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Prediction of hemispheric asymmetry as measured by handedness from digit length and 2D:4D digit ratio

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Hemispheric asymmetry is widely theorised as having a basis in prenatal androgen levels. However, these theories ignore a second round of asymmetrical changes in the brain, which occur at the same time as post-puberty surges in androgens. Hemispheric asymmetry in adults might therefore be explained in terms of the joint effects of prenatal and post-pubertal androgen levels. Evidence is emerging that the ratio between the length of the second and fourth digits (2D:4D) is related to prenatal androgen exposure, and that digit length is related to post-puberty levels of androgen exposure. In this study, hemispheric asymmetry is measured as handedness, prenatal androgen levels as 2D:4D, and post-puberty androgen levels as digit length. Right-handedness is associated with consistent prenatal and post puberty androgen release whereas left-handedness is associated with mixed levels of androgen release. Age, race, and sex effects were explored but were not significant.

The aim of this research is to develop and test a theory that links digit characteristics to hemispheric asymmetry. It is argued that hemispheric asymmetry (measured by handedness) should be predicted from digit ratio, in interaction with digit length. This is on the basis that hemispheric asymmetry has a likely basis in androgen release, and that digit ratio and digit length are likely markers of the two stages of major androgen release during development.

One of the most obvious indications of lateralisation of functions in the human brain is handedness. Handedness is defined as the hand that humans use or habitually prefer across a variety of tasks (Annett, 1985). Handedness is generally seen as depending primarily on prenatal factors, such as genetics (Annett, 1985; Gangestad et al., 1996; McManus, 1985; Yeo, Gangestad, & Daniel, 1993) and prenatal or perinatal environmental events (Bishop, 1990; for a critical review see Searleman, Porac, & Coren, 1989). Indirect evidence for the early ontogeny of handedness includes studies of foetuses that

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disproportionately move their right hands (McCartney & Hepper, 1999) and suck their right thumbs (Hepper, Shahidullah, & White, 1991).

Handedness is also widely regarded as a good measure of lateralisation of cortical functions (e.g., Coulson & Lovett, 2004; Hopkins & Cantalupo, 2004; Jansen, Floel, Menke, Kanowski, & Knecht, 2005). Recent studies in humans have provided evidence that asymmetries associated with regions of the primary motor cortex are related to handedness (Amunts et al., 1996; White, Lucas, Richards, & Purves, 1994). Neuroanatomical studies in humans have identified an area of the precentral gyrus known as the knob that is related to the representation of contralateral hand and fingers on the motor strip (Hlustik, Solodkin, Gullapalli, Noll, & Small, 2001; Maldjian, Gottschalk, Patel, Detre, & Alsop, 1999; Yousry et al., 1997). Functional imaging studies (including fMRI and positron-emission tomography) provide evidence that handedness is associated with the dorsal primary motor cortex in the hemisphere contralateral to the active hand (Pizzella, Tecchio, Romani, & Rossini, 1999). Transcranial magnetic stimulation studies also provide evidence in favour of the contralateral relationship between handedness and hemispheric activity (Boroojerdi et al., 1999; Triggs, Subramanium, & Rossi, 1999). Overall, these studies suggest that the neurobiological basis for control of the hand and hand preference is localised to the contralateral dorsal area of the primary motor cortex and provide evidence that handedness is a useful index of at least some aspects of hemispheric lateralisation.

The androgen theories, which are the focus of the current paper, predict that prenatal exposure to testosterone influences cell death in the foetal brain. Two main theories account for individual differences in hemispheric asymmetry and both share the notion that hemispheric lateralisation occurs early in development in response to androgen exposure (Becker, Breedlove, & Crews, 1992; Sisk, Schulz, & Zehr, 2003).

The first theory is commonly referred to as the "GBG" theory (Geschwind & Behan, 1982; Geschwind & Galaburda, 1987). GBG theory proposes that prenatal testosterone influences hemispheric asymmetry such that high levels of testosterone slow growth of certain regions of the left hemisphere, leading to both right-hemisphere language dominance and increased incidence of left-handedness. Kelley (1993) extends the theory to argue that testosterone inhibits ontogenetic cell death in the left hemisphere. Support for this theory remains equivocal, with some authors confirming its predictions (see Tan, 1991), while others report findings in opposition to predictions (see Elkadi, Nicholls, & Clode, 1999; Gadea, Gómez, González-Bono, Salvador, & Espert, 2003). While noting that GBG theory is highly criticised (Bryden, McManus, & Bulman-Fleming, 1994; McManus & Bryden, 1991; Previc, 1991; Tønnessen, 1997), the general prediction from GBG is that increased prenatal levels of testosterone will affect brain structure, leading to right hemispheric dominance and consequently left-handedness.

The second theory hypothesises that androgens may differentially influence naturally occurring axonal loss in each side of the corpus callosum, thereby explaining the mechanism underlying the embryological development of hand preference (Witelson & Nowakowski, 1991). To test this theory, Grimshaw, Bryden, and Finegan (1995) assessed testosterone concentrations in amniotic fluid and lateralisation 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, but did not find this effect for boys. This theory predicts that increased levels of prenatal testosterone are associated with greater lateralisation towards the left hemisphere and right-handedness.

Recent research suggests that an accurate marker of prenatal sex steroid exposure is the ratio between the length of the second digit (the index finger) and the length of the fourth digit (the ring finger). This finger length ratio is commonly termed 2D:4D, and is negatively related to prenatal testosterone and positively associated with prenatal oestrogen (Manning et al., 1998).

The relationship between 2D:4D and sex steroids can be summarised as follows: (i) males tend to show lower values of 2D:4D than females (Phelps, 1952; Manning, Scutt, Wilson, & Lewis-Jones, 1998); (ii) Some sexually dimorphic traits that occur more frequently in males (e.g., autism, Aspergers, fast running speed) are associated with low 2D:4D (Manning, Baron-Cohen, Wheelwright, & Sanders, 2001; Manning & Taylor, 2001), while other dimorphic traits that occur more frequently in females (e.g., good verbal fluency and breast cancer) are associated with high 2D:4D ratios (Manning, 2002); (iii) Women and men with smaller digit ratios have more masculine characteristics (Csatho et al., 2003; Neave, Laing, Fink, & Manning, 2003; Wilson, 1983); (iv) Mothers with a high waist–hip ratio (associated with high testosterone and low oestrogen), tend to have children with low 2D:4D ratios (Manning, Trivers, Singh, & Thornhill, 1999).

The evidence that the link between 2D:4D and sex steroids is prenatal, biological, and genetic can be summarised as follows: (i) sex differences in 2D:4D are present in children as young as 2 years (Brown, Hines, Fane, & Breedlove, 2002; Manning et al., 1998; Okten, Kalyoncu, & Yaris, 2002); (ii) High sensitivity to testosterone, as measured by the structure of the testosterone receptor, is associated with low 2D:4D (Manning, Bundred, Newton, & Flanagan, 2003); (iii) 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 the mothers' amniotic fluid (Lutchmaya, Baron-Cohen, Raggatt, Knickmeyer, & Manning, 2004; Manning, 2002).

Given the likely common underlying link of prenatal testosterone as a basis of 2D:4D and hemispheric asymmetry (as indexed by handedness), it is strange that no direct link between 2D:4D and handedness has been reported in the literature. This is surprising since less direct relationships have been uncovered. Manning, Trivers, Thornhill, and Singh (2000), for example, in a sample of Afro-Caribbean Jamaican children, have shown that low 2D:4D is associated with faster left-hand speed relative to right-hand speed in a peg-moving test. They also found that participants with lower 2D:4D in their right hand had comparatively faster left-hand speed. Fink, Manning, Neave, and Tan (2004) have confirmed such findings in a Caucasian population.

The reason why a relationship between 2D:4D and handedness has not been identified previously may be because there is a second element influencing the development of hemisphericity aside from the prenatal effects which have already been described. Is the post-puberty release of androgens also likely to have an effect on hemispheric asymmetry?

It has already been noted that hemispheric asymmetry seems to have a prenatal origin associated with androgens. However this perspective ignores the post-puberty surge of androgens and oestrogens that occur in many animals including humans, primates, and rats (Becú-Villalobos, Iglesias, Diaz-Torga, Hockl, & Libertun, 1997; Styne, 1994). Adolescence represents a secondary pattern of hormone release similar to the one that occurs at ontogeny. At puberty, pulsatile release of gonadotropin-releasing hormone (GnRH) is re-established that was evident perinatally. This leads to increased release of both follicle-stimulating hormone and luteinising hormone, which in turn stimulate release of androgens and oestrogens (Spear, 2000). Release of growth hormone also increases substantially during the growth spurt of adolescence (Loche, Casini, & Faedda, 1996). As a result of these processes, secondary sexual characteristics emerge in human adolescents (Benson & Migeon, 1975) as well as physical growth (Grumbach & Styne, 2002; Loche et al., 1996; Spear, 2000). Androgens appear to have their effect primarily after being converted to oestrogens by the enzyme aromatase (Reiter & Rosenfeld, 2002). Thus, the effects of sex steroids on skeletal growth may be influenced by aromatase levels in various tissues.

Therefore it is unsurprising that average digit length differences across the sexes become increasingly apparent after puberty, such that boys typically have a greater average digit length. Based on the known relationships between post-pubertal release of sex steroids and skeletal growth, Lippa (2006) argues that digit length (as opposed to 2D:4D) is likely to be highly influenced by post-puberty sex steroids. Lippa (2006) does note that digit length may also be related to prenatal effects, although effects are likely to be small since digit length differences are only slight before puberty.

Puberty is also associated with a second round of synaptic downsizing in the neocortex (Spear, 2000). This secondary pruning is likely to be related to developmental plasticity whereby the brain is ontogenetically sculpted on the basis of experience to effectively accommodate environmental needs (Rakic, Bourgeois, & Goldman-Rakic, 1994). Similar to the prenatal pruning, this secondary pruning may also be related to (i) a marked increase in the degree to which the two cerebral hemispheres can process information independently (Merola & Liederman, 1985), and (ii) an increase in the amount of hemispheric asymmetry evident in EEG (Anokhin, Lutzenberger, Nikolaev, & Birbaumer, 2000).

It has already been noted that there are two prominent theories arguing that prenatal testosterone is the basis for hemispheric asymmetry (GBG as proposed by Geschwind & Behan, 1982; Geschwind & Galaburda, 1987, and "collosal pruning" theory by Witelson & Nowakowski, 1991). Such models could plausibly be extended to argue that post-pubertal levels of androgens in interaction with prenatal levels of androgens could predict hemispheric asymmetries, based on the observations that post-pubertal and prenatal androgen release both occur at times of asymmetrical hemispheric sculpturing of the brain. Results obtained by Moffat and Hampson (1996) provide some support for this proposition; they reported that testosterone found in the saliva of adults was related to hand preference and cerebral functional asymmetry. Their study is generally interpreted as providing evidence in support of the prenatal theories of the relationship between testosterone and handedness, but crucially note that testosterone in saliva is a measure of current and not prenatal testosterone levels.

As far as is known, no study has investigated these relationships. Given the divergent views of the effects of prenatal testosterone on hemispheric asymmetry based on "GBG theory" or "collosal pruning" theory, coupled with the completely unknown additional effects of post-pubertal sex hormones on hemispheric asymmetry, no directional hypotheses can be made. Thus, the hypothesis to be tested is as follows:

The 2D:4D ratio, in interaction with Average Digit Length, will predict hemispheric asymmetry as measured by handedness.

Results in favour of the hypothesis would provide evidence that hemispheric asymmetry in adults is a function of prenatal and post-puberty androgen release.

METHOD

Participants

A total of 360 participants (267 female, 93 male; 9% left-handed, 81% right-handed; 72% white origin, 18% Chinese and SE Asia Origin; average age = 19.20 yrs, *SD* = 1.57) took part in the study in exchange for partial course credit at The University of Queensland, Australia.

Procedure

Participants completed a battery of electronically administered questionnaires, which included questions on handedness in terms of Hand Use and Hand Preference. At the end of the questionnaire the digit characteristics of the participants were directly measured by a research assistant.

Measures

Measures of hemispheric asymmetry were assessed in terms of handedness:

i. *Hand Use as a measure of asymmetry.* Participants were simply asked whether they were right- or left-handed. Right-handers were scored as "1" and left handers were scored as "0". A total of 265 participants provided this information.
ii. *Hand Preference as a measure of asymmetry.* The Hand, Ear, and Eye preference Questionnaire (HEEP) is a modified form of the lateral preference questionnaire developed by Coren, Porac, and Duncan (1979). The current version has been used in recent lateral preference research (e.g., Jackson, 2005, 2007), and has 10 items assessing hand preference. Scores for each scale are summed and divided by the number of relevant scale items to produce a five-point measure, with higher scores indicating a right preference and lower scores indicating a left preference. The questions determine Hand Preference for a variety of tasks (e.g., throwing a ball, using an eraser, using a comb). Only the Hand Preference scale is reported in the current study.

Finger characteristics (digit length and 2D:4D ratio). Finger length was measured directly in this study in contrast to other studies that use photocopied hands (e.g., Fink et al., 2004). Direct measurement was chosen for four reasons: (1) There can be magnification problems with photocopying machines; (2) Pre-study trials showed that increasing pressure when a hand is placed on the photocopier relates to increasing finger length;

(3) Pre-study trials also indicated increasing occasional differential increase in finger length between the digits as hands were placed on the photocopier; (4) Concern was expressed that males might use increased pressure compared to females.

Following the process employed by Lippa (2006), 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 were directly measured using a precision ruler. A ruler provides a flat surface against which digits can be measured and from this perspective is potentially a superior measurement instrument compared to callipers. Callipers do not provide a flat surface and therefore digit length may be affected by differential tendon tension and elasticity. Where there was a band of creases at the base of the digit, the most proximal of these was used. Measurement was judged to be accurate to 1 mm.

To achieve improved accuracy of digit length measurement in the current study, averaging procedures across relevant digits were used. Average Digit Length was recorded as the average length of the four digits measured (i.e., the second and fourth digits of each hand). The 2D:4D ratio was calculated as the average second to fourth digit ratio across left and right hands. Average values across left and right hands were used, since evidence has suggested 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, and there is some support for this tendency in 2D:4D (Manning, 2002). As a consequence, average values across both hands were felt to provide a more stringent test of the theory as well as a more accurate measure of the variables than use of either left or right hand digits alone. Moreover, in a study that aims to predict laterality effects, it was felt particularly appropriate to use independent variables averaged across both left and right hands.

However as a consequence of Manning's (2002) observations, and Tan (1990a, 1990b) who reports that right-handed skills were related to serum testosterone in men and women, it was also decided to analyse right and left hand digit characteristics separately. In line with Fink et al. (2004), it is argued that right digit characteristics are more likely to predict handedness than left.

Statistical analysis

After examination of the descriptive statistics and correlations, hierarchical moderated regression was used to predict Hand Preference and hierarchical moderated logistic regression was used to predict Hand Use. Prior to entry into the regression, all independent variables were standardised to reduce effects of collinearity.

Two regression models were used with three sets of independent variables (left, right, and average of left and right) in the separate prediction of Hand Use and Hand Preference:

i. *Complete model*: In this regression model, the effects of Race, Sex, Average Digit Length, and 2D:4D are examined. In Step 1, Age, Sex, Race (a dichotomous variable), Digit Length, and 2D:4D were entered. In Step 2, Sex $\times$ Digit length, Sex $\times$ 2D:4D and Digit Length $\times$ 2D:4D were entered. In Step 3, the three-way interaction between Sex, Average Digit Length, and Average 2D:4D was entered. By this means the effects of Race as a main effect and Sex as a possible further moderating variable could be examined on the proposed interaction between Digit Length and 2D:4D.
ii. *Significant terms only model*: Non-significant effects are removed and the analysis re-run. In effect this resulted in the following: In Step 1, 2D:4D and Digit Length were entered. At Step 2, 2D:4D $\times$ Digit Length was entered.
iii. The simple slopes of significant interactions were plotted using standard methods and significance of simple slopes in hierarchical moderated regression is reported (Jaccard, Turrisi, & Wan, 1990).

RESULTS

To assess the reliability of digit-length measures, the two measures of digit length (i.e., from left hand and from right hand) of each of the digits assessed were correlated. These correlations were: .87 between left and right D2 and .88 between left and right D4. The correlation and between right D2 and right D4 was .75 and between left D2 and left D4 was .77. The correlation between left D2 and right D4 was .75, and between right D2 and left D4 was .76 (all $p < .001$). These correlations are very similar to those reported by Lippa (2006).

Digit characteristics averaged across both hands

Descriptive statistics and correlations between the variables are shown in Table 1. Alpha reliabilities of Average Digit Length (i.e., based on the four measured digits) and Hand Preference were 0.94 and 0.95 respectively. Hand Use was found to have a positive correlation with Hand Preference ($r = .84$, $p < .001$) and Average Digit Length had a small significant correlation with Average 2D:4D ($r = -.18$, $p < .001$). No other correlations were significant.

TABLE 1
Descriptive statistics and correlations between variables using digit characteristics averaged across left and right hands

Variable	*M*	*SD*	*α*	*DL*	*Hand*	*HP*
Average 2D:4D	0.98	.05	.94	−.181**	.017	−.010
Average Digit Length (DL)	71.93	5.04			−.092	−.034
Hand Use (Hand)	1.88	.33	–			.835**
Hand Preference (HP)	43.05	9.13	.95			

$n = 360$. Just one alpha is reported for Average 2D:4D and Average Digit Length since they are both derived from the same four unique digit lengths of the second and fourth fingers of the left and right hand. High scores of handedness (Hand use and Hand Preference) indicate right-handedness and are commonly interpreted in terms of left hemispheric dominance.

As noted above, two different regression models were employed. First a complete terms regression model was employed. In the prediction of Hand Use (using hierarchical moderated logistic regression) and Hand Preference (using hierarchical moderated regression), Average Digit Length × Average 2D:4D was significant ($\beta = -.75$, $p = .020$; $\beta = -2.30$, $p = .022$ respectively). No other terms were significant. The complete regression models ruled out possible moderating effects of sex[1] as well as possible main effects of age and race.

Accordingly, a significant terms only model was used. In the prediction of Hand Use (using hierarchical moderated logistic regression) and Hand Preference (using hierarchical moderated regression) the interaction remained significant in the prediction of both dependent variables ($\beta = -.57$, $p = .020$; $\beta = -.144$, $p = .007$ respectively). No other terms were significant.

Simple slopes analysis of the interaction in the prediction of Hand Preference (as shown in Figure 1) shows that, when average Digit Length is short, there is a trend for greater right Hand Preference as 2D:4D digit ratio increases ($\beta = 1.25$), $t(358) = 1.72$, $p = .086$; when average digit length is long there is a significant tendency for greater left Hand Preference as 2D:4D digit ratio increases ($\beta = -1.89$), $t(358) = -2.37$, $p = .018$. At low Average 2D:4D (i.e., high prenatal preponderance of masculinising hormones) the effect is small, but long digit length is associated with greater right-hand preference and short digit length is associated with left-hand preference. However, at high average 2D:4D ratios (i.e., low levels of prenatal masculinising hormones), hemispheric asymmetry is more strongly related to average Digit Length such that long digit length is now associated with greater left-hand preference and short digit length is associated with

[1] Regression weights of females and males were very similar when analysed separately, again suggesting a sex effect is minimal in this analysis.

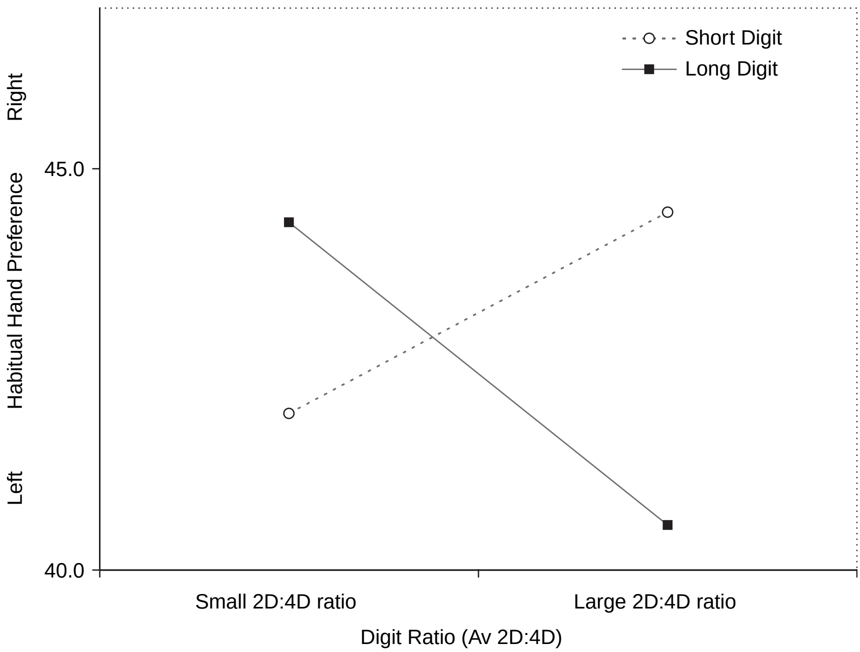

Figure 1. The interaction between Average 2D:4D and Average Digit length in the prediction of Hand Preference.

right-hand preference. The plot of the simple slopes of the interaction in the prediction of Hand Use showed a very similar relationship.

Left and right digit characteristics

Table 2 presents the correlations between left and right digit characteristics. As could be expected, left and right average Digit Lengths (the average of left ring and left index digits and the average of right ring and right index digits respectively) are highly correlated ($r = .924$, $p < .001$) and left and right 2D:4D ratios are also highly correlated ($r = .570$, $p < .001$). There are also some minor but significant correlations between left and right 2D:4Ds and left and right average Digit Lengths. There is just one small but significant correlation between all the digit characteristics and Hand Use. No digit characteristics predict Hand Preference.

When the complete regression model is employed using right digit characteristics only, a right Average Digit Length × Right 2D:4D effect is close to significance in the prediction of Hand Use and significant in the prediction of Hand Preference ($\beta = -.625$, $p = .098$, $\beta = -.155$, $p = .050$

TABLE 2
Descriptive statistics and correlations for left and right digit characteristics

	M	*SD*	*Left DL*	*Right 2D:4D*	*Right DL*	*Hand*	*HP*
Left 2D:4D	0.98	.05	−.190**	.570**	−.179**	.057	.017
Left Av Digit Length (DL)	71.95	5.10		−.139*	.924**	−.135*	−.054
Right 2D:4D	0.76	.06			−.155**	.013	.003
Right Av Digit Length (DL)	71.90	5.16				−.106	−.070
Hand Use (Hand)	1.88	.33					.835**
Hand Preference (HP)	43.05	9.13					

respectively). No other terms are significant. Using just left digit characteristics, there are no significant effects.

When the significant effects only regression model is employed in the prediction of Hand Preference, the right Average Digit Length × right 2D:4D interaction remains significant ($\beta = -.144$, $p = .008$).

The interaction plot using the right digit characteristics only is shown in Figure 2. When right Average Digit Length is short, there is a tendency for greater right Hand Preference as 2D:4D digit ratio increases ($\beta = .84$),

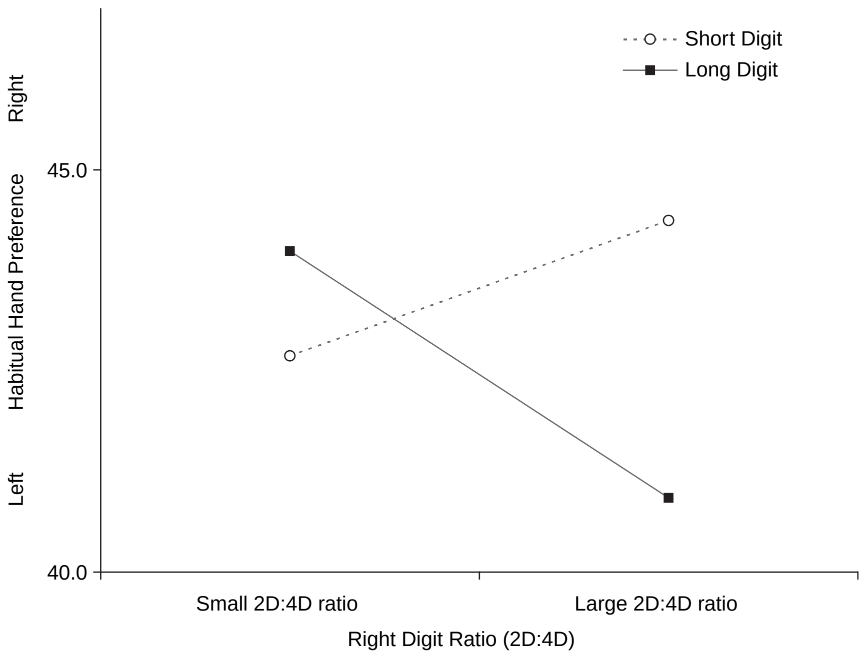

Figure 2. The interaction between right 2D:4D and right Digit length in the prediction of Hand Preference.

$t(358) = 1.43$, $p = .154$, and when right Average Digit Length is long there is a significant tendency for greater left Hand Preference as 2D:4D digit ratio increases ($\beta = -1.53$), $t(358) = -2.12$, $p = .035$. At low 2D:4D, the effect of right digit length is smaller than at high 2D:4D. Clearly, Figure 1 and Figure 2 are very similar.

DISCUSSION

The high alphas of all the scales suggest that all measurements were reliable. Left hand 2D was highly correlated with right hand 2D and left hand 4D was highly correlated with right hand 4D, and there is a high correlation between Hand Use and Hand Preference. Lippa (2006) makes the point that digit length is likely to be mainly related to post-puberty sex hormones but that there may also be a prenatal basis. The small but significant correlation between digit length and 2D:4D confirms this possibility, yet the small correlation suggests that the overlap is not large. These results suggests that the study has psychometric integrity when examined from a variety of perspectives.

The results of this study show support for the hypothesis. Evidence indicates that Digit Length, in interaction with 2D:4D ratio, is a significant predictor of handedness (measured as Hand Use and Hand Preference). Handedness is widely regarded to be a marker of contralateral hemispheric asymmetry with a prenatal origin (e.g. White et al., 1994). Results of this study show that a small Average 2D:4D ratio leads to relatively small changes in handedness and, therefore, suggests that high levels of prenatal testosterone are not strongly related to hemispheric asymmetries associated with handedness. Nevertheless, the small effect that is apparent supports Witelson and Nowakowski's (1991) model, based on the evidence that long digit length is related to right-handedness *but as a post-puberty effect rather than a prenatal effect*.

In contrast, when Average 2D:4D is high, long Average Digit Length is more strongly associated with left-handedness (indicative of right hemispheric activity) and short Average Digit Length is almost significantly associated with right-handedness (indicative of left hemispheric activity). The direction of this effect is in support the GBG theory, *but as a post-puberty effect as opposed to a prenatal effect*.

Although the effects on handedness for small 2D:4D ratios are small, the following consistent picture can be derived which explains the effects of androgens on handedness and hemispheric asymmetry:

- Masculinisation prenatal and masculinisation post-puberty = right-handed

- Feminisation prenatal and feminisation post-puberty = right-handed
- Masculinisation prenatal and feminisation post-puberty = left-handed
- Feminisation prenatal and masculinisation post-puberty = left-handed

These results are quite robust since they are found in the prediction of two measures of handedness, and found when using digit characteristics averaged across left and right hands as well as for right digit characteristics on their own. However there were no significant effects when using just left digit characteristics. In this study, results were stronger and more consistent when using digit characteristics averaged across both hands as opposed to just the right hand. In a study of the laterality of handedness it is useful to show that the effect can be found using averaged values across left and right digit characteristics, since this increases reliability of measurement and provides a more stringent test of the hypothesis. Nevertheless this finding is somewhat contrary to a trend in the literature to find strongest effects with right digit characteristics. However the finding that left digit characteristics are not predictive of handedness does fit in with this trend in the literature (e.g. Manning, 2002).

In this study no significant effects were found for age and race as main effects and for sex as a potential further moderating variable. It was therefore safe to remove these variables from the regression model to focus on the significant effects. This is not surprising because the proposed model concerns the prediction of hemispheric asymmetry from androgen release and there is likely to be a lot of variation in such a relationship within race and sex as well as between race and sex.

A further question raised in this research is the possibility that handedness may change during childhood and there seems scant research into this possibility. However research looking at such changes could really add to the results of this initial research.

In summary, these results argue that lateralisation effects of androgens are complex. They have indicated that prenatal testosterone is more important in hemispheric asymmetry if the foetus is exposed to low levels of androgen (as indicated by a high Average 2D:4D ratio) but otherwise the effect is less. When prenatal androgens are low, higher levels of post-puberty androgen (as indicated by higher Average Digit Length) are associated with increasing left-handedness and right hemispheric dominance. In contrast, when prenatal androgens are high, the effect is smaller but in the opposite direction.

As far as is known, this is the first study to make links between prenatal and post-pubertal digit characteristics and hemispheric asymmetries as measured by handedness. This study does follow a long tradition of digit characteristics research in which digit characteristics are regarded as proxy measures for the actions of hormones at various stages of development.

There seems to be a growing acceptance in the literature that 2D:4D is a valid measure of prenatal androgens, but digit length is still an emerging measure of post-puberty androgen release (see Lippa, 2006). Moreover, while a ruler has many advantages for measuring digit characteristics, it might be argued that this represents an inferior method to the use of photocopies or callipers. The results need to be interpreted in light of these limitations.

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