The 2nd:4th digit ratio and asymmetry of hand performance in Jamaican children

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Testosterone, particularly prenatal testosterone, has been implicated in the aetiology of many extragenital sexually dimorphic traits. It is difficult to test directly for the effect of prenatal testosterone in humans. However, Manning, Scutt, Wilson, and Lewis-Jones (1998b) have recently shown that the ratio of the length of the 2nd and 4th digits (2D:4D) in right hands negatively predicts testosterone levels in men. As digit ratios are fixed *in utero* it may be that the 2D:4D ratio is associated with many prenatally determined sexually dimorphic traits. We tested this for one case by examining the relationship between lateralised hand performance (LHP), as measured by an Annett peg board, and 2D:4D ratio in rural Jamaican children. 2D:4D ratio was measured from photocopies and X rays of hands. A low 2D:4D ratio in the right hand of boys and girls (photocopies) and the right hand of boys only (X rays) was associated with a reduction in rightward performance asymmetry. In both samples the difference in 2D:4D ratio between the hands (2D:4D left hand–2D:4D right hand) showed the strongest relationship with LHP i.e. high ratio in the left and low in the right correlated with a tendency towards a fast performance with the left hand. It is suggested that the 2D:4D ratio may be associated with the expression of other sexually dimorphic behavioural traits.

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INTRODUCTION

Prenatal testosterone has been implicated as an important factor in the development of extragenital sexual dimorphism including the differentiation of the nervous system (Bardin & Caterall, 1981; McEwen, 1981; MacLusky & Naftolin, 1981). One such dimorphism may be seen in the expression of hand preferences (Geschwind & Behan, 1982; Geschwind & Galaburda, 1985; Hassler & Gupta, 1993). Geschwind and Galaburda (1985) have hypothesised that testosterone may slow growth within some areas of the left hemisphere and promote growth of certain areas in the right hemisphere. Such a process may mean that high levels of testosterone *in utero* would be associated with left-handedness and this left-preference could be seen in higher frequencies in males.

The Geschwind and Galaburda model is controversial. The model predicts association between left-handedness and lateralised hand performance and such things as auto-immune disorders, autism, and dyslexia. Not all of these predictions are convincingly supported by available data (Bryden, McManus, & Bulman-Fleming, 1994). A more powerful test of the model would be to relate the expression of left-handedness and other traits directly to prenatal testosterone.

It is very difficult to test directly for the effect of prenatal testosterone on left-handedness and lateralised hand performance in humans. However, *in utero* exposure to testosterone may leave morphological markers which could be used to test the relationship indirectly. Prenatal testosterone comes from maternal testosterone, which may pass across the placenta and enter the foetal bloodstream, and from the foetus itself, which secretes increasing amounts from about 8 weeks (the time of Leydig cell differentiation) to mid-gestation (George, Griffin, Leshin, & Wilson, 1981; Jamison, Meier, & Campbell, 1991). From that point levels slowly decrease until a few months after birth when it has reached the low level characterising childhood (Tanner, 1990). The foetal source is dependent on the differentiation of the testes (Lording & Dekretser, 1972). Manning et al. (1998a,b) have pointed out that the differentiation of the gonads and the digits and toes is under the common control of the *Hox* genes and particularly the posterior-most *Hoxd* and *Hoxa* genes (Kondo, Zakamy, Innis, & Duboule, 1997; Peichel, Prabhakaram, & Vogt, 1997). Therefore patterns of formation of the digits would relate to the function of the gonads. In support of this Manning et al. (1998a) have found that digit asymmetry is negatively related to sperm numbers per ejaculate and to measures of sperm viability such as the Sperm Migration Test. In addition the ratio between the length of the 2nd digit or index finger and that of the 4th digit or ring finger (2D:4D ratio) was sexually dimorphic. Men tended to have a lower 2D:4D ratio than women, and in men 2D:4D was negatively related to sperm numbers and testosterone levels and positively related to oestrogen and LH levels. In women 2D:4D was positively correlated with oestrogen and LH. They also found that all relationships were stronger for the 2D:4D ratio of the right hand compared to that of the left

(Manning et al., 1998a). Relative digit length is determined early in foetal growth. Garn, Burdi, Babler, & Stinson (1975) have found that adult bone-to-bone ratios of the phalanges are established by 13 weeks. The correlations between 2D:4D ratios and adult hormone levels are therefore likely to relate also to foetal hormone levels.

The purpose of this work was to examine the relationship between 2D:4D ratio and measures of lateralised hand preference. The work was carried out within a large long-term study, the Jamaican Symmetry Project, which is concerned with patterns of developmental instability in rural Jamaican children (Manning et al., 1997; Trivers, Manning, Thornhill, & Singh, 1999). Our prediction was that low 2D:4D ratio would be related to an increase in the speed of performance with the left hand relative to the right.

METHOD

Our Jamaican study population is described in detail in Trivers et al. (1999) and Manning et al. (1997). Our total sample was 285 children (156 boys and 129 girls) drawn from Southfield in the parish of St Elizabeth. The children were recruited from three schools in the area (Top Hill Primary, Mayfield All/Age, and Epping Forest All/Age) and the sample had an age range of 5–11 years. Subjects' age, height, and weight were recorded.

We assessed relative hand performance by the Annett peg-moving test (Annett, 1985, 1987). Trials were carried out in January 1996. A peg board with two rows of ten holes was used. Participants moved, with one hand, ten pegs from a row or holes to an empty row of holes situated about five inches in front. Each trial was timed from the moment the hand touched the first peg until the last peg was placed in its hole. There were ten trials in all, five for each hand. Mean left and right hand times were then calculated. Lateralised hand performance (LHP) was calculated by subtracting the mean left hand time from the mean right hand time, i.e. the greater the LHP the greater the tendency to perform faster with the left hand relative to the right hand. Subjects who had a faster time with the left hand compared to the right hand had an LHP > 1. There were 250 participants with a mean LHP of -1.77 ± 1.14SD seconds and a range of -5.27 to 2.80 seconds. Boys had a significantly higher mean LHP than girls (boys, $n = 134$, $\bar{x} = 11\ 1.58 \pm 1.08$ seconds and girls, $n = 116$, $\bar{x} = -1.99 \pm 1.17$ seconds, unpaired t test, $t = 2.89$, $P = 0.004$).

The 2D:4D ratio was measured in two ways:

1. Photocopies were made of the right and left hands of 152 children (78 boys and 74 girls) in June 1998. The subjects placed their hands palm down on the centre of the glass plate and one photocopy per hand was made. Care was taken to ensure that details of major creases could be seen on the hands. When quality was poor a second photocopy was made. Vernier callipers measuring to 0.01 mm

were used to measure the length of the 2nd and 4th photocopied digits from the ventral basal crease of each digit to the tip. Repeatabilities of similar measurements made directly on digit length have been high in previous studies (Manning, 1995; Trivers et al., 1999). We calculated our repeatabilities (r_1) of 2D:4D ratios in the form of intra-class correlation coefficients using Model II single factor ANOVA tests as follows:

$$r_1 = \frac{\text{groups mean squares} - \text{error mean squares}}{\text{groups mean squares} + \text{error mean squares}}$$

In addition we used repeated measures ANOVA tests to calculate the ratio (F) between groups mean squares (i.e. the real differences between individuals) and the error mean squares (i.e. the error in our repeated measures; Zar, 1984).

Repeatabilities were obtained by measuring the 2nd and 4th digits twice from 30 hands. The r_1 values of the 2D:4D ratios were: right hand $r_1 = 0.77$ and left hand $r_1 = 0.65$. The between-individual variance was greater than the measurement error for both hands (right hand $F = 8.00$, $P = .0001$, left hand $F = 4.62$, $P = .0002$). We concluded that our measurements reflected real differences between the 2D:4D ratios of different subjects.

2. X rays of the right and left hands of 244 participants (135 boys and 109 girls) were taken in January 1996. The X rays were taken from the dorsal surface of the hand at 70kVp, 10mA and 1 second at a collimator distance of 70cm. Measurements of the 2nd and 4th digits were made from the proximal tip of the shaft of phalanx 1 to the distal tip of phalanx 3. Measurements were made with vernier callipers measuring to 0.01mm. The hands of 30 children were measured twice. Repeatabilities of the 2D:4D ratios were: right hand $r_1 = 0.77$ and left hand $r_1 = 0.79$. The F ratios were highly significant (right hand $F = 7.87$, $P = -.0001$, left hand $F = 8.52$, $P = .0001$). We concluded our measurements reflected real differences in 2D:4D ratios between subjects.

There were photocopies and X rays from 135 children. The 2D:4D ratio calculated from the photocopies was significantly correlated with the ratio from the X rays (right hand, $r = 0.46$, $F = 34.89$, $P = .0001$; left hand, $r = 0.47$, $F = 38.90$, $P = .0001$). As the photocopies were made approximately 2.5 years after the X rays this indicates the 2D:4D ratio is stable over time and our two different modes of measurement were recording real differences between subjects.

RESULTS

Study 1: Photocopies of the hands

Mean 2D:4D ratios were right hand $\bar{x} = 0.935 \pm 0.035$SD, left hand $\bar{x} = 0.934 \pm 0.036$SD. The ratios of left and right hands were significantly correlated ($r = 0.68$, $F = 124.79$, $P = .0001$). As in the English sample (Manning et al., 1998b) there was evidence of sexual dimorphism in the ratio with boys showing a lower ratio than girls. The difference was significant for the right hand but not for the left (right hand, boys $\bar{x}=0.929 \pm 0.037$SD and girls, $\bar{x}=0.941 \pm 0.032$SD, unpaired t test, $t=2.12$, $P=.03$; left hand, boys, 0.932 ± 0.36SD and girls, 0.936 ± 0.036SD, $t=0.78$, $P=0.43$).

Age, height (cm), and weight (kg) were not strong predictors of 2D:4D with only one relationship, that of age and left hand 2D:4D, showing significance (simple linear regressions, age; right hand, $b=0.003$, $F=1.75$, $P=.19$, left hand, $b=0.006$, $F=8.82$, $P=.004$: weight; right hand, $b=0.0002$, $F=1.59$, $P=.21$, left hand, $b=0.0002$, $F=0.93$, $P=.34$: height, right hand, $b=0.001$, $F=0.47$, $P=.49$, left hand, $b=0.001$, $F=1.3$, $P=.25$). Manning et al. (1998b) found no relationship between age and ratio in their English data.

There were 130 subjects (63 boys and 67 girls) with LHP scores and photocopies of their hands. Descriptive statistics (means and standard divisions) of the sample were as follows; 2D:4D ratio, right hand $\bar{x}=0.936 \pm 0.036$, left hand $\bar{x}=0.936 \pm 0.036$: LHP $\bar{x}=0.87 \pm 0.07$: Age $\bar{x}=7.82 \pm 1.45$ years: weight $\bar{x}=24.79 \pm 5.35$kg: height $\bar{x}=128.98 \pm 9.37$cms. Table 1 shows the results of simple linear regressions of LHP on 2D:4D calculated from photocopies. The 2D:4D ratio of the right hand was a significant negative predictor of LHP (Fig. 1) i.e. subjects with low 2D:4D ratio had a greater tendency towards low left hand times than subjects with high 2D:4D ratios. Left hand 2D:4D ratio did not predict LHP. A regression of LHP on 2D:4D left hand—2D:4D right hand showed a significant positive association ($b=9.68$, $F=7.83$, $P=.006$, Fig. 2). This means that a low 2D:4D ratio in the right hand relative to a high ratio in the left hand correlates with a tendency towards faster performance with the left hand relative to the right.

We found some evidence that LHP was associated with asymmetry of the 2nd and 4th digits. Absolute asymmetry was calculated by subtracting the length of

TABLE 1
Linear Regression Analyses: Photocopies

Trait	*beta*	*F*	*p*
2D:4D Right Hand (boys and girls)	–6.24	4.65	0.03
2D:4D Right Hand (boys and only)	–6.05	2.51	0.11
2D:4D Right Hand (girls only)	–4.04	0.88	0.35
2D:4D Left Hand (boys and girls)	–0.73	0.06	0.80
2D:4D Left Hand (boys only)	–5.30	1.74	0.19
2D:4D Left Hand (girls only)	4.62	1.40	0.24

The results of simple linear regression analyses of LHP (lateralised hand preference) regressed on 2D:4D ratio for right hands and left hands measured from photocopies (boys and girls $n=130$, boys $n=60$, girls $n=67$).

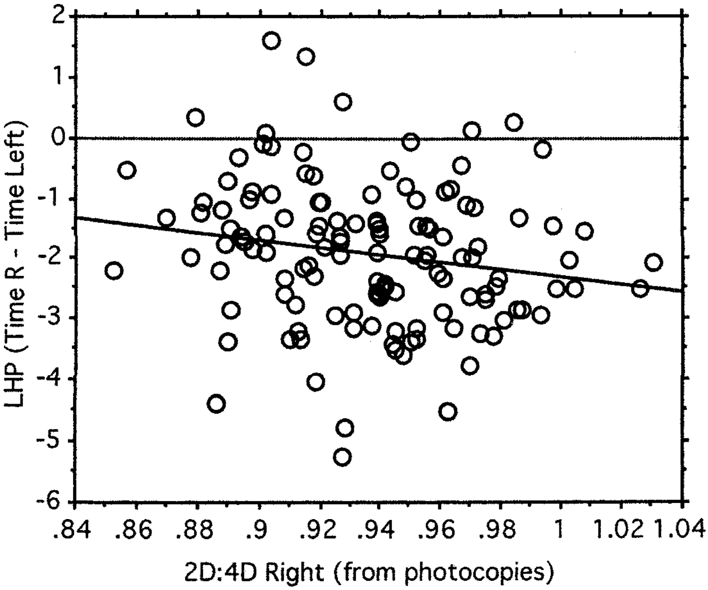

FIG. 1. The relationship of lateralised hand performance (LHP) regressed on 2D:4D (measured from photocopies) of the right hand of 130 boys and girls (y=–6.24 × 1.21). Higher LHP values indicate an increased speed of left hand performance.

the right side of the trait from the length of the left side (L–R). Descriptive statistics of asymmetries are in Table 2. Dermatoglyphic asymmetry has been reported to show a curvilinear relationship with hand preference (Yeo, Gangestad, & Daniel, 1993). We found a similar and significant U-shaped relationship between composite asymmetry of the 2nd and 4th digit and LHP (Table 2).

Study II: X rays of the Hands

Mean 2D:4D ratios calculated from the X rays were lower than those from the photocopies (X rays, right hand $\bar{x}=0.907 \pm 0.02$, left hand $\bar{x}=0.903 \pm 0.02$). Also there was no evidence of sexual dimorphism in the data (right hand, boys $\bar{x}=0.907 \pm 0.02$, girls $\bar{x}=0.907 \pm 0.02$: left hand, boys $\bar{x}=0.905 \pm 0.02$, girls $\bar{x}=0.901 \pm 0.02$). These differences presumably reflect the different types of measurement i.e. bone to bone compared to soft tissue measurements.

As with the ratios calculated from the photocopies we found that age, height, and weight were not strong predictors of 2D:4D ratio (simple linear regressions; age, right hand, $b=0.0001$, $F=0.02$, $P=.89$, left hand, $b=0.0002$, $F=0.05$, $P=.83$: height, right hand, $b=0.0001$, $F=0.58$, $P=.45$, left hand, $b=0.0002$,

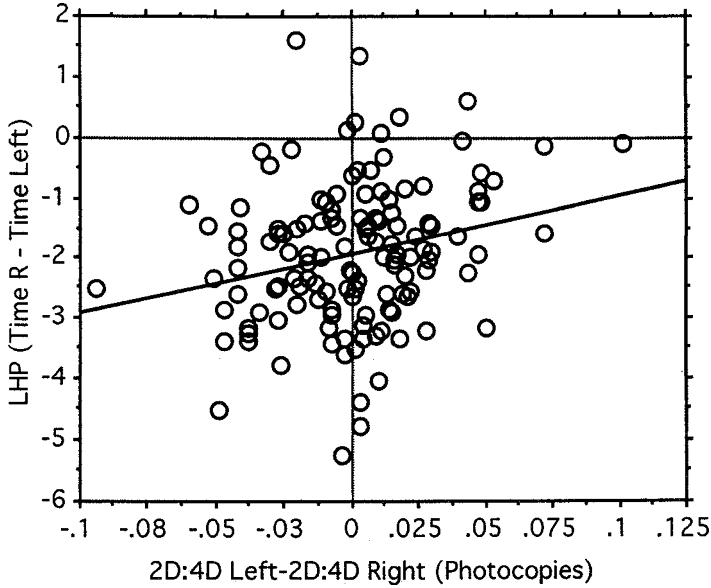

FIG. 2. The relationship of lateralised hand performance (LHP) regressed on 2D:4D left hand–2D:4D right hand (measured from photocopies) of 130 boys and girls (y = 9.68 × 1.92). Higher LHP values indicate an increased speed of left hand performance.

TABLE 2
Descriptive Statistics: Photocopies

Tests of Directional Asymmetry (one-sample t tests, mean at zero)	
2nd digit,	$x = -0.08$mm, $t = 0.65$, $P = .52$.
4th digit,	$x = -0.05$mm, $t = 0.32$, $P = .75$.
No evidence of directional asymmetry.	
Tests of Skewness (g_1) and kurtosis (g_2)	
2nd digit	$g_1 = 0.25$, $Z = 1.27$, $P = .10$
	$g_2 = 0.09$, $Z = 0.23$, $P = .41$.
4th digit	$g_1 = 0.45$, $Z = 2.26$, $P = .01$.
	$g_2 = 3.47$, $Z = 8.89$, $P = .0001$.
There was evidence that the asymmetries of the 4th digit were skewed and leptokurtotic.	
2nd Order Polynomial Regressions of Digit Asymmetry on LHP	
2nd digit	$r^2 = 0.03$, $F = 2.03$, $P = .14$.
4th digit	$r^2 = 0.03$, $F = 1.98$, $P = .14$.
Composite Asymmetry	$r^2 = 0.06$, $F = 3.58$, $P = .03$.

Descriptive statistics of absolute asymmetries calculated (L–R) from the lengths of the 2nd and 4th digits measured from photocopies.

$F=2.01$, $P=.16$: weight, right hand, $b=0.0002$, $F=0.39$, $P=.53$, left hand, $b=0.0002$, $F=0.91$, $P=.34$).

There were 215 subjects (116 boys and 99 girls) with LHP scores and X rays of their hands. Descriptive statistics (means and standard deviations) of the sample were as follows; 2D:4D ratio, right hand $\bar{x}=0.907 \pm 0.023$, left hand $\bar{x}=0.904 \pm 0.023$: LHP $\bar{x}=0.87 \pm 0.07$: age $\bar{x}=8.30 \pm 1.72$ years: weight $\bar{x}=25.85 \pm 6.10$: height $\bar{x}=129.99 \pm 10.33$cms) (Fig. 3). Table 3 shows the results of simple linear regressions of LHP on 2D:4D calculated from X rays. The 2D:4D ratio of the right hand in boys was a significant negative predictor of LHP. That is, in boys those individuals with low 2D:4D ratio in the right hand had a higher tendency towards left handedness than boys with high ratios. The remaining relationships were not close to significance. A regression of LHP on L–R 2D:4D again showed a positive and significant association ($b=10.03$, $F=4.69$, $P=.03$, Fig. 4). That is a low 2D:4D in the right hand and high 2D:4D in the left hand gave a tendency towards a faster performance with the left hand compared to the right.

In this sample we found no evidence that LHP was related to asymmetry of the 2nd and 4th digits as measured from X rays. Absolute asymmetry was calculated as previously (Table 4) and there was no U-shaped relationship between composite asymmetry of the 2nd and 4th digit and LHP.

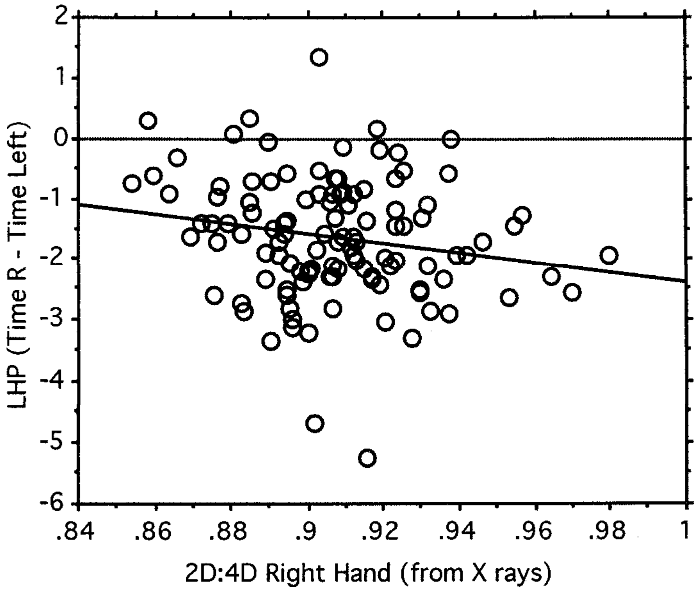

FIG. 3. The relationship of lateralised hand performance (LHP) regressed on 2D:4D right hand (measured from X rays) of 116 boys (y=–7.99 × 1.39). Higher LHP values indicate an increased speed of left hand performance.

TABLE 3
Linear Regression Analyses: X Rays

Trait	*beta*	*F*	*P*
2D:4D Right Hand (boys and girls)	–3.59	1.23	0.27
2D:4D Right Hand (boys only)	–7.99	4.12	0.04
2D:4D Right Hand (girls only)	1.70	0.11	0.74
2D:4D Left Hand (boys and girls)	1.19	0.14	0.71
2D:4D Left Hand (boys only)	–3.82	1.02	0.32
2D:4D Left Hand (girls only)	6.58	1.60	0.21

The results of simple linear regression analyses of LHP (lateralised hand performance) regressed on 2D:4D ratio (measured from X rays) for right hands and left hands (boys and girls $n=215$, boys $n=116$ and girls $n=99$).

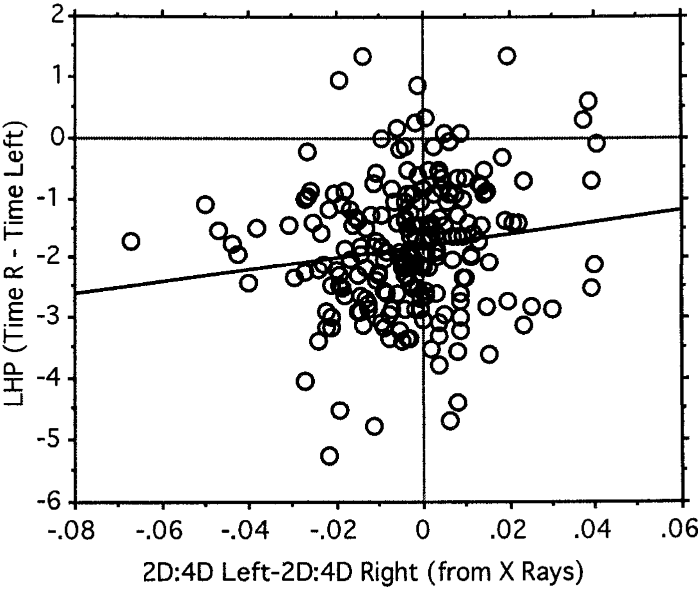

FIG. 4. The relationship of lateralised hand performance (LHP) regressed on 2D:4D left hand–2D:4D right hand (measured from X rays) of 215 boys and girls (y = 10.03 6–1.78). Higher LHP values indicate an increased speed of left hand performance.

TABLE 4
Descriptive Statistics: X Rays

Tests of Directional Asymmetry (one-sample t tests, mean at zero)	
2nd digit,	$x = 0.31$mm, $t = 5.51$, $P = .0001$.
4th digit,	$x = 0.11$mm, $t = 1.87$, $P = .07$.
Evidence of directional asymmetry in the asymmetries of digit 2.	
Tests of Skewness (g_1) and kurtosis (g_2)	
2nd digit	$g_1 = 0.22$, $Z = 1.37$, $P = .09$.
	$g_2 = 0.08$, $Z = 0.25$, $P = .40$.
4th digit	$g_1 = 0.55$, $Z = 3.43$, $P = .003$.
	$g_2 = 4.15$, $Z = 13.21$, $P = .0001$.
There was evidence that the asymmetries of the 4th digit were skewed and leptokurtotic.	
2nd Order Polynomial Regressions of Digit Asymmetry on LHP	
2nd digit	$r^2 = 0.01$, $F = 1.30$, $P = .27$.
4th digit	$r^2 = 0.01$, $F = 0.9$, $P = .40$
Composite Asymmetry	$r^2 = 0.001$, $F = 0.10$, $P = .91$.

Descriptive statistics of absolute asymmetries calculated (L–R) from the lengths of the 2nd and 4th digits measured from X rays.

DISCUSSION

We have found evidence that low 2D:4D ratios in the right hand correlate with a reduction in left-hand performance times. This effect is seen in our male and female sample combined in Study I and in males only in Study II. Left hand 2D:4D ratios alone did not predict LHP in either study. The strongest correlate of LHP in both studies was L–R 2D:4D ratio.

There are two possible interpretations of our results. (1) They could arise from a direct effect of relative 2nd and 4th digit lengths on manual dexterity. For example, a hand with a 2D:4D ratio = 1 may be more dextrous than a hand with a ratio of say 0.90. If this was so, an individual with a low ratio in the right hand and a high ratio in the left might favour the use of the latter hand over the former. We do not think this is a correct interpretation of our data. If low ratios were correlated with preferred use of the other hand then simple linear regressions of LHP on 2D:4D ratio of the left hand would show strong positive relationships, in addition to the negative relationships of the right hand. An explanation involving both left and right hand 2D:4D ratios is necessary. (2) An alternative explanation is the following model: (a) it is known that adult testosterone levels are negatively correlated with 2D:4D in the right hand, this suggests that foetal levels of testosterone show similar association; (b) foetal testosterone may inhibit the growth of the left hemisphere (Geschwind & Galaburda, 1985) and may also lower the 2D:4D ratio of the right hand (Manning et al., 1998B); (c) a reduction in growth of the left hemisphere could be associated with an enhanced growth rate of the right hemisphere but perhaps the effect of testosterone on the 2D:4D ratio of the left hand is less marked; (d) an increase in dexterity of the left hand is facilitated by this relative effect on right and left hemisphere growth and is negatively correlated with 2D:4D ratio of the right hand and positively with L–R 2D:4D ratio. In support of this model it is known that dermatoglyph asymmetry, which is determined in the first trimester of pregnancy, is related to hand preference (Yeo et al., 1993) and to testosterone levels in adults (Jamison et al., 1993). Against the model is the lack of direct evidence that foetal testosterone is related to cerebral lateralisation (Grimshaw, Bryden, & Finnegan, 1995). We are at present investigating the relationship between foetal testosterone and 2D:4D ratio.

Testosterone production may be ultimately dependent on *Hox* gene function. The posterior-most *Hoxd* and *Hoxa* genes are essential for limb and genital development (Herault, Fradeau, & Zakany, 1997; Peichel et al., 1997). In humans the hand–foot–genital syndrome is marked by anatomical defects in digits and genitalia, and is the result of mutation within *Hoxa* (Mortlock & Innis, 1997). Polymorphisms within *Hoxd* and *Hoxa* may therefore result in variation in gonad and digit form and function. The former could then affect Leydig cell differentiation and therefore the production of testosterone.

If the 2D:4D ratio (particularly the ratio for the right hand) is a marker of *in utero* testosterone levels it may be useful as a predictor of other extragenital traits. Geschwind and Galaburda (1985) have implicated testosterone in the aetiology of autism, dyslexia, migraine, stammering, autoimmune disease, sexual preferences, and spatial, language, music, and mathematical abilities. We suggest that these traits will also correlate with 2D:4D ratios of the right hand and L–R 2D:4D ratios.

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