Supporting Information

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SI Text

Heritability and Evolvability of Head Size and Pelvic Dimensions. Evolutionary change of a quantitative trait requires additive genetic variance on which selection can act (1, 2). The hypothesis that we tested further assumes a genetic basis of variation in head size; otherwise, the mother's head size would be unrelated to the neonate's head size. The measure most often reported in this context is the (narrow sense) heritability $h^2 = V_A/V_P$, the ratio of additive genetic variance to total phenotypic variance of a trait.

It is well established that variation in head size has a genetic basis in humans (3–5) (summarized in Table S1). Intracranial volume has a heritability of 0.73 in newborns and 0.88 in adults (4, 5). Heritability of head circumference is low at birth ($h^2 =$ 0.14) but increases rapidly after the first months of life (3). This discrepancy likely results from the highly plastic head shape at birth (due to cranial deformations during birth) that affects head circumference but not intracranial volume. Because of the deformable head shape, intracranial volume may be a more relevant measure of cephalo-pelvic mismatch than head circumference, but the circumference is much easier to measure and is typically reported in the obstetric literature.

It is not primarily the heritability but rather the additive genetic variance present in a population that determines a trait's capacity to evolve (1, 6, 7). The low heritability of head circumference at birth is accompanied by a very large phenotypic variance, compared with the later months (table 1 in ref. 3). Hence, even for head circumference, genetic variance is not as small as the low heritability value seems to suggest, but instead environmental variance is particularly large. Hansen et al. (2011) (6) suggested a novel measure of "evolvability," computed as the ratio of additive genetic variance to the squared mean value m of a trait—that is, the squared coefficient of variation of the additive genetic variance component:

$$e = \frac{V_A}{m^2} = \frac{h^2 \cdot V_P}{m^2}.$$

This evolvability value, multiplied by 100, can be interpreted as the expected percent change in a trait under a unit strength of selection (6). The evolvabilities for head circumference, intracranial volume, and pelvic dimensions (Table S1) indicate considerable evolutionary potential for all those measures, well within the range of evolvabilities reported for other traits and other species (6). Interestingly, although the heritability of head circumference at birth is only $h^2 = 0.14$ (3), its evolvability amounts to 88% of the evolvability of head circumference at 8 mo of age, where its heritability is $h^2 = 0.92$.

1. Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits* (Sinauer Associates, Sunderland, MA), 1st Ed.
2. Falconer DS, Mackay TFC (1996) *Introduction to Quantitative Genetics* (Benjamin Cummings, Essex, UK), 4th Ed.
3. Smit DJA, et al. (2010) Heritability of head size in Dutch and Australian twin families at ages 0-50 years. *Twin Res Hum Genet* 13(4):370–380.
4. Gilmore JH, et al. (2010) Genetic and environmental contributions to neonatal brain structure: A twin study. *Hum Brain Mapp* 31(8):1174–1182.
5. Baaré WFC, et al. (2001) Quantitative genetic modeling of variation in human brain morphology. *Cereb Cortex* 11(9):816–824.
6. Hansen TF, Pélabon C, Houle D (2011) Heritability is not evolvability. *Evol Biol* 38(3): 258–277.
7. Houle D (1992) Comparing evolvability and variability of quantitative traits. *Genetics* 130(1):195–204.

Table S1. Heritabilities and evolvabilities for head and pelvic dimensions

Measure	Mean	SD	Heritability, h^2	Evolvability, *e* %	Reference
Head					
Circumference, mm					
Neonate	351	25.4	0.14	0.0733	(1)
6–8 mo	441	13.3	0.92	0.0837	(1)
Adult 50 y	566	23.2	0.75	0.1260	(1)
Intracranial volume, cm^3					
Neonate	460.11	62.36	0.73	1.3410	(2)
Adult female	1,342.4	117.8	0.88	0.6777	(3)
Pelvis					
Biiliac diameter, mm					
Adult female	217.8	12.0	0.88	0.2691	(4)
Bituberous diameter, mm					
Adult female	117.9	8.6	0.56	0.2984	(4)

Means, SDs, and heritabilities are taken from the literature as indicated. The corresponding evolvabilities were calculated following ref. 5. Intracranial volume is the variable with the highest evolvability. It is higher than the evolvability of head circumference, probably due to large plasticity in head shape but not volume at birth. For a neonate, the evolvability of head circumference is almost as large (88%) as at 6–8 mo. Evolvability of female adult pelvic dimensions lies in between the values for intracranial volume and head circumference.

1. Smit DJA, et al. (2010) Heritability of head size in Dutch and Australian twin families at ages 0-50 years. *Twin Res Hum Genet* 13(4):370–380.
2. Gilmore JH, et al. (2010) Genetic and environmental contributions to neonatal brain structure: A twin study. *Hum Brain Mapp* 31(8):1174–1182.
3. Baaré WFC, et al. (2001) Quantitative genetic modeling of variation in human brain morphology. *Cereb Cortex* 11(9):816–824.
4. Sharma K (2002) Genetic basis of human female pelvic morphology: A twin study. *Am J Phys Anthropol* 117(4):327–333.
5. Hansen TF, Pélabon C, Houle D (2011) Heritability is not evolvability. *Evol Biol* 38(3):258–277.

Table S2. List of landmarks

No.	Landmark
Unpaired	
1	Promontorium
2	Pubic symphysis
3	S1 body, posterior
4	Sacral canal, anterior floor
5	Sacral canal, anterior roof
6	S1 spine
7	S2 spine
8	Caudion, posterior
9	Sacral canal, posterior roof
10	S1 center
11	First segment union point
12	Second segment union Point
13	Inflection
14	Third segment union point
15	Fourth segment union point
16	Caudion, anterior
Paired	
17	Superior pole, pubic symphysis
18	Iliospinale
19	S1 body, lateral
20	Lateral alar-auricular point
21	Posterior alar-auricular point
22	Superior articular facet, medial superior
23	Superior articular facet, lateral superior
24	Superior articular facet, medial inferior
25	Superior articular facet, lateral inferior
26	Sacral canal, anterior wall
27	Posterior sacral tubercle
28	Anterior alar point
29	Mid alar point
30	Caudion, lateral
31	Inferior sacro–iliac junction
32	Iliospinale, cristale
33	Iliospinale, anterior lateral
34	Anterior segment midpoint, lateral
35	Anterior segment midpoint, medial
36	Iliocristale, summum
37	Posterior segment point, lateral 1
38	Posterior segment point, medial 1
39	Posterior segment point, lateral 2
40	Posterior segment point, medial 2
41	Posterior segment point, lateral 3
42	Posterior segment point, medial 3
43	Iliocristale, posterior
44	Posterior superior iliospinale
45	Superior sciatic notch point
46	Apex of sciatic notch
47	Anterior sciatic notch point
48	Posterior ischial border point
49	Medial tuberosity point
50	Inferior tuberosity point
51	Lateral tuberosity point
52	Superior tuberosity pole
53	Ischiale
54	Superior ischial pubic ramus
55	Anterior inferior ischial pubic ramus
56	Obturator tubercle point
57	Inferior obturator foramen point
58	Inferior symphyseal pole
59	Anterior symphyseal point
60	Posterior symphyseal point
61	Pubotubercle

Table S2. Cont.

No.	Landmark
62	Pubic eminence point
63	Posterior inlet point
64	Intermediate inlet point
65	Anterior inlet point
66	Anterior iliac base point
67	Acetabulion, anterior
68	Acetabulion, superior
69	Acetabulion, posterior
70	Acetabulion, inferior
71	Acetabulion, center point

The 126 3D data points that were measured on each pelvis consist of 16 unpaired landmarks and 55 landmarks on the left and right hemipelvis each.

Table S3. Summary statistics (mean and SD) for selected linear pelvic measurements, calculated from the 3D data

		Females, mm		Males, mm	
Pelvic distance	Description	Mean	SD	Mean	SD
Biiliac diameter	Distance between anterior superior iliac spines	232.9	18.8	234.6	16.2
Anteroposterior diameter of the inlet	Sacral promontory to dorsomedial superior pubic symphysis	118.8	11.5	109.1	8.6
Transverse diameter of the inlet	Maximum distance between lineae terminalis	131.0	8.1	124.8	7.2
Sacral breath	Straight distance across ventral surface of sacrum where sacrum meets apex of auricular surface of ilium when pelvis is articulated	104.0	8.4	104.2	6.4
Oblique diameter of the inlet	From the right sacroiliac joint to the left iliopectineal eminence	123.5	6.9	120.0	5.6
Biacetabular diameter	Distance between centers of acetabula	129.7	9.5	126.4	9.4
Pubic symphysis length	Superior-medial border pubic symphysis to inferior-medial border pubic symphysis	33.6	3.3	40.0	4.3
Anteroposterior diameter of the midplane	From junction of fourth and fifth sacral vertebrae to dorsomedial inferior pubic symphysis	128.7	9.9	122.3	7.7
Anteroposterior diameter of the outlet	From the tip of the sacrum to dorsomedial inferior pubic symphysis	118.3	10.4	111.0	7.6
Bituberous diameter	Distance between the inner aspects of the ischial tuberosities	113.7	13.1	96.9	11.6
Sacral length	Sacral promontory to midpoint of the antero-inferior margin of the last sacral segment	104.8	12.3	112.5	14.3
Hip bone length	From most superior point on iliac crest to most inferior point of ischial tuberosity	195.7	10.9	216.3	9.9

Definitions of these pelvic distances as in the literature (refs. 1–4). Sacral length is modified from ref. 1.

1. Tague RG (1995) Variation in pelvic size between males and females in nonhuman anthropoids. *Am J Phys Anthropol* 97(3):213–233.
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