ELSEVIER

Evolution and Human Behavior 21 (2000) 163–183

Evolution and Human Behavior

The 2nd:4th digit ratio, sexual dimorphism, population differences, and reproductive success: evidence for sexually antagonistic genes?

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Manuscript received July 16, 1999; revised manuscript January 25, 2000

Abstract

The ratio between the length of the 2nd and 4th digit (2D:4D) is sexually dimorphic, with mean male 2D:4D lower than mean female 2D:4D. It recently was suggested that 2D:4D is negatively correlated with prenatal testosterone and positively correlated with prenatal estrogen. It is argued that high prenatal testosterone and low estrogen (indicated by low 2D:4D) favors the male fetus and low prenatal testosterone and high estrogen (indicated by high 2D:4D) favors the female fetus. The patterns of expression of 2D:4D are interpreted in terms of sexually antagonistic genes.

We report data on the following. (a) reproductive success and 2D:4D from England, Germany, Spain, Hungary (ethnic Hungarians and Gypsy subjects), Poland, and Jamaica (women only). Significant negative associations were found between 2D:4D in men and reproductive success in the English and Spanish samples and significant positive relationships between 2D:4D in women and reproductive success in the English, German, and Hungarian samples. The English sample also showed that married women had higher 2D:4D ratios than unmarried women, suggesting male choice for a correlate of

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PII: S1090-5138(00)00029-5

high ratio in women, and that a female 2D:4D ratio greater than male 2D:4D predicted high reproductive success within couples. Comparison of 2D:4D ratios of 62 father:child pairs gave a significant positive relationship. This suggested that genes inherited from the father had some influence on the formation of the 2D:4D ratio. Waist:hip ratio in a sample of English and Jamaican women was negatively related to 2D:4D. (b) Sex and population differences in mean 2D:4D in samples from England, Germany, Spain, Hungary (including ethnic Hungarians and Gypsy subjects), Poland, Jamaica, Finland, and South Africa (a Zulu sample). Significant sex and population differences in mean 2D:4D were apparent.

Keywords: 2nd:4th digit ratio; Sexual dimorphism; Reproductive success; Sexually antagonistic genes

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It has been known for some time that the ratio between the length of the 2nd and 4th digits (2D:4D) is a sexually dimorphic trait (Baker, 1888; George, 1930). In general, mean 2D:4D has been found to be lower in men compared to women (Phelps, 1952). The differentiation of the digits is under the control of Homeobox or *Hox* genes (the posterior-most *Hoxd* and *Hoxa* genes), which also control the differentiation of the testes and ovaries (Peichel et al., 1997; Herault et al., 1997). This common control of the distal limbs and genital bud may be seen when progressive removal of posterior *Hox* gene function results in loss of digits, genital bud derivatives, and fertility (Kondo et al., 1997; Peichel et al., 1997; Mortlock & Innis, 1997). Manning et al. (1998) suggested that the common control of the differentiation of the gonads and digits may mean that the functioning of the former may be reflected in the formation of the latter. Patterns of 2D:4D ratios may therefore reflect aspects of gonadal function such as the production of testosterone and estrogen.

Manning et al. (1998) showed in a sample of 58 men and 40 women attending an infertility clinic that (a) in men 2D:4D ratio is negatively related to serum testosterone levels and sperm numbers per ejaculate and positively related to estrogen and luteinizing hormone (LH), i.e., men with low 2D:4D ratio have more testosterone and sperm but less estrogen and LH than men with high ratios, while (b) in women 2D:4D ratio is positively related to estrogen and LH levels, i.e., women with high 2D:4D ratios have more estrogen and LH than women with low ratios. There is evidence that digit ratios are determined in utero by about the 14th week (Phelps, 1952; Garn et al., 1975; Manning et al., 1998). Correlations between 2D:4D ratios and hormonal levels in adults may therefore originate in associations between 2D:4D and prenatal hormonal levels.

A fetus is exposed to testosterone from two sources, the fetal testes and the fetal adrenal glands (Morishima et al., 1995), while the main source of prenatal estrogen appears to be the aromatase conversion of testosterone from the adrenal glands and the placenta (George et al., 1981; Tanner, 1990; Morishima et al., 1995). A correlate of maternal levels of testosterone and estrogen is waist:hip ratio (WHR). Women with low ratios have low testosterone and high estrogen, while women with high WHR have high testosterone and low estrogen (Evans et al., 1983). The WHR of women has in turn been found to correlate with the 2D:4D ratio of their children, i.e., women with low WHR have male and female children with high 2D:4D, and mothers with high WHR have low 2D:4D ratio children of both sexes (Manning et al., 1999). We argue that 2D:4D may be a marker for sexually antagonistic genes (Rice, 1996a, 1996b; Rice and Holland, 1997) that exert their effects prenatally. On the one hand, low

2D:4D may indicate prenatal exposure to high testosterone and low estrogen levels, a situation that enhances fertility in males but reduces it in females. On the other hand, high 2D:4D ratios may correlate prenatally with low testosterone and high estrogen and be associated with low fertility in males and high in females.

The selective consequences of sexually antagonistic genes are best seen by comparing their sex-dependent effects on reproductive success. In humans, the mean number of children per adult is likely to be strongly influenced by factors such as the economic value of children (Harris, 1989) and rates of infant mortality (Lopreato and Yu, 1988), but underlying biological factors such as sperm numbers, hormonal levels, and behavioral patterns still may account for some of the variance in offspring number within populations. The purpose of this work was to consider (1) the correlation between 2D:4D and reported numbers of children in samples obtained from England, Germany, Spain, Hungary, Poland, and Jamaica; and (2) sex differences and between-population differences in mean 2D:4D in these samples together with samples from Finland and South Africa.

1. Materials and methods

The length of the 2nd and 4th digits was measured on the ventral surface of the hand from the basal crease of the digit to the tip of the digit. Vernier callipers measuring to the nearest 0.01 mm were used throughout this study. It is known that this measurement of digit length can be made with high repeatability (Manning, 1995). Subjects with injuries to the digits were not included in the study. The digit ratio was calculated by dividing the length of the 2nd digit by that of the 4th (2D:4D). Some samples were measured directly from the fingers (English, Spanish, Polish, Hungarian, and South African) and others from photocopies of the palm of the hand (German, Finnish, and Jamaican).

In order to establish that direct measures of digits and measures from photocopies produce comparable 2D:4D ratios, digit length was measured directly from fingers and from photocopies in 30 hands from 30 subjects. Mean digit lengths and 2D:4D ratios were very similar (means and standard deviations: digit measurements, 2D $= 72.87 \pm 4.39$, 4D $= 74.61 \pm 3.27$, 2D:4D $= 0.97 \pm 0.04$; photocopy measurements, 2D $= 72.33 \pm 4.10$, 4D $= 74.73 \pm 3.72$, 2D:4D $= 0.97 \pm 0.04$). Model II single-factor analysis of variance was used to calculate repeatabilities (r_1) (Zar, 1994) of the digit and photocopy measurements:

$$r_1 = (\text{groups MS} - \text{error MS})/(\text{groups MS} + \text{error MS})$$

where MS = mean squares. The ratio between differences between individuals (groups MS) and measurement error (error MS) was calculated using repeated measures analysis of variance (ANOVA) tests. Repeatabilities were 2D $r_1 = 0.91$, 4D $r_1 = 0.97$, 2D:4D $r_1 = 0.91$. For all three traits, there was significantly greater variance in between-subject differences than between digit and photocopy measurements (repeated measures ANOVA, 2D $F = 64.60$, $p = .0001$, 4D $F = 64.00$, $p = .0001$, 2D:4D $F = 21.99$, $p = .0001$). We concluded that 2D:4D ratios calculated from direct digit measurement are essentially the same as 2D:4D ratios calculated from photocopies of the hands.

All subjects in Study I concerning reproductive success were necessarily adults. Study II was concerned with sex and population differences of 2D:4D. Manning et al. (1998) found no evidence of a change with age in 2D:4D over a range of 2 to 25 years, and relative digit length has been shown to be determined by the 14th week of pregnancy (Garn et al., 1975). The Jamaican and Finnish samples in Study II were obtained from children (in the case of the Jamaican sample 2D:4D of female children was compared with that of Jamaican women and found to be very similar), and we feel that their means also reflect those of the adult population. WHR was measured in two populations (English and Jamaican). Measurements were made on subjects who were standing and wearing light outdoor clothes. The waist was measured at the narrowest part between the ribs and the iliac crest, and the hips were measured at the level of the greatest protrusion of the buttocks.

2. Study I—2D:4D and fertility

2.1. English sample

We recruited 300 subjects (117 men and 183 women) with a minimum age of 30 years from the Merseyside area. Participants were from social groups of elderly retired people and mature university students. A wide range of socioeconomic backgrounds was represented. In addition to digit measurements, participants were required to report the number and sex of their putative biological children. From the sample of 300 subjects we identified 60 couples and we recruited a further 30 ($n = 90$). These pairs were asked to report number of children from their partnership. We measured the 2nd and 4th digit length twice in 100 hands from 100 subjects.

2.1.1. Results

Repeatabilities of 2D:4D from 100 hands were as follows: males, $n = 50$, $r_1 = 0.86$; females $n = 50$, $r_1 = 0.92$. There was significantly greater variance between subjects than within-subject error (repeated measures ANOVA: males, $F = 13.70$, $p = .0001$; females, $F = 23.22$, $p = .0001$). We concluded that our measurements represented real differences between subjects.

In accord with previous work, the male 2D:4D ratio was smaller than that of the female ratio but the difference in this instance was not significant (2D:4D right hand: males $x = 0.98 \pm 0.03$, females $x = 0.99 \pm 0.04$, $t = 1.66$, $p = .09$; 2D:4D left hand, males $x = 0.98 \pm 0.04$, females $x = 0.99 \pm 0.04$, $t = 0.88$, $p = .38$). The 2D:4D ratio was negatively related to age in our sample, but the association was weak and not significant for either sex or hand (simple linear regressions of 2D:4D on age: males, right hand $b = -0.001$, $F = 3.68$, left hand $b = -0.0004$, $F = 1.28$, $p = .25$; females, right hand $b = -0.0002$, $F = 1.73$, $p = .19$, left hand $b = -0.00002$, $F = 1.72$, $p = .19$). The mean number of children was $x = 1.77$, $\pm$ 1.37. In males there were negative relationships between number of reported children and 2D:4D ratio (for right hand, see Fig. 1). The associations between 2D:4D and number of children were as follows: number of children regressed on 2D:4D: right hand $b = -6.14$, $F = 5.10$, $p = .01$; left hand $b = -5.01$, $F = 4.39$, $p = .02$. One-tailed tests were used throughout, with a negative relationship predicted for males and a positive association for females. Multiple regression was performed with number of children as the dependent variable and age (as number of children and age were likely to show collinearity they were forced into the analysis simultaneously) and 2D:4D as independent variables. The 2D:4D ratio remained significantly

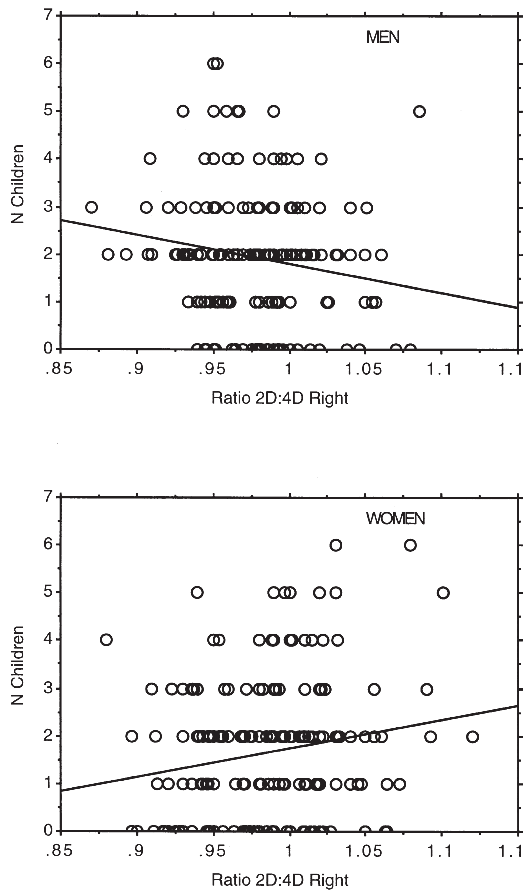

Fig. 1. Reported number of children regressed on 2D:4D ratio of the right hand of English men (n = 117) and women (n = 183).

negatively related to fecundity for the right and left hand. Age was significantly positively associated with fecundity (Table 1).

In females there were positive relationships between number of children and 2D:4D ratio (for right hand, see Fig. 1). The associations were significant for right and left hands (simple linear regressions, number of children regressed on 2D:4D: right hand $b = 6.02$, $F = 6.91$, $p = .005$; left hand $b = 6.34$, $F = 7.35$, $p = .004$). Multiple regression analyses with numbers of children as the dependent variable and age and 2D:4D ratio as independent variables forced simultaneously into the analyses are shown in Table 1. The 2D:4D ratio remained significantly positively related to number of children. Age was positively but nonsignificantly related to fecundity.

Data on marital status were reported by 112 men and 166 women. There were 104 men who were or had been married and 8 who had never been married. There were no differences in the 2D:4D ratio between married and not married men (t-test, 2D:4D right hand: married $\bar{x} = 0.98$, not married 0.98, $t = 0.35$, $p = .73$; 2D:4D left hand; married $\bar{x} = 0.98$, not married 0.98, $t =$

Table 1
Results of multiple regression analyses of the English, Spanish, German, Hungarian, Polish, and Jamaican samples

	Right Hand				Left Hand			
	b	*SE*	*t*	*p*	*b*	*SE*	*t*	*p*
England: Males								
2D:4D	−5.40	2.68	2.01	.02 (.04)	−4.70	2.35	2.00	.02 (0.02)
Age	0.02	0.01	2.56	.02	0.02	0.01	2.55	.02
England: Females								
2D:4D	5.33	2.34	2.27	.01 (0.01)	6.71	2.37	2.83	.0025 (0.005)
Age	−0.01	0.01	0.84	.40	−0.01	0.01	1.00	.32
Spain: Males								
2D:4D	−9.74	4.27	2.28	.015 (0.03)	−5.84	4.98	1.17	.125 (0.125)
Dur Marriage	0.08	0.01	6.19	.0005	0.08	0.01	5.83	.0001
Spain: Females								
2D:4D	6.93	4.58	1.51	.07 (0.07)	−2.12	4.93	0.43	.34 (0.68)
Dur Marriage	0.09	0.01	7.12	.0001	0.08	0.01	6.49	.0001
Germany: Males								
2D:4D	−1.74	3.03	0.57	.29 (0.58)	−1.46	2.94	0.50	.36 (0.36)
Age	0.07	0.01	7.97	.0001	0.07	0.01	8.10	.0001
Germany: Females								
2D:4D	6.91	2.90	2.38	.01 (0.01)	7.10	2.83	2.51	.005(0.01)
Age	0.05	0.01	5.23	.0001	0.05	0.01	5.10	.0001
Hungary: Males								
2D:4D	−3.87	8.61	0.45	.235 (0.47)	−0.86	8.75	0.10	.46 (0.46)
Age	0.08	0.04	2.02	.05	30.08	0.04	2.02	.052
Ethnicity	0.36	0.56	0.63	.53	0.41	0.56	0.74	.46
Hungary: Females								
2D:4D	11.45	5.05	2.27	.015 (0.03)	10.04	5.43	1.85	.035 (0.035)
Age	0.05	0.02	2.44	.02	0.05	0.02	2.60	.01
Ethnicity	1.32	0.36	3.70	.0004	1.16	0.35	3.30	.0002
Poland: Males								
2D:4D	3.55	4.06	0.87	.38 (0.76)	2.35	3.00	0.79	.43 (0.43)
Age	0.03	0.01	2.73	.007	0.03	0.01	2.70	.01
Poland: Females								
2D:4D	−4.93	4.04	0.21	.23 (0.46)	−2.29	4.71	0.49	.63 (0.63)
Age	0.03	0.01	3.02	.003	0.03	0.01	2.96	.004
Jamaica: Females								
2D:4D	6.88	0.04	1.08	.15 (0.15)	9.32	5.65	1.65	.055 (0.11)
Age	0.07	0.22	1.75	.09	0.06	0.04	1.57	.12

The prediction is that males will show negative and females positive relationships between 2D:4D and offspring number after removing the effects of age or duration of marriage. The *p* values shown for the 2D:4D ratios are therefore one-tailed and are Bonferroni adjusted (brackets) for two tests (one for each hand) per sex.

0.03, $p = .98$). There were 152 women who were or had been married and 16 who had never been married. The married women had significantly higher 2D:4D ratio than the unmarried women (*t*-test, 2D:4D right hand married $\bar{x} = 0.99$, not married $\bar{x} = 0.97$, $t = 2.09$, $p = .03$; left hand married $\bar{x} = 0.99$, not married $\bar{x} = 0.96$, $t = 2.94$, $p = .004$).

If 2D:4D ratio is a predictor of fecundity in single subjects, it should explain a greater percentage of the variance of fecundity if it is known for both partners. We recruited 90 couples

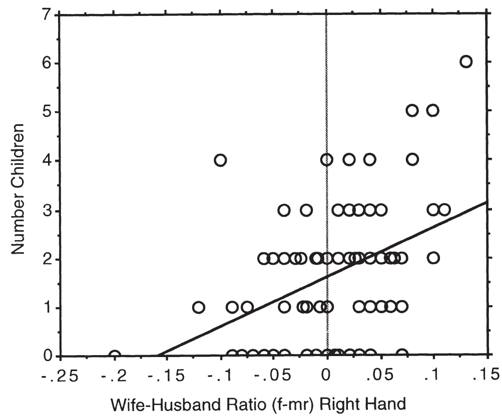

Fig. 2. Reported number of children per couple regressed on 2D:4D of female partner minus 2D:4D of male partner in 90 English couples.

with a mean duration of relationship of 27 $\pm$ 11.92 years. In our data, large family size was related to high 2D:4D ratio in women and low 2D:4D ratio in men. We therefore calculated female 2D:4D $-$ male 2D:4D (f-m_r) as a predicted correlate of fecundity per couple. We found strong positive relationships between f-m_r and number of reported children per couple (simple linear regression analysis of number of children regressed on f-m_r, right hand $b = 10.16$, $F = 18.29$, $p = .0001$; left hand $b = 9.27$, $F = 12.39$, $p = .0007$; see Fig. 2 for right hands). The results of multiple regression analyses with number of children as the dependent variable and relationship duration of f-m_r as independent variables forced into the analysis simultaneously are shown in Table 2. The f-m_r remained a strong positive predictor of fecundity. Relationship duration also was positively related to fecundity. We found no evidence for nonrandom assortment of subjects on the basis of 2D:4D (simple linear regressions of 2D:4D male partner regressed on 2D:4D female partner: right hand $b = 0.13$, $F = 2.01$, $p = .15$; left hand $b = 0.12$, $F = 1.66$, $p = .21$).

The fetus is thought to be isolated from the effects of maternal sex hormones by the action of enzymes secreted by the placenta (Simpson et al., 1994; Morishima et al., 1995). How-

Table 2
Results of multiple regression analyses with number of children per couple as the dependent variable and female 2D:4D $-$ male 2D:4D (f-m_r) and duration of relationship as independent variables

	β	*SE*	*t*	*p*
Right hand				
f-m_r	10.16	2.45	4.15	.0001
Duration of relationship	0.03	0.01	2.20	.03
Left hand				
f-m_r	9.23	2.68	3.44	.001
Duration of relationship	0.04	0.01	3.44	.001

ever, it may be that paternal inheritance is ineffective in determining 2D:4D ratio and that some form of maternal influence may be the important factor in the formation of relative digit length. In order to exclude this possibility, we measured 2D:4D in a sample of 62 father:child pairs (28 male and 34 female offspring). All pairs were from the Liverpool area and were drawn from inner-city and suburban populations with a wide socioeconomic mix. Mean ages were as follows: fathers $\bar{x} = 41.71 \pm 6.3$ and children $\bar{x} = 12.58 \pm 4.34$. Repeated measurements on 15 hands gave a significant repeatability score ($r_1 = 0.81$, $F = 9.56$, $p = .0001$, repeated measures ANOVA). The mean 2D:4D ratios were similar for fathers and offspring (fathers, $\bar{x} = 0.99 \pm 0.03$; offspring, $\bar{x} = 0.99 \pm 0.04$). A regression of offspring 2D:4D on father 2D:4D ratio gave a significant positive relationship ($b = 0.35$, $F = 5.94$, $p = .02$, Fig. 3).

WHR was measured in 95 female subjects who were not represented in the previous sample. Repeat measurements on 10 subjects gave a significant repeatability ($r_1 = 0.72$, $F = 7.9$, $p = .004$). The mean WHR was 0.77 ± 0.08 SD. Means and standard deviations for age and number of children were: age $\bar{x} = 55.73 \pm 16.76$ and number of children $\bar{x} = 1.72 \pm 1.40$. There was a positive but nonsignificant association between age and WHR ($b = 0.001$, $F = 3.08$, $p = .08$) and a weak negative relationship between numbers of children and WHR ($b = -0.85$, $F = 0.21$, $p = .65$). There was a negative nonsignificant relationship between 2D:4D of the right hand and WHR ($b = -0.08$, $F = 1.97$, $p = .16$) and a weak positive relationship between left 2D:4D and WHR ($b = 0.03$, $F = 0.38$, $p = .54$).

2.2. Spanish sample

There were 98 subjects (44 men and 54 women). Participants were 30 years of age or older and recruited mainly from the Granada area of Spain. Marital status was a predictor of fertility in our data (there were eight unmarried subjects, all with no children). Therefore, duration of marriage, as a likely correlate of numbers of children, was recorded.

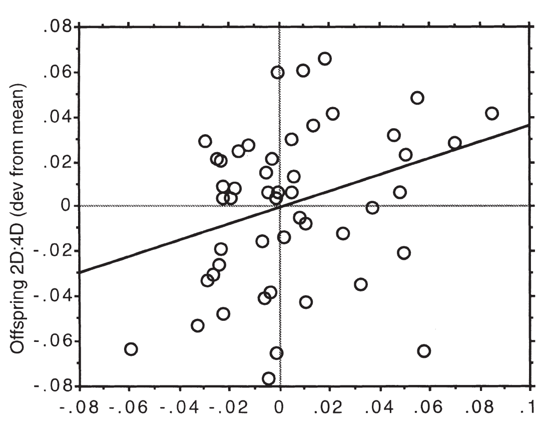

Fig. 3. Offspring 2D:4D (expressed as deviation from offspring mean) regressed on father 2D:4D (expressed as deviation from father mean). The equation for the line of best fit is $y = 0.35x - 0.0003$.

2.2.1. Results

Repeatability for 2D:4D from 98 hands was $r_1 = 0.91$, $F = 20.54$, $p = .0001$.

In the complete sample, the mean number of children was $\bar{x} = 2.29 \pm 1.65$. In males there were negative but nonsignificant relationships between 2D:4D and numbers of children (right hand, $b = -8.49$, $F = 2.10$, $p = .16$; left hand, $b = -5.78$, $F = 0.76$, $p = .39$, Fig. 4). Multiple regression analyses with 2D:4D and duration of marriage as independent variables gave a significant negative relationship between right hand 2D:4D and numbers of children. Duration of marriage was a strong positive predictor of numbers of children and was used to partial out effects of "opportunity" for reproduction (Table 1).

In females there were no significant relationships between 2D:4D and numbers of children (right hand, $b = 1.14$, $F = 0.03$, $p = .43$; left hand, $b = -9.18$, $F = 2.02$, $p = .07$, Fig. 4). Multiple regression analyses with 2D:4D and duration of relationship as independent variables revealed no significant association between 2D:4D and numbers of children but showed a significant positive relation between duration of relationship and numbers of children (Table 1).

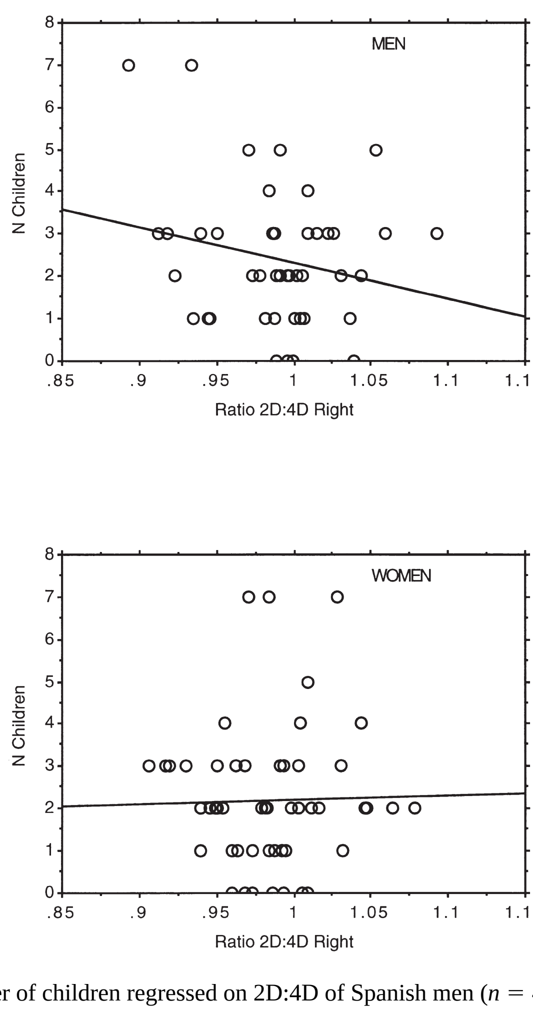

Fig. 4. Reported number of children regressed on 2D:4D of Spanish men (n = 44) and women (n = 54).

2.3. German sample

We recruited 238 participants of whom 205 (109 men and 96 women) were aged 30 years and over. Recruitment was from the staff of the Universities of Kiel, Kassel, and Hannover and from subjects attending tango dance studios in Bielefeld, Hannover, Hamburg, and Kassel.

2.3.1. Results

The repeatability from 96 hands was $r_1 = 0.98$, $F = 91.3$, $p = .0001$. There was significantly greater variance between subjects than within-subject error (repeated measures ANOVA: $F = 91.30$, $p = .0001$.

In the complete sample, the mean number of children was $\bar{x} = 2.29 \pm 1.65$. In males there were negative but nonsignificant relationships between numbers of children and 2D:4D ratio (right hand, $b = -5.77$, $F = 2.35$, $p = .06$; left hand, $b = -4.41$, $F = 1.43$, $p = .12$, Fig. 5).

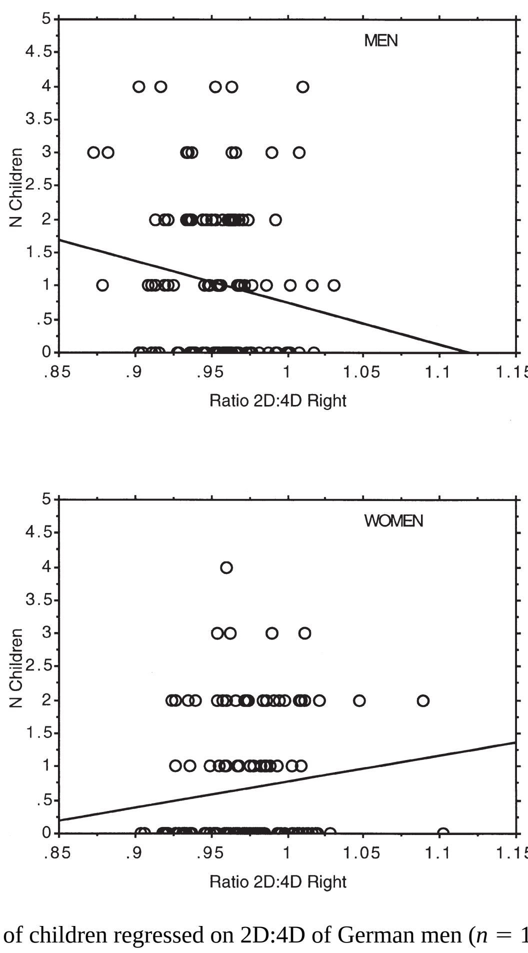

Fig. 5. Reported number of children regressed on 2D:4D of German men ($n = 109$) and women (n = 96).

Multiple regression tests (dependent variable numbers of children and independent variables 2D:4D and age, the latter forced into the analysis simultaneously) showed age positively and significantly related to numbers of children but 2D:4D remained nonsignificant (Table 1).

In females there were positive relationships between numbers of children and 2D:4D that were significant for the right and left hand (right hand, $b = 6.50$, $F = 3.92$, $p = .03$; left hand, $b = 7.58$, $F = 5.68$, $p = .02$, Fig. 5). Multiple regression tests with 2D:4D and age as independent variables showed significant relationships between right and left hand 2D:4D and number of children (Table 1).

2.4. Hungarian sample

There were 132 subjects in our sample. Of these 96 were 30 years or older, and our analyses were confined to this group. Subjects were recruited in and around Pecs, a city in Southern Hungary. Measurements were made in the university and, with the help of district nurses, in homes in the suburbs and rural areas around the city. A wide range of socioeconomic backgrounds characterized our participants. The sample contained two distinct ethnic groups, ethnic Hungarian men ($n = 12$) and women ($n = 39$) and Hungarian Gypsy men ($n = 15$) and women ($n = 30$). In the few cases of doubt, ethnicity was confirmed by the participants and/or the district nurse. In order to establish repeatability, digit measurements were made twice on 90 hands before the start of the study.

2.4.1. Results

Repeatability was high and significant ($r_1 = 0.90$, $F = 19.27$, $p = .0001$).

There were differences in the mean number of children between ethnic Hungarians and Gypsies (non-Gypsies, $\bar{x} = 2.41 \pm 1.15$ SD, Gypsies, $\bar{x} = 3.48 \pm 1.75$ SD, $t = 3.56$, $p = .0006$). In males a multiple regression analysis with 2D:4D ratio, age, and ethnicity (dummy coded, ethnic Hungarians = 1, Gypsies = 2) and number of children as the dependent variable showed no significant relationships with 2D:4D (Fig. 6 and Table 1). The lack of relationship may well have been the result of the small sample size ($n = 27$).

In women a similar multiple regression analysis showed a significant positive relationship between right hand 2D:4D and number of children with the Gypsy regression line lying above the ethnic Hungarian line (Fig. 6 and Table 1). Age and ethnicity also showed significant positive associations (Table 1).

2.5. Polish sample

There were 210 subjects (107 men and 103 women) aged over 30 years recruited from the Poznan area of Poland. The subjects were from a range of socioeconomic backgrounds.

2.5.1. Results

Repeatability of 2D:4D was high from repeated measurements of 210 hands ($r_1 = 0.97$). There was significantly greater variance between-subjects than between measurements ($F = 71.45$, $p = .0001$) indicating that our measurement error was much smaller than the real differences between subjects.

In the complete sample, the mean number of children was $\bar{x} = 2.14 \pm 1.19$.In contrast to previous relationships, there were positive associations between 2D:4D and numbers of chil-

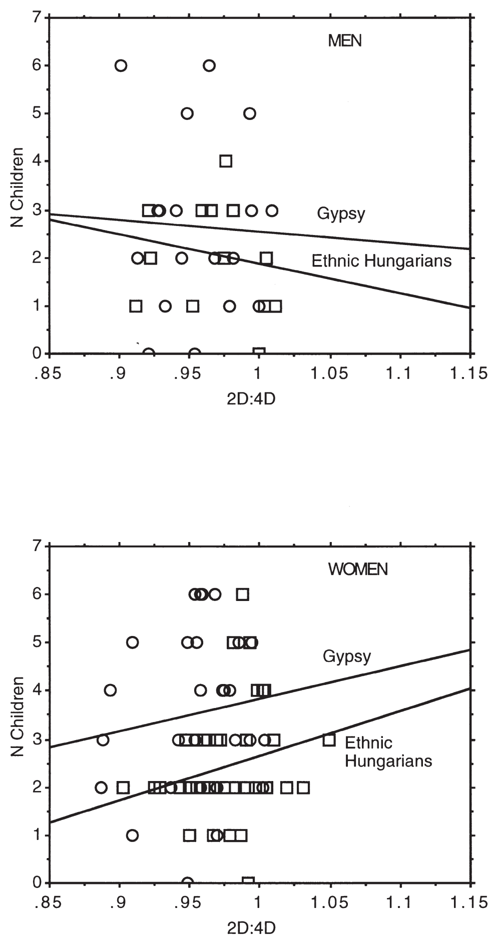

Fig. 6. Reported number of children regressed on 2D:4D of Hungarian men and women (ethnic Hungarians ($n = 51$) and Gypsies ($n = 45$)).

dren in males and negative associations in females. However, none of these relationships were significant (males: 2D:4D right, $b = 5.89$, $F = 2.08$, $p = .15$, left, $b = 4.27$, $F = 2.07$, $p = .15$; females: right, $b = -3.99$, $F = 0.91$, $p = .34$, left, $b = -0.31$, $F = 0.004$, $p = .95$; two-tailed tests; Fig. 7).

Multiple regression analyses with independent variables 2D:4D and age and dependent variable number of children showed that 2D:4D was not significantly related to number of children, but age was positively associated (Table 1).

2.6. Jamaican sample

Our Jamaican sample was obtained from Southfield in the parish of St. Elizabeth and the participants were part of a long-term study of developmental stability (the Jamaican Symmetry Project) (Trivers et al., 1999). Measurements were made on women only. Subjects were

Table 3
Bonferroni adjusted *p* values for cross-cultural associations between 2D:4D and offspring number for males and females and right and left hands

	Men		Women	
	Right	Left	Right	Left
England	0.04 (0.16)	0.02 (0.10*)	0.01 (0.06*)	0.005 (0.03*)
Spain	0.03 (0.15)	0.125	0.07 (0.21)	0.68
Germany	0.58	0.36	0.01 (0.05*)	0.01 (0.05*)
Hungary	0.65	0.46	0.03 (0.12)	0.035 (0.14)
Poland	0.76	0.43	0.46	0.63
Jamaica			0.15	0.11

Significance level is 10% (see text for discussion of significance values).
*Significant at the 10% level after Bonferroni adjustment.

mothers who had at least one child attending primary school; therefore, an important difference in this sample was that nulliparous women were not represented. This was likely to weaken the relationship between 2D:4D and numbers of children. Women who were 30 years and older ($n = 60$) were selected from the sample.

2.6.1. Results

Repeatability of 2D:4D on 30 hands was $r_1 = 0.90$, $F = 27.72$, $p = .0001$.

The mean number of children was x = 2.93 ± 1.58. There were no significant relationships between mean 2D:4D and numbers of children, but left hand 2D:4D showed a positive and significant association (right hand: $b = -6.09$, $F = 0.88$, $p = .35$; left hand: $b = 9.98$, $F = 3.05$, $p = .04$; the strongest relationship is shown in Fig. 8). Multiple regression analyses with 2D:4D and age as the independent variables showed no significant relationships between 2D:4D and numbers of children (Table 1).

WHR was measured in 93 women. Ten subjects were measured twice and repeatability was significant ($r_1 = 0.79$, $F = 8.43$, $p = .001$). The mean WHR ($\bar{x} = 0.79 \pm 0.07$ SD) was larger than that of the English sample, but the difference was not significant ($t = 1.33$, $p = .18$). There was a negative but nonsignificant relationship between WHR and 2D:4D (right hand: $b = -0.32$, $F = 2.15$, $p = .14$; left hand: $b = -0.12$, $F = 0.35$, $p = .55$). When amalgamated, the English and Jamaican samples gave a significant negative association between right hand 2D:4D and WHR (right hand, $b = -0.33$, $F = 6.03$, $p = .02$, Fig. 9; left hand, $b = -0.07$, $F = 0.31$, $p = .58$). Partialing out age increased the association between right hand 2D:4D and WHR (multiple regression, 2D:4D, $b = -036$, $t = 2.60$, $p = .01$; age, $b = -0.0003$, $t = 1.11$, $p = .27$).

2.7. Total sample

We do not think it appropriate to pool these 2D:4D data. The frequency of sexually antagonistic genes may differ in different populations at different times with changes in the intensity of sexual selection (see Discussion). However, that does not remove the need to adjust for multiple tests. Table 3 shows *p* values for the relationships between 2D:4D and offspring number for males and females and right and left hands. For males the sample from England (right and left hands) and Spain (right hand) show significant negative relationships from two

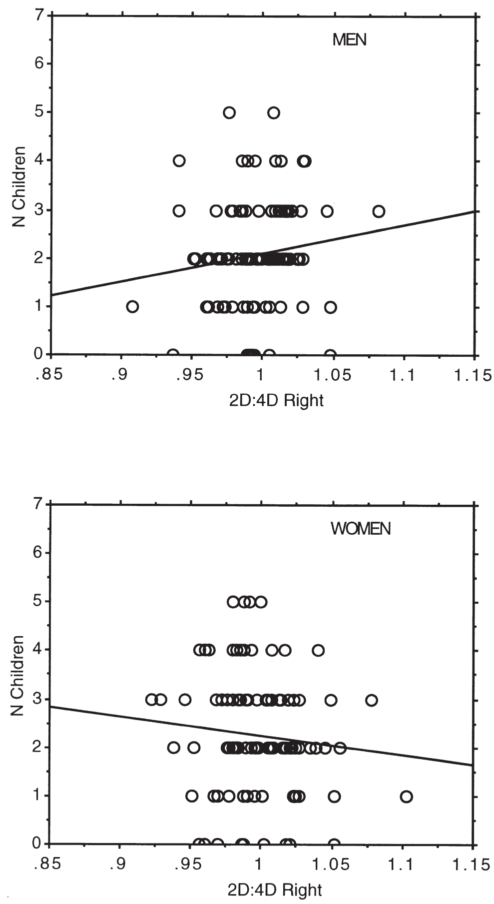

Fig. 7. Reported numbers of children regressed on 2D:4D of Polish men ($n = 107$) and women ($n = 103$).

of the five cultures. For females there were significant positive relationships (both hands) in the English, German, and Hungarian (caucasian and gypsy) samples, i.e., from three of the six cultures sampled. Bonferroni correction of the *p* values is shown in Table 3. Strict application of this method severely reduces the power of tests (Wright, 1962), but such sacrificial loss of power can be avoided by choosing an error rate higher than the usually accepted 5%. We used 10% as suggested by Wright (1962) and Chandler (1995). Significant relationships remained for the English sample for left hand (males), right and left hand (females), and in the German sample for left and right hand (females). This suggests that these relationships, although relatively weak, are nevertheless real.

3. Study II—sex and population differences in 2D:4D

Early work on 2D:4D considered the trait as discontinously distributed into two classes, 2D $<$ 4D and 2D $>$ 4D, and was mainly based on measurements of subjects in the United

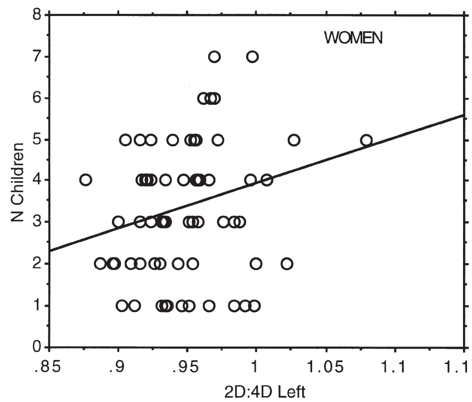

Fig. 8. Reported number of children regressed on 2D:4D of Jamaican women ($n = 60$). Note all subjects had at least one child (see text).

States and Canada (for review see Phelps, 1952). In all these studies both classes are common. Figures 1 to 7 show that in some samples (German, Hungarian, and Jamaican) the class 2D $>$ 4D is quite rare. In order to examine this question in more detail, further samples were obtained as follows.

3.1. Helsinki, Finland

A sample of 41 children (24 males and 17 females) was obtained from a primary school with an intake comprising a wide range of socioeconomic levels. The mean age was 5.29 $\pm$ 1.27 years. Children of this age tend to move in an unpredicable way during measurement; therefore, photocopies of the hand were made. Callipers were used to measure digit length from the photocopies. A subset of 25 hands was measured twice in order to establish repeatabilities.

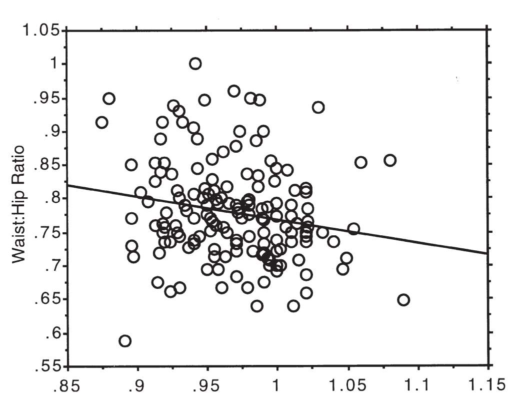

Fig. 9. Relationship between 2D:4D and waist-hip ratio in 188 English ($n = 95$) and Jamaican ($n = 93$) women.

3.2. Natal, South Africa

This sample comprised 120 adult subjects (60 males and 60 females) recruited from urban zulu students of the University of Natal. The 2nd and 4th digit was measured twice on all subjects using callipers. The mean age was 23 ± 81 years.

3.3. Southfield, Jamaica

Our data on adult Jamaicans in Study I comprised only females. A sample of 151 children (78 males and 73 females) was recruited from primary schools (mainly Top Hill Primary School) in the Southfield area. The mean age was 7.66 ± 1.40 SD years. Measurements of the 2nd and 4th digits were made from photocopies. The digits were measured twice in a subset of 30 hands.

3.4. Results

Repeatabilities were significant for all three samples: Finnish, $r_1 = 0.67$, $F = 5.92$, $p =$ .0001; Zulu, $r_1 = 0.99$, $F = 204.99$, $p = .0001$; Jamaican, $r_1 = 0.77$, $F = 8.00$, $p = .0001$ were: Finnish, female $\bar{x} = 0.95 \pm 0.04$, male $\bar{x} = 0.93 \pm 0.03$; Zulu, female $\bar{x} = 0.95 \pm 0.04$, male $\bar{x} = 0.95 \pm 0.04$; Jamaican, female $\bar{x} = 0.94 \pm 0.03$, male $\bar{x} = 0.93 \pm 0.04$. There was no significant difference between the mean 2D:4D of Jamaican girls and Jamaican women (girls $\bar{x} = 0.94 \pm 0.03$, women $\bar{x} = 0.95 \pm 0.04$, $t = 1.68$, $p = .10$). This was further evidence that 2D:4D does not change after birth.

Amalgamating data from Study I and II gave mean 2D:4D ratios ranging from 1.00 for Polish females to 0.93 for male Finns and Jamaicans (Fig. 10). There were significant differences between populations and between sexes (two-factor ANOVA: population $F = 53.49$, $p =$ .0001; sex $F = 13.76$, $p = .0001$).

4. Discussion

We do not argue that the 2D:4D ratio is important mechanistically or as a display trait in mate choice. Most probably it affords us a window into prenatal hormonal conditions. There

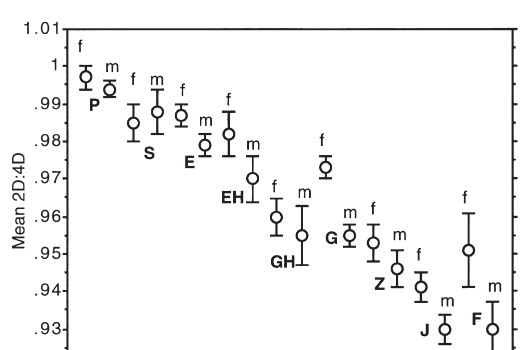

Fig. 10. Population (P = Poland; S = Spain; E = England; H = Hungary [EH = ethnic Hungarians, HG = Hungarian Gypsies]; G = Germany; Z = Zulu; J = Jamaica; F = Finland) and sex differences (f = female and m = male) in mean 2D:4D with standard error bars.

is accumulating evidence for an association between gonad and digit differentiation. Testosterone and dihydroxytestosterone (DHT) are known to affect development of the epidermis and dermis of the digits. Jamison et al. (1993) found a positive association between dermatoglyphic asymmetry, which is determined *in utero*, and testosterone in adult males. Mid-phalangeal hair growth has been shown to be positively associated with DHT in !Kung San and Kavango men (Winkler and Christiansen, 1993). The presence of hair on the middle phalanges has been the subject of much research. Danforth (1921) was the first to call attention to its presence and distribution. The presence of mid-phalangeal hair, i.e., on phalanx 2 (P2), is thought to be dominant over its absence (Garn, 1951). However, the expression of this trait is not equal across the digits. When combinations of digits are affected, the 4th is always affected but the 2nd is least often affected. This pattern of expression may result from a high sensitivity to DHT in the 4th digit and particularly low sensitivity in the 2nd digit. Moreover, the growth of P2 is strongly related to fertility in mice and humans through the action of *Hox* genes. The posterior-most *Hoxd* and *Hoxa* genes are essential for limb and genital development (Peichel et al., 1997; Herault et al., 1997). P2 bones are the last to form in the limb (Shubin and Alberch, 1986), and they are reduced or absent in all *Hox* targeted mutations (Peichel et al., 1997). In humans, anatomical defects in digits and genitalia occur in the hand-foot-genital syndrome, which results from mutation within *Hoxa* (Mortlock and Innis, 1997). In mice, deregulation of *Hoxd* genes alters the relative lengths of P2 and affects the growth of the genital bud (Peichel et al., 1997).

Our results indicate significant differences in mean 2D:4D between populations and confirm that the trait is sexually dimorphic. There was also a trend for 2D:4D to be negatively related to reproductive success in males (the English and Spanish samples) and positively in females (the English, German, and Hungarian Caucasian and Gypsy samples). There are many cultural and biological factors that intervene between fertility and reproductive success. Perhaps the most important is the fertility of the long-term partner. In an English sample we found high reproductive success in partnerships in which the male had lower 2D:4D than his partner and low reproductive success when 2D:4D was higher than that of his partner. When English and Jamaican data were pooled, there was some evidence of a weak negative association between WHR and 2D:4D in women.

Our data are best explained by reference to the action of sexually antagonistic genes (Rice, 1996a, 1996b; Rice and Holland, 1997). There is evidence that behavioral and physiological advantages accrue to the male fetus when exposed to high testosterone and low estrogen levels and to the female fetus when exposed to low testosterone and high estrogen such that the following occur. (a) In males, testosterone is necessary for the differentiation of the testes and for spermatogenesis (Wu, 1993). The 2D:4D ratio is negatively related to testosterone and to sperm numbers (Manning et al., 1998). Our Finnish sample had very low male 2D:4D, and it is known that Finnish men have sperm counts that are nearly double that of men word-wide (Suominen and Vierula, 1993; Vierula et al., 1996).

Testosterone/estrogen levels also are important for the *in utero* differentiation and subsequent maintenance of the male vascular system. First trimester exposure to elevated levels of estrogen is associated with cardiovascular, genital, and digit malformations in the male fetus (Levy et al., 1973; Nora et al., 1976; Heinonen et al., 1977; Lorber et al., 1979). Myocardial infarction (MI, heart attack) in young men is correlated with low testosterone and high estrogen levels (Aksut et al., 1986; Phillips et al., 1994). Consistent with this, age at first MI is negatively correlated with 2D:4D in men (Manning and Bundred, in press; Manning and Bundred, in preparation). Elevated incidence of premature MI and 2D:4D in men could indicate poor cardiovascular performance and compromised athleticism, even in young men. The homeostasis of blood glucose levels also may be associated with *in utero* levels of testosterone (Manning and Bundred, in press), but it is not yet known whether diabetes incidence is correlated with 2D:4D. Prenatal testosterone has been implicated in superior spatial judgment and in the development of musical ability (Geschwind and Galaburda, 1985). It remains to be seen whether 2D:4D correlates with spatial ability, but there is evidence that low 2D:4D is associated with musicality (Sluming and Manning, 2000). Good spatial ability, an efficient cardiovascular system, effective control of blood glucose, and prolific production of sperm are important factors in direct male-male competition and sperm competition, while musical ability may be an honest male display trait indicating fertility (Sluming and Manning, 2000). (b) Prenatal estrogen is important to females in the differentiation of ovaries and the formation of breast buds (Trichopoulos, 1990). Breasts are probably a sexually selected female display trait and breast asymmetry predetermined *in utero* and accentuated in puberty may be negatively correlated with fertility (Møller et al., 1995; Manning et al., 1997). A proxy of high testosterone levels in females, i.e., high WHR, is associated with cardivascular disease, elevated incidence of diabetes, and lowered fertility (for review see Singh, 1993). Low WHR and low breast asymmetry have been shown to be attractive to men (Singh and Young, 1995).

We suggest the following model. Consider a man who has had high testosterone and low estrogen exposure *in utero*, i.e., he has a low 2D:4D ratio. It would be of advantage to him if his sons shared these characters. They may therefore make many grandchildren to him. However, what of his daughters? High testosterone and low estrogen could compromise the development of their reproductive system and therefore reduce their fitness. Similarly, a woman with low testosterone and high prenatal exposure to estrogen may produce fertile daughters but low-fertility sons. In such a situation, modifiers of genes controlling sex-limited prenatal testosterone and estrogen exposure may arise and spread. Eventually, we may expect complete sex dependence to characterize the expression of genes that influence prenatal hormonal levels.

The distribution of the 2D:4D ratio shows a high degree of overlap between males and females. This suggests that sex-limited expression is incomplete. Why is this so? Sex limitation is a complex adaptation, involving the evolution of sex-specific regulatory sequences (Rice, 1996a). It will therefore evolve slowly. However, other things being equal, it will eventually evolve. So do we simply need more time or are there other factors operating here? One possibility is the occurence of cycles of intragenomic conflict. Males, because they produce low-cost sperm, are able to fertilize many eggs. Females, because they produce high-cost ova, are limited to smaller numbers of offspring. In populations with polygyny or frequent extra-pair copulations (EPCs), the variance of male reproductive success is high. That is, a small proportion of successful males may fertilize a high proportion of eggs. When strict monogamy is practiced by most females, the variance in male reproductive success is similar to that of females. In such a situation, polygyny or EPCs may be a successful female strategy if there is substantial heritable variance in male fitness. If there is little such variance, female monogamy would be favored. Suppose there are two loci controlling *in utero* hormonal exposure:

one influencing testosterone levels and the other estrogen. A mutation arises at the testosterone locus of a male, which increases *in utero* exposure. He has high testosterone levels and sperm counts, and these traits are passed on to his sons. However, because sex limitation is incomplete, his daughters have reduced fertility. The existence of such a male or small numbers of such males increases the variance in male fitness and favors a polygynous or EPC strategy in females. The high testosterone mutation will spread and with it the frequency of polygyny or EPCs. However, as the mutation becomes common, the variance in male fitness declines and females switch to increasing frequencies of monogamy. Now conditions favor the spread of a mutation at the estrogen locus, which increases *in utero* estrogen exposure. Alternating cycles of high prenatal testosterone and high prenatal estrogen will ccur. This is interlocus coevolution of sexually anagonistic genes. Such coevolution has the characteristics of the Red Queen process (Rice and Holland, 1997). Sexually antagonistic genes should affect fertility and, because of population cycles, may be at different frequencies in different populations. In populations with high prenatal exposure to testosterone in both males and females, there may be substantial differences in the variance in male and female reproductive success. A negative relationship between 2D:4D and offspring number would be expected in males and a positive association in females. In addition, there will be selective pressure for the accumulation of modifiers that cause sex-limited expression. A population that is highly estrogenized *in utero* would have no marked difference in variance of male and female reproductive success, no strong correlation between 2D:4D ratio and offspring number, and little selective pressure for sex-limited expression of prenatal genes.

Other factors may be important in 2D:4D differences between populations. Male mate preference for high WHR women could ensure high prenatal testosterone exposure for their sons who would have low 2D:4D (Manning et al., 1999). High WHR women also tend to have an excess of sons (Manning et al., 1996; Singh and Zambarano, 1997; Manning et al., 1999). Daughters from such a pairing would presumably be exposed to high prenatal testosterone and have health and fertility problems. Preference for low WHR women would favour oestrogenised daughters and sons. The latter would have compromised health and fertility. Where polygyny is strong or EPC rates are high male WHR preferences may drive mean 2D:4D values up or down. Men in westernised societies appear to prefer low WHR women but there is some evidence for preference for at least heavy women in traditional societies (Singh, 1993; Manning et al., 1996; Yu and Sheppard, 1998). High 2D:4D ratio may be associated with preference for low WHR and low 2D:4D with a preference for heavy tubular women. A drive toward low 2D:4D may be limited by the negative effects of very high prenatal testosterone exposure on some males (e.g., autism, dyslexia, migraine, various cancers) (Manning and Bundred, in press). The spread of high 2D:4D ratios may be halted by the deleterious effects of excess prenatal estrogen (e.g., breast and ovarian cancers; see Manning and Bundred, in press).

The prenatal period, particularly, the first trimester of pregnancy, is very important for the organization of the central nervous system, urinogenital system, and cardiovascular system. Prenatal testosterone and estrogen have their impact on differentiation when systems show sex-limited differences. Therefore, it is likely that 2D:4D will prove to be a marker for many traits that show sex-limited expression. These may include behavioral traits such as handedness, verbal fluency, spatial judgment, autism, schizophrenia, and depression. Sexually antagonistic genes have beneficial effects in one sex and harmful effects in the other sex. This means that natural selection cannot remove them, and each sex comes to contain numerous deleterious traits that are advantageous in the other sex (Rice, 1996b). The etiology of many major human diseases may be understandable in terms of sexually antagonistic genes. Examples may include tendencies toward adult-onset diseases of the cardiovascular system and cancers such as breast, ovarian, and prostate. 2D:4D ratio may prove to be a predictor of susceptibility to such diseases (Manning and Bundred, in press).

Acknowledgments

We are grateful to Varpu Lindstrom and Louise Barrett for help with data collection.

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