



Second to fourth digit ratio and hand skill in Austrian children

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Abstract

Prenatal exposure to testosterone is thought to promote the development of the right-hemisphere and increase the incidence of sinistrality. A direct test of this hypothesis has previously been problematic because of the difficulty of indirectly assessing prenatal sex steroid exposure. Evidence now suggests that the ratio between the length of the second and fourth digits ($2D:4D$) is related to prenatal testosterone exposure. We tested whether digit ratio is related to the degree of hand skill such that low $2D:4D$ (indicating high levels of testosterone in utero) may be correlated with enhanced left-hand performance. In right-handed children, high $2D:4D$ correlated with improved right-hand skill and low $2D:4D$ correlated with enhanced left-hand skill. Correlations were found to be similar for girls and for boys. Since low $2D:4D$ has been previously reported to be associated with faster left-hand speed compared to right in Afro-Caribbean children with very low mean $2D:4D$, the present finding in a Caucasian population with high mean $2D:4D$ suggests that a tendency of improved left-hand performance due to prenatal testosterone may be found across ethnic groups.

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1. Introduction

Individual differences in lateralization are well known, for example Annett (1985) noted that between 8–12% of the population are left-handed; moreover cognitive function also appears to be lateralized, with most right-handers processing language in the left hemisphere, and visuoperceptual processes in the right (Bryden, 1982). Several theories have been proposed to account for individual differences in lateralization, all have in common the notion that lateralization occurs early in development in response to sex steroid exposure.

The ‘sexual differentiation’ theory (Hines and Shipley, 1984) argues that early exposure to testosterone causes masculinization of physiology, anatomy and behaviour (for review see Goy and McEwen, 1980). In support, males display higher rates of left-handedness (Perelle and Ehrman, 1994) and there appears to be a clear link between handedness and sexual orientation (Lalumière et al., 2000).

A second ‘callosal’ theory (Witelson and Nowakowski, 1991) posits that cerebral lateralization occurs via the testosterone-mediated pruning of callosal axons during early development. A clear prediction of this theory is that increased levels of prenatal testosterone would be associated with greater cerebral lateralization, and a stronger right-hand preference. In support, Grimshaw et al. (1995) assessed testosterone concentrations in amniotic fluid and lateralization of speech, emotion and handedness in children at age 10. They reported that girls exposed to higher prenatal testosterone were more strongly right-handed and had stronger left hemisphere speech representation.

The third ‘GBG’ hypothesis (Geschwind and Behan, 1982; Geschwind and Galaburda, 1987), proposes that in utero levels of testosterone influence cerebral development such that high levels of testosterone slows growth of certain regions of the left hemisphere, leading to right-hemisphere language dominance and increased left-handedness. Support for the theory remains equivocal with some authors confirming its predictions (see Tan, 1991b) while others report findings directly opposed to its predictions (see Elkadi et al., 1999; Gadea et al., 2003). Indeed, the clear predictions between left-handedness and auto-immune disorders, and developmental disorders are not convincingly supported (Bryden et al., 1994). The original theory has undergone several modifications. For example, Kelley (1993) proposed that testosterone inhibits ontogenetic cell death in the left hemisphere though with prolonged exposure both hemispheres are affected leading to anatomical asymmetry. While this modification suggests a different role for testosterone the predictions remain the same, namely that increased levels of this hormone are associated with an increase in left-handedness.

A key problem in assessing the theories is that evidence has typically come from studies of atypical populations. Where normal populations have been utilised, measures of prenatal testosterone exposure are limited to sampling amniotic fluid which may not reflect hormone exposure during early critical periods of development, and may simply reflect maternal levels (Reinisch and Sanders, 1984). Recent research suggests that an accurate window into prenatal steroid exposure may be provided by analysis of finger length patterns. There is accumulating evidence that the ratio between the length of the second digit (the index finger) and the length of the fourth digit (the ring finger) ($2D:4D$) is sexually dimorphic and is largely determined prenatally (Manning, 2002). Males tend to show lower values of $2D:4D$

than do females, i.e., males have on average longer fourth digits relative to their second than females (Phelps, 1952; Manning et al., 1998). Relative finger lengths are determined before birth (Garn et al., 1975), the sex difference in $2D:4D$ is present in children as young as 2 years (Manning et al., 1998), and sex differences in $2D:4D$ are robust across a number of ethnic groups and races (Manning, 2002; Peters et al., 2002).

The sexual dimorphism in $2D:4D$ has been known for many years (e.g., see Baker, 1888). However, it has only recently been suggested that sex differences in $2D:4D$ arise from in utero concentrations of sex steroids, with $2D:4D$ negatively related to prenatal testosterone and positively associated with prenatal oestrogen (Manning et al., 1998). The evidence for these relationships with sex hormones is as follows: (i) some sexually dimorphic traits with an excess of males are associated with low $2D:4D$ ratios (autism and Aspergers syndrome (Manning et al., 2001); fast running speed (Manning and Taylor, 2001)). Other dimorphic traits with an excess of females are associated with high $2D:4D$ ratios (good verbal fluency and breast cancer (Manning, 2002)); (ii) mothers with a high waist-hip-ratio, (associated with high testosterone and low oestrogen), tend to have children with low $2D:4D$ ratios (Manning et al., 1999); (iii) children with congenital adrenal hyperplasia (CAH), a condition associated with high prenatal androgens, have lower $2D:4D$ ratios than controls (Brown et al., 2002; Okten et al., 2002); (iv) high sensitivity to testosterone, as measured by the structure of the testosterone receptor, is associated with low $2D:4D$ (Manning et al., 2003); (v) mothers with low $2D:4D$ tend to have children with low $2D:4D$ ratio and their children have high concentrations of testosterone relative to oestrogen in their amniotic fluid (Manning, 2002; Lutchmaya et al., 2004).

Manning et al. (2000a) have shown in a sample of Afro-Caribbean Jamaican children that low $2D:4D$ was associated with faster left-hand speed relative to right-hand speed in a peg moving test. In addition they found that participants with lower $2D:4D$ in their right-hand compared to their left ($D[r-l]$) had faster left-hand speed in comparison to right-hand speed. $D[r-l]$ received attention because sexual dimorphic traits in general, and the $2D:4D$ ratio in particular, tend to be expressed in the “male form” more strongly on the right side of the body in men, and this pattern is reversed in females (Tanner, 1990). Consequently, Manning et al. (2000a) suggested that low $D[r-l]$ and low $2D:4D$ were indicators of high prenatal testosterone. There are substantial ethnic differences in mean $2D:4D$. Afro-Caribbean Jamaicans have very low mean $2D:4D$ ratios while many white Caucasian populations have high mean $2D:4D$ ratios (Manning et al., 2000a). The association between hand preference and prenatal testosterone may not hold across the range of possible $2D:4D$ ratios. The aim of the present study was to determine whether digit ratio is related to the degree of hand skill in right-handed children by confirming and extending the results of Manning et al. (2000a) in a white Caucasian Austrian population. In this regard, the studies of Tan (1990a,b, 1991a,b, 1992) suggest a very careful examination of left- and right-hand skills in children and adults. In particular, Tan (1990a,b) found that only the right-hand skill showed a direct correlation and an inverse correlation with serum testosterone for men and women. Therefore we decided to put the focus on right-hand skill and the associations with digit ratio in the present study. We hypothesized that for right-handed children a low $2D:4D$ would be positively related to the degree of left-hand skill, whereas a high $2D:4D$ would be more common among individuals with enhanced right-hand skill.

2. Method

Our total sample was 93 white Caucasian children (45 boys and 48 girls) between the ages of 6–11 years recruited from an elementary school in Lower Austria (Austria). Parental permission was obtained for the testing and the methodology was agreed by the local ethical committee. Hand performance was assessed with the “Hand Dominance Test” (HDT) (Steingrüber and Lienert, 1976). This test comprises three dexterity tasks, each to be performed with maximal speed and precision over 15 s, separately for the right and left-hand (tracing lines, dotting circles, and dotting squares). In this regard, dominance refers to the performance advantage of one hand relative to the other. It is scored for each task according to the following formula:

$$D = \frac{\text{right hand performance} - \text{left hand performance}}{\text{right hand performance} + \text{left hand performance}} \times 100$$

the ratio (D) reflects the relative amount of the advantage of the dominant hand of the summary score. It results in scores from -100 (extreme left-handedness) to $+100$ (extreme right-handedness). These values are subsumed then and make up the summary score of the hand dominance inventory.

For the measurements of finger lengths photocopies were made of the ventral surface of the hand. In contrast to soft-tissue measurements taken directly from the hands, this method photocopying has advantages in terms of accuracy and practicability especially in children which normally show a high level of activity. Several studies have shown that measurements from photocopies produce similar results compared with other methods (e.g., soft-tissue measurements, X-rays; see Manning, 2002). The participants were asked to place their hands palm down on the centre of the glass plate of the photocopier 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. We measured the lengths of the second and fourth digits of the left and right-hands from the ventral proximal crease of the digit to the finger tip from the photocopies. Where there was a band of creases at the base of the digit, we measured from the most proximal of these. The measurements were made twice with the second measurement made blind to the first. All measurements were made with a digital Vernier calliper (Preisser Products, Germany) measuring to 0.01 mm. Children who reported injuries to the second or fourth digits were discarded from the analyses.

We used repeated measures ANOVA to calculate the ratio (F) between measurement error (the differences between successive measures of $2D:4D$) and between participant differences. We found that between individual differences were significantly greater than measurement error in $2D:4D$ (right-hand $F(32, 33) = 5.67$, $P < 0.0001$; left-hand $F(32, 33) = 4.93$, $P < 0.0001$). We concluded that our calculated values of $2D:4D$ reflected real differences between individuals.

We used unpaired t -tests for determining possible group-differences in $2D:4D$. A one-sample Kolmogorov–Smirnov test revealed that not all variables were normally distributed (i.e., tracing lines was not). We therefore used two-tailed Spearman correlation coefficients (ρ) for assessing the relationship between $2D:4D$ and hand preference scores.

Table 1
Spearman correlation coefficients (rho) for the relationship of hand performance scores with 2D:4D right-hand and 2D:4D left-hand

	Boys and girls (<i>n</i> = 79)	Boys (<i>n</i> = 38)	Girls (<i>n</i> = 41)
2D:4D right-hand			
Total score	0.248*	0.111	0.213
Subscore tracing lines	0.141	−0.012	0.160
Subscore dotting circles	0.091	0.108	0.036
Subscore dotting squares	0.233*	−0.036	0.200
2D:4D left-hand			
Total score	0.431**	0.366*	0.358*
Subscore tracing lines	0.135	−0.108	0.133
Subscore dotting circles	0.227	0.204	0.226
Subscore dotting squares	0.414*	0.382*	0.347*

* $P < 0.05$, two-tailed.

** $P < 0.01$.

3. Results

According to the results of the hand dominance inventory 79 children from the original sample of $N = 93$ boys and girls were classified right-handers (i.e., those who had a summary score of > 0). These were 38 boys (mean age = 8.96, S.D. = 1.38) and 41 girls (mean age = 8.52, S.D. = 1.16). Only those children were included in the subsequent analyses.

In accordance with previous reports (Manning et al., 2000a,b; Manning, 2002), 2D:4D ratio in boys was significantly lower for both hands than the girls' ratio (unpaired t -tests, 2D:4D right-hand: boys $x = 0.95 \pm 0.03$, girls $x = 0.98 \pm 0.03$, $t(77) = -3.677$, $P < 0.01$; 2D:4D left-hand, boys $x = 0.95 \pm 0.03$, girls $x = 0.97 \pm 0.03$, $t(77) = -3.483$, $P < 0.05$).

There was a significant sex difference for the hand dominance summary score, with greater right-hand dominance in girls compared to boys (boys: $x = 35.78 \pm 23.90$, girls: $x = 52.72 \pm 32.41$, $t(77) = -2.705$, $P < 0.05$), the subscore for tracing lines (boys: $x = 4.05 \pm 12.51$, girls: $x = 9.75 \pm 12.46$, $t(77) = -2.025$, $P < 0.05$), and the subscore for dotting squares (boys: $x = 10.42 \pm 14.97$, girls: $x = 20.73 \pm 18.20$, $t(77) = -2.738$, $P < 0.05$). No sex difference was found for the dotting circles subscore.

Table 1 shows the correlations between hand dominance and performance scores and right and left-hand 2D:4D for the total sample and for boys and girls separately. Basically, hand performance scores were found to be positively correlated with high 2D:4D, i.e. low prenatal testosterone was associated with better right-hand performance, whereas low 2D:4D (higher prenatal testosterone) was associated with increased left-hand performance. The associations were found to be stronger for left-hand digit ratio. In girls, left-hand 2D:4D was significantly positively correlated with the total hand performance score (see Fig. 1a), and also with the subscore for dotting squares. Girl's right-hand 2D:4D was also positively associated with hand performance but was found non-significant for the total score and the subscores. The associations between hand performance scores and left-hand 2D:4D in boys (see Fig. 1b) were found to be significantly positively associated with the total hand

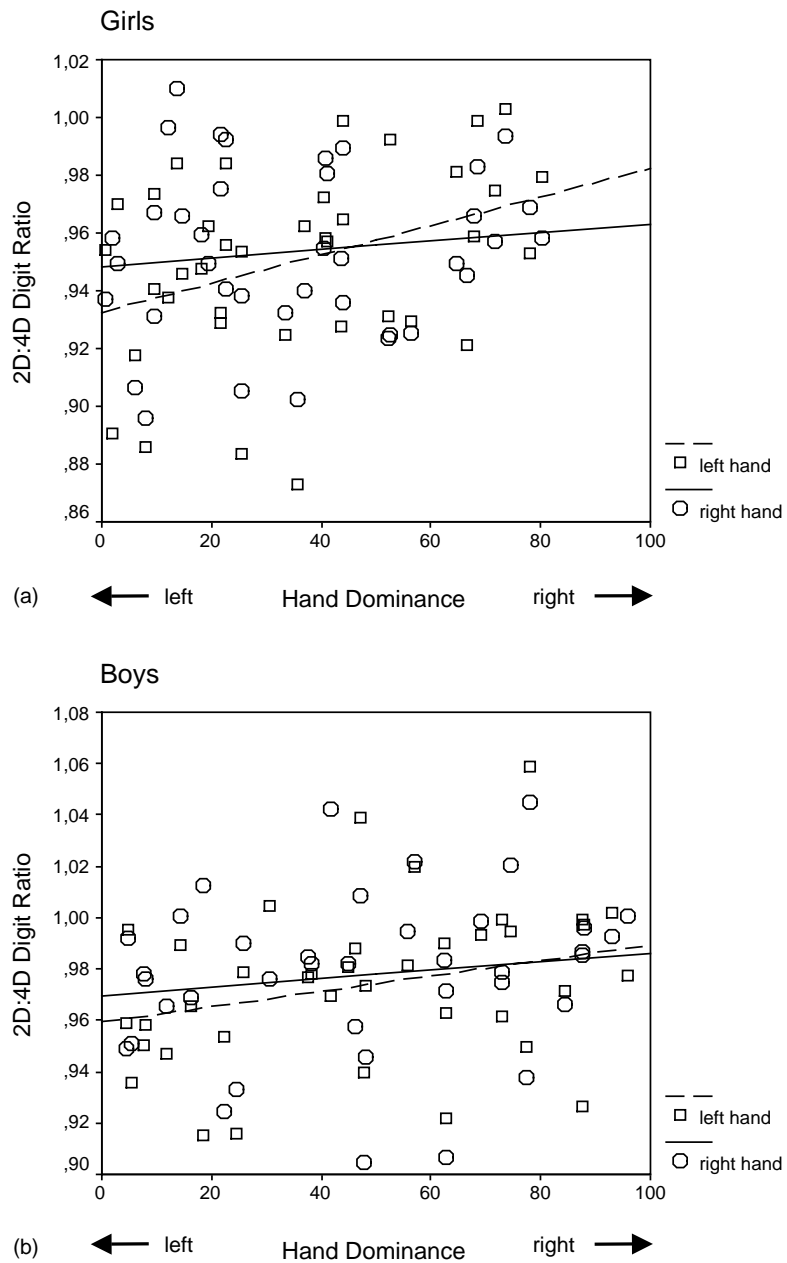


Fig. 1. Scatterplot of left and right-hand 2D:4D digit length ratios and hand dominance total scores in girls (a) and boys (b). Higher scores for hand dominance indicate better right-hand performance relative to left-hand performance.

performance score and with the subscore for dotting squares. No significant correlations were found for right-hand *2D:4D* in boys. Also, no significant associations were found for the difference between right and left-hand digit ratio ($D[r-l]$) and hand performance (total and subscores) as suggested in previous studies (Manning et al., 2000a; Manning, 2002).

Since digit ratio and also hand performance scores (except the subscore for dotting circles) were found to be significantly different between boys and girls we were interested in the associations between left and right-hand *2D:4D* and hand skill when sex was controlled. Partial correlations (r_p) between *2D:4D* ratio and test scores showed that, in general, digit ratio was positively associated with hand performance but the strongest effects were found for left-hand *2D:4D* and the total hand performance score ($r_p = 0.332$, $P < 0.05$, two-tailed) and for left-hand *2D:4D* and the subscore for dotting squares ($r_p = 0.318$, $P < 0.05$, two-tailed).

Finally we analysed whether age had a significant effect on (total) hand performance scores. This was only the case for the subscore tracing lines for girls ($\rho = 0.382$, $P < 0.05$, two-tailed). However, left-hand *2D:4D* was found to be significantly related to age in boys ($\rho = -0.477$, $P < 0.05$). Partial correlations with age held constant revealed that the associations between total hand performance scores and *2D:4D* ratio remained significant for the total sample and for left-hand *2D:4D* in boys (total sample: right-hand, $r_p = 0.248$, $P < 0.05$; left-hand, $r_p = 0.433$, $P < 0.01$; boys: right-hand $r_p = 0.129$, n.s.; left-hand, $r_p = 0.457$, $P < 0.05$). In addition, left-hand *2D:4D* in boys was also found to be significantly correlated with the subscore for dotting squares ($r_p = 0.533$, $P < 0.01$). Girls *2D:4D* ratio was positively associated with hand performance scores but remained non-significant after controlling for age.

4. Discussion

The results of this study provide further evidence that *2D:4D* is a sexually dimorphic trait in right-handed children in addition to adults, with boys having a significantly lower ratio than girls.

With regard to associations between *2D:4D* and hand skill, we found all correlation coefficients between test scores and left and right *2D:4D* to be positive and significant for right-handed subjects of the total sample. This included all three test subscales (tracing lines, dotting circles, and dotting squares) and the total score. This finding provides some support to our prediction concerning a positive association between *2D:4D* and hand performance. Considering the whole sample, as predicted there were significant positive associations between right and left *2D:4D* and test scores which included the dotting squares subscore and total test score. However, this effect was not equal between left and right *2D:4D*. We found left-hand *2D:4D* to be significantly positively correlated with the total hand dominance scores and the subscore for dotting squares for the total sample and boys and girls separately, but for right-hand *2D:4D* in the total sample only.

Similar results were found when sex was controlled, i.e. the association between hand dominance scores and *2D:4D* ratio remained significant for the left-hand in the way that low *2D:4D* ratio was associated with lower degree of right-handedness. With respect to the effects of in utero levels of testosterone we may speculate that high levels during early

development influence cerebral development in both, girls and boys, such that they slow growth of certain regions of the left hemisphere, leading to increased left-hand skill.

We found some indication that age is correlated with *2D:4D* but this was only significant for the left-hand in boys and girls as well as in the total sample. Manning et al. (1998) have found no association between age and *2D:4D* in a large sample aged 2–25 years. In our present data the overall sample showed a negative association between *2D:4D* and age, while Williams et al. (2003) reported a weak but significant positive correlation between age and *2D:4D*. More data are required to clarify the situation. However, at present it appears that relationships between age and *2D:4D* are either weak or non-existent.

Overall our data provide some support for the reported associations in children between low *2D:4D* and faster left-hand performance as compared to right (Manning et al., 2000a). Our finding was for Caucasian Austrian children and those of Manning et al. (2000a) were for rural Afro-Caribbean Jamaican children. As expected the former had higher mean *2D:4D* ratios than the latter (Males: right-hand, Austria 0.95 ± 0.03 , Jamaica 0.93 ± 0.04 , left-hand, Austria 0.95 ± 0.03 , Jamaica 0.93 ± 0.04 ; Females: right-hand, Austria 0.98 ± 0.03 , Jamaica 0.94 ± 0.03 , left-hand, Austria 0.97 ± 0.03 , Jamaica 0.94 ± 0.04). An association between low *2D:4D* and high left-hand performance scores may therefore be found across geographically and ethnically widespread populations with a range of mean *2D:4D* ratios. However, there were some differences in our findings and those of the Jamaican study. In the latter significant effects were restricted to the right-hand and were strongest in boys. Our data indicate stronger effects in the left-hand of girls. These differences may of course be due to sampling effects and more data may indicate significant associations between right and left *2D:4D* and handedness in both boys and girls. However, there is the possibility of both sex and lateralization effects here. Manning (2002) has reviewed evidence that sexually dimorphic traits tend to take the male form of the trait more intensely on the right side of the body and the female form of the trait on the left. There is some support for this tendency in *2D:4D*, with a number of studies showing lower *2D:4D* in the right-hand. In addition low $D[r-1]$ has been found to be predictive of left-handedness and some other traits that are more intensely expressed in males such as high waist-to-hip ratio and fast running speed (Manning, 2002).

We have found that a proxy for high prenatal testosterone, i.e. low values of *2D:4D*, is associated with enhanced left-hand performance. This is supportive of the GBG theory (Geschwind and Behan, 1982; Geschwind and Galaburda, 1987) and its later modifications in that prenatal testosterone appears to compromise the development of the right-hemisphere leading to improved left-hand performance. This conclusion is also supported by the finding among Jamaican children that higher left-hand relative to right-hand speed in the performance of a peg test was related to low *2D:4D* values (Manning et al., 2000a). In summary it appears that low *2D:4D* is a correlate of fast left-hand performance relative to right, and that this tendency may be found across ethnic groups with different mean *2D:4D* ratios. However, more data is required before we can say whether this effect is most strongly developed in one sex than the other or in one hand than the other. Future studies should consider the investigation of associations in consistent left-handed subjects to possibly confirm the effect of early testosterone in terms of the theory of cerebral lateralization (Geschwind and Behan, 1982).

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References

- Annett, M., 1985. *Left right, hand and brain: the right shift theory*. London, Erlbaum.
- Baker, F., 1888. Anthropological notes on the human hand. *American Anthropologist* 1, 51–76.
- Brown, W.M., Hines, M., Fane, B.A., Breedlove, S.M., 2002. Masculinized finger length patterns in human males and females with congenital adrenal hyperplasia. *Hormones and Behavior* 42, 380–386.
- Bryden, M.P., 1982. *Laterality: functional asymmetry in the intact brain*. Academic Press, New York.
- Bryden, M.P., McManus, I.C., Bulman-Fleming, M.B., 1994. Evaluating the empirical support for the Geschwind-Behan-Galaburda model of cerebral lateralisation. *Brain and Cognition* 26, 103–167.
- Elkadi, S., Nicholls, M.E.R., Clode, D., 1999. Handedness in opposite and same-sex dizygotic twins: testing the testosterone hypothesis. *Neuroreport* 10, 333–336.
- Gadea, M., Gómez, C., González-Bono, E., Salvador, A., Espert, R., 2003. Salivary testosterone is related to both handedness and degree of linguistic lateralization in normal women. *Psychoneuroendocrinology* 28, 274–287.
- Garn, S.M., Burdi, A.R., Babler, W.J., 1975. Early prenatal attainment of adult metacarpal-phalangeal rankings and proportions. *American Journal of Physical Anthropology* 43, 327–332.
- Geschwind, N., Behan, P., 1982. Left-handedness: associations with immune disease, migraine, and developmental learning disabilities. *Proceedings of the National Academy of Sciences* 79, 5097–5100.
- Geschwind, N., Galaburda, A.M., 1987. *Cerebral lateralization, biological mechanisms, associations, and pathology*. MIT Press, Cambridge, MA.
- Goy, R.W., McEwen, B.S., 1980. *Sexual differentiation of the brain*. MIT Press, Cambridge, MA.
- Grimshaw, G.M., Bryden, M.P., Finegan, J.-A., 1995. Relations between prenatal testosterone and cerebral lateralization in children. *Neuropsychology* 9, 68–79.
- Hines, M., Shipley, C., 1984. Prenatal exposure to diethylstilbestrol (DES) and the development of sexually dimorphic cognitive abilities and cerebral lateralization. *Developmental Psychology* 20, 81–94.
- Kelley, D.B., 1993. Androgens and brain development: possible contributions to developmental dyslexia. In: Galaburda, A.M. (Ed.), *Dyslexia and development: neurobiological aspects of extra-ordinary brains*. Harvard University Press, Cambridge, MA, pp. 21–41.
- Lalumière, M.L., Blanchard, R., Zucker, K.J., 2000. Sexual orientation and handedness in men and women: a meta-analysis. *Psychological Bulletin* 126, 575–592.
- Lutchmaya, S., Baron-Cohen, S., Raggatt, P., Knickmeyer, R., Manning, J.T., 2004. 2nd to 4th digit ratios, fetal testosterone and estradiol. *Early Human Development* 77 (1–2), 23–28.
- Manning, J.T., 2002. *Digit ratio: a pointer to fertility, behaviour and health*. Rutgers University Press, New Jersey.
- Manning, J.T., Barley, L., Lewis-Jones, I., Walton, J., Trivers, R.L., Thornhill, R., Singh, D., Rhode, P., Berechzei, T., Henzi, P., Soler, M., Sved, A., 2000b. The 2nd to 4th digit ratio, sexual dimorphism population differences and reproductive success: evidence for sexually antagonistic genes. *Evolution and Human Behavior* 21, 163–183.
- Manning, J.T., Baron-Cohen, S., Wheelwright, S., Sanders, G., 2001. The 2nd to 4th digit ratio and autism. *Developmental Medicine & Child Neurology* 43, 160–164.
- Manning, J.T., Bundred, P.E., Newton, D.J., Flanagan, B.F., 2003. The 2nd to 4th digit ratio and variation in the androgen receptor gene. *Evolution and Human Behavior* 24, 399–405.
- Manning, J.T., Scutt, D., Wilson, J., Lewis-Jones, D.I., 1998. The ratio of 2nd to 4th digit length: a predictor of sperm numbers and concentrations of testosterone luteinizing hormone and oestrogen. *Human Reproduction* 13, 3000–3004.

- Manning, J.T., Taylor, R.P., 2001. 2nd to 4th digit ratio and male ability in sport: implications for sexual selection in humans. *Evolution and Human Behaviour* 22, 61–69.
- Manning, J.T., Trivers, R.L., Singh, D., Thornhill, R., 1999. The mystery of female beauty. *Nature* 399, 214–215.
- Manning, J.T., Trivers, R.L., Thornhill, R., Singh, D., 2000a. The 2nd:4th digit ratio and asymmetry of hand performance in Jamaican children. *Laterality* 5, 121–132.
- Okten, A., Kalyonku, M., Yaris, N., 2002. The ratio of second-and-fourth digit lengths and congenital adrenal hyperplasia due to 21-Hydroxylase deficiency. *Early Human Development* 70, 47–54.
- Perelle, I.B., Ehrman, L., 1994. An international study of human handedness. *Behaviour Genetics* 24, 217–227.
- Peters, M., Tan, U., Kang, Y., Teixeira, L., Mandal, M., 2002. Sex-specific finger-length patterns linked to behavioral variables across human populations. *Perceptual and Motor Skills* 94, 171–181.
- Phelps, V.R., 1952. Relative index finger length as a sex-influenced trait in man. *American Journal of Human Genetics* 4, 72–89.
- Reinisch, J.M., Sanders, S.A., 1984. Prenatal gonadal steroidal influences on gender-related behaviour. In: De Vries, G.J., De Bruin, J.P.C., Uylings, H.G.M., Corner, M.A. (Eds.), *Progress in brain research*, vol. 61. Sex Differences in the Brain, Elsevier, Amsterdam, pp. 407–416.
- Steingrüber, H.J., Lienert, G.A., 1976. *Hand-Dominanz-Test (HDT)*. Hogrefe, Göttingen, Toronto, Zürich.
- Tan, U., 1990a. Testosterone and hand skill in right-handed men and women. *International Journal of Neuroscience* 53 (2–4), 179–189.
- Tan, U., 1990b. Testosterone and hand performance in right-handed young adults. *International Journal of Neuroscience* 54 (3–4), 267–276.
- Tan, U., 1991a. The relationship between serum testosterone and visuomotor learning in hand skill in right-handed young women. *International Journal of Neuroscience* 56 (1–4), 13–18.
- Tan, U., 1991b. Serum testosterone levels in male and female subjects with standard and anomalous dominance. *International Journal of Neuroscience* 58, 211–214.
- Tan, U., 1992. Testosterone and estradiol in right-handed men but only estradiol in right-handed women is inversely correlated with the degree of right-hand preference. *International Journal of Neuroscience* 66 (1/2), 25–34.
- Tanner, J.M., 1990. *Foetus into man: physical growth from conception to maturity*. Harvard University Press, Cambridge, Massachusetts.
- Williams, J.H.J., Greenhalgh, K.D., Manning, J.T., 2003. Second to fourth finger ratio and possible precursors of developmental psychopathology in preschool children. *Early Human Development* 72, 57–65.
- Witelson, S.F., Nowakowski, R.S., 1991. Left out axons make men right: a hypothesis of the origin of handedness and functional asymmetry. *Neuropsychologia* 28, 327–333.