Quantification of ancient human intelligence has become possible with recent advances in polygenic prediction. Intelligence is a complex trait that has both environmental and genetic components and high heritability. Large-scale genome-wide association studies based on ~270,000 individuals have demonstrated highly significant single-nucleotide polymorphisms (SNPs) associated with intelligence in present-day humans. We utilized those previously reported 12,037 SNPs to estimate a genetic component of intelligence in ancient Funadomari Jomon individual from 3700 years BP as well as four individuals of Afanasievo nuclear family from about 4100 years BP and who are considered anatomically modern humans. We have demonstrated that ancient individuals could have been not inferior in intelligence compared to present-day humans through assessment of the genetic component of intelligence. We have also confirmed that alleles associated with intelligence tend to spread equally between ancestral and derived origin suggesting that intelligence may be a neutral trait in human evolution.
have demonstrated a trend of increasing brain sizes as well as higher metabolic neuronal activity suggesting an upward rise of human cognitive abilities in AMHs compared to Neanderthal and *Australopithecus* [15, 16].

The aim of this study was to assess a genetic component of intelligence in ancient individuals who are considered AMHs through genome analysis. Intelligence as a complex trait has been demonstrated in ancient genomes from ancient individuals (Table 1) including Funadomari Jomon individual discovered in Hokkaido, Japan with high coverage sequencing and peak depth of 48x (estimated age about 3700 years BP) [17]. Four other ancient genomes data originated from a nuclear family of four—a mother, a father, and their two sons from Afanasievo Culture discovered in modern Russia, who lived about 4100 thousand years BP (https://reich.hms.harvard.edu/datasets) [18].

Our analysis was aimed at elucidating a genetic component of intelligence in late AMHs (largely originating within 10,000 years ago) such as individuals from Jomon and Afanasievo cultures. The reason for that is the GWAS summary statistics obtained from present-day humans around the globe aligned to more archaic genomes like Denisovans and Neanderthal has a high likelihood of non-interpretable results due to considerable population divergence time (up to 170,000–700,000 years between Denisovans and present-day humans) [19]. We compared intelligence PGS derived from genomic data of ancient individuals (considered as AMHs) to 2504 present-day humans from the 1000 Genome Project Phase 3 [20]. We also inferred absolute IQ scores for ancient individuals compared to general population based on a genetic component of intelligence.

**METHODS**

**Selection of SNPs for polygenic scoring**

Genetic markers of intelligence were obtained from a large-scale meta-analysis of GWAS on cognitive abilities with 269,867 participants from 14 European epidemiological cohorts [3]. Genome-wide significance (*p* < 5 × 10^{-8}) in association with intelligence was confirmed for total number of 12,110 SNPs. Polygenic risk score prediction demonstrated that around 5.2% variation in intelligence can be explained by those SNPs. We estimated ancestral state of the majority of SNPs associated with intelligence by multiple alignment of reference genome of modern human (GRCh37) to bonobo, chimpanzee, gorilla, orang utan, gibbon, and macaque using “Orthrus” method implemented in ENSEMBLE database [21]. Fisher’s exact test of independence was used to assess any nonrandom association between ancestral state and effect on intelligence (Table 2).

**Calculating intelligence polygenic scores**

We built PGS using 12,037 SNPs that reached genome-wide significance (*p* < 5 × 10^{-8}) in the GWAS summary statistics. We utilized publicly available datasets from 1000 genome project phase 3 data (2504 individuals across global 26 populations) to construct PGS for each individual. The Funadomari Jomon genome sequence was selected for analysis due to high sequencing coverage (peak depth of 48x) considered as “the reference Jomon genome”. Four ancient European genomes with high-quality sequence belonging to Afanasievo culture were used for comparison as well (Table 1). Although the intelligence-associated SNPs have been identified in European populations we proceeded with evaluation of genetic component of intelligence in above mentioned ancient high-quality genomes in spite of estimated age of 3900–4100 BP. We used PLINK version 1.9 [22] and R version 4.0.2 [23] to compute intelligence PGS. Data visualization was done through ggplot2 implemented in R [24]. Genetic intelligence scores were obtained by summing up the GWAS meta-analysis output beta regression coefficients identified for effective alleles in independent UK Biobank data subset for educational attainment replication. Each subject score was calculated as a sum of SNP effects considering number of effect allele presence (0, 1, or 2) multiplied by reported beta regression coefficients using polygenic risk score calculation [25].

We calculated genetic component of intelligence by constructing PGS through a linear model for each individual of the study cohort. Intelligence PGS for each individual was defined in the form of:

$$PGS = \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k + \beta_0,$$

where $\beta_k$ represents per-allele beta coefficient of logistic regression for intelligence at SNP $k$ and $x_k$ based on allele dosage of 0, 1, or 2 for SNP $k$ with total n number of SNPs included in PGS.

We used two subsets of SNPs from total 12,037 SNPs for PGS derivation: one set comprised of 9128 SNPs (p value threshold $p < 5 \times 10^{-8}$) as well as a smaller set of 1402 SNPs (p value threshold $p < 4 \times 10^{-11}$) replicated in an independent UK Biobank cohort and having top association in the original GWAS study. We decided to build two PGS based on different threshold of p values for SNPs reported in the original GWAS study according to generally accepted guidelines on performing PGS analysis through comparison of PGS and absolute IQ scores for ancient genomes to present-day humans [26]. Functions for calculating PGS and data visualization are available as R scripts on GitHub (https://github.com/Kays3/Ancient_intelligence.git).

**Statistical inference**

The overall PGS of the intelligence data was tested for normality (Shapiro–Wilks’s test) and plotted assuming normal distribution. PLINK version 1.9 was used to extract the genotype data calculating eigenvalues for principal component analysis (PCA), and building matrices for computing genetic intelligence scores for each subject. Population structure demonstrated by PCA was built based on subset of 9128 SNPs and 1402 SNPs shared by modern and ancient human genomes. We also inferred absolute values of IQ for ancient individuals based on PGS results and compared them to a general human population mean of 100 and standard deviation (SD) of 15 [27] using open-access software designed for translating PGS into relevant absolute values of phenotypical traits [28].

**RESULTS**

We have built genotypes based on 12,037 SNPs highly associated with intelligence from genome sequences of 2504 individuals from 1000 Genome Project Phase 3. We also constructed two sets of genotypes comprised of 9148 SNPs and 1402 SNPs for genomes of Funadomari Jomon individual, Afanasievo family of four individuals as well as 1000 Genome Project subjects. Intelligence PGS constructed for total 2509 individuals were tested for

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**Table 1.** Ancient genomes used for polygenic estimation of intelligence

| Sample name          | Average coverage | Reference                  |
|----------------------|------------------|----------------------------|
| Funadomari Jomon     | 48x              | Kanzawa-Kiriyama et al. [16]|
| Afanasievo mother    | 21.2x            | Wohns et al. [17]          |
| Afanasievo father    | 25.3x            | Wohns et al. [17]          |
| Afanasievo son1      | 10.8x            | Wohns et al. [17]          |
| Afanasievo son2      | 25.8x            | Wohns et al. [17]          |

**Table 2.** Ancestral state analysis of SNPs associated with intelligence

| Regression direction | Ancestral | Derived | Total   |
|----------------------|-----------|---------|---------|
| Positive             | 2542      | 3333    | 5875    |
| Negative             | 3262      | 5752    | 9014    |
| Total                | 5032      | 6595    | 11,627  |
normality using Shapiro–Wilk test. Intelligence PGS were indeed normally distributed \((W = 0.99964, p value = 1.22 \times 10^{-15})\).

The PGS of intelligence based on highly significant 1402 SNPs \((p value threshold p < 5 \times 10^{-13})\) demonstrated Funadomari Jomon individual’s value within 1 SD above population mean of 1000 Genome Project \((z = 0.34)\), while Afanasievo mother had a score lower than 2 SD of the mean \((z = −2.94)\), Afanasievo father score was also below 2 SD from the mean \((z = −1.77)\). Afanasievo sons scores were located between the maternal and paternal values where Son1 had a score of \(z = −2.36\) and Son2 \(z = −2.88\) (Fig. 1A).

The PGS of intelligence based on 9128 SNPs \((p value threshold p < 5 \times 10^{-8})\) placed Funadomari Jomon individual within 1 SD below population mean of 1000 Genome Project \((z = −1.29)\), while Afanasievo mother had score lower than 2 SD of the mean \((z = −3.59)\), Afanasievo father score was below 1 SD from the mean \((z = −2.03)\). Afanasievo sons scores were located between the maternal and paternal scores where Son1 score \(z = −2.44\) and Son2 with \(z = −2.99\) (Fig. 1B).

Absolute IQ score inference based on variance explained by intelligence PGS (5.2%) with mean of the trait of 100 and SD of 15 demonstrated following scores for ancient individuals: for the 1402 SNPs PGS Funadomari Jomon individual IQ = 101 (95% CI = 72.58–129.74), while Afanasievo mother’s IQ = 89 (95% CI = 60.96–118.12), Afanasievo father IQ = 94 (95% CI = 65.2–122.36). Afanasievo sons scores were located between the maternal and paternal scores where Son1’s IQ = 92 (95% CI = 63.17–120.3) and Son2’s IQ = 90 (95% CI = 61.54–118.7) (Fig. 2A).

Absolute IQ score estimates for PGS based on 9128 SNPs demonstrated Funadomari Jomon individual’s IQ = 95 (95% CI = 66.88–124.04), while Afanasievo mother’s IQ = 87 (95% CI = 57.96–115.12), Afanasievo father IQ = 93 (95% CI = 64.3–121.46). Afanasievo sons scores were similarly located between the maternal and paternal scores where Son1 had IQ = 91 (95% CI = 62.87–120.02) and for Son2: IQ = 89 (95% CI = 60.96–118.12) (Fig. 2B).

PCA based on 1402 SNPs demonstrated close genetic relationships between ancient Funadomari Jomon individual to modern East Asian populations while Afanasievo family individuals clustered with modern European populations from the 1000 Genome Project (Fig. 3A). PCA based on 9128 SNPs did not reveal any clear population structure with Funadomori Jomon individual clustered in proximity to East Asian populations compared to Afanasievo family (Fig. 3B).

We assessed ancestral state of 12,037 SNPs used for PGS construction in 1000 Genome Populations through alignment with six primate genomes including bonobo, chimpanzee, gorilla, orangutan, gibbon, and macaque using “Orthoeus” method implemented in ENSEMBLE database [21]. The alignment results between ancestral species and GWAS summary statistics used for polygenic scoring was available only for 11,627 SNPs (96.6%) accessible from ENSEMBLE database. SNPs contributing to positive effect and negative effect on intelligence demonstrated no association with derived state \((p value = 0.985, OR with 95% CI = 1.00 [0.93–1.10])\) based on Fisher exact test (Table 2). Ancestral state analysis of SNPs highly associated with intelligence did not demonstrate any
DISCUSSION

We have demonstrated first ever insight into genetic component of intelligence through PGS in ancient individuals from around 3700–4100 BP. The performed calculations indicate a possibility that people living on the territory of modern Hokkaido and Russia in that period being not less intelligent than modern humans. Absolute IQ values inferred from PGS in Afanasievo individuals and Funadomari Jomon individual tends to be within the 95% range of mean general human population suggesting similarity of intelligence of humans living 3700 BP and modern humans. Although intelligence PGS of Afanasievo family tend to fluctuate on the lower tail of normal distribution of the scores of 1000 Genome project these scores translate to absolute IQ values within mean of general population given the low variance explained by intelligence PGS ($R^2 = 5.2\%$).

We used two different $p$ value thresholds for constructing PGS of intelligence, since there is no clear consensus on how selection of SNPs may affect the predictive power of the analysis. Previous work on PGS of intelligence demonstrated that different thresholds may actually have association with particular aspects of cognition like memory or verbal intelligence [29].

Previous studies on PGS prediction confirmed lower applicability and reproducibility of the majority of GWAS reported in global populations due to the fact that most data used in the discovery phase came from people of European descent [30, 31]. However, recent development in derivation of absolute trait values from PGS confirmed potential clinical utility and rationale of polygenic prediction in context of complex traits and clinical decision making [32, 33].

Even though there is a possibility that SNPs associated with cognition may have lower predictive abilities when applied to non-Europeans, there have not been any other studies reporting intelligence prediction of ancient individuals through genetic data to our knowledge. This analysis is an example of application of GWAS findings toward assessment of cognitive abilities in individuals living around 4000 years ago. Previous studies on polygenic prediction of height as well disease risk in ancient DNA confirmed similar predictive power in ancient humans to modern individuals [34, 35].

Modern concept on intelligence measured by IQ holds on principle of dual contribution of genetic and environmental components (socioeconomic aspects, medical care) forming essential cognitive functions. IQ measures have been implicated with survival, adaptation to environment, and mental functioning [8]. Digital genomic biobank DNA.Land as well as various genetic applications like GenePlaza, 23andMe previously reported polygenic prediction of a number of complex traits including

![Fig. 2](image_url)

**Fig. 2** Absolute IQ values inferred from intelligence polygenic scores in ancient individuals compared to modern humans. **A** Absolute IQ values inference based on variance explained by intelligence polygenic score build from 1402 SNPs ($p$ value threshold $p < 4 \times 10^{-11}$) demonstrated Funadomari Jomon individual’s IQ = 101 (95% CI = 72.58–129.74), while Afanasievo mother’s IQ = 89 (95% CI = 60.96–118.12), Afanasievo father IQ = 94 (95% CI = 65.2–122.36). Afanasievo sons scores were located between the maternal and paternal scores where Son1 score had IQ = 92 (95% CI = 63.17–120.3) and Son2 IQ = 90 (95% CI = 61.54–118.7). Variance explained by intelligence polygenic score ($R^2 = 5.2\%$), mean IQ = 100 with SD = 15 (95% CI = 71.42–128.58) in modern human general population. **B** Absolute IQ values inference based on variance explained by intelligence polygenic score build from 9128 SNPs ($p$ value threshold $p < 5 \times 10^{-8}$) demonstrated Funadomari Jomon individual’s IQ = 95 (95% CI = 66.88–124.04), while Afanasievo mother’s IQ = 87 (95% CI = 57.96–115.12), Afanasievo father IQ = 93 (95% CI = 64.3–121.46). Afanasievo sons scores were similarly located between the maternal and paternal scores where Son1 had IQ = 91 (95% CI = 62.87–120.02) and for Son2: IQ = 89 (95% CI = 60.96–118.12).
increase in predictive power of intelligence based solely on cognitive functions and mental disorders [3]. Likely such a modest coding and non-coding DNA elements highly associated with PGS, large number of those SNPs have been mapped to protein study only explain about 5.2% variance in intelligence through Land study was about 4.8%. Although 12,110 SNPs we used in our variance of intelligence explained by polygenic scoring in DNA.

Fig. 3 Intelligence-associated genetic relationship based on principal component analysis between ancient and modern humans. A Principal component analysis based on 1402 top significant SNPs out of 12,110 SNPs (p value threshold $p < 4 \times 10^{-11}$) shared by ancient individuals and subjects from 1000 Genomes Project. Ancient individuals including Funadomari Jomon (F23), Afanasievo family—Mother (AM), Father (AF), Son1 (AS1), Son2 (AS2) and modern humans defined in accordance with the groupings in the 1000 Genomes Project: European (EUR), admixed American (AMR), East Asian (EAS), African (AFR) and South Asian (SAS); B principal component analysis based on 9128 SNPs out of 12,110 SNPs (p value threshold $p < 5 \times 10^{-8}$) in high association with intelligence based on GWAS findings [36, 37]. Although the predictions have the potential to elucidate individual traits in comparison to massive digital databanks, a small percent of genetic contribution to the traits is still the most important limiting factor in wider applicability of any predictions [38].

DNA.Land platform has previously demonstrated evaluation of intelligence PGS using GWAS findings based on 72 SNPs [2]. The variance of intelligence explained by polygenic scoring in DNA. Land study was about 4.8%. Although 12,110 SNPs we used in our study only explain about 5.2% variance in intelligence through PGS, large number of those SNPs have been mapped to protein coding and non-coding DNA elements highly associated with cognitive functions and mental disorders [3]. Likely such a modest increase in predictive power of intelligence based solely on genetic factors suggests a need for alternative intelligence prediction tools incorporating environment and socioeconomic factors.

A common approach in studying quantitative traits like intelligence in humans has been based on monozygotic and dizygotic twins [39]. Previous studies on three-dimensional brain mapping in twins supported correlation between gray-matter volumes in genetically identical twins and high heritability for brain areas responsible for IQ, speech, and language [40, 41]. High heritability of intelligence has also been criticized due to overlap of cognitive ability measurements with various factors like presence of IQ statistics, socioeconomic influence, and other environmental influences [42].

Intelligence as a phenotypic trait with underlying effects of DNA polymorphism has been likely shaped by evolutionary processes. Majority of mutations in genes affecting underlying cognition used in this study tend to interact in extremely complex networks with higher activity in hippocampal as well as somatosensory neurons [3]. Since not only humans, but primates have active neurogenesis in those brain areas [43] we hypothesize that genetic contribution to intelligence through mutations are shared to some extent with human ancestral species. High abundance of shared SNPs related to intelligence in primates and humans observed in our study may suggest that most mutations in genomic regions associated with intelligence of ancient humans and their ancestors are in line with neutral theory of evolution [44]. We have demonstrated conserved state of half of causative SNPs in primates and humans (Table 2). Since the ancestral state inference was done in relation to primates, there is no clear boundary between alleles contributing to higher intelligence being more common in modern humans than in ancestral species.

We demonstrated that genomic data from ancient individuals can be used to evaluate a genetic component of intelligence. Funadomari Jomon as well as Afanasievo family individuals demonstrated intelligence PGS as well as IQ scores in line with modern humans. DNA evidence may indicate a possibility of intelligence being a neutral trait in human evolution suggesting that ancient individuals living 3700–4100 years BP could have been as intelligent as modern humans.

REFERENCES

1. Zabaneh D, Krapohl E, Gaspar HA, Curtis C, Lee SH, Patel H, et al. A genome-wide association study for extremely high intelligence. Mol Psychiatry. 2018;23:1226–32.

2. Snikkers S, Stringer S, Watanabe K, Jansen PR, Coleman JR, Krapohl E, et al. Genome-wide association meta-analysis of 78,308 individuals identifies new loci and genes influencing human intelligence. Nat Genet. 2017;49:1107–12.

3. Savage JE, Jansen PR, Stringer S, Watanabe K, Bryois J, de Leeuw CA, et al. Genome-wide association meta-analysis in 269,867 individuals identifies new genetic and functional links to intelligence. Nat Genet. 2018;50:912–9.

4. Fawns-Ritchie C, Deary I. Reliability and validity of the UK Biobank cognitive tests. PLoS ONE. 2020;15:e0231627.

5. Miller CJ, Li Y, Abecasis GR. METAL: fast and efficient meta-analysis of genome-wide association scans. Bioinformatics. 2010;26:2190–1.

6. Arias TD, Jorge LF, Barrantes R. Uses and misuses of definitions of genetic polymorphism. A perspective from population pharmacogenetics. Br J Clin Pharm. 1991;31:117–20.

7. Sternberg RJ, Detterman DK. What is intelligence?: Contemporary viewpoints on its nature and definition. Norwood, NJ: Ablex Pub. Corp.; 1986.

8. Braaten EB, Norman D. Intelligence (IQ) testing. Pediatr Rev. 2006;27:403–8.

9. Lyall DM, Cullen B, Allerhand M, Smith DJ, Mackay D, Evans J, et al. Cognitive test scores in UK Biobank: data reduction in 480,416 participants and longitudinal stability in 20,346 participants. PLoS ONE. 2016;11:e0154222.

10. Holloway RL. The evolution of the hominid brain. In: Henke W, Tattersall I, editors. Handbook of paleoanthropology. Berlin, Heidelberg: Springer; 2015. p. 1961–87.

11. Montgomery S. Hominin brain evolution: the only way is up? Curr Biol. 2018;28:R788–90.

12. Shultz S, Nelson E, Dunbar RIM. Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. Philos Trans R Soc B Biol Sci. 2012;367:2130–40.
13. Renfrew C, Frith C, Malafouris L, Stout D, Toth N, Schick K, et al. Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. Philos Trans R Soc B Biol Sci. 2008;363:1939–49.

14. Putton SS, Wijekumakum S, Franciscur RS, Spencer JP. The functional brain networks that underlie Early Stone Age tool manufacture. Nat Hum Behav. 2017;1:1–8.

15. Pearce E, Stringer C, Dunbar RM. New insights into differences in brain organization between Neanderthals and anatomically modern humans. Proc R Soc B Biol Sci. 2013;280:20130168.

16. Seymour RS, Bosiocic V, Snelling EP, Chikezie PC, Hu Q, Nelson TJ, et al. Cerebral blood flow rates in recent great apes are greater than in Australopithecus species that had equal or larger brains. Proc R Soc B Biol Sci. 2019;286:20192208.

17. Kanzawa-Kiymama H, Jinam TA, Kawai Y, Sato T, Hosomichi K, Tajima A, et al. Late Jomon male and female genome sequences from the Funadomari site in Hokkaido, Japan. Anthropol Sci. 2019;127:83–108.

18. Wohns AW, Wang Y, Jeffery B, Akbair A, Mallick S, Pinhasi R, et al. A unified genealogy of modern and ancient genomes: unified, inferred tree sequences of 1000 Genomes, Human Genome Diversity, and Simons Genome Diversity Projects with ancient samples. 2021. https://doi.org/10.5281/zenodo.5512994.

19. Meyer M, Kircher M, Gansauge M-T, et al. A high-coverage genome sequence from an Archaic Denisovan Individual. Science. 2012;338:48376.

20. The 1000 Genomes Project Consortium. A global reference for human genetic variation. Nature. 2015;526:68–74.

21. Paten B, Herrero J, Fitzgerald S, Beal K, Flicek P, Holmes I, et al. Genome-wide nucleotide-level mammalian ancestor reconstruction. Genome Res. 2008;18:1829–43.

22. Purcell S, Neale B, Todd-Brown K, Thomas L, Ferreira MA, Bender D, et al. PLINK: a tool set for whole-genome association and population-based linkage analyses. Am J Hum Genet. 2007;81:559–75.

23. Wickham H. ggplot2: elegant graphics for data analysis. NY: Springer; 2014.

24. Wickham H. ggplot2: elegant graphics for data analysis. NY: Springer; 2014.

25. Liu JZ, Erlich Y, Pickrell JK. Case studies on the application of whole-genome association analyses. Nat Protoc. 2020;15:2759–74.

26. Genç E, Schlüter C, Fraenz C, Arning L, Metzen D, Nguyen HP, et al. Polygenic risk score usage and performance in diverse human populations. Nat Genet. 2018;50:160.

27. Laurin M. A framework to collect genomes and phenomes in the era of abundant genetic information. Nat Rev Genet. 2018;50:160.

28. Plomin R, von Stumm S. The new genetics of intelligence. Nat Rev Genet. 2010.

29. Yuan J, Gordon A, Speyer D, Aufrichtig R, Zielinski D, Pickrell J, et al. DNA. Land is available at http://www.nature.com/nature/journal/v503/n7475/full/nature12770.html.

30. Coghill MN, Batty GD, Ferris TF, Lawlor DA, Wannamethee G, Shaper AG. Lots of walking: associations with measures of physical fitness, physical activity, and general health among the elderly. J Epidemiol Comm Health. 2002;56:694–701.

31. Kanzawa-Kiymama H, Jinam TA, Kawai Y, Sato T, Hosomichi K, Tajima A, et al. Late Jomon male and female genome sequences from the Funadomari site in Hokkaido, Japan. Anthropol Sci. 2019;127:83–108.

32. Wohns AW, Wang Y, Jeffery B, Akbair A, Mallick S, Pinhasi R, et al. A unified genealogy of modern and ancient genomes: unified, inferred tree sequences of 1000 Genomes, Human Genome Diversity, and Simons Genome Diversity Projects with ancient samples. 2021. https://doi.org/10.5281/zenodo.5512994.

33. Meyer M, Kircher M, Gansauge M-T, et al. A high-coverage genome sequence from an Archaic Denisovan Individual. Science. 2012;338:48376.

34. The 1000 Genomes Project Consortium. A global reference for human genetic variation. Nature. 2015;526:68–74.

35. Paten B, Herrero J, Fitzgerald S, Beal K, Flicek P, Holmes I, et al. Genome-wide nucleotide-level mammalian ancestor reconstruction. Genome Res. 2008;18:1829–43.

36. Burki T. Genetic apps: raising more questions than they answer? Lancet Digit Health. 2020;2:e13–4.

37. Yuan J, Gordon A, Speyer D, Aufrichtig R, Zielinski D, Pickrell J, et al. DNA. Land is a framework to collect genomes and phenomes in the era of abundant genetic information. Nat Genet. 2018;50:160.

38. Plomin R, von Stumm S. The new genetics of intelligence. Nat Rev Genet. 2010;11:148–59.

39. Neale MC, Cardon LR. Methodology for genetic studies of twins and families. Dordrecht; London: Springer; 2011.

40. Posthuma D, De Geus EJC, Baaré WFC, Pol HEH, Kahn RS, Boomsma DI. The association between brain volume and intelligence is of genetic origin. Nat Neurosci. 2002;5:83–4.

41. Thompson PM, Cannon TD, Narr KL, van Erp T, Poutanen V-P, Huttunen M, et al. Genetic influences on brain structure. Nat Neurosci. 2001;4:1253–8.

42. Visscher PM, Hill WG, Wray NR. Heritability in the genomics era—concepts and misconceptions. Nat Rev Genet. 2008;9:255–66.

43. Gould E, Reeves AJ, Fallah M, Tanapat P, Gross CG, Fuchs E. Hippocampal neuropathology in adult Old-World primates. Proc Natl Acad Sci USA. 1999;96:5263–7.

44. Kimura M. The neutral theory of molecular evolution. Cambridge, New York: Cambridge University Press; 1983.

AUTHOR CONTRIBUTIONS
Kaisar Dauyey conducted all the data analyses, and Naruya Saitou supervised his analyses.

COMPETING INTERESTS
The authors declare no competing interests.

ADDITIONAL INFORMATION
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