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# Sex Differences in the Inheritance of Some Anthropometric Characters in Twins

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Biometrical genetical techniques have been applied to the analysis of certain anthropometric characters measured in 134 pairs of adult twins. After allowing for assortative mating it appears that there is a family environment ($E_2$) component for variation in height larger than previously reported. "Fatness" traits – weight, ponderal index, and skinfold thickness – all show higher heritabilities in males and substantial $E_2$ components in females, and reasons for this are discussed. The same is true for cephalic index and forearm length but the reason for these differences is not so obvious. Head length shows a much higher heritability than head breadth. A larger sample of DZ opposite-sex pairs would allow more powerful discrimination, but the variety of patterns of variation revealed by the model-fitting approach used here justify its use over more traditional techniques.

**Key words: Height, Weight, Cephalic index, Sex differences, Twins**

## INTRODUCTION

As well as having intrinsic interest, the genetical analysis of anthropometric traits in twins has long been popular in providing a benchmark against which the analysis of psychological variables could be judged. It has been supposed that "simple" and "reliable" physical measures would be much more susceptible to genetical analysis than "complex" and "labile" psychological ones. Vandenberg [14] summarises six earlier twin studies and da Rocha [1] reports a seventh more recent one, all of which list F ratios demonstrating a heritable component in a great variety of anthropometric traits.

Few of these, however, consider complications such as the relative importance of individual and family environmental effects, the role of assortative mating, or the possibility that size of genetical and environmental components of variation may be quite different in males and females. Most studies specifically exclude dizygotic opposite-sex pairs (DZOS) on the ground that they will introduce the complication of sex differences, rather than take advantage of the opportunity these pairs provide to see whether the causes of varia-

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*TABLE 1. Age, Sex, and Zygosity Composition of the Sample*

| | MZ males | MZ females | DZ males | DZ females | DZ opposite sex |
|---|---|---|---|---|---|
| Number of pairs | 23 | 45 | 20 | 33 | 13 |
| Mean age (years) | 24.39 | 26.16 | 20.95 | 25.52 | 20.85 |
| Age range | 17–53 | 15–64 | 17–37 | 16–47 | 17–31 |

tion are the same in males and females. Nearly all studies (including the present one) are too small to allow reliable discrimination between alternative models of variation in traits that are probably of intermediate inheritance.

In the present study of some anthropometric characters in twins, we have tried to remedy some of these deficiencies by applying the techniques of biometrical genetical analysis, first advocated by Jinks and Fulker [7] and developed by Eaves and his colleagues [3].

## SAMPLE AND MEASUREMENTS

A sample of 134 twin pairs was ascertained in the Sydney area by appeals in the press. The sex, zygosity, and age distribution of the sample is shown in Table 1. There is the familiar excess of female pairs over male observed in all volunteer twin studies, so we shall have better discrimination between alternative models for variation in females. Most of the twins are in their twenties but there are sufficient older pairs to create some problems in the analysis of variables heavily dependent on age. Inferences about the causes of variation can only really apply to this young age group. The twins are mainly of Northern European ancestry but the inclusion of a proportion of Southern European ancestry may inflate genetic variance between pairs our of proportion to within-pair variance.

A blood sample was taken and zygosity was diagnosed by typing with the following antisera; anti-A, $A_1$, B, C, c, D, E, e, M, N, S, s, $Fy^a$, K, and $P_1$. In addition, twin pairs were typed for HLA, using up to 29 antisera and for the serum protein haptoglobin, the enzyme red cell acid phosphatase, and the immunoglobulin Gc. Secretor, colour vision, and P.T.C. tasting status were also determined. Eye colour, hair colour, and earlobe form were noted. It is very unlikely, therefore, that any twins have been misclassified with respect to zygosity.

The folowing characters were measured or calculated according to specifications in Weiner and Lourie [16]: standing height (mm), weight (kg), inverse ponderal index height (mm) $/\sqrt[3]{\text{weight (kg)}}$, skinfold thickness – triceps ($m \times 10^{-4}$), head breadth (mm), head length (mm), cephalic index (head breadth $\times$ 100/head length), length right forearm (mm), length left forearm (mm). Forearm length was measured by placing the elbow against the back wall of a specially constructed box and moving a slide to touch the tip of the extended fingers.

Other data collected on skin reflectance and haematological and dermatoglyphic characters will be analyzed in future publications.

Some variables were not measured on all subjects and where these missing values occur will be obvious from the tables. In certain variables, extreme values were considered outliers and were excluded from the analysis. Two values for head breadth (from two different DZ female pairs) were 6.21 and 6.36 SDs above the mean. Four values for both left and right forearm length from one MZ and three different DZ female pairs were between 3.74

and 4.28 SDs below the sample mean. These values were either the result of abnormalities or recording errors. Their retention completely disrupted the genetical analysis of the normal range of variation.

## METHODS OF ANALYSIS

### Scaling

Jinks and Fulker [7] showed that certain types of genotype × environment interaction (G × E) could be detected by regressing the absolute differences of MZ pairs (a measure of individual environmental differences – $E_1$) on their pair sums (a measure of genotype (G) and/or family environment ($E_2$)). Martin and Eysenck [9] showed that such interactions could be detected with great sensitivity but that they could nearly always be removed by a transformation of the scale of measurement that lessened departures from normality. It was also found that, in most cases, such transformations had a negligible effect on the results of model-fitting to variance components and in the light of this experience we have used only one standard transformation in this analysis. Skinfold thickness was transformed using $100 \log_{10} (x - 18)$ where $x$ is the caliper reading in 0.1 mm [4].

The raw data for skinfold thickness show a significant proportion of within-pairs variance accounted for by linear and quadratic regression of absolute pair differences on pair sums. However, the transformation almost totally removes such interaction, but for the sake of interest we shall report results for both transformed and untransformed skinfold thickness to illustrate the effect of this systematic G × E on the analysis.

### Tests of Sampling

Before attempting to fit models to explain trait variation, it is important to ensure that MZ and DZ groups have been sampled in the same range, ie, that the subgroup means and variances are comparable. No significant differences between MZ and DZ means in males nor between these zygosity means in females were found. However, several significant differences between MZ and DZ total variances were found and these may cause failure of the models which we shall fit.

The same danger may apply if we attempt to fit models simultaneously to male and female data, with the added complication that any large sex difference will inflate the within-pairs mean square for DZOS pairs.

### Correction for Sex Differences and Regression on Age

The raw data to which models of variation are fitted are the between- and within-pairs mean squares from an analysis of variance of each separate group of $n$ twin pairs:

| Source | Degrees of freedom | Expected mean squares |
|---|---|---|
| Between pairs | $n-1$ | $\sigma^2_w + 2\sigma^2_b$ |
| Within pairs | | $\sigma^2_w$ |

If a variable is strongly age-dependent, then heterogeneity between age structures of subgroups will inflate differentially the between-pairs mean squares. Thus it is important to correct the between-pairs sum of squares by subtracting the sum of squares for re-

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*TABLE 2. Characters Showing Significant Correlations With Age*

| Variable | Males | Females |
|---|---|---|
| Weight | 0.49*** | 0.23** |
| Ponderal index | −0.51*** | −0.29*** |
| Skinfold thickness | 0.29** | 0.44*** |
| Transformed skinfold thickness | 0.30** | 0.34*** |

*0.01 < P < 0.05.
**0.001 < P < 0.01.
***P < 0.001.

*TABLE 3. Total Sample Means and Standard Deviations for Males and Females. Significance of Differences in Means is Indicated*

| | Males | | Females | |
|---|---|---|---|---|
| Variable | Mean | SD | Mean | SD |
| Height*** | 1,750.87 | 64.95 | 1,622.99 | 64.11 |
| Weight*** | 68.76 | 9.23 | 57.11 | 9.12 |
| Ponderal index* | 428.69 | 18.10 | 423.20 | 21.35 |
| Skinfold thickness*** | 82.31 | 30.52 | 193.56 | 91.39 |
| Head breadth*** | 153.95 | 6.64 | 146.82 | 4.99 |
| Head length | 191.62 | 7.42 | 183.92 | 6.69 |
| Cephalic index | 80.45 | 4.43 | 79.93 | 3.73 |
| Length right forearm*** | 478.70 | 20.34 | 431.39 | 26.03 |
| Length left forearm*** | 476.19 | 20.55 | 429.50 | 25.12 |

gression of pair means on age. Table 2 shows the significant linear age correlations in the variables where this correction was made. The corresponding degrees of freedom are reduced by one to $n$-2 for this correction.

The corrections are all quite predictable: variables associated with weight – skinfold thickness, ponderal index – increase with age, whereas the lack of correlation with other body measurements indicates that bone growth has ceased.

A large difference in the means of males and females will inflate the within-pairs mean square (WMS) of DZ opposite-sex pairs by an amount $n/2\ (\bar{M}-\bar{F})^2$, where there are $n$ pairs, $\bar{M}$ is the male mean and $\bar{F}$ is the female mean. Because there were only 13 DZ opposite-sex pairs, it was decided that a more reliable correction would be obtained by using total sample values of $\bar{M}$ and $\bar{F}$. The residual WMS (now with $n$-1 df) is given by $n/n-1$ [WMS $-$ ½ $(\bar{M}-\bar{F})^2$].

Male and female means for the total sample are given in Table 3 and the DZOS within mean square has been corrected in variables showing a significant difference in these means.

## Fitting Models

For each variable we now have a set of ten mean squares, corrected for age and sex differences where appropriate and these are listed in Table 4. We can fit models of variation to these mean squares using the method of weighted least-squares, which has now been discussed extensively in the literature [3, 8].

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*TABLE 4. Observed Mean Squares Used for Model Fitting*

| | Height[b] | | Weight[a,b] | | Ponderal[a,b] index | | Transformed skinfold thickness[a, b] | | Head breadth[b] | | Head length[b] | | Cephalic[b] index | | Length right forearm[b] | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Statistic | df | Observed MS | df | Observed MS | df | Observed MS | df | Observed MS | df | Observed MS | df | Observed MS | df | Observed MS | df | Observed MS |
| $MZM_b$ | 22 | 9,320.6 | 21 | 151.76 | 21 | 446.55 | 20 | 482.87 | 22 | 84.13 | 22 | 78.80 | 22 | 46.50 | 21 | 765.08 |
| $MZM_w$ | 23 | 362.7 | 23 | 11.30 | 23 | 30.26 | 22 | 58.86 | 23 | 18.28 | 23 | 10.26 | 23 | 6.03 | 22 | 24.43 |
| $MZF_b$ | 44 | 8,890.8 | 43 | 126.71 | 43 | 690.61 | 43 | 426.74 | 44 | 41.92 | 44 | 66.97 | 44 | 19.58 | 43 | 771.74 |
| $MZF_w$ | 45 | 317.5 | 45 | 21.70 | 45 | 142.91 | 45 | 173.69 | 45 | 5.93 | 45 | 8.27 | 45 | 3.10 | 44 | 27.84 |
| $DZM_b$ | 19 | 5,784.4 | 18 | 78.11 | 18 | 360.01 | 18 | 503.16 | 19 | 63.92 | 19 | 102.61 | 19 | 15.86 | 19 | 741.29 |
| $DZM_w$ | 20 | 1,160.4 | 20 | 19.21 | 20 | 120.34 | 20 | 308.50 | 20 | 25.08 | 20 | 57.10 | 20 | 13.10 | 20 | 257.55 |
| $DZF_b$ | 32 | 6,882.9 | 31 | 137.76 | 31 | 645.20 | 31 | 414.03 | 31 | 40.13 | 32 | 77.98 | 31 | 26.09 | 28 | 1,000.34 |
| $DZF_w$ | 33 | 1,434.4 | 33 | 37.17 | 33 | 214.17 | 33 | 214.21 | 32 | 11.24 | 33 | 32.30 | 32 | 5.99 | 29 | 125.30 |
| $DZO_b$ | 12 | 4,387.1 | 10 | 120.61 | 10 | 361.19 | 10 | 400.48 | 11 | 31.45 | 12 | 37.90 | 11 | 22.36 | 12 | 359.27 |
| $DZO_w$ | 12 | 1,877.4 | 11 | 33.90 | 11 | 273.65 | 11 | 431.42 | 11 | 10.54 | 12 | 20.90 | 12 | 12.97 | 12 | 230.84 |

[a]Between pairs mean squares corrected for regression on age.
[b]$DZO_w$ mean square corrected for mean difference between males and females.

*TABLE 5. Full Model for Mean Squares of MZ and DZ Twins Reared Together*

| | $D_R$ | $H_R$ | $E_1$ | $E_2$ |
|---|---|---|---|---|
| MZ between pairs | $1 + \frac{A}{1-A}$ | ½ | 1 | 2 |
| MZ within pairs | 0 | 0 | 1 | 0 |
| DZ between pairs | $¾ + \frac{A}{1-A}$ | $\frac{5}{16}$ | 1 | 2 |
| DZ within pairs | ¼ | $\frac{3}{16}$ | 1 | 0 |

The complete model for variation in MZ and DZ mean squares is shown in Table 5. $E_1$ is environmental variance within families and as such it is specific to the individual and will include error variance. $E_2$, however, includes sources of environmental variance shared by members of a family but differing between families. It will thus embrace the lasting effects of cultural and class differences and parental rearing practices. $D_R$ is that part of the genetic variation due to the additive effects of genes in the absence of assortative mating, whereas $H_R$ is variation due to dominance at loci affecting the trait. In practice it is extremely difficult to detect dominance variance in classical twin studies, even under ideal conditions, and it will usually be confounded with $D_R$ and $E_2$. A further complication arises from assortative mating which, at equilibrium, increases the additive genetic variance between families by an amount $½D_R$ (A/1−A) where A (Fisher's assortative mating parameter) is the correlation between the additive deviations of spouses and is related to the marital correlation $\mu$ by $A = h^2\mu$ ($h^2$ is the narrow heritability). As can be seen from the model, the coefficients of this extra additive variance are the same as for $E_2$ and will be completely confounded with it. It is better to think of a parameter $\hat{B} = E_2 + ½D_R$ (A/1−A).

Inference about the composition of $\hat{B}$ will depend on the size of the marital correlation. Since this model specifies that the total variances of MZ and DZ twins are equal, the model matrix is not of full rank, and a maximum of three parameters can be estimated. A sensible hierarchy of models is to first fit $E_1$ alone. Failure of this most simple model will indicate that there is significant between-families variation. A model incorporating $E_1$ and $E_2$ will test whether the between-families variation is entirely environmental in origin, and the $E_1 D_R$ model will test whether it is entirely genetic. If both two-parameter models fail, then a model incorporating all three sources of variation must be considered. As we have already indicated, the model is not of full rank, so a model comprising $E_1$, $D_R$, and $H_R$ will yield the same chi-square as the $E_1 BD_R$ model, the remaining degree of freedom simply testing the equality of MZ and DZ variances. We must decide which is the more appropriate of these two models by seeing which parameter estimates are more sensible. Because it is so difficult to detect dominance in classical twin studies, in nearly all cases it is the $E_1 BD_R$ model we shall be interested in.

There is no necessary reason why the components of variation will be the same in males and females, so we start by fitting models to the sexes separately and then the eight statistics together. At this stage we can calculate a heterogeneity chi-square for $\kappa$ df by adding the two male and female chi-squares for 4−$\kappa$ df and subtracting from the chi-square (8−$\kappa$ df) for the corresponding model of $\kappa$ parameters fitted to all eight statistics. The heterogeneity

chi-square for $\kappa$ df will indicate whether the same parameters are appropriate for both sexes. If it is not significant, then the DZOS data may be added and the same model fitted to all ten statistics.

As we shall see, different characters are best summarised by quite different models, so we shall discuss the results for each character separately.

## RESULTS

### Height

The data for stature show near perfect consistency over sexes and are summarised in Table 6. The $E_1 E_2$ (or $E_1 B$) model fails badly, indicating that sources other than these account for a significant part of the total variation. However, the data are consistent with an $E_1 D_R$ model and males and females are homogeneous for its fit ($\chi^2_2 = 0.15$), so we are justified in fitting the same model to all ten statistics. This yields $\chi^2_8 = 6.49$ and a heritability of 0.92 ± 0.02.

This is an adequate model to explain variation in stature, but we note that the fitting of a third parameter (B) produces a significant drop in chi-square ($\chi^2_1 = 3.85$) to $\chi^2_7 = 2.64$ and a significant estimate of B, so we judge this to be the most appropriate model. As discussed above, the relative contributions of $E_2$ and extra additive variance due to assortative mating (A.M.) will depend on the marital correlation ($\mu$) for stature. Spuhler [13] summarizes many studies of assortative mating for physical characteristics. A median value for stature in Northern European populations is about $\mu = 0.3$ and we can use this to estimate $A$ from the equation $A = h^2\mu$, which in the present case becomes

$$A = \mu \left[ \frac{\tfrac{1}{2} D_R \left(1 + \frac{A}{1-A}\right)}{\hat{E}_1 + \hat{B} + \tfrac{1}{2} \hat{D}_R} \right]$$

For $\mu = 0.3$ we find $\hat{A} = 0.21$ and the extra additive variance due to assortative mating $A.M. = \tfrac{1}{2} D_R \, (A/1-A) = 603.89$, or 39% of the variance estimated as $\hat{B}$. Of the total variance for height we can thus say that 7.9% is $E_1$, 23.1% is $E_2$, $\tfrac{1}{2}D_R$ is 54.5%, and 14.5% is extra additive variance due to assortative mating. The total proportion of variance due to genetic causes is thus 69%, a heritability somewhat lower than the 80–90% found in earlier studies [1, 14] employing Holzinger's [6] classical analysis of twin data. Rao et al [12] found evidence for a significant family environment component for height accounting for about 20% of the variance (in a Brazilian population) although their model explicitly excluded assortative mating and dominance. Any dominance variation for height will be confounded with $E_2$ or $D_R$ and we can make no inferences here about its possible importance.

### Weight

The data for weight are consistent with both an $E_1 E_2$ or an $E_1 D_R$ model (Table 7). Power calculations have shown [10] that, for traits of intermediate heritability, large numbers (eg, more than 600 pairs) may be required to discriminate reliably between alternative models of variation. This appears to be the case here since either two-parameter model would fit the complete data set. However, as with height, there is a significant reduction in chi-square ($\chi^2_1 = 4.04$) to $\chi^2_7 = 6.34$ when all three parameters are fitted. There is a suggestion that the heritability may be slightly higher in males than in females. Female $E_1$ variance is double

*TABLE 6. Summary of Model Fitting to Data for Height*

| Data set | Model | $\hat{E}_1$ | $\hat{B}$ | $\hat{D}_R$ | $\chi^2$ | df | $h^2$ |
|---|---|---|---|---|---|---|---|
| Males | $E_1B$ | 733.70*** | 3,474.10*** | – | 7.40* | 2 | |
| | $E_1D_R$ | 346.39*** | – | 6,836.33*** | 2.93 | 2 | 0.91 ± 0.03 |
| | $E_1BD_R$ | 359.92*** | 2,108.17* | 3,342.41* | 0.67 | 1 | 0.40 ± 0.20 |
| Females | $E_1B$ | 790.03*** | 3,627.67*** | – | 19.60*** | 2 | |
| | $E_1D_R$ | 309.54*** | – | 7,576.27*** | 2.74 | 2 | 0.92 ± 0.17 |
| | $E_1BD_R$ | 316.87*** | 1,802.54** | 4,538.51** | 0.12 | 1 | 0.52 ± 0.17 |
| Eight statistics | $E_1B$ | 770.01*** | 3,574.00*** | – | 27.48*** | 6 | |
| | $E_1D_R$ | 322.39*** | – | 7,309.87*** | 5.82 | 6 | 0.92 ± 0.02 |
| | $E_1BD_R$ | 331.56*** | 1,915.52** | 4,101.20*** | 1.13 | 5 | 0.48 ± 0.13 |
| Ten statistics | $E_1B$ | 869.92*** | 3,359.81*** | – | 32.06*** | 8 | |
| | $E_1D_R$ | 321.79*** | – | 7,133.40*** | 6.49 | 8 | 0.92 ± 0.02 |
| | $E_1BD_R$ | 331.06*** | 1,565.47** | 4,543.54*** | 2.64 | 7 | 0.55 ± 0.13 |

*TABLE 7. Summary of Model Fitting to Weight*

| Data set | Model | $\hat{E}_1$ | $\hat{B}$ | $\hat{D}_R$ | $\chi^2$ | df | $h^2$ |
|---|---|---|---|---|---|---|---|
| Males | $E_1$ | 63.87*** | – | – | 33.02*** | 3 | |
| | $E_1B$ | 14.98*** | 51.39*** | – | 3.39 | 2 | |
| | $E_1D_R$ | 10.38*** | – | 98.47*** | 3.81 | 2 | 0.83 ± 0.06 |
| | $E_1BD_R$ | 11.05*** | 35.90* | 36.57 | 1.57 | 1 | |
| Females | $E_1$ | 78.44*** | – | – | 33.35*** | 3 | |
| | $E_1B$ | 28.24*** | 51.55*** | – | 2.92 | 2 | |
| | $E_1D_R$ | 20.71*** | – | 115.04*** | 2.45 | 2 | 0.74 ± 0.06 |
| | $E_1BD_R$ | 21.98*** | 30.04 | 56.55 | 0.35 | 1 | |
| Eight statistics | $E_1$ | 73.33*** | – | – | 64.25*** | 7 | |
| | $E_1B$ | 23.53*** | 51.56*** | – | 10.98 | 6 | |
| | $E_1D_R$ | 17.06*** | – | 109.66*** | 9.79 | 6 | 0.76 ± 0.05 |
| | $E_1BD_R$ | 18.12*** | 31.85* | 49.92* | 6.37 | 5 | 0.33 ± 0.18 |
| Ten statistics | $E_1$ | 73.48*** | – | – | 67.64*** | 9 | |
| | $E_1B$ | 24.39*** | 50.89*** | – | 11.28 | 8 | |
| | $E_1D_R$ | 16.91*** | – | 110.03*** | 10.38 | 8 | 0.76 ± 0.05 |
| | $E_1BD_R$ | 18.13*** | 30.96** | 52.09* | 6.34 | 7 | 0.35 ± 0.17 |

that in males, suggesting that weight in females is more subject to individual environmental experiences than in males. Fashions in dieting and fluctuations due to menstrual cycle may partially account for this difference, although the total observed variance for females is the same as for males (Table 3).

However, any such heterogeneity between sexes is not sufficient to cause model failure, and it appears that a model in which $E_1$ accounts for 24% of total variance, additive genetic variance is 35% and the remaining between-families component is 41% will give an adequate account of the joint data for males and females. Vandenberg [15] quotes a marital correlation of 0.23 for weight, and using this value, assortative mating would only account for a trivial proportion (3.4%) of the total variance. Thus family rather than individual environment appears to be an important influence on weight, which is slightly surprising given that most of our twins are in their twenties.

### Ponderal Index

Many compound indices of body build have been proposed but we shall use the most common, viz inverse ponderal index = height (mm)/$_3\sqrt{\text{weight}}$ (kg). The results of model-fitting are presented in Table 8 and clearly show a much greater genetic component for males than for females. $\hat{E}_2$ appears to be a negligible component of variation in males but as important as genetic variation in females. This heterogeneity is reflected in the failure of attempts to fit models jointly to the eight and ten statistics.

It appears that there are different-sized $\hat{E}_1$ and $\hat{D}_R$ components for males and females and that $\hat{E}_2$ is substantial in females but negligible in males.

A full model incorporating different-sized $E_1$, $D_R$, and $E_2$ effects for males and females has been developed by Eaves [2], illustrated in Eaves et al [3] and is shown in Table 9. $D_{RMF}$ is the covariance between the genetical effects in males and the genetical effects in females. If the genes affecting a trait in males are quite different from those affecting the trait in females then we expect $\hat{D}_{RMF}$ to be zero. If the genes acting in males and females are exactly the same but produce scalar differences in the two sexes then we expect the correlation between the effects

$$r_{D_R} = \frac{D_{RMF}}{\sqrt{D_{RM} \cdot D_{RF}}}$$

to be one. A similar argument applies to $E_{2\,MF}$, the covariation between $E_2$ effects acting in males and females. Clearly, however, fairly large numbers of opposite-sex pairs will be needed to make reliable inferences about the size of $D_{RMF}$ and $E_{2\,MF}$ and we have a maximum of only 13 such pairs in this study.

If $\hat{D}_{RMF}$ and $\hat{E}_{2MF}$ are zero, then we expect that the between and within mean squares for DZOS pairs will be equal; ie, the intraclass correlation for DZOS pairs will be zero. For ponderal index we find no significant difference ($F_{10,11} = 1.32$) between the two mean squares for DZOS pairs so we can fit a model to the ten statistics which yields the following estimates:

$$\begin{aligned}
\hat{E}_{1F} &= 143.22 \pm 29.90^{***} \\
\hat{E}_{1M} &= 29.89 \pm 8.74^{***} \\
\hat{E}_{2F} &= 139.09 \pm 110.37 \\
\hat{D}_{RF} &= 276.91 \pm 232.80 \\
D_{RM} &= 407.75 \pm 85.75^{***}
\end{aligned}$$

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*TABLE 8. Summary of Model Fitting to Data for Ponderal Index*

| Data set | Model | $\hat{E}_1$ | $\hat{B}$ | $\hat{D}_R$ | $\chi^2$ | df | $h^2$ |
|---|---|---|---|---|---|---|---|
| Males | $E_1$ | 231.23*** | – | – | 22.88*** | 3 | |
| | $E_1B$ | 72.16*** | 167.23*** | – | 8.56* | 2 | |
| | $E_1D_R$ | 29.89*** | – | 409.92*** | 0.13 | 2 | 0.87 ± 0.04 |
| | $E_1BD_R$ | 30.26*** | 29.25 | 359.72** | 0.0004 | 1 | |
| Females | $E_1$ | 415.76*** | – | – | 27.69*** | 3 | |
| | $E_1B$ | 173.06*** | 249.26*** | – | 1.66 | 2 | |
| | $E_1D_R$ | 135.69*** | – | 557.81*** | 1.29 | 2 | 0.67 ± 0.07 |
| | $E_1BD_R$ | 143.36*** | 140.37 | 277.82 | 0.01 | 1 | |
| Eight statistics | $E_1$ | 351.10*** | – | – | 56.11*** | 7 | |
| | $E_1B$ | 137.20*** | 221.47*** | – | 15.20* | 6 | |
| | $E_1D_R$ | 99.97*** | – | 501.18*** | 15.62* | 6 | |
| | $E_1BD_R$ | 104.86*** | 106.29 | 294.89* | 13.22* | 5 | |
| Ten statistics | $E_1$ | 348.15*** | – | – | 57.33*** | 9 | |
| | $E_1B$ | 148.57*** | 206.88*** | – | 18.51* | 8 | |
| | $E_1D_R$ | 100.91*** | – | 496.87*** | 16.02* | 8 | |
| | $E_1BD_R$ | 104.66*** | 68.33 | 363.89* | 14.73* | 7 | |

*TABLE 9. Model for the Covariation of Genetical and of Environmental Effects in Mean Squares of DZ Opposite-Sex Twin Pairs*

| | $E_{1m}$ | $E_{1f}$ | $E_{2m}$ | $E_{2f}$ | $E_{2mf}$ | $D_{Rm}$ | $D_{Rf}$ | $D_{Rmf}$ |
|---|---|---|---|---|---|---|---|---|
| $MZB_{males}$ | 1 | · | 2 | · | · | 1 | · | · |
| $MZW_{males}$ | 1 | · | · | · | · | · | · | · |
| $MZB_{females}$ | · | 1 | · | 2 | · | · | 1 | · |
| $MZW_{females}$ | · | 1 | · | · | · | · | · | · |
| $DZB_{males}$ | 1 | · | 2 | · | · | ¾ | · | · |
| $DZW_{males}$ | 1 | · | · | · | · | ¼ | · | · |
| $DZB_{females}$ | · | 1 | · | 2 | · | · | ¾ | · |
| $DZW_{females}$ | · | 1 | · | · | · | · | ¼ | · |
| $DZB_{m\text{-}f}$ | ½ | ½ | ½ | ½ | 1 | ¼ | ¼ | ¼ |
| $DZW_{m\text{-}f}$ | ½ | ½ | ½ | ½ | −1 | ¼ | ¼ | −¼ |

$D_{RM}$ = $D_R$ effect for males.
$D_{RF}$ = $D_R$ effect for females.
$D_{RMF}$ = covariance of $D_{RM}$ and $D_{RF}$.
Similarly for $E_2$ and $E_1$.

Fitting separate parameters for males and females has caused a reduction of chi-square from $\chi^2_7 = 14.73$ to $\chi^2_5 = 0.34$. Neither $\hat{E}_{2F}$ nor $\hat{D}_{RF}$ is significant, which is not surprising given that we have fairly small numbers and that there is a negative correlation of –0.87 between these parameter estimates. Most striking is the large difference between the (nonsignificant) heritability of 0.33 ± 0.28 for females and the value of 0.87 ± 0.04 for males, demonstrating the much greater importance to females of environmental influences, both individual and shared by sisters, on this measure of body build.

### Skinfold Thickness

Not surprisingly, the results for skinfold thickness are very similar to those for ponderal index. The results of model-fitting to the untransformed data have been included here (Table 10) to illustrate the difference that an appropriate transformation can make to the data analysis in certain cases. Comparing these with the results for the transformed data (Table 11), it can be seen that transformation has particularly improved the model-fitting to female data.

Once again it appears that there is a high heritability for males but larger $\hat{E}_1$ and $\hat{E}_2$ components for females. This is despite the fact that the total variance for males is almost double that in females. The DZOS between-pairs mean square is not significantly greater than the within-pairs mean square (we have fitted the same model as for ponderal index) so the joint transformed data yield the following estimates:

$$\hat{E}_{1F} = 176.42 \pm 36.07^{***}$$
$$\hat{E}_{1M} = 63.81 \pm 18.98^{***}$$
$$\hat{E}_{2F} = 61.47 \pm 101.20$$
$$\hat{D}_{RF} = 145.54 \pm 233.93$$
$$\hat{D}_{RM} = 646.85 \pm 140.52^{***}$$

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*TABLE 10. Summary of Model Fitting to Untransformed Skinfold Thickness Data*

| Data set | Model | $\hat{E}_1$ | $\hat{B}$ | $\hat{D}_R$ | $\chi^2$ | dg | $h^2$ |
|---|---|---|---|---|---|---|---|
| Males | $E_1$ | 761.85*** | – | – | 13.15** | 3 | |
| | $E_1B$ | 397.89*** | 383.11** | – | 10.72* | 2 | |
| | $E_1D_R$ | 137.62*** | – | 1,456.62*** | 2.51 | 2 | 0.84 ± 0.06 |
| | $E_1BD_R$ | 129.68*** | −290.90 | 2,052.35** | 0.66 | 1 | |
| Females | $E_1$ | 7,056.84*** | – | – | 26.11*** | 3 | |
| | $E_1B$ | 4,410.61*** | 2,717.75** | – | 8.25* | 2 | |
| | $E_1D_R$ | 4,192.56*** | – | 5,559.45** | 9.06* | 2 | |
| | $E_1BD_R$ | 4,259.62*** | 1,390.88 | 2,787.25 | 8.64** | 1 | |
| Eight statistics | $E_1$ | 4,886.15*** | – | – | 92.28*** | 7 | |
| | $E_1B$ | 4,410.61*** | 1,947.14*** | – | 61.26*** | 6 | |
| | $E_1D_R$ | 2,839.55*** | – | 3,987.70*** | 63.57*** | 6 | |
| | $E_1BD_R$ | 2,906.16*** | 1,210.72 | 1,574.25 | 62.09*** | 5 | |
| Ten statistics | $E_1$ | 4,640.63*** | – | – | 112.94*** | 9 | |
| | $E_1B$ | 2,884.90*** | 1,820.49*** | – | 71.16*** | 8 | |
| | $E_1D_R$ | 2,729.86*** | – | 3,702.46*** | 74.21*** | 8 | |
| | $E_1BD_R$ | 2,815.04*** | 1,367.13 | 978.84 | 71.90*** | 7 | |

*TABLE 11. Summary of Model Fitting to Transformed Skinfold Thickness Data*

| Data set | Model | $\hat{E}_1$ | $\hat{B}$ | $\hat{D}_R$ | $\chi^2$ | df | $h^2$ |
|---|---|---|---|---|---|---|---|
| Males | $E_1$ | 377.24*** | – | – | 12.29** | 3 | |
| | $E_1B$ | 177.74*** | 157.37** | – | 10.34** | 2 | |
| | $E_1D_R$ | 64.18*** | – | 614.32*** | 2.66 | 2 | 0.83 ± 0.06 |
| | $E_1BD_R$ | 60.02*** | – 14.55 | 881.83** | 0.89 | 1 | |
| Females | $E_1$ | 303.09*** | – | – | 11.17** | 3 | |
| | $E_1B$ | 190.83*** | 115.29** | – | 0.44 | 2 | |
| | $E_1D_R$ | 168.74*** | – | 273.26** | 0.38 | 2 | 0.45 ± 0.11 |
| | $E_1BD_R$ | 175.32*** | 500.62 | –477.24 | 0.03 | 1 | |
| Eight statistics | $E_1$ | 311.41*** | – | – | 24.32*** | 7 | |
| | $E_1B$ | 186.25*** | 129.64*** | – | 10.26 | 6 | |
| | $E_1D_R$ | 141.20*** | – | 355.97*** | 7.10 | 6 | 0.56 ± 0.08 |
| | $E_1BD_R$ | 139.94*** | – 12.42 | 382.69* | 7.12 | 5 | |
| Ten statistics | $E_1$ | 320.15*** | – | – | 24.07** | 9 | |
| | $E_1B$ | 206.84*** | 117.50*** | – | 15.51* | 8 | |
| | $E_1D_R$ | 148.00*** | – | 364.07*** | 10.20 | 8 | 0.55 ± 0.08 |
| | $E_1BD_R$ | 140.74*** | – 56.52 | 491.30** | 9.44 | 7 | |

Allowing for sex-limited parameters has caused a large reduction in chi-square to $\chi^2_5 = 2.97$. As for ponderal index, the female heritability is small and nonsignificant ($0.23 \pm 0.37$) whereas that for males is very high ($0.84 \pm 0.06$).

### Head Breadth

Males have both a larger mean and a larger variance than females for head breadth. The data for both sexes are compatible both with an $E_1 E_2$ and $E_1 D_R$ model, and the heritability on the simple genetic model is slightly higher for females (Table 12). It appears that both $D_R$ and $E_2$ make substantial contributions to variance in both males and females but that these will differ in both relative and absolute size. Assortative mating is negligible [5, 13].

A model allowing different $E_1$ and $D_R$ parameters (and also $D_{RMF}$) for males and females does not adequately account for the data ($\chi^2_5 = 11.92$, $P = 0.036$) but when separate $E_2$ parameters are also included in the model there is a large reduction of $\chi^2_2 = 10.34$ to $\chi^2_3 = 1.58$ and the following estimates are obtained:

$$\begin{aligned}
\hat{E}_{1F} &= 5.95 \pm 1.25^{***} \\
\hat{E}_{1M} &= 17.63 \pm 5.13^{***} \\
\hat{E}_{2F} &= 8.15 \pm 5.96 \\
\hat{E}_{2M} &= 12.28 \pm 16.40 \\
\hat{D}_{RF} &= 20.30 \pm 11.80 \\
\hat{D}_{RM} &= 30.40 \pm 36.31 \\
\hat{D}_{RMF} &= 92.17 \pm 24.69^{***}
\end{aligned}$$

We cannot resolve how much of the significant covariance term is actually $D_{RMF}$ or $E_{2MF}$ since these parameters would have identical coefficients in the model. So the interpretation of the parameter listed as $D_{RMF}$ must be left open. It is surprising, however, that the unequivocal additive genetic component in head breadth is so low ($h^2_{female} = 0.42 \pm 0.24$, $h^2_{male} = 0.34 \pm 0.40$).

### Head Length

Similar problems occur in the analysis of head length. Male mean and variance are higher than those for females but the importance of additive genetic effects is identical in males and females (Table 13). There is a tendency to heterogeneity ($\chi^2_2 = 4.95$) when the $E_1 D_R$ model is fitted to the sexes jointly and a substantial reduction ($\chi^2_3 = 5.50$) is achieved by fitting separate parameters for males and females to the ten statistics to yield $\chi^2_5 = 8.47$ and the following parameter estimates

$$\begin{aligned}
\hat{E}_{1F} &= 8.53 \pm 1.77^{***} \\
\hat{E}_{1M} &= 11.31 \pm 3.28^{***} \\
\hat{D}_{RF} &= 74.09 \pm 12.34^{***} \\
\hat{D}_{RM} &= 102.86 \pm 22.26^{***} \\
\hat{D}_{RMF} &= 116.61 \pm 43.99^{**}
\end{aligned}$$

However, the heritabilities remain identical ($h^2_{female} = 0.81 \pm 0.05$, $h^2_{male} = 0.82 \pm 0.06$) and the correlation between additive effects acting in males and females is not significantly different from one, indicating that the same genes are acting in the two sexes but are producing their effects on different scales.

*TABLE 12. Summary of Model Fitting for Head Breadth*

| Data set | Model | $\hat{E}_1$ | $\hat{B}$ | $\hat{D}_R$ | $\chi^2$ | df | $h^2$ |
|---|---|---|---|---|---|---|---|
| Males | $E_1$ | 47.47*** | – | – | 14.28** | 3 | |
| | $E_1B$ | 21.44*** | 26.66** | – | 0.91 | 2 | |
| | $E_1D_R$ | 17.03*** | – | 59.93** | 0.64 | 2 | 0.64 ± 0.11 |
| | $E_1BD_R$ | 17.95*** | 14.08 | 31.67 | 0.16 | 1 | 0.33 ± 0.39 |
| Females | $E_1$ | 24.44*** | – | – | 35.20*** | 3 | |
| | $E_1B$ | 8.14*** | 16.52** | – | 4.00 | 2 | |
| | $E_1D_R$ | 5.68*** | – | 36.77*** | 1.66 | 2 | 0.76 ± 0.06 |
| | $E_1BD_R$ | 5.96*** | 8.50 | 20.55* | 0.07 | 1 | 0.42 ± 0.24 |
| Eight statistics | $E_1$ | 32.64*** | – | – | 63.41*** | 7 | |
| | $E_1B$ | 12.91*** | 20.07*** | – | 23.78*** | 6 | |
| | $E_1D_R$ | 9.63*** | – | 45.37*** | 22.92*** | 6 | |
| | $E_1BD_R$ | 10.10*** | 9.90 | 25.91 | 21.21*** | 5 | |
| Ten statistics | $E_1$ | 31.64*** | – | – | 70.01*** | 9 | |
| | $E_1B$ | 12.71*** | 19.24*** | – | 25.86** | 8 | |
| | $E_1D_R$ | 9.44*** | – | 43.31*** | 26.01*** | 8 | |
| | $E_1BD_R$ | 10.03*** | 10.44* | 22.75* | 23.69** | 7 | |

*TABLE 13. Summary of Model Fitting for Head Length*

| Data set | Model | $E_1$ | $E_2$ | $D_R$ | $H_R$ | $x^2$ | df | $h^2$ |
|---|---|---|---|---|---|---|---|---|
| Males | $E_1B$ | 32.05*** | 28.89** | – | – | 11.78** | 2 | |
| | $E_1D_R$ | 11.19*** | – | 113.74*** | – | 3.56 | 2 | 0.84 ± 0.06 |
| | $E_1BD_R$ | 10.55*** | −23.12 | 156.36* | – | 2.07 | 1 | |
| | $E_1D_RH_R$ | 10.55*** | – | 17.63 | 184.97 | 2.07 | 1 | |
| Females | $E_1B$ | 18.44*** | 26.59*** | – | – | 16.40*** | 2 | |
| | $E_1D_R$ | 8.54*** | – | 77.04*** | – | 1.99 | 2 | 0.82 ± 0.04 |
| | $E_1BD_R$ | 8.44*** | − 3.73 | 83.97** | – | 1.92 | 1 | |
| | $E_1D_RH_R$ | 8.44*** | – | 61.58 | 29.85 | 1.92 | 1 | |
| Eight statistics | $E_1B$ | 23.27*** | 27.36*** | – | – | 37.95*** | 6 | |
| | $E_1D_R$ | 9.47*** | – | 90.07*** | – | 10.50 | 6 | 0.83 ± 0.03 |
| | $E_1BD_R$ | 9.17*** | −11.39 | 111.01*** | – | 8.53 | 5 | |
| | $E_1D_RH_R$ | 9.17*** | – | 42.66 | 91.13 | 8.53 | 5 | |
| Ten statistics | $E_1B$ | 22.96*** | 25.65*** | – | – | 40.42*** | 8 | |
| | $E_1D_R$ | 9.45*** | – | 84.20*** | – | 13.97 | 8 | 0.82 ± 0.04 |
| | $E_1BD_R$ | 9.14*** | − 9.86 | 102.52*** | – | 11.83 | 7 | |
| | $E_1D_RH_R$ | 9.14*** | – | 43.37 | 78.87 | 11.83 | 7 | |

### Cephalic Index

This compound variable is different from both its elements, head breadth and head length. Variation is clearly largely genetic in males but there is a substantial $E_2$ component in females. This heterogeneity leads to failure of models fitted to the joint data (Table 14) and a model allowing separate $E_1$ and $D_R$ parameters (and $D_{RMF}$) for males and females fits badly ($\chi^2_5 = 13.45$). However, inclusion of an $E_2$ parameter for females leads to a dramatic reduction of $\chi^2_1 = 8.96$ to $\chi^2_5 = 4.49$ and the parameter estimates resulting from this model are:

$$\begin{aligned}
\hat{E}_{1F} &= 3.17 \pm 0.67^{***} \\
\hat{E}_{1M} &= 5.93 \pm 1.69^{***} \\
\hat{E}_{2F} &= 5.36 \pm 3.17^{*} \\
\hat{D}_{RF} &= 9.99 \pm 6.13 \\
\hat{D}_{RM} &= 28.98 \pm 7.35^{***} \\
\hat{D}_{RMF} &= 17.36 \pm 18.35
\end{aligned}$$

Although the genetic component of variation in females is much smaller ($h^2_{female} = 0.37 \pm 0.23$, $h^2_{male} = 0.71 \pm 0.09$), it should be noted that there is a perfect correlation between the genetic effects in males and females ($r_{D_R} = 1.02$).

### Forearm Length

The results for left and right forearm length are so similar that only those for the latter will be discussed (Table 15). An $E_1 D_R$ model is adequate for males and a high heritability is indicated. However, both simple models fail for females and significant $\hat{E}_2$ and $\hat{D}_R$ parameters are estimated when the three-parameter model is fitted. Although the joint data are consistent ($\chi^2_8 = 9.60$) with an $E_1 D_R$ model and a high heritability ($0.94 \pm 0.01$), a large reduction of $\chi^2_4 = 6.5$ to $\chi^2_4 = 3.10$ is achieved by fitting separate parameters for either sex and an $E_2$ parameter for females yielding the following estimates:

$$\begin{aligned}
\hat{E}_{1F} &= 27.95 \pm 5.96^{***} \\
\hat{E}_{1M} &= 24.58 \pm 7.40^{***} \\
\hat{E}_{2F} &= 239.19 \pm 88.51^{**} \\
\hat{D}_{RF} &= 369.56 \pm 127.91^{**} \\
\hat{D}_{RM} &= 817.61 \pm 153.03^{***} \\
\hat{D}_{RMF} &= 612.65 \pm 446.01
\end{aligned}$$

Once again, we see a high heritability for males ($h^2_{male} = 0.94 \pm 0.02$), a much lower one for females ($h^2_{females} = 0.41 \pm 0.15$) and a perfect correlation ($r_{DR} = 1.11$) between additive genetic effects acting in males and females.

## DISCUSSION

The range of models appropriate for different characters and the apparent differences in genetic architecture between males and females for some traits fully justify the more sensitive biometrical genetical analysis employed here over the traditional techniques used by earlier authors. In particular, the inclusion of opposite-sex twins, far from complicating the analysis, allows us to see whether the genetical and environmental causes of variation are the same in males and females. It is only unfortunate that the number of DZOS pairs

*TABLE 14. Summary of Model Fitting for Cephalic Index*

| Data set | Model | $\hat{E}_1$ | $\hat{B}$ | $\hat{D}_R$ | $\chi^2$ | df | $h^2$ |
|---|---|---|---|---|---|---|---|
| Males | $E_1$ | 20.54*** | – | – | 25.12*** | 3 | |
| | $E_1B$ | 9.31*** | 11.49*** | – | 7.66* | 2 | |
| | $E_1D_R$ | 5.92*** | – | 28.67*** | 2.99 | 2 | 0.71 ± 0.09 |
| | $E_1BD_R$ | 5.73*** | – 5.54 | 40.11* | 2.31 | 1 | |
| Females | $E_1$ | 13.17*** | – | – | 38.08*** | 3 | |
| | $E_1B$ | 4.30*** | 8.99*** | – | 5.01 | 2 | |
| | $E_1D_R$ | 2.98*** | – | 20.29*** | 4.56 | 2 | 0.77 ± 0.05 |
| | $E_1BD_R$ | 3.17*** | 5.33* | 9.96 | 1.54 | 1 | |
| Eight statistics | $E_1$ | 15.79*** | – | – | 74.87*** | 7 | |
| | $E_1B$ | 6.10*** | 9.86*** | – | 28.40*** | 6 | |
| | $E_1D_R$ | 3.99*** | – | 23.44*** | 16.16* | 6 | |
| | $E_1BD_R$ | 4.07*** | 2.31 | 19.03** | 16.09** | 5 | |
| Ten statistics | $E_1$ | 15.94*** | – | – | 74.60*** | 9 | |
| | $E_1B$ | 6.72*** | 9.40*** | – | 31.12*** | 8 | |
| | $E_1D_R$ | 4.03*** | – | 23.90*** | 16.20* | 8 | |
| | $E_1BD_R$ | 4.08*** | 1.00 | 21.98*** | 16.26* | 7 | |

*TABLE 15. Summary of Model Fitting for Length of Right Forearm*

| Data set | Model | $\hat{E}_1$ | $\hat{B}$ | $\hat{D}_R$ | $\chi^2$ | df | $h^2$ |
|---|---|---|---|---|---|---|---|
| Males | $E_1$ | 43.71*** | – | – | 22.01*** | 3 | |
| | $E_1B$ | 135.44*** | 309.17*** | – | 15.52*** | 2 | |
| | $E_1D_R$ | 24.56*** | – | 868.87*** | 0.35 | 2 | 0.95 ± 0.02 |
| | $E_1BD_R$ | 24.53*** | − 12.98 | 889.88** | 0.36 | 1 | |
| Females | $E_1$ | 458.70*** | – | – | 56.60*** | 3 | |
| | $E_1B$ | 66.56*** | 397.67*** | – | 19.33*** | 2 | |
| | $E_1D_R$ | 27.22*** | – | 815.06*** | 7.69* | 2 | |
| | $E_1BD_R$ | 27.98*** | 256.74** | 374.25** | 1.20 | 1 | 0.40 ± 0.15 |
| Eight statistics | $E_1$ | 450.85*** | – | – | 79.33*** | 7 | |
| | $E_1B$ | 91.71*** | 365.61*** | – | 52.10*** | 6 | |
| | $E_1D_R$ | 26.39*** | – | 834.09*** | 7.91 | 6 | 0.94 ± 0.01 |
| | $E_1BD_R$ | 26.83*** | 148.97* | 583.60*** | 5.74 | 5 | 0.62 ± 0.16 |
| Ten statistics | $E_1$ | 435.90*** | – | – | 86.52*** | 9 | |
| | $E_1B$ | 104.86*** | 336.42*** | – | 51.66*** | 8 | |
| | $E_1D_R$ | 26.41*** | – | 806.78*** | 9.60 | 8 | 0.94 ± 0.02 |
| | $E_1BD_R$ | 26.80*** | 106.29 | 631.39*** | 7.75 | 7 | 0.70 ± 0.16 |

*TABLE 16. Correlation of MZ Absolute Pair Differences With Age*

| | Height | Weight | Ponderal index | Transformed skinfold thickness |
|---|---|---|---|---|
| MZ males | −0.24 | 0.33 | 0.25 | 0.08 |
| MZ females | 0.02 | 0.33* | 0.30 | 0.38* |

in this study was too small to obtain the fine discrimination possible with these models, and it should be an object of future studies to increase rather than exclude the sample of opposite-sex pairs.

The role of assortative mating and the surprisingly large $E_2$ component for height have already been mentioned, as has the contrast in the low heritability of head breadth, compared with the high heritability of head length. Several other features of the analysis, however, bear further discussion.

The consistency of the results for weight, ponderal index, and skinfold thickness is impressive. All are measures of body build or fatness and all show the much greater importance to females of environmental experiences, both individual and shared with twin sister, than in their male counterparts. Whether this reflects or justifies the interest of modern Western women with this subject is open to debate.

One surprising feature is the continuing influence of family environmental effects on these fatness traits in women who presumably are no longer living together. This may reflect some continuing permanent effect of some early shared dietary practice, in which case one would expect the $E_2$ effect to remain constant with age. However, it may reflect the continuation of dietary habits acquired together as children, in which case one might expect these $E_2$ effects to attenuate with age and changes in individual habits to be reflected in increasing $E_1$ differences. To test these possibilities we regressed absolute pair differences in MZ twins (a measure of $E_1$) on age for the three "fatness" traits and height as a control. The correlation coefficients are shown in Table 16 and are most striking for MZ females where there are significant (or near significant) correlations for all three "fatness" traits, indicating the increasing importance of individual habits with age. This suggests that some of the shared environmental effects ($E_2$) influencing "fatness" at an early age become individual environmental effects ($E_1$) later in life. Clearly, however, these correlations will not explain all of the rather large $E_2$ effects for "fatness" that continue into adulthood.

It has been found that the number of adipocytes produced in young rats depends on diet and exercise regime and that, in adult humans, increased cell number plays a more important role in the development of the grossly overweight condition than does cell size [11]. One can therefore see how a family environmental effect of diet at an early age could continue to manifest itself as an $E_2$ effect in adult life when twins are no longer living together.

There is a striking similarity between results for forearm length and those for cephalic index. While one can rationalize sex differences in heritability for fatness traits, the reasons for the substantial between-families effect for cephalic index and forearm length in females are not clear. This difference is not obvious in earlier reported studies but many authors have pooled data across sexes or sample sizes are too small to detect such differences. The possibility of some oddity in sampling cannot be ruled out. Nevertheless, such differences if real may reveal interesting contrasts in the genetic and environmental influences to which males and females are subject during development.

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