum disorder; SCZ, schizophrenia.
12

1

Gene	SNP	Syndromic	Score	Top-ranking gene sets
<i>TBR1</i>	rs4500960	ID, ASD	6	Developmental biology, decreased brain size, abnormal cerebral cortex morphology
<i>MEF2C</i>	rs7277187	ID, ASD	5	ErbB signaling pathway, abnormal sternum ossification, regulation of muscle cell differentiation
<i>ZSWIM6</i>	rs61160187	–	5	Transcription factor binding, negative regulation of signal transduction, PI3K events in ErbB4 signaling
<i>BCL11A</i>	rs2457660	ASD	5	Dendritic spine organization, abnormal hippocampal mossy fiber morphology, SWI/SNF-type complex
<i>CELSR3</i>	rs11712056	SCZ	5	Dendrite morphogenesis, dendrite development, abnormal hippocampal mossy fiber morphology
<i>MAPT</i>	rs192818565	ID	5	Dendrite morphogenesis, abnormal hippocampal mossy fiber morphology, abnormal axon guidance
<i>SBNO1</i>	rs7306755	SCZ	5	Protein serine/threonine phosphatase complex
<i>NBAS</i>	rs12987662	–	5	–
<i>NBEA</i>	rs9544418	SCZ	4	Developmental biology, signaling by Robo receptor, dendritic shaft
<i>SMARCA2</i>	rs1871109	ID	4	–
<i>MAP4</i>	rs11712056	ASD	4	Developmental biology, signaling by Robo receptor, SWI-SNF-type complex
<i>LINC00461</i>	rs10061788	–	4	Decreased brain size, abnormal cerebral cortex morphology, abnormal hippocampal mossy fiber morphology
<i>POU3F2</i>	rs9320913	–	4	Dendrite morphogenesis, developmental biology, decreased brain size
<i>RAD54L2</i>	rs11712056	SCZ	4	Decreased brain size, SWI/SNF-type complex, nBAF complex
<i>PLK2</i>	rs2964197	–	4	Negative regulation of signal transduction, PI3K events in ErbB4 signaling

2

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