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## Genetic and Environmental Variation of Ridge-Counts on Fingers, Palms, Soles and Toes: A Twin Study

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**Abstract:** A multivariate procedure for estimating heritable components from twin data was applied to ridge counts obtained from the entire dermatoglyphic system. Covariance matrices of MZ and DZ within-pair differences were used to estimate genetic correlation matrices for 20 finger ridge counts, 6 palmar interdigital counts, 20 toe counts, 4 hallucal counts, and 6 sole interdigital counts. The proportion of genetic variation was found to be greater in ridge counts of patterns than in ridge counts of interdigital areas. On digits, finger counts are more highly heritable than toe counts. Each of the dermatoglyphic areas yielded several independent genetic components, ranging from general to specific. Environmental variation was found to be local and to frequently involve reciprocal interaction between twin pairs.

**Key words:** Twins, Dermatoglyphics, Genetic factors, Multivariate analysis

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### INTRODUCTION

The genetics of ridge counts, primarily finger ridge counts, has been investigated intensively for many years. Twins have played a central role in attempting to sort out genetic from environmental variation [11,21,23]. The majority of such studies have focused on total ridge count or other summary features, an approach which necessarily ignores the multidimensional nature of ridge count variation. Holt [12] attempted to deal with the problem by maximizing the intraclass correlation between monozygotic twins, using the larger count for each digit, both hands summed. She concluded that there was very little improvement over using the total ridge count itself, although she confined her attention to the linear function associated with the largest root.

Closely related to the maximization of the intraclass correlation is the multivariate

generalization of the classical twin model where the dizygotic/monozygotic (DZ/MZ) is maximized [4]. This procedure has been applied to a variety of human biological data [18,19,20]. To our knowledge, Nance et al's [19] study represents the only application of this technique to dermatoglyphic data. Their data were limited to finger ridge counts plus some direct measurements and angles of the palm.

Fulker [10] has discussed the assumptions of this model; it assumes only additive genetic variance, no genotype-environment interaction, and that MZ and DZ twins share relevant aspects of their environment. The model does provide a straightforward multivariate solution to the problem of genetic components. Since little is known about genetic and environmental components of ridge counts, apart from those of fingers, we apply the model to ridge counts derived from the entire dermatoglyphic system.

## MATERIALS AND METHODS

The samples consist of 141 MZ and 110 DZ same-sex twin pairs. Twins were sampled from three areas, Freiburg, Baden-Württemberg (71 MZ and 63 DZ), Vienna (45 MZ and 37 DZ) and Knoxville (25 MZ and 10 DZ).

Zygoty was determined using non-dermatoglyphic morphological features. These include external characteristics of the face, ears, fingers and toes; several dental, tongue and palate details; body weight and height; hair and eye color. Use of the morphological methods is described in Martin and Saller [16]. In 18 ambiguous cases serological tests were carried out (see Brehme [5] for details of sampling and zygosity testing).

The variables are ridge counts, each individual being represented by 20 finger counts (radial and ulnar count for each digit), 6 palmar interdigital counts (a-b, b-c, and c-d for each hand), 20 toe counts (tibial and fibular count for each toe), 4 hallucal counts (tibial and distal count for each foot's thenar/I area), and 6 interdigital sole counts (a-b, b-c, and c-d counts for each foot). All ridge counting was carried out by the second author according to the precise rules given by Brodhage and Wendt [8] and Baitsch and Schwarzfischer [2]. Individuals with more than four missing toe or finger values due to missing or damaged prints were excluded, otherwise the missing values were replaced by regression. Very few individuals were excluded from the analysis for this reason.

The interdigital counts of the sole in whites present a special problem, in that it is frequently not possible to count the ridges at all because of the occurrence of distally closed patterns in the areas II to IV. Excluding those twin pairs where one or both could not be counted reduced sample size by about two-thirds for each of the zygosity types, resulting in 46 MZ and 33 DZ twins for interdigital sole variables.

Each morphological area was analysed separately, yielding five analyses. Analysing in such a way may bias the number of independent genetic components upward if there is correlation between the different areas. Such correlation has been shown between finger and toe counts [7] and between different pattern areas of the entire epidermal pattern system [28]. The level of correlation generally seems to be low, so the overestimation of the number of genetic components should be slight. Moreover, most investigators tend to focus attention on the dermatoglyphic areas individually rather than on the system as a whole, so it is desirable at this stage to present the analyses separately for each area.

The method used is the multivariate generalization of the DZ/MZ ratio as given by Bock and Vandenberg [4] where details can be found. If  $V_{DZ}$  and  $V_{MZ}$  are the intrapair covariance matrices for DZ and MZ twins respectively, the roots of  $V_{DZ} (V_{MZ}^{-1})$  represent the maximized variance ratios, and the associated eigenvectors are the weighted linear functions maximizing the  $V_{DZ}/(V_{MZ})$  ratio. An intraclass correlation coefficient expressing the proportion of heritable variation of each root can be calculated as:

$$r_1 = \lambda_1 - 1/\lambda_1$$

Equations suggested by Burnaby [9] were solved using the MATRIX procedure in the SAS package [25]. Given a matrix  $V_{MZ}$ , find a matrix A such that  $A'A = V_{MZ}$ . If  $m$  = the eigenvectors of the symmetric matrix  $A(V_{DZ})A'$ , then the canonical vectors are  $X = A'm$ .

Bock and Vandenberg [4] also present a procedure for obtaining the genetic covariance matrix from the latent roots and canonical vectors of  $V_{DZ}(V_{MZ})$ :

$$E_h = (X^{-1})^\lambda (\lambda^* - 1) (X^{-1})$$

where I is the identity matrix and  $\lambda^*$  is the diagonal matrix of latent roots modified by setting those less than one equal to unity. It is necessary to calculate  $E_h$  in this manner rather than using the unbiased estimate  $V_{DZ}-V_{MZ}$ , because the latter is usually not positive semidefinite.

Tests of significance were carried out by means of Bartlett's  $\chi^2$ . This test assumes multivariate normality, a condition which is probably not met in some of our data. Certainly many of the individual variables are not normally distributed (eg, ulnar ridge counts on fingers), although it has been noted [27] that the linear functions will be more normally distributed than the original variables. We feel that the significance tests are generally reliable, particularly when probabilities are low. In any case, nonnormality will not influence the direction of the axes of heritable variation take in multidimensional space and morphological interpretations should be valid.

Analysis of structure was carried out by converting the genetic and MZ intrapair covariance matrices to correlation matrices and subjecting them to principal factor analysis with varimax rotation (SAS FACTOR procedure). In the case of the genetic correlation matrices the number of factors retained corresponds to the number of dimensions of the  $V_{DZ}(V_{MZ})$  ratio exhibiting a positive correlation with heritable variation. For the MZ intrapair correlations, principal components associated with eigenvalues greater than 1.0 were retained for rotation.

## RESULTS

### Heritable Dimensions

Values for the roots extracted from the  $V_{DZ}(V_{MZ})$  matrix, their correlations with heritable variation, and Bartlett's  $\chi^2$  test are given in Tables 1-5. It may be observed that several roots show positive correlation with heritable variation, but are not statistically significant. We follow Bock and Vandenberg [4] in including these roots and their associated discriminant functions in the computation of the genetic covariance matrix.

Table 1 - Canonical Roots and Bartlett's Chi Square for the  $V_{DZ}/(V_{MZ}^{-1})$  Ratio of 20 Finger Ridge Counts

Root no.	Root	Correlation with heritable variation	$\chi^2$	df	P
0	...	...	3998.35	2200	< 0.001
1	26.33	0.96	3428.84	2071	< 0.001
2	9.79	0.90	3028.84	1944	< 0.001
3	8.25	0.88	2656.57	1819	< 0.001
4	5.87	0.83	2337.66	1696	< 0.001
5	4.34	0.77	2063.30	1575	< 0.001
6	3.18	0.69	1832.07	1456	< 0.001
7	2.81	0.64	1616.61	1339	< 0.001
8	2.52	0.60	1414.72	1224	< 0.001
9	2.07	0.52	1236.51	1111	< 0.01
10	1.88	0.47	1069.02	1000	≅ .13
11	1.66	0.40	914.75	891	ns
12	1.54	0.35	768.20	784	ns
13	1.36	0.26	634.34	679	ns
14	1.26	0.21	507.46	576	ns
15	1.09	0.08	393.36	475	ns

Roots < 1.0

**Table 2 - Canonical Roots and Bartlett's Chi Square for the  $V_{DZ}/(V_{MZ}^{-1})$  Ratio of 6 Palmar Interdigital Ridge Counts**

Root no.	Root	Correlation with heritable variation	$\chi^2$	df	P
0	...	...	1168.26	654	< 0.001
1	9.61	0.90	759.01	540	< 0.001
2	3.96	0.75	489.98	428	< 0.05
3	2.15	0.53	302.07	318	ns
4	1.05	0.04	188.31	210	ns
.	Roots < 1.0				
6					

**Table 3 - Canonical Roots and Bartlett's Chi Square for the  $V_{DZ}/(V_{MZ}^{-1})$  Ratio of 20 Toe Ridge Counts**

Root no.	Root	Correlation with heritable variation	$\chi^2$	df	P
0	...	...	3423.12	2140	< 0.001
1	14.01	0.93	2972.91	2014	< 0.001
2	8.83	0.89	2598.18	1890	< 0.001
3	6.10	0.84	2280.97	1768	< 0.001
4	5.56	0.82	1977.52	1648	< 0.001
5	3.42	0.71	1742.39	1530	< 0.001
6	3.01	0.67	1524.05	1414	< 0.05
7	2.34	0.57	1336.60	1300	ns
8	2.05	0.51	1164.20	1188	ns
9	1.90	0.47	999.92	1078	ns
10	1.77	0.43	843.41	970	ns
11	1.57	0.36	698.94	864	ns
12	1.24	0.20	576.77	760	ns
13	1.08	0.08	466.50	658	ns
14	1.01	0.01	361.45	558	ns
.	Roots < 1.0				
.					
20					

**Table 4 - Canonical Roots and Bartlett's Chi Square for the  $V_{DZ}/(V_{MZ}^{-1})$  ratio of 4 Hallucal Ridge Counts**

Root no.	Root	Correlation with heritable variation	$\chi^2$	df	P
0	...	...	892.06	436	< 0.001
1	5.49	0.82	572.39	324	< 0.001
2	4.75	0.79	274.89	214	< 0.01
3	1.70	0.41	112.82	106	ns
4	1.03	0.03	...	...	

Table 5 - Canonical Roots and Bartlett's Chi Square for the  $V_{DZ}/(V_{MZ}^{-1})$  Ratio of 6 Sole Interdigital Ridge Counts

Root no.	Root	Correlation with heritable variation	$\chi^2$	df	P
0	...	...	323.93	198	< 0.001
1	6.00	0.83	225.52	160	< 0.001
2	2.94	0.66	158.56	124	< 0.05
3	2.05	0.51	105.13	90	ns
4	1.53	0.35	61.37	58	ns
5	1.17	0.15	25.44	28	ns
6	Root < 1.0				

Most noteworthy is the large number of significant dimensions seen in finger and toe ridge counts, ten and seven respectively. While, as noted, nonnormality of some of the variables may cause the tests to be only approximate, the high dimensionality of heritable variation should still be evident. The palm and sole counts each yield three significant heritable components. Somewhat surprising is the hallucal area, which, with only four variables, yields three significant heritable dimensions, and all four show positive correlation with heritable variation.

The roots and associated discriminant functions were used to calculate genetic covariance matrices, which represent that part of the total DZ intrapair variation due to genetic variation. An idea of the proportion of genetic variation can be obtained by calculating the ratio  $\text{Tr}(E_h)/\text{Tr}(V_{DZ})$ . These ratios are, for fingers 0.738, for palmar interdigitals 0.647, for toes 0.706, for hallucals 0.708 and for sole interdigitals 0.565. It is evident from these figures that ridge counts of patterns have higher heritabilities than interdigital ridge counts.

The genetic covariance matrices were converted to correlation matrices and subjected to principal axis factor analysis with varimax rotation. Factor patterns are shown in Tables 6-10. The factor patterns provide insight into covarying genetic entities and are presented below under their respective morphological categories. Only the most important factors are discussed, as judged from the number of significant genetic components.

#### Finger ridge counts

*Factor 1 (22.33%)*, IV-V radial count factor: There is a gradient of decreasing radial count weights radially across the hand, and a small contribution from the ulnar counts of right IV and right I.

*Factor 2 (15.12%)*, V-IV ulnar count factor: There is a gradient of decreasing weights radially across the hand. It might be taken as an ulnar count counterpart to Factor 1 above, except that the polar digit is V rather than IV. The higher left than right loading of ulnar IV should be noted.

*Factor 3 (11.77%)*, radial thumb count factor: There are only small contributions from other digits, namely, radial III and ulnar I of the left hand.

*Factor 4 (9.87%)*, III ulnar count factor: There is a tendency for ulnar count weights to decrease in both radial and ulnar directions across the hand.

*Factor 5 (5.96%)*, left ulnar thumb count factor: The right thumb possesses the next highest weight, but this is clearly a case of an asymmetrical factor.

*Factor 6 (11.04%)*, II radial count factor: Also a tendency for radial counts to decrease toward the ulnar side of the hand.

*Factor 7 (3.84%)*, right thumb ulnar count factor: May be regarded as the complement of Factor 5, expressing the opposite degree of asymmetry.

Table 6 - Rotated Factor Pattern of Genetic Correlations for Finger Ridge Counts

Variable	Factor Loadings (x 100)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
LIR	08	06	93	07	12	16	07	05	-07	06	-04	22	00	00	-09
LIU	14	13	31	06	87	16	17	02	18	02	05	14	-00	02	00
LIIR	37	13	12	06	16	87	08	-05	05	15	06	09	-04	02	06
LIIU	29	05	02	22	29	23	21	08	77	04	10	27	00	03	00
LIIIR	59	15	41	12	12	38	-01	02	20	42	19	18	02	02	01
LIIIU	19	47	04	75	02	01	-03	03	37	05	10	-02	13	-05	02
LIVR	91	14	08	19	-05	15	02	10	10	-05	03	05	07	-20	-12
LIVU	33	72	-02	28	07	27	01	25	24	29	16	03	17	07	-00
LVR	75	12	28	08	11	28	21	-10	19	06	01	11	02	37	-01
LVU	15	96	08	04	01	12	02	-00	10	-05	-07	01	-14	-01	03
RIR	25	14	91	03	17	07	09	03	10	10	10	-04	01	03	10
RIU	28	07	25	17	32	23	72	-04	23	-00	02	30	-00	03	00
RIR	35	26	22	05	05	78	13	22	18	-15	11	02	05	02	-08
RIIU	16	07	24	37	18	10	21	05	22	03	05	80	00	01	00
RIIIR	59	11	12	20	14	39	03	04	23	07	59	11	-00	01	00
RIIIU	11	17	07	92	05	08	12	05	00	-00	02	27	07	03	-01
RIVR	88	23	08	07	11	25	10	15	05	15	06	11	05	04	16
RIVU	50	49	05	25	07	26	-09	56	17	01	03	14	-01	-04	00
RVR	79	26	23	03	24	21	13	01	07	-12	10	-00	-23	23	-01
RVU	14	88	18	28	14	06	09	01	-17	02	09	10	11	02	-04
Variance	4.74	3.02	2.35	1.97	1.19	2.21	0.77	0.48	1.20	0.33	0.48	1.06	0.15	0.25	0.07

Table 7. Rotated Factor Pattern of Genetic Correlations for Toe Ridge Counts

Variable	Factor loadings (x 100)													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
LIT	09	19	93	07	-13	16	06	03	07	-00	-16	-06	-02	03
LIF	-00	92	27	02	-03	14	19	02	-05	10	-01	02	-11	-02
LIIT	33	19	32	31	-07	56	50	09	-04	01	27	-03	04	05
LIIF	39	18	-00	19	07	21	75	19	09	-01	-02	34	03	-00
LIIT	89	04	11	13	08	11	24	08	02	30	-02	01	-08	-00
LIIF	88	08	-02	13	-04	22	22	-04	10	-28	-07	04	-01	00
LIVT	69	08	05	31	02	27	37	41	05	02	-10	09	-13	01
LIVF	41	10	02	39	14	68	20	03	26	-06	02	08	26	01
LVT	24	14	03	91	02	08	17	13	-03	-12	04	-12	03	03
LVF	-06	-06	-15	-03	98	04	02	-00	02	-00	-00	01	00	-00
RIT	-02	09	97	01	-04	-14	-06	04	-03	01	16	06	02	-03
RIF	09	96	03	18	-05	03	05	-03	06	-10	02	-01	09	01
RIIT	34	26	25	56	12	33	47	06	05	-00	29	-02	02	-04
RIIF	39	10	-10	16	-04	25	83	03	-08	01	-01	-19	-01	-00
RIIT	81	-06	-04	12	-03	23	12	26	-36	14	17	-07	02	02
RIIF	84	02	00	09	-32	23	21	13	-03	-17	09	-00	18	-02
RIVT	54	-07	09	33	-02	11	16	74	-05	00	03	01	02	-00
RIVF	36	06	-10	12	-02	85	27	10	-16	02	-05	-02	-11	-01
RVT	07	06	02	96	-07	15	07	08	03	11	-04	11	-02	-02
RVF	-25	51	45	14	44	-20	-03	-06	45	06	06	00	02	01
Variance	4.68	2.29	2.31	2.71	1.35	2.10	2.25	0.90	0.47	0.27	0.27	0.21	0.17	0.01

**Table 8 - Rotated Factor Pattern of Genetic Correlations for Palmar Interdigital Ridge Counts**

Variable	Factor loadings (x 100)			
	1	2	3	4
L c-d	07	96	25	09
L b-c	33	12	94	-01
L a-b	95	24	21	07
R a-b	95	05	29	-08
R b-c	21	38	90	01
R c-d	21	96	17	-09
Variance	2.00	2.07	1.91	0.03

**Table 9 - Rotated Factor Pattern of Genetic Correlations for Hallucal Ridge Counts**

Variable	Factor loadings (x 100)			
	1	2	3	4
Lt	-03	96	27	11
Ld	97	-03	-17	-17
Rt	-03	96	-26	-10
Rd	97	-02	17	17
Variance	1.89	1.84	0.20	0.08

**Table 10 - Rotated Factor Pattern of Genetic Correlations for Sole Interdigital Ridge Counts**

Variable	Factor loadings (x 100)				
	1	2	3	4	5
L c-d	13	97	05	-19	01
L b-c	96	-02	17	17	13
L a-b	16	-28	-05	95	-02
R a-b	51	12	46	63	34
R b-c	92	24	24	16	-08
R c-d	24	04	97	00	02

*Factor 9 and 12* (5.98% and 5.28% respectively), left and right digit II ulnar count factors: These two may be considered together since they are asymmetrical complementary factors. Both exhibit a gradient of decreasing weights in the ulnar direction for their respective hands. Factor 12 also gets a small contribution from the ulnar count of right I.

*Factors 10 and 11* (1.64% and 2.42% respectively), left and right III radial count factors respectively: Only Factor 11 falls within the 10 most important factors, but both are included because they are asymmetrical and complementary factors. All weights except those defining the factors are negligible, and even these are low.

#### **Palmar interdigital ridge counts**

*Factor 1* (33.34%), a-b ridge count factor: Weights on the a-b counts define the factor unambiguously, with only minor contributions from the other variables.

*Factor 2* (34.43%), c-d ridge count factor: As in Factor 1, the weights clearly and unambiguously define the factor.

*Factor 3* (31.75%), b-c ridge count factor: The principal weights are only slightly less pronounced than the previous two factors.



**Toe ridge counts**

*Factor 1* (23.41%), mesial digit factor: The highest weights are on digit III, including both tibial and fibular counts, with a gradient of decreasing weights proceeding both tibially and fibularly.

*Factor 2* (11.46%), fibular large toe count factor: The weights, apart from those defining the factor are nearly negligible with only a small contribution from the fibular count of right digit V.

*Factor 3* (11.57%), large toe tibial count factor: May be considered the tibial counterpart of Factor 2 above, again with only small contribution from the fibular count of digit V.

*Factor 4* (13.58%), IV tibial count factor: The main weights are well defined, but there are, in addition, some secondary loadings. In decreasing order of importance these are right tibial II, left fibular IV, right tibial IV, left tibial IV and left tibial II.

*Factor 5* (6.75%), left fibular V factor: The right fibular V count is the second highest weight, but it is substantially smaller than the left, making this an instance of an asymmetrical factor. The smaller but negative contribution of the right III fibular count should also be noted.

*Factor 6* (10.51%), fibular IV factor: This is an ill-defined factor. The main weights are not especially high and are somewhat asymmetrical. Secondary loadings include left tibial II, and right tibial II.

*Factor 7* (11.26%), fibular II factor: This factor also receives some contribution from the tibial counts of digit II and a small contribution from left tibial IV.

**Interdigital sole ridge counts**

*Factor 1* (35.63%), b-c factor: Primary weights are unambiguous, but a secondary contribution of right a-b should be noted.

*Factor 2* (18.27%), left c-d factor: This is a well defined factor, clearly asymmetrical, the homologous ridge count on the right sole contributing virtually nothing. The secondary weights are right b-c and a negative loading for left a-b.

*Factor 3* (20.65%), right c-d factor: The complement of Factor 2 above, but with a fairly strong secondary contribution from right a-b.

*Factor 4* (23.11%), a-b factor: Although weights are clearly on the a-b counts, the different contributions of right and left hands should be noted.

**Ridge counts of the hallucal area (plantar thenar/I)**

*Factor 1* (47.21%), distal count factor: Clear and unambiguous.

*Factor 2* (45.93%), tibial count factor: Again clear and unambiguous.

*Factor 3* (4.92%), hallucal asymmetry: This is a relatively unimportant factor, but presents an easily interpretable pattern. Homologous counts on right and left feet carry opposite weights expressing asymmetry.

**Environmental Components**

The MZ intrapair correlation matrices representing environmental variation and covariation, were subjected to principal axis factor analysis retaining those factors with eigenvalues greater than one for rotation. Factor patterns are shown in Tables 11-15, and their interpretation is given below under their respective morphological categories.

**Finger ridge counts**

*Factor 1* (7.56%), right ulnar III: There is a secondary contribution from right radial V, and several small weights distributed over both hands. This is an ill-defined factor in the sense that the two heaviest weights account for only about 65% of the variance of the factor overall, the small and essentially uninterpretable small weights making up the remainder.

*Factor 2* (7.40%), right ulnar I: Secondary weights include left thumb, both radial and ulnar and right ulnar IV. This factor may be interpreted as reflecting mainly environmental influences on the thumb, but asymmetrical influences are clearly important. The left thumb includes both radial and ulnar weights of about equal magnitude, but the ulnar count of the right thumb makes virtually no contribution, and in fact is negative.

*Factor 3* (7.15%), left digit II radial-ulnar contrast: A reciprocal interaction between twin pairs is apparently reflected in this factor. It is unambiguous and receives very little from other variables. The small contribution of left ulnar I should be noted, which goes along with adjacent negative loading digit II.

Table 11 - Rotated Factor Pattern of MZ Intrapair Correlations for Finger Ridge Counts

Variable	Factor loadings (x 100)								
	1	2	3	4	5	6	7	8	9
LIR	-19	55	11	14	25	-05	30	19	01
LIU	02	42	-29	02	-32	14	-12	14	-06
LIIR	19	-02	-74	-05	22	-04	-08	09	-05
LIIU	14	10	75	-00	10	-09	-05	05	00
LIIR	13	-10	12	-02	-09	07	01	11	69
LIUU	-14	06	-02	19	04	78	04	13	25
LIVR	-22	04	-01	60	-19	-06	-02	25	-28
LIVU	35	-08	24	08	21	23	-05	17	-60
LVR	20	-14	-16	59	17	-06	04	-23	-04
LVU	-02	-07	05	08	06	-05	-03	-88	-07
RIR	10	-06	-01	12	56	-10	-06	36	-20
RIU	09	83	16	03	03	-03	-12	-06	-03
RIIR	07	-15	17	-10	26	09	68	-04	20
RIIU	-05	-08	10	-05	19	12	-82	-03	10
RIIR	-10	15	-11	-12	69	05	03	-25	-08
RIIU	79	05	01	-04	-10	-05	12	01	-04
RIVR	05	19	16	65	-07	16	01	-05	06
RIVU	39	42	-11	-37	-02	13	19	-03	-15
RVR	60	-04	-02	44	15	-10	-14	06	21
RVU	-05	04	07	16	09	-71	11	11	35
Variance	1.51	1.48	1.43	1.61	1.29	1.31	1.36	1.22	1.28

*Factor 4 (8.05%), radial IV-V:* Involves the digits of both hands, although right radial V is somewhat weaker. A secondary negative contribution is seen on right ulnar IV, but has no counterpart on the left hand.

*Factor 5 (6.44%), right radial III and I:* The primary weights are not especially strong and there are a number of secondary weights, most notably left I, both radial and ulnar. These secondary weights are opposite in sign, which again signifies reciprocal relationships between twin pairs.

*Factor 6 (6.53%), left ulnar III and right ulnar V contrast:* The factor is unambiguous in the sense that there are no secondary weights of any consequence.

*Factor 7 (6.81%), right digit II, radial-ulnar contrast:* Essentially the right hand counterpart of Factor 3 above, but with some small contributions from other variables, the largest of which left radial I.

*Factor 8 (6.12%), left ulnar V:* There are a number of secondary weights, mainly on the left hand, making this an ill-defined factor. The primary and several of the secondary weights bear opposite signs, again suggestive of negative interaction between twin pairs.

*Factor 9 (6.39%), left ulnar IV and left radial III contrast:* The primary weights bear opposite signs, so the factor reflects negative interaction between twin pairs. Several secondary weights are involved in this negative interaction, most importantly left radial IV, left ulnar III and right V, both radial and ulnar.

#### Palmar interdigital ridge counts

*Factor 1 (23.38%), right c-d b-c contrast.* A clearly defined factor with only one additional small weight on right a-b. Since right b-c is negative and the other two right variables are negative, the reciprocal interaction involves the right hand generally.

*Factor 2 (22.92%), right a-b left c-d:* Both primary weights are positive, so the environmental influences here are seen to act across hands and across sides of hands. A secondary weights is left b-c, which is negative. To some extent this may be seen as complementary to Factor 1.

*Factor 3 (17.32%), left a-b:* Secondary weights are left b-c and right a-b.

Table 12 - Rotated Factor Pattern of MZ Intrapair Correlations for Palmar Interdigital Ridge Counts

Variable	Factor loadings (x 100)		
	1	2	3
L c-d	-12	70	12
L b-c	02	-55	-24
L a-b	07	13	91
R a-b	23	72	-27
R b-c	-84	-13	14
R c-d	79	-14	23
Variance	1.40	1.38	1.04

Table 13 - Rotated Factor Pattern of MZ Intrapair Correlations for Toe Ridge Counts

Variable	Factor loadings (x 100)							
	1	2	3	4	5	6	7	8
LIT	20	42	13	-10	-48	13	16	15
LIF	-00	56	17	22	05	11	-28	10
LIIT	-17	59	-04	03	-25	22	20	-11
LIIF	11	81	-01	-03	18	-07	-04	07
LIIT	15	14	-04	16	05	17	40	-54
LIIF	04	12	19	08	13	70	00	-03
LIVT	-07	-02	02	01	08	-12	84	02
LIVF	08	07	73	22	-02	-02	-13	-17
LVT	19	18	42	-01	20	-63	12	-14
LVF	-06	05	-06	-87	-01	03	-06	10
RIT	-36	16	54	-19	-23	-07	30	10
RIF	-08	02	-12	-06	72	-02	-02	22
RIIT	30	-07	05	08	-18	24	56	-08
RIIF	44	-35	44	-09	-02	03	17	12
RIIT	87	11	-11	-00	-05	-00	05	-11
RIIF	16	28	25	-15	05	49	15	-08
RIVT	07	09	05	02	69	12	05	-13
RIVF	-15	-01	73	01	-05	29	04	16
RVT	-02	14	-01	20	04	06	06	08
RVF	-08	16	04	81	-02	06	03	27
Variance	1.38	1.86	1.92	1.67	1.47	1.42	1.51	1.26

Table 14 - Rotated Factor Pattern of MZ Intrapair Correlations for Hallucal Ridge Counts

Variable	Factor loadings (x 100)	
	1	2
Lt	68	27
Ld	-75	27
Rt	36	62
Rd	-21	79
Variance	1.21	1.14

Table 15 - Rotated Factor Pattern of MZ Intrapair Correlations for Sole Interdigital Ridge Counts

Variable	Factor loadings (× 100)		
	1	2	3
L c-d	60	-22	60
L b-c	71	13	-23
L a-b	29	62	15
R a-b	-13	23	87
R b-c	-03	84	01
R c-d	74	13	12
Variance	1.51	1.22	1.21

### Toe ridge counts

*Factor 1 (6.92%)*, right tibial III: Secondary weights are right digit II, both tibial and fibular, and right tibial I, which is negative. The factor can be seen as a contrast between the mesial ridge counts and the tibial side, but the organization of the weights into the form of a gradient should be noted.

*Factor 2 (9.32%)*, left fibular II: Secondary weights are left tibial II and tibial and fibular counts of digit I. This factor may be seen as reflecting environmental influences on the tibial side of the left digits generally. There is a slight contrast to be observed in the small negative loadings on left fibular II.

*Factor 3 (9.58%)*, fibular IV: Secondary weights are right tibial I and right fibular II. The factor can be seen as reflecting bilateral environmental influences on the fibular side of IV, but with some asymmetrical involvement from the right hands as well.

*Factor 4 (8.37%)*, fibular V contrast. No other loadings of consequence to be noted.

*Factor 5 (7.38%)*, right fibular I and right tibial IV: A negative secondary weight on left tibial I indicates a slight contrast with the two primary loadings.

*Factor 6 (7.12%)*, left fibular III and left tibial V contrast: There is also a secondary weight on right fibular III.

*Factor 7 (7.55%)*, left tibial IV: A secondary weight on right tibial II and several small loadings make this an ill-defined factor.

*Factor 8 (6.30%)*, right tibial V: A negative secondary weight permits interpretation as a contrast between right tibial V and left tibial III.

### Hallucal ridge counts

*Factor 1 (30.19%)*, left hallucal distal and hallucal tibial contrast: The principal loadings are clearly on the left, but there is a similar contrast to be seen on the right hallucal counts as well.

*Factor 2 (28.62%)*, right hallucal, both counts.

### Plantar interdigital ridge counts

*Factor 1 (25.16%)*, c-d, left b-c: Factor may be seen as reflecting environmental influences on fibular sides of the feet, more pronounced on the left than the right.

*Factor 2 (20.30%)*, right b-c, left a-b: Strongest weight is left a-b, but right b-c makes a substantial contribution. Environmental influences are seen to influence nonhomologous counts of the two hands.

*Factor 3 (20.13%)*, right a-b, left c-d: Right a-b makes the strongest contribution, but the left c-d weight is substantial. Like Factor 2 above, nonhomologous counts are involved.

## DISCUSSION

Ridge counts fall into two categories, counts of patterns and counts between triradii. In the present study, pattern counts include those on fingers, toes and the hallucal area of the sole, and counts between triradii include the palmar and sole interdigital counts. These two kinds of ridge counts must result from rather different morphogenetic processes.

The most commonly accepted model explaining patterns draws on developmental timing relationships of fetal pad formation and regression in relation to ridge formation [1,17]. Less attention has been devoted to the determinants of interdigital counts, but they result from hand or foot growth in size, the development of the primary pads II-IV [26], the placement of the triradii and the width of ridges which fill the interdigital spaces [26]. It is convenient to discuss the results under the two categories of ridge counts.

### Ridge Counts of Patterns

The most striking result to emerge from all pattern areas is the highly multidimensional nature of the genetic components, providing statistical substantiation of the inadvisability of limiting observations to summary characters such as total or absolute ridge count. Looking at the factor analysis of the genetic correlation matrix provides some insight into the action of the morphogenetic processes which result in ridge count phenotypes.

Taking fingers first, it is evident that radial and ulnar sides of the digits load on different factors, which may be taken as evidence that different morphogenetic processes influence their development. In no case do both radial and ulnar sides of a digit constitute the primary weights on a single factor. In those instances where ulnar sides load on a radial factor or vice versa, they are secondary loadings. These findings are consistent with previous principal components or factor analyses of population samples, where similar radial-ulnar independence has been observed [14,22,29].

We should mention that the decision to rotate the factors extracted from the genetic correlation matrix may alter the interpretation somewhat from the unrotated case. This problem has been discussed in reference to dermatoglyphics [24]. It is generally agreed that rotation facilitates morphological interpretations if a rational decision can be reached as to how many factors to rotate. In the present instance, this is decided by the tests of significance of the  $V_{DZ}/(V_{MZ})$  ratio, so rotation would seem to be the method of choice. Inspecting the unrotated axes (not shown), however, reveals a general factor with positive loadings on all 20 ridge counts, as has been noted on population data as well [13,24]. Thus, a general size factor emerges from the genetic correlation matrix, but largely disappears under rotation, although remnants of it are to be seen in Factor 1.

Finger ridge-count factors do not, in general emerge with unique weights which specify particular variables to the exclusion of others. Rather, there is a tendency for the weights to define gradients, with a polar digit assuming the high weight and adjacent weights declining with distance from the polar digit. The existence of gradients is consistent with the idea of overlapping morphogenetic fields [14,24,29]. Thus, a digit's individuality is expressed by its assuming the polar loading for a particular factor, while at the same time its relationship to other digits is expressed by its participation in gradients where neighboring digits assume the polar loading.

Factors range from fairly general, ie, finger Factors 1, 2, 4 and 6, to very specific, ie, Factors 3, 5 and 7. The latter involve the thumb and emphasize its developmental independence. The most surprising feature of the factor analysis is the emergence of factors specific to individual hands. The more important of these involve the thumb, and are consistent with the observation that the thumb exhibits more directional variation than any of the other digits. Our results contrast with those of Nance et al [19], who found factor loadings to be uniformly symmetrical.

Finger environmental components are not as strongly patterned as the genetic ones. In general, the level of correlation is much lower, emphasizing the relative predominance of genetic influence on ridge count variation. Environmental factors tend to reflect local

environmental influences, involving no more than two ridge counts and are often marked by weights which contrast one count against another. Of the nine environmental factors retained in the analysis, four (finger Factors 3, 6, 7, 9) are characterized by primary loadings where one variable is positive and the other negative. These contrasts appear to involve either radial and ulnar sides of the same digit or digits of the same hand, or ulnar contrasts of right-left ridge counts. In addition to the factors mentioned, several others contain elements of these contrasts in secondary loadings, so it is a recurring theme throughout the factor structure.

Since fingers and toes are homologous structures, one might expect similar morphogenetic processes to be reflected in their respective genetic correlation matrices. This expectation is only partly met. The most fundamental difference concerns the unity of tibial and fibular counts, in contrast to the relative independence of radial and ulnar counts on fingers. Factor 1, by far the most important of the toe count factors, defines the mesial digits as a unit and incorporates both tibial and fibular counts. The polarity of this important factor also differs from fingers, in that it assumes a mesial rather than an ulnar position. Knussmann [15] observed a similar factor in his analysis of the correlation matrix presented in Brehme et al [7]. In spite of rotation, Factor 1 retains characteristics of general size.

There also appears to be less of a tendency to exhibit gradients in toes than in fingers, although gradients are clearly evident in toe Factor 1. Tibial and fibular counts of the large toe, like radial and ulnar thumb counts, are independent of the other counts, but lack the asymmetrical tendencies. Apart from the first factor, there is no tendency for tibial and fibular counts to load on the same factor.

Hallucal counts, even though possessing the lowest maximized variance, present a clear and simple structure. The distal and tibial counts are almost completely independent, and to the extent that there is any interaction at all, it is negative. Hallucal counts, therefore, are more similar to finger counts than to toe counts in the independence of different sides of the patterns.

Toe counts exhibit environmental variation which is similar to fingers in a number of respects. Contrasts are evident (ie, especially Factor 6), but they seem less pervasive than in fingers. There is also evidence that environmental influences might be slightly more general, especially Factor 2, which reflects environmental influences on all digits of one foot. Other factors, like fingers, reflect environmental features local in nature.

Hallucal counts also give a clear indication of contrasts between the two counts (Factor 1), and some evidence of general environmental influences, effecting all counts in the same direction.

Overall, environmental variation in patterns shows that environmental influences are local in nature, and frequently involve reciprocal interactions of different sides of the same digit or pattern.

### **Interdigital Ridge Counts of Palms and Soles**

Palmar interdigital ridge counts yield logical patterns of genetic variation. The three significant genetic components result in three factors, each of which loads bilaterally on one particular ridge count. Thus, we can speak of each of the interdigital counts as more or less genetically independent. There is, however, evidence of gradients in the factor loadings, although to a lesser degree than seen in the fingers. In general, loadings decrease with distance from the polar loading, except on the left hand of the c-d factor, where left a-b is larger than left b-c. As in fingers, we may see interdigital counts as

responding to overlapping genetic fields, each count being to a considerable degree independent of the others, but also to some extent integrated into the interdigital ridge count system as a whole.

Environmental correlations are moderate for some variables and the resulting environmental factors are clearly defined. Environmental factors are all characterized by contrasts, some of them quite strong. As in fingers, these contrasts involve right-left counts as well as different counts on the same hand. These contrasts reflect negative interaction between twin pairs. That some of these negative interactions involve nonhomologous counts on different hands (ie, Factors 2 and 3) is a puzzling problem difficult to interpret in morphogenetic terms.

Sole interdigital counts provide somewhat more tentative interpretations due to the necessity of omitting individuals lacking the counts. This may result in underestimating the genetic variation if DZ twins are discordant for missing counts more often than MZ twins. This does not appear to be the case, the proportion of persons included in the sample being about the same in both kinds of twins. Compared to palmar interdigital counts, sole counts are characterized by greater genetic independence of the two sides. Factor 1 contains strongly bilateral loadings, but all four significant factors include an asymmetrical loading of some sort. This may explain why sole interdigital counts, particularly c-d and to a lesser extent a-b, have asymmetrical mean values [6]. There is no evidence of gradients in the sole counts. Sole interdigital counts, therefore, do not seem to be organized in the same way as palmar counts.

Interdigital sole counts also exhibit different environmental influences than palms. They are not characterized by marked contrasts and environmental influences seem more general. Both c-d counts are influenced by common environmental influences, which contrasts to the genetic situation, where they are independent.

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