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Genetic and Environmental Factors in Head and Face Measurements of Belgian Twins

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Seventeen head and face measurements of 205 twin pairs, aged 18 to 25 years, are analyzed. In both sexes a significant genetic variance component is found for head length, head breadth, and frontal breadth, for seven breadth measurements of the face, for physio-face height, and nose height. A significant genetic variance component is found for nasion-gnathion, nasion-stomion, and lips height in males and for the two ear measurements in females. We suggest that the sex difference for heritability may be due to random factors and to continued growth from 18 to 25 years in males.

Key words: Twins, Dominance, Heritability

INTRODUCTION

Estimates of heritability coefficients are relative to the studied population in its specific environment and time [9] and with its specific gene pool. The comparison of the heritability estimates is sometimes difficult, and several factors must be taken into account such as sex, age, dominance, X linkage, and the often positively correlated environments of relatives.

Studies on head and face measurements are not numerous and are often limited to a few characteristics such as head length and breadth. Among the larger ones, Howells [13] and Schreider [19] examined samples of brothers, Howells [14] of sibs, and Susanne [21,22] and Bernhard et al [1] of parent-children and sibs. On twins, some authors analyzed the F values relating the DZ and the MZ intrapair variances, Dahlberg [5] and von Verschuer [29] on twins with a zygosity diagnosis based on the physical resemblance, and Clark [4], Vogel and Wendt [28], Osborne and De George [17], Vandenberg and Strandskov [27] on twins diagnosed with blood groups (eight, nine, nine, and four groups, respectively). The twins' ages were very variable: 3 to 80 years for Dahlberg; 2 to 63 for von Verschuer; 12 to 20 for Clark; 6 to 19 for Vogel and Wendt; 18 to 55 for Osborne and DeGeorge; 12 to 78 for Vandenberg and Strandskov. In the twin studies, most authors used Holzinger's controversial heritability estimate [12].

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Another difficulty is that the parent-offspring correlations vary in function of the age of the children [23,24], with the highest values observed after puberty. To avoid at least some of the pitfalls we have just mentioned, we have chosen for the study of head and face a sample of twins of 18 to 25 years, homogeneous for age, geographical, ethnological, and, as far as possible, for socio-economic origin. We analyze the measurements with the methodology proposed by Christian et al [2,3].

MATERIALS AND METHODS

The sampling of Belgian same-sexed twins, aged 18 to 25 years, started in 1979 and is now finished, with 57 MZ and 39 DZ male pairs and 67 MZ and 42 DZ female pairs, making a total of 205 pairs. The zygosity is based on at least 22 blood groups for which details are given in Defrise-Gussenhoven et al [6]. The twins are Belgians of caucasian origin born in Flanders or near Brussels, and they were reared together; most of them are high school or university students. Roughly 66% of the fathers of the twins belong to the professional classes, the remaining 34% having a manual occupation; the corresponding values for the fathers of our Belgian conscripts are 41% and 59%, respectively, a nearly reverse proportion.

The measurements were taken according to the technique of Martin and Saller [15], revised by Twiesselmann [25] and illustrated in a growth study of 14,300 Belgian children [26]; most of the measurements were taken by the same person (CS) in order to reduce the "noise" variation; only 20 of the 205 pairs were measured by a young colleague, R. Hauspie.

RESULTS

Most of the calculations were performed with the program of Christian et al [2,3].

Table 1 gives the mean and the variance of the measurements in each of the four groups: MZ and DZ males, MZ and DZ females. Table 2 lists the probabilities for the tests of equality of means and variances in MZ and DZ twins.

We did not find, as was the case for the body measurements [8], the means for MZ twins to be smaller than those of the DZ twins. Only the mean bigonial breadth was significantly lower in MZ than in DZ male twins ($P = 0.009$). Neither do the variances, estimated by the sum of mean squares within and among pairs [2], show a systematic tendency to be smaller in MZ twins, as was the case for body measurements [8]. Since the expected values of the variances are

$$E(AMZ + WMZ) = 2(\sigma_g^2 + 2\sigma_{ge} + \sigma_{eMZ}^2) \tag{1}$$

and

$$E(ADZ + WDZ) = 2(\sigma_g^2 + 2\sigma_{ge} + \sigma_{eDZ}^2) \tag{2}$$

a significant difference may be caused by the inequality of the variance components due to environmental effects. As the power of the F′ test performed to detect $\sigma_{eMZ}^2 \neq \sigma_{eDZ}^2$ is low, we adopted the increased significance level $\alpha = 0.20$ recommended by Christian et al [3].

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TABLE 1. Means and Variances

Measurement	Mean $\bar{x}$				Variance $\hat{\sigma}^{2a}$			
	♂		♀		♂		♀	
	MZ	DZ	MZ	DZ	MZ	DZ	MZ	DZ
Head length	19.21	19.21	18.54	18.48	0.843	1.075	0.766	0.766
Head breadth	15.22	15.31	14.67	14.71	0.819	0.573	0.646	0.386
Frontal breadth	10.83	10.79	10.50	10.58	0.374	0.333	0.374	0.441
Bizygomatic breadth	13.73	13.84	13.16	13.11	0.669	0.497	0.451	0.330
Bigonial breadth	9.86	10.08	9.35	9.31	0.467	0.451	0.546	0.589
Physio-face height	18.78	18.71	17.51	17.52	2.121	1.644	1.327	1.129
Nasion-gnathion height	12.38	12.27	11.53	11.56	0.988	0.795	0.571	0.801
Nasion-stomion	7.75	7.70	7.24	7.26	0.526	0.626	0.372	0.410
Nose height	5.52	5.51	5.17	5.21	0.349	0.478	0.251	0.278
Nose breadth	3.44	3.47	3.17	3.20	0.102	0.130	0.084	0.084
Internal biocular breadth	3.06	3.03	2.97	2.94	0.123	0.100	0.105	0.129
External biocular breadth	9.07	9.16	8.76	8.88	0.324	0.328	0.290	0.329
Interpupillary breadth	6.36	6.35	6.11	6.16	0.246	0.320	0.195	0.163
Lips height	1.72	1.78	1.65	1.64	0.238	0.197	0.146	0.125
Mouth breadth	4.93	4.99	4.71	4.76	0.294	0.135	0.174	0.177
Ear height	6.21	6.21	5.85	5.88	0.223	0.324	0.221	0.238
Ear breadth	3.38	3.38	3.13	3.20	0.220	0.356	0.244	0.298
Total number of twins	114	78	134	84	114	78	134	84

$^a\hat{\sigma}^2$, Estimates of two times the population variance. See text for details.

TABLE 2. Probabilities of the t' Tests (α = 0.05) and the F' Tests (α = 0.20) for Equality of Means and Variances

Measurement	Probability				Intraclass corr coeff			
	t' Test		F' Test					
	$H_0:\bar{x}_{MZ}=\bar{x}_{DZ}$		$H_0:\sigma^2_{MZ} = \sigma^2_{DZ}$		♂♂		♀♀	
	♂	♀	♂	♀	MZ	DZ	MZ	DZ
Head length	0.980	0.610	0.328	0.999	0.845	0.391	0.781	0.472
Head breadth	0.410	0.638	0.152	0.032	0.853	0.414	0.767	0.503
Frontal breadth	0.544	0.317	0.624	0.466	0.792	0.270	0.730	0.481
Bizygomatic breadth	0.259	0.507	0.288	0.177	0.839	0.368	0.711	0.446
Bigonial breadth	0.009	0.700	0.880	0.745	0.792	0.149[a]	0.863	0.461
Physio-face height	0.714	0.948	0.312	0.484	0.881	0.441	0.745	0.383
Nasion-gnathion height	0.391	0.757	0.393	0.149	0.824	0.509	0.751	0.570
Nasion-stomion	0.627	0.726	0.507	0.667	0.870	0.745	0.683	0.655
Nose height	0.880	0.514	0.224	0.657	0.802	0.123[a]	0.710	0.558
Nose breadth	0.454	0.448	0.317	0.999	0.779	0.493	0.722	0.415
Internal biocular breadth	0.436	0.432	0.365	0.382	0.678	0.124[a]	0.856	0.435
External biocular breadth	0.242	0.122	0.962	0.596	0.840	0.341	0.777	0.592
Interpupillary breadth	0.965	0.320	0.283	0.443	0.803	0.537	0.756	0.514
Lips height	0.351	0.804	0.436	0.495	0.845	0.292	0.621	0.433
Mouth breadth	0.281	0.241	0.001	0.944	0.670	−0.055[a]	0.633	0.277
Ear height	0.972	0.650	0.130	0.745	0.760	0.529	0.807	0.483
Ear breadth	0.925	0.367	0.074	0.413	0.807	0.840	0.831	0.706
Critical value at 5% level					0.220	0.267	0.203	0.257
Mean for the 17 variables					0.805	0.383	0.750	0.493
Mean for the 12 variables with significant GT in both sexes (Table VI)					0.799	0.300	0.754	0.461
Total number of pairs					57	39	67	42

[a] Intraclass correlation coefficients not significant for a one-sided test (α = 0.05).

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In Table 2, the intraclass correlation coefficients, ρ_{MZ} and ρ_{DZ}, estimated by the difference of among and within mean squares divided by their sum are also listed. A one-sided test shows them to be significantly positive at the 5% level, except for bigonial breadth, nose height, internal biocular breadth, and mouth breadth in DZ males.

We have not listed the tests for $\hat{\rho}_{MZ} - \hat{\rho}_{DZ}$, but, except for ear breadth in males, all the correlations for MZ pairs are higher than those of DZ pairs, and most of the differences are highly significant; only nose breadth ($P = 0.1$) in males and nasion-gnathion height ($P = 0.053$), nasion stomion ($P = 0.399$), nose height ($P = 0.102$), and lips height ($P = 0.097$) in females do not reach the 5% level. On the whole, the results indicate, as expected, a stronger resemblance in MZ than in DZ twins for head and face measurements, the mean correlation coefficients of all the measurements being 0.805 vs 0.383 in males and 0.750 vs 0.493 in females. The contrast is more marked in males, with ♂ $\hat{\rho}_{MZ}$ > ♀ $\hat{\rho}_{MZ}$ > ♀ $\hat{\rho}_{DZ}$ > ♂ $\hat{\rho}_{DZ}$ in most cases.

Table 3 lists the mean squares, among and within pairs, with the corresponding degrees of freedom, and Table 4 gives two estimates of the fraction

$$GT = \tfrac{1}{2}\sigma_a^2 + \tfrac{3}{4}\sigma_d^2 + (1 - f)\sigma_i^2 \tag{3}$$

of the genetic variance $\sigma_g^2 = \sigma_a^2 + \sigma_d^2 + \sigma_i^2$, and the corresponding probabilities. The two estimates of GT are

$$\begin{aligned} &\hat{G}WT = WDZ - WMZ \text{ with} \\ &E(\hat{G}WT) = GT + CMZ - CDZ + 2(\sigma_{ge} - \overset{*}{\sigma}_{ge}) + \sigma_{eDZ}^2 - \sigma_{eMZ}^2 \end{aligned} \tag{4}$$

and

$$\begin{aligned} &\hat{G}CT = (WDZ - WMZ + AMZ - ADZ)/2 \text{ with} \\ &E(\hat{G}CT) = GT + CMZ - CDZ + 2(\sigma_{ge} - \overset{*}{\sigma}_{ge}). \end{aligned} \tag{5}$$

CMZ and CDZ are the covariances among environmental effects between members of a twin pair, σ_{ge} is the covariance between genetic and environmental effects in the same individual, and $\overset{*}{\sigma}_{ge}$ is the covariance between genetic effects on twin A of a pair and environmental effects of twin B of that pair. The notations are those of Christian et al [3], and if we accept the model in which CDZ = CMZ and $\sigma_{ge} = \overset{*}{\sigma}_{ge}$, it is clear that $\hat{G}WT$ is a good estimate of GT when the F′ test comparing σ_{eMZ}^2 and σ_{eDZ}^2 is not significant. However, when $\sigma_{eMZ}^2 \neq \sigma_{eDZ}^2$, the estimate $\hat{G}CT$ must be preferred although its variance is larger than that of $\hat{G}WT$, about 4.3 times larger in males and 3.7 times larger in females according to our data.

DISCUSSION

The most interesting parts of the statistical analysis are, of course, the tests evaluating the genetic component, GT, in the variance of a measurement. We first test whether the variances of the two twin types differ at the 20% level of significance. We admit the presence of GT in either of the following situations: 1) when the variances are not significantly different and $\hat{G}WT$ is significant at the 5% level; 2) when the variances are unequal and $\hat{G}CT$ is significant at the 5% level (Tables 2 and 4).

According to these rules, the presence of GT is found in all the measurements of the females except nasion-stomion, lips height, and nasion-gnathion height. However, we

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TABLE 3. Mean Squares Among and Within Twin Pairs

	♂♂				♀♀			
	MZ		DZ		MZ		DZ	
Measurement	AMZ	WMZ	ADZ	WDZ	AMZ	WMZ	ADZ	WDZ
Head length	0.781	0.062	0.747	0.327	0.683	0.084	0.564	0.202
Head breadth	0.759	0.060	0.405	0.168	0.570	0.075	0.290	0.096
Frontal breadth	0.335	0.039	0.211	0.121	0.323	0.051	0.327	0.115
Bizygomatic breadth	0.615	0.054	0.340	0.157	0.386	0.065	0.239	0.091
Bigonial breadth	0.418	0.048	0.259	0.192	0.508	0.037	0.430	0.159
Physio-face height	1.994	0.126	1.184	0.459	1.178	0.149	0.781	0.348
Nasion-gnathion height	0.901	0.087	0.560	0.195	0.500	0.071	0.629	0.172
Nasion-stomion	0.491	0.034	0.547	0.080	0.313	0.059	0.340	0.071
Nose height	0.315	0.035	0.401	0.077	0.215	0.036	0.216	0.061
Nose breadth	0.091	0.011	0.097	0.033	0.072	0.012	0.059	0.025
Internal biocular breadth	0.103	0.020	0.056	0.044	0.098	0.008	0.093	0.037
External biocular breadth	0.298	0.026	0.220	0.108	0.258	0.032	0.262	0.067
Interpupillary breadth	0.220	0.024	0.246	0.074	0.172	0.024	0.123	0.040
Lips height	0.220	0.018	0.127	0.070	0.118	0.028	0.090	0.035
Mouth breadth	0.246	0.049	0.064	0.071	0.142	0.032	0.113	0.064
Ear height	0.196	0.027	0.248	0.076	0.199	0.021	0.176	0.062
Ear breadth	0.199	0.021	0.327	0.028	0.223	0.021	0.254	0.044
Degrees of freedom	56	57	38	39	66	67	41	42

TABLE 4. Within Pair (ĜWT) and Among Component (ĜCT) Estimates of Genetic Variance GT and the Corresponding Probabilities ($\alpha = 0.05$)

	♂♂				♀♀			
Measurement	ĜWT	P	ĜCT	P	ĜWT	P	ĜCT	P
Head length	0.266	0.000	0.150	0.124	0.118	0.000	0.119	0.106
Head breadth	0.107	0.000	0.230	0.005	0.021	0.179	0.150	0.007
Frontal breadth	0.083	0.000	0.103	0.010	0.064	0.001	0.030	0.277
Bizygomatic breadth	0.103	0.000	0.189	0.006	0.026	0.107	0.087	0.028
Bigonial breadth	0.143	0.000	0.151	0.004	0.121	0.000	0.100	0.086
Physio-face height	0.333	0.000	0.571	0.011	0.199	0.001	0.298	0.021
Nasion-gnathion height	0.109	0.003	0.205	0.040	0.101	0.000	−0.013	0.574
Nasion-stomion	0.046	0.002	−0.005	0.533	0.011	0.246	−0.007	0.569
Nose height	0.042	0.003	−0.022	0.666	0.025	0.028	0.012	0.365
Nose breadth	0.022	0.000	0.008	0.316	0.013	0.003	0.013	0.101
Internal biocular breadth	0.024	0.003	0.035	0.003	0.029	0.000	0.017	0.132
External biocular breadth	0.082	0.000	0.080	0.031	0.035	0.004	0.015	0.351
Interpupillary breadth	0.050	0.000	0.012	0.380	0.016	0.032	0.032	0.071
Lips height	0.051	0.000	0.072	0.005	0.008	0.180	0.018	0.119
Mouth breadth	0.023	0.092	0.102	0.000	0.032	0.006	0.031	0.063
Ear height	0.050	0.000	−0.001	0.523	0.040	0.000	0.032	0.138
Ear breadth	0.007	0.154	−0.060	0.945	0.023	0.003	−0.004	0.556

note that the latter variable has, with unequal variances (P = 0.149), a significant ĜWT value with P = 0.001; we also note that the test for $\hat{\rho}_{MZ} - \hat{\rho}_{DZ}$ reaches the 5.3% level.

In males, only the two measurements of the ear fail to reveal the presence of GT; again it seems worthwhile to note that ear height has unequal variances (P = 0.130) but a significant ĜWT value (P = 0.000) and that the test for $\hat{\rho}_{MZ} - \hat{\rho}_{DZ}$ is significant with P = 0.029.

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To discuss the results in more detail, we first look again at the intraclass correlation coefficients (Table 2). We have already seen that in most cases the coefficients for the males have extreme values as compared to those of the females, with ♂$\hat{\rho}_{\mathrm{MZ}}$ $>$ ♀$\hat{\rho}_{\mathrm{MZ}}$ $>$ ♀$\hat{\rho}_{\mathrm{DZ}}$ $>$ ♂$\hat{\rho}_{\mathrm{DZ}}$. A possible explanation is that between 18 and 25 years the regression coefficients for head and face measurements on age are significantly positive more often in boys than in girls [7], as is shown in Table 5 where the values for 722 (or 724 in some cases) boys and 598 girls of caucasian origin from the schools of Brussels are recorded. The fact that growth for head and face goes on after 18 years more markedly in boys than in girls indicates age as a disturbing factor in our twin analysis; it leads to an artificially greater similarity of features in male MZ than in female MZ twins. Indeed, for four measurements, we observe that the differences ♂$\hat{\rho}_{\mathrm{MZ}}$ $-$ ♀$\hat{\rho}_{\mathrm{MZ}}$ are significantly positive for a one-sided test: bizygomatic breadth, $P < 0.05$; physio-face height, $P < 0.025$; nasion-stomion and lips height, $P < 0.005$. There are only four negative differences: bigonial breadth, the two ear measurements, and internal biocular breadth, and the difference for the latter variable is significant at $P < 0.025$.

On the other hand, since it is known that during growth, the differences between DZ twins increase, we expect DZ male twins to become more dissimilar with advancing age, whereas the female DZ twins are already more or less stabilized at 18 years. This might account for the fact that ♀$\hat{\rho}_{\mathrm{DZ}}$ $>$ ♂$\hat{\rho}_{\mathrm{DZ}}$. Another reason for this inequality could be the effect of X-linked characters, which tend to be more similar in sisters, who share the paternal X-chromosome, than in brothers. We tested the differences ♀$\hat{\rho}_{\mathrm{DZ}}$ $-$ ♂$\hat{\rho}_{\mathrm{DZ}}$. In 12 cases this difference is positive, and none of the five negative values is significant. For nose height and mouth breadth the difference is significantly positive at the 2.5% level for a one-sided test. Nevertheless, we cannot point out these two measurements as candidates for X-linkage, because the growth factor, present in males, cannot be cancelled out and also because in a family study Susanne [21] has found no evidence of X-linkage for nose height and mouth breadth.

TABLE 5. Regression Coefficients of Measurements on Age of 722 (or 724 in Four Cases) Males and 598 Females Between 18 and 25 Years From Brussels Schools

	$b_{x/\mathrm{age}}$	
Measurement	Males	Females
Head length	0.027**	0.019
Head breadth	0.037**	0.028**
Frontal breadth	0.001	−0.012
Bizygomatic breadth	0.046***	0.025*
Bigonial breadth	0.062***	0.016
Nasion-gnathion height	0.061***	0.025*
Nasion-stomion height	0.039***	0.013
Nose height	0.035***	0.016*
Nose breadth	0.004	0.008
External biocular breadth	0.024***	0.009
Lips height	−0.014**	0.016*
Mouth breadth	0.031***	0.029
Ear height	0.034***	0.004
Ear breadth	0.007	0.006

One sided t test; $^{*}P < 0.05$; $^{**}P < 0.025$; $^{***}P < 0.01$.

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So we observe that the contrast between the degrees of similarity in the two twin types is more marked in boys than in girls, and this fact leads naturally to the results obtained for heritability coefficients, defined in twins as $H^2_{tw} = 2GT/\sigma^2_{tw}$, $\sigma^2_{tw} = \sigma^2_g + 2\sigma_{ge} + (\sigma^2_{eMZ} + \sigma^2_{eDZ})/2$ being the variance of the population of twins, estimated by

$$\hat{\sigma}^2_{tw} = (AMZ + WMZ + ADZ + WDZ)/4 \qquad (6)$$

The estimates of H^2_{tw} are listed in Table 6; they are calculated with the significant values of GT, either $\hat{G}WT$ when $\sigma^2_{eMZ} = \sigma^2_{eDZ}$ or $\hat{G}CT$ when $\sigma^2_{eMZ} \neq \sigma^2_{eDZ}$. For instance, $\hat{H}^2_{tw}$ for head length is 1.108 in males and 0.618 in females. This means that if the hypotheses CMZ = CDZ and $\sigma_{ge} = \overset{*}{\sigma}_{ge}$ hold, the GT components are 55.4 and 20.9%, respectively, of the total variances. As GT is only a part of the genetic variance, σ^2_g (3), we can admit that head length is mostly determined by genes, and more so in males than in females. Heritability is also found in the other measurements, with the exception of nasion-gnathion, nasion-stomion, and lips height in females and the two ear measurements in males. We cannot explain, except by continued growth in males, why three of the height

*TABLE 6. Comparison of Heritability Coefficients Estimated With Twin and Family Data and Noted $\hat{H}^2_{tw}$ and $\hat{\hat{h}}^2_{fa}$, Respectively**

Measurement	Twins				Families studied by Susanne
	Males		Females		
	$\hat{H}^2_{tw} = 2\hat{G}WT/\hat{\sigma}^2_{tw}$ $\hat{\sigma}^2_{eMZ} = \hat{\sigma}^2_{eDZ}$	$\hat{H}^2_{tw} = 2\hat{G}CT/\hat{\sigma}^2_{tw}$ $\hat{\sigma}^2_{eMZ} \neq \hat{\sigma}^2_{eDZ}$	$\hat{H}^2_{tw} = 2\hat{G}WT/\hat{\sigma}^2_{tw}$ $\sigma^2_{eMZ} = \sigma^2_{eDZ}$	$\hat{H}^2_{tw} = 2\hat{G}CT/\hat{\sigma}^2_{tw}$ $\sigma^2_{eMZ} \neq \sigma^2_{eDZ}$	$\hat{\hat{h}}^2_{fa} = 2r_{pc}/1 + m_p$
Head length	1.108		0.618		0.554
Head breadth		1.326		1.166	0.614
Frontal breadth	0.934		0.628		0.668
Bizygomatic breadth	0.710			0.890	0.606
Bigonial breadth	1.250		0.854		0.662
Physio-face height	0.708		0.646		0.650
Nasion-gnathion height	0.486			GT NS	0.582
Nasion-stomion height	0.318		GT NS		0.520
Nose height	0.406		0.378		0.392
Nose breadth	0.752		0.614		0.640
Internal biocular breadth	0.858		0.986		0.630
External biocular breadth	1.006		0.448		0.662
Interpupillary breadth	0.708		0.350		0.650
Lips height	0.944		GT NS		0.636
Mouth breadth		0.904	0.726		0.482
Ear height		GT NS[a]	0.702		0.602
Ear breadth		GT NS	0.342		0.598
Mean of the 12 heritability coef. *with sign. GT in* both sexes	0.972		0.692		0.600
Total number of pairs	96		109		564

*Neglecting σ^2_i, the theoretical values are $H^2_{tw} = (\sigma^2_a + {}^3/_2\ \sigma^2_d)/\sigma^2_{tw}$ and $h^2_{fa} = \sigma^2_a/\sigma^2_{fa}$. See text for details.

[a] NS, not significant.

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variables show influence of genes in males and fail to do so in females. However, we note that in both sexes the observed variation coefficients ($100\hat{\sigma}/\bar{x}$) are rather large, with means for the four twin groups equal to 7.40 and 9.22, respectively, for nasion-gnathion and nasion-stomion height and to a very large value, 24.51, for lips height. Now, it is well known in biometry that large variation coefficients may partly be due to measurement errors obscuring the heritability tests.

The two ear variables have no significant GT component in males, which may also be due to the fact that the variation coefficients are 8.28 and 16.09, respectively, for ear height and breadth, whereas the corresponding values for head length and breadth are only 4.91 and 5.15, respectively. On the other hand, it is known by other studies [1] that the dimensions of the ear are not highly influenced by genetic factors.

Susanne [20] measured subjects of 125 Brussels families of same ethnic origin as our twins. He used Fisher's model [10] to calculate heritability coefficients defined as $h^2_{fa} = \sigma^2_a/\sigma^2_{fa}$, with population variance σ^2_{fa} equal to $\sigma^2_a + \sigma^2_d + \sigma^2_e$, epistasis and covariance, σ_{ge}, being ignored.

The estimate of h^2_{fa} is

$$\hat{h}^2_{fa} = 2r_{pc}/(1 + m_p) \tag{7}$$

with r_{pc} and m_p equal to the correlation coefficients respectively of parent-child and father-mother. The family estimate of the heritability coefficient for head length is $\hat{h}^2_{fa} = 0.554$, a much smaller figure than that for male twins (Table 5).

The difference is possibly due to dominance factors, since

$$h^2_{fa} = \sigma^2_a/\sigma^2_{fa} \text{ and } H^2_{tw} = (\sigma^2_a + {}^3/_2\, \sigma^2_d)/\sigma^2_{tw} \tag{8}$$

when σ^2_i is ignored.

Taken over the twelve measurements with significant GT values in both sexes, the means of $\hat{H}^2_{tw}$ in males, of $\hat{H}^2_{tw}$ in females, and of h^2_{fa} in families are 0.972, 0.692, and 0.600, respectively, a decreasing order.

That heritability is on the whole greater in males than in females was to be foreseen with our analysis of the correlation coefficients. Only for bizygomatic breadth and internal biocular breadth are the results reversed.

We must still understand why parent-offspring estimates are smaller than twin values in nearly all the cases. We suggest that dominance variance, detectable in twins but not in parent-child studies, may be a cause for greater heritability coefficients in twins (equation 8). This explanation holds if we admit the equality of the population variances of the twins (σ^2_{tw}) and of the families (σ^2_{fa}). We could not test this hypothesis of equality because Susanne [27], working with correlation coefficients, used only standardized (normalized) variables. However, as at the time they were measured the families lived in Brussels and the twins are scattered over a wider region, we are tempted to admit that the variances of the families are not as a rule higher than those of the twins and cannot therefore be the cause for smaller h^2_{fa} values. Another explanation for smaller $\hat{h}^2_{fa}$ values is that, since $\hat{h}^2_{fa}$ is proportional to r_{pc} (equation 7), its lower values could be due to different environmental experiences in parents and children. The same kind of argument has been used by Furusho [11], Rao et al [18], and Mueller [16] to explain higher correlation coefficients observed between sibs closer together in age and higher correlation coefficients between parents and children when parents are younger.

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CONCLUSIONS

Heritability

A significant genetic variance component, GT, was found in both sexes for the three head measurements: head length, head breadth, and frontal breadth; for seven breadth measurements of the face: bizygomatic and bigonial breadth, nose breadth, internal and external biocular breadth, interpupillary breadth and mouth breadth; and for two height variables: physio-face height and nose height. Three height measurements have a significant GT component in males but not in females: nasion-gnathion height, nasion-stomion height, and lips height. The two ear measurements have a significant GT component in females but not in males. We suggest that the difference for heritability between the sexes may be caused by random deviations and by a nonrandom factor, age, since growth proceeds in boys after 18 years, whereas it practically stops in girls at the same age.

Dominance

Comparison of heritability coefficients in twins and in families of same origin shows that dominance variance is probably present in head length and breadth, internal biocular breadth, and mouth breadth.

X-Linkage

We found no sufficient evidence for X-linkage.

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