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Hand Asymmetry in Heterosexual and Homosexual Men and Women: Relationship to 2D:4D Digit Ratios and Other Sexually Dimorphic Anatomical Traits

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Abstract Sexual differentiation leads to the development of distinctive anatomical structures (e.g., gonads and genitalia); it also produces less obvious anatomical shifts in brain, bones, muscles, etc. This study is a retrospective analysis of growth patterns in the hands in relation to sex and sexual orientation. Using data from three published studies, we analyzed four hand traits in adults: hand width, hand length, second digit length, and fourth digit length. Using these measurements, we derived estimates of trait laterality (directional asymmetry or DA) and developmental instability (fluctuating asymmetry or FA). High FA is a putative indicator of interference with the cellular and molecular mechanisms regulating development. We focused on how these derived variables were related to sex, sexual orientation, and putative markers of early sex steroid exposure (e.g., the second to fourth digit ratio or 2D:4D). Our data point to three principal conclusions. First, individual differences in DA appeared to be a major source of variation in the 2D:4D ratio. The 2D:4D ratios of heterosexual men differed depending on whether they had leftward or rightward DA in their digits. Homosexual women showed the same pattern. Individuals with leftward DA in both digits had lower 2D:4D ratios than those with rightward DA. This effect was absent in heterosexual women and homosexual men. This led to sex differences in 2D:4D and sexual orientation differences in 2D:4D in the leftward DA group, but not in the rightward DA group. The second conclusion was that DA in digit length and hand width varied with sex; women were more likely to have rightward asymmetry than men. Homosexual men and women were generally sex typical in DA. The third conclusion was that homosexuality is unlikely to be a result of increased developmental instability. Although limited in scope, the present evidence actually suggests that homosexuals have lower FA than heterosexuals, raising the question of whether the positive fitness components associated with low FA may contribute to selection that maintains homosexuality in a population.

Keywords 2D:4D ratio · Fluctuating asymmetry · Directional asymmetry · Laterality · Sex differences · Sexual orientation

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Introduction

Asymmetry

Bilateral anatomical structures, such as the arms and hands, are not perfectly symmetrical but rather exhibit relatively small deviations. This asymmetry can be of two general types. When a trait is larger on one side, i.e., the left side or the right side, in a preponderance of individuals in a population, the asymmetry is referred to as directional asymmetry (DA). DA is a measure of laterality. It is not clear what developmental mechanisms lead to laterality, but sexual dimorphism in various lateralized traits has led investigators to hypothesize that sex steroids are involved (Geschwind & Galaburda, 1985; McCormick, Witelson, & Kingstone, 1990).

A second type of asymmetry is referred to as fluctuating asymmetry (FA), because, in a group of individuals, the mean left-right difference in the trait fluctuates around 0. Because there is no tendency for the trait to be greater on the left or right, FA presumably has no adaptive value. Rather, these small deviations are thought to reflect interference with the developmental mechanisms that maintain bilateral symmetry. This interference may be caused by genetically or externally induced disturbances in growth. For example, individuals who were exposed during fetal development to cigarette smoke have greater FA in some morphological traits than individuals who were not exposed (Kieser, Groeneveld, & Da Silva, 1997), and individuals with known genetic or chromosomal abnormalities have greater FA than controls (Barden, 1980; Peretz et al., 1988; Thornhill & Moller, 1997). Individuals with elevated FA may also experience lowered reproductive fitness and increased susceptibility to illness (Milne et al., 2003; Thornhill & Gangestad, 2006).

Thus, DA may represent a proxy measure of sex steroid exposure and FA may be thought of as a measure of developmental instability. Both unusual sex steroid exposure and increased developmental instability have been proposed as etiological mechanisms to explain homosexuality and differences between homosexuals and heterosexuals in both DA and FA have been explored. For example, homosexuals are known to have a higher frequency of atypical lateralization for some functional traits, such as handedness (Lalumière, Blanchard, & Zucker, 2000) and dichotic listening (McCormick & Witelson, 1994), and there is also evidence that homosexuals have a higher frequency of atypical lateralization for at least one anatomical trait—fingerprint ridges (Hall & Kimura, 1994). However, studies by Rahman and Wilson (2003), Rahman (2005a), and Mustanski, Bailey, and Kaspar (2002) did not find higher FA in homosexuals. These studies were limited, however, because the traits examined (e.g., digit lengths and finger ridges) also show DA, and the factors causing DA are presumably different from those causing FA. Where DA is present and different between groups, FA may not reflect developmental instability unless DA is statistically controlled.

Anatomical Ratios

Numerous anatomical traits that are sexually dimorphic in the adult (e.g., stature) become so as a result of differential hormone exposure in late childhood and early adolescence (Harrison, Weiner, Tanner, & Barnicot, 1964). Differences in sex steroid exposure account for a considerable portion of the variance in long bone growth of the legs, arms, and hands prior to and during adolescence. Traits corrected for differences in overall size or stature may also be sexually dimorphic. The width-to-length ratio of the hand and the arm length-to-stature ratio are sexually dimorphic anatomical traits (Martin & Nguyen, 2004). The second to fourth digit ratio (2D:4D) also differs between men and women (Manning, Scutt, Wilson, & Lewis-Jones, 1998; Phelps, 1952), possibly from as early as the end of the first trimester of gestation (Malas, Dogan, Evcil, & Desdicioglu, 2006). These sex differences have led to speculation that adult arm length:stature ratio, hand width:length ratio, 2D:4D, etc., can serve as proxy estimates of early (neonatal or prenatal) exposure to sex steroids (Manning, 2002; Manning et al., 1998; Martin & Nguyen, 2004). Some evidence supports this assertion. For example, digit ratios have been found to be more masculine in individuals with CAH, a condition characterized by elevated prenatal androgen levels (Brown, Hines, Fane, & Breedlove, 2002; Okten, Kalyoncu, & Yaris, 2002), although one study using radiographic measurements did not find an effect of CAH on digit ratios (Buck, Williams, Hughes, & Acerini, 2003). Sexual dimorphism in arm length:stature ratios begins early in childhood and the sex difference becomes progressively larger until adulthood (Harrison et al., 1964; Maresh, 1955).

Working under the hypothesis that these ratios and sexual orientation are both affected by early sex steroids, several investigators have demonstrated correlations between 2D:4D and sexual orientation (McFadden et al., 2006; Putz, Gaulin, Sporter, & McBurney, 2004; Williams et al., 2000) and between sexual orientation and arm length:stature and hand width:length (Martin & Nguyen, 2004). However, significant numbers of homosexuals have ratios in the range of heterosexuals or even beyond the heterosexual mean; thus, one can conclude either that these ratios are imprecise markers of steroid exposure and/or that differences in steroid exposure play a limited role in determining sexual orientation. It is also possible that, in addition to steroids, other developmental factors can lead independently to homosexuality. Lippa (2003) and Rahman (2005b) have summarized the evidence for and against developmental instability, birth trauma and brain injuries, and maternal immunological attack as alternative causes. The concept of maternal immunological attack as an etiological factor in male homosexuality is based on the arguments of Gualtieri and Hicks (1985) that Y-chromosome related antigens in a male fetus cause the mother's immune system to develop antibodies which may adversely affect subsequent male fetuses and on the observations of Blanchard and Bogaert (1996) that homosexual men have more older brothers than heterosexual men.

Since previous studies comparing homosexuals and heterosexuals in terms of FA and digit ratios did not control for laterality, in this study we examined FA and 2D:4D after correction for DA. We also explored whether homosexual men with anatomical ratios similar to heterosexual men, and hence presumably exposed to normal or adequate sex steroids during development, might have elevated FA that could account for their atypical sexual orientation.

Method

Participants

Three different datasets were used in these analyses. The measurement protocols and the demographics of these three samples differed as shown in Table 1. The subject recruitment and data collection protocols have been previously published (Martin & Nguyen, 2004; Putz et al., 2004; Williams et al., 2000). Data collected by Martin and Nguyen are referred to here as the multi-site data. Data collected by Putz et al. are referred to as the Pittsburgh data, while those collected by Williams et al. are referred to as the Berkeley data.

The multi-site data were drawn from 514 participants who were recruited in California, Utah, West Virginia, and the District of Columbia for a study that was approved by the IRB at Western University of Health Sciences and by the IRB at Brigham Young University. Exclusion criteria for that study were non-Caucasian ancestry and age of <20 or >50 years. Of the 514 recruits, 411 described themselves as exclusively heterosexual or homosexual and only their data were included in the present study.

The Pittsburgh data were drawn from a pool of psychology students at the University of Pittsburgh who had participated in one of two separate experiments. All were undergraduates between 18 and 30 years of age. The first of the two experiments was open only to exclusively heterosexual men; data from a total of 111 of these men were included in the present study (Group A Males). In the second experiment in which participants were initially recruited without respect to sexual orientation, a questionnaire was used to identify sexual orientation. From these individuals, 120 women and 119 men (Group B Males) indicated they were exclusively heterosexual, and their data were included in the present study.

The Berkeley data were drawn from 717 individuals who were solicited in public settings in northern California without regard to ethnicity or age. Of these 717 individuals, 483 had reported themselves as exclusively heterosexual or exclusively homosexual on an anonymous questionnaire, and only their data were used in the present study except for the frequency distributions comparing men and women (Fig. 1b) which included all participants for whom hand width or length measurements were available, regardless of how they rated their sexual orientation.

Measures

Multi-site Data

Participants were weighed, measured for hand width and length, and then asked to complete a questionnaire, which

Table 1 Comparison of subjects from the three study populations

Characteristic	Data	Men						Women					
		Heterosexual			Homosexual			Heterosexual			Homosexual		
		Berk	Multi	Pitt	Berk	Multi	Pitt	Berk	Multi	Pitt	Berk	Multi	Pitt
Age													
	Mean	41.6	31.4	18.9	40.6	32.5	–	39.5	32.6	–	41.4	34.2	–
	SEM	1.547	.745	.115	.825	.714	–	3.648	.897	–	1.29	.902	–
	N	92	118	111	196	117	–	119	109	–	83	68	–
Handedness													
	RH	73	–	–	170	–	–	105	–	–	79	–	–
	NRH	21	–	–	27	–	–	14	–	–	8	–	–
Ethnicity		M	C	M	M	C	–	M	C	M	M	C	–
Second Digit	*N*	91	–	108	189	–	–	116	–	103	80	–	–
Fourth Digit	*N*	92	–	106	193	–	–	113	–	104	81	–	–
Hand Width	*N*	18	118	–	18	116	–	29	109	–	11	68	–
Hand Length	*N*	44	118	–	64	116	–	53	109	–	26	68	–

M = Mixed ethnicity, C = Caucasian, RH = Right handed, NRH = Non-right handed

Berk = Berkeley dataset of Williams et al. (2000)

Multi = Multi-site dataset of Martin and Nguyen (2004)

Pitt = Pittsburgh dataset of Putz et al. (2004)

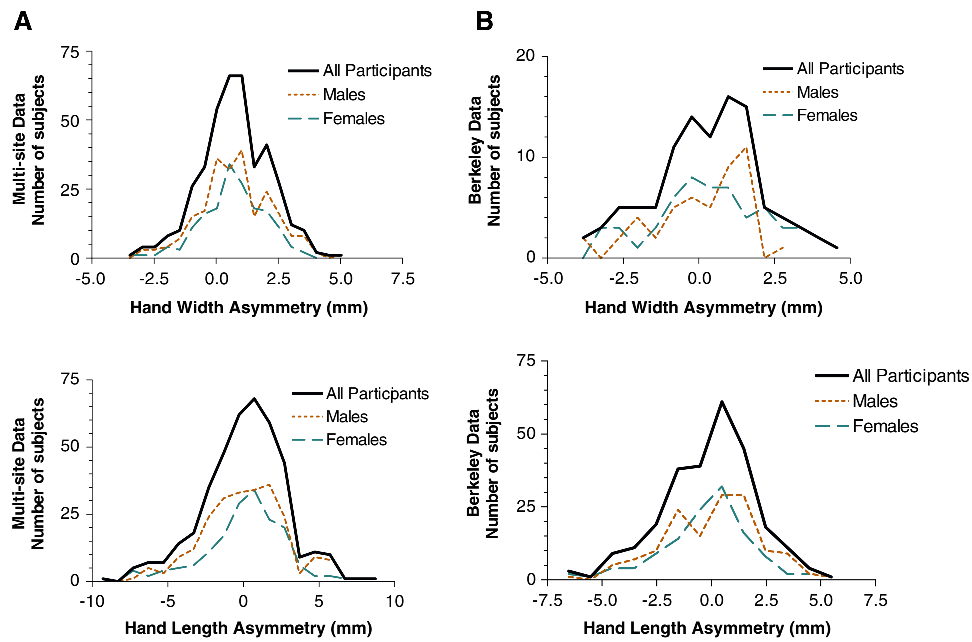

Fig. 1 Frequency distribution of unadjusted hand width and length asymmetries according to sex and data source. Each frequency distribution includes all "Right minus Left" asymmetry values in the multi-site data (**a**) and in the Berkeley data (**b**) regardless of sexual orientation

solicited information about sexual orientation and about several variables not related to this study. For sexual orientation, participants were asked to select a category (exclusively heterosexual, predominately heterosexual, predominately homosexual, or exclusively homosexual). To provide anonymity and encourage honest answers, no personal identifying information was solicited or recorded, and participants were asked to fold and deposit their questionnaire into a closed box along with those of other participants. In the multi-site data, all physical measurements were made directly on participants by the same investigator (D.N.) using a digital caliper measuring to the nearest .01 mm. Hand lengths were measured on the ventral (palm) surface with the lower arm and hand pronated on a flat surface. The participant was asked to keep the fingers touching and to remove rings and watches. The caliper was extended from the most distal skin crease at the center of the wrist to the tip of the third digit. Widths were measured from the most medial point of the second metacarpal to the most lateral surface of the fifth metacarpal. Various other anthropometric measures were made (Martin & Nguyen, 2004); however, finger lengths were not measured. Repeated measures of a single individual indicated that the coefficient of variation for caliper measurement of hand width was in the .5–.67% range, whereas the coefficient of variation for hand length was in the .27–.39% range. Technical error of measurement (TEM) in a related study (Diehl & Martin, 2006), which used the same methodology, calipers, and landmarks was .81 mm for hand width, and the %TEM was 1.01%. TEM for hand length was 1.71 mm, while the %TEM was .94%, which is comparable to the values reported by Weinberg, Scott, Neiswanger, and Marazita (2005) for hand width.

Pittsburgh Data

In the Pittsburgh data, digit lengths were measured from photocopies by two investigators using a digital caliper precise to .01 mm. For the 111 men in Group A, two photocopies were made of each hand, alternating left and right, and measurements from both photocopies were averaged. For the 120 women and 119 men in Group B, only one photocopy of each hand was measured. Ten percent of hand photocopies were re-measured to assess intra-measurer reliability. Correlations between repeated measures were ≥.99.

Berkeley Data

In the Berkeley data, digit length and palm length were measured on photocopies by a single investigator. Hand length was the sum of palm length plus the third digit length. Hand width measures were obtained from photocopies for those participants whose thumb did not obscure the lateral margin of the hand. Slightly different landmarks were used to measure hand width in this dataset from those used in the multi-site dataset; width was measured from the point of intersection of the medial palmar flexion crease with the medial margin of the hand to the point of intersection of the lateral palmar flexion crease with the lateral margin of the hand.

Procedure

From the four traits that were measured (hand length, hand width, second digit length, and fourth digit length), we derived measures of DA and FA for each of these traits. These two derived measures, along with the ratio of the second and fourth digit lengths on each hand (2D:4D), were the primary variables reported in the results. DA was defined as the difference in length between the right and left side, i.e., (R–L), for a given individual in any of the four traits. FA was defined as the individual's unsigned DA for that particular trait divided by the average of the individual's right and left side measurements for that trait. As is common in studies of FA, we have reported here single trait FA as well as the composite of several trait FAs.

With respect to DA in the digits (Table 2), we categorized the individual as having leftward, rightward, or no asymmetry in the second digit (and also the fourth digit) using the following scheme. We used a ruler to measure the photocopies of the digits in the Berkeley data to the nearest half-millimeter. For purposes of categorizing the Pittsburgh participant's digits, we applied the Berkeley level of precision retrospectively. Participants with a digit DA of $\geq$+.25 were classified as having rightward asymmetry, and those with DA of $\leq -.25$ were classified as having leftward asymmetry for that digit. Hence, any Pittsburgh participant falling between $-.25$ and +.25 mm of asymmetry was categorized as symmetrical in that digit. In order to determine whether DA was present in the digits in a given group, we used the chi-square Goodness of Fit statistic to test whether the number of individuals with rightward and leftward asymmetries among the participants differed from the predicted 50:50 (Table 2). Additionally, we used the Fisher's Exact Test to determine whether there were laterality differences between groups by treating DA as a categorical variable (Table 2).

In order to study the relationship of digit laterality to digit ratios, we further divided the Berkeley and Pittsburgh participants into one of three categories: (1) those with both digits showing leftward DA; (2) those with both digits showing rightward DA; and (3) all others (see 2D + 4D in Table 2; see also Figs. 3 and 4).

In order to make accurate measurement of FA in a trait where there is DA, the DA in that trait must first be factored out; otherwise, measures of developmental instability are confounded with developmentally normal growth asymmetries. For a discussion of the problems measuring FA in traits that show DA, see Palmer and Strobeck (2003) and Graham, Emlen, Freeman, Leamy, and Kieser (1998). This is particularly important in comparing groups where the frequency distribution of asymmetries is skewed differently between groups. Because some groups, but not others, have significant DA in the second and fourth digits, all groups were first normalized so that the mean lateralization of each group was 0. Consequently, following normalization, because a preliminary analysis indicated that, in heterosexual men, but not other groups, hand size (width $\times$ length) was correlated with asymmetry measures, all measurements of digit FA were adjusted for trait size in order to standardize the measurements from different sexes and sources. This adjustment was done by dividing the individual's absolute asymmetry measurement by that individual's mean (left and right) trait size. An individual's composite FA was calculated by averaging the individual asymmetries from different traits. Another important aspect of analysis of data for FA is identification and evaluation of outliers, which might be caused by injuries, transcription errors, failure to reset the caliper, etc. (Palmer & Strobeck, 2003). In the studies reported here, past injuries that would bias the asymmetry measures were not recorded. The FA data for each group were, therefore, evaluated for outliers using Grubb's test with a rejection region of $p =$ .025, and individual data points that exceeded the statistic were omitted from the analysis.

Results

Directional Asymmetry

Multi-site Data

Hand Width. Averaged over all participants in the multi-site data, the right hand was wider than the left, as shown by a significant rightward median asymmetry of +.72 mm (Fig. 1a top; $t = 10.93$, df = 399, $p < .0001$). When width asymmetry was treated as a continuous variable, both sexes had significant rightward DA and there was no significant sex difference in DA. Comparing sexual orientation groups (Fig. 2 top), there was a significantly greater rightward DA in heterosexual women than in homosexual women ($\text{median}_{\text{ht women}} = .87$ mm; $\text{median}_{\text{hm women}} = .50$ mm; $U =$ 2650, $p = .042$). Heterosexual and homosexual men did not differ significantly in hand width DA.

Hand Length. Hand length exhibited no significant DA across all participants (Fig 1a, bottom). When the four groups were examined separately for hand length asymmetry as a continuous variable, heterosexual women had significant rightward DA (median = +.50; Wilcoxon Signed Ranks Test $W = 1128$, $p = .044$); however, homosexual men and women, as well as heterosexual men, did not have DA in hand length (Fig. 2a and b, bottom). The four groups also did not differ significantly from each other.

Relationship between Width and Length Asymmetry. An analysis of the relationship between individual subject's width asymmetry and length asymmetry was done using signed asymmetry values from the multi-site data. There was a statistically significant positive correlation between these two measures of hand asymmetry in heterosexual men ($r = .24$, df = 113, $p < .01$) and women ($r = .19$, df = 107,

Table 2 Directional asymmetry in second and fourth digits in homosexuals and heterosexuals

Trait	Asymmetry	Frequency							
		Heterosexual men		Homosexual men		Homosexual women		Heterosexual women	
		N	(%)	*N*	(%)	*N*	(%)	*N*	(%)
Berkeley									
2D	Left	47	51[a]	94	49[c]	34	43	33	28[a]
	Right	37	40	66	34	36	44	60	51[e]
	Equal	8	9	32	17	11	13	24	21
4D	Left	43	46	72	37	24	30[d]	52	46[d]
	Right	38	41	88	45	46	57[f]	49	43
	Equal	12	13	36	18	11	14	12	11
2D + 4D	Left	25	27	39	20	13	16	16	14
	Right	16	17	34	17	19	23	23	20
	Other	51	55	123	63	50	61	74	65
Pittsburgh									
2D	Left	110	53[b,c]	–	–	–	–	32	31[b]
	Right	77	37					60	58[e]
	Equal	22	11	–	–	–	–	12	12
4D	Left	88	42	–	–	–	–	32	31
	Right	96	46	–	–	–	–	62	60[f]
	Equal	25	12	–	–	–	–	10	9
2D + 4D	Left	52	26[g]	–	–	–	–	16	15[g]
	Right	45	22	–	–	–	–	39	37[e]
	Other	105	52	–	–	–	–	49	47

[a] Sex difference, Fisher's exact test, $p = .007$

[b] Sex difference, Fisher's exact test, $p = .0002$

[c] Leftward asymmetry, $\chi^2 = 4.9$ and 5.82, $p < .05$

[d] Sexual orientation difference, Fisher's exact test, $p = .028$

[e] Rightward asymmetry heterosexual women, $\chi^2 = 6.70$ and 8.52 and 9.57, $p < .01$

[f] Rightward asymmetry homosexual females, $\chi^2 = 6.91$, $p < .01$

[g] Sex difference, Fisher's exact test, $p = .003$

% = Percentage of the group

Other = Individuals without both digits lateralized to the same side

Equal = Both digits of the same length within measurement error

$p < .05$). The slopes of these relationships of length to width were not different between heterosexual men and heterosexual women. In homosexual men and women, hand width asymmetry and length asymmetry were not significantly correlated. The slopes of these relationships of length to width were significantly different between heterosexual men and homosexual men ($F(1, 229) = 4.07$; $p = .0447$), but not between the two female groups.

Berkeley Data

Hand Width. Similar patterns of DA in hand width were found in the Berkeley data which included, in addition to exclusively heterosexual or homosexual participants, 25 participants who were not exclusively heterosexual or homosexual (Fig. 1b, top). There was a significant rightward DA in hand in the combined groups (Wilcoxon Signed Rank $W = 1056$; $N = 103$; $p = .039$). Broken down by sex, females had significant rightward DA (median of +.29 mm) ($W = 403$; $N = 56$; $p = .046$), but males did not ($W = 1132$; $N = 47$). Women, however, did not differ statistically from men and there was no significant difference due to sexual orientation.

Hand length. There was no significant overall DA in length asymmetry (Fig. 1b, bottom), and none of the groups when analyzed separately had significant DA.

Second Digit. DA of digits is summarized in Table 2, in which digit length was treated as a categorical variable with three categories: digit(s) longer on the right, digit(s) longer

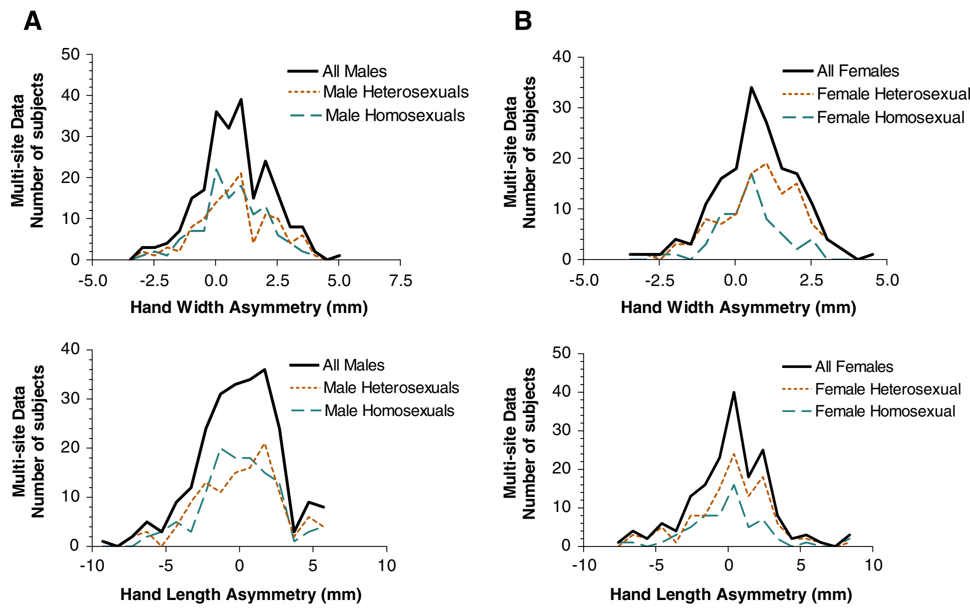

Fig. 2 Frequency distribution of unadjusted hand width and length asymmetries according to sexual orientation in the multi-site data. Each frequency distribution includes all "Right minus Left" asymmetry values in the multi-site data for hand width (top) and for hand length (bottom) for men (**a**) and for women (**b**)

on the left, or indeterminate due to measurement error. Statistical comparisons were made only between the first two categories; the third category was omitted from the frequency analysis.

Heterosexual women showed right-sided DA in the second digit (χ^2(df = 1, N = 79) = 7.84, p < .01) and differed significantly from heterosexual men in DA (Fisher's Exact Test, p = .007). Men in this dataset did not show significant DA.

Homosexual women, in contrast, showed no significant asymmetry in the second digit; however, they were not significantly different from heterosexual women. Homosexual men showed significant leftward DA in the second digit (χ^2(df = 1, N = 160) = 4.90, p < .05), but they did not differ from heterosexual men in frequency of leftward asymmetry (Table 2).

Fourth Digit. The fourth digit pattern of DA was different from that of the second digit (Table 2). Neither heterosexual women nor heterosexual men showed DA in this digit. Homosexual women showed rightward DA (χ^2(df = 1, N = 70) = 6.91, p < .01), and they were significantly different from heterosexual women (Fisher's Exact Test, p = .028). Homosexual men showed no DA in the fourth digit.

Combined Digits. None of the four groups had a greater frequency of individuals with leftward versus rightward asymmetry in both digits, and there were no significant differences between groups in the proportions of individuals lateralized to the left versus to the right (Table 2).

Pittsburgh Data

Second Digit. In heterosexual women, there was right-sided DA similar to that in the Berkeley data (χ^2(df = 1, N = 92) = 8.52, p < .01). In heterosexual men, the Group A participants showed significant leftward DA (χ^2(df = 1, N = 101) = 6.40, p < .05); however, the Group B men did not. These two groups of men differed in that Group A individuals had responded to a recruitment advertisement stipulating heterosexuals only, whereas Group B men were recruited without reference to sexual orientation, and then identified themselves as exclusively heterosexual in a questionnaire. Heterosexual women differed significantly in DA from their Group B heterosexual male counterparts (Fisher's Exact Test, p = .019), as well as from Group A and B men combined (Fisher's Exact Test, p = .0002) (Table 2). The number of homosexuals in the Pittsburgh dataset was too small for analysis.

Fourth Digit. Heterosexual women showed rightward asymmetry in the fourth digit (χ^2(df = 1, N = 94) = 9.57, p < .01); however, they did not differ from the heterosexual men, which did not show DA in this digit (Table 2).

Combined Digits. Among the subgroup of heterosexual women in which both digits were lateralized on the same side, there was significantly more rightward asymmetry than leftward asymmetry (χ^2(df = 1, N = 55) = 9.62, p < .01). Furthermore, the rightward versus leftward distribution of asymmetries among these women differed significantly from that of the combined Group A and B heterosexual men (Fisher's Exact Test, p = .004). The subgroup of men that had both digits lateralized on the same side did not show DA (Table 2).

Fluctuating Asymmetry

Multi-site Data

Hand Width. FA data can be presented as the mean or medians of simple unadjusted, unsigned asymmetries (|R–L|) or as means or medians of asymmetries adjusted for individual differences in trait size and for group differences in DA (Tables 3 and 4). Since adjusting the data for these potential sources of bias compounds the measurement error in the results, we have chosen to provide the analysis of the multi-site FA data as both unadjusted (frequency distributions in Figs. 1 and 2) and adjusted (medians in Tables 3 and 4). Comparison of the unadjusted estimates of FA using a Kruskal–Wallis Test showed no significant difference between heterosexual men and women, i.e., no sex effect (Fig. 1a, top). There was, however, a significantly lower FA in homosexual women than in heterosexual women (Fig. 2b, top) (Kruskal–Wallis = 8.68, $p = .034$; Dunn's multiple comparison test, $p < .05$). The male heterosexual and homosexual groups did not differ significantly (Fig. 2a, top).

When the data were adjusted for hand size and DA (Table 3), a two-factor ANOVA of these hand width data indicated no significant effect of sex or sexual orientation, although the F value for the sexual orientation factor was close to being significant ($p = .069$).

Hand Length. In the corresponding analysis of hand length asymmetries, there was no statistically significant effect of sex or sexual orientation (Figs. 1a, bottom, 2a and b, bottom; Table 3).

Composite. The composite FA, which averages hand width and hand length (Table 3), was analyzed using a two-factor ANOVA. There was no sex effect, but FA was significantly lower in homosexuals than in heterosexuals ($F(1, 405) = 4.91$, $p = .027$). There was no significant interaction between sex and sexual orientation.

Berkeley Data

Hand Width. The width asymmetry measurements in the Berkeley data were made from different points on the hand margins than in the multi-site data. A two-way ANOVA indicated an effect of sex ($F(1, 72) = 4.18$, $p = .045$) but not of sexual orientation; however, the sample size was small ranging from 11 to 29 (Table 3).

Hand Length. Non-parametric analysis of unadjusted asymmetry in hand length indicated a significant difference between groups (Kruskal–Wallis = 9.11, $p < .028$; heterosexual women > homosexual men); however, these Berkeley hand length data were not statistically significant if adjusted for individual differences in hand size (Table 3).

Digits. Measurements for FA in the digits are reported as group medians in Table 4, where all data were adjusted for trait size and for DA. Heterosexual men and women did not differ significantly in FA in either second or fourth digit or in the composite of both digits. The only significant statistical comparison was between heterosexual men and homosexual men in which the latter group had significantly lower FA (Mann–Whitney $U = 7309.5$, $p = .042$).

Pittsburgh Data

Digits. In the Pittsburgh data, Putz et al. (2004) had previously reported a significant sex effect for the composite FA of second and fourth digits with women having greater FA. That report involved data that were not adjusted for DA, and included both heterosexual and homosexual participants.

Table 3 FA in hand width and hand length after adjustment for trait size and DA

Data Source	Statistic	Trait											
		Width				Length				Composite			
		Men		Women		Men		Women		Men		Women	
		Hm	Ht	Hm	Ht	Hm	Ht	Hm	Ht	Hm	Ht	Hm	Ht
Multi-site													
	Median	.0100	.0121	.0089	.0119	.0086	.0105[c]	.0093[c]	.0099	.0106[a]	.0123[a]	.0101[a]	.0114[a]
	Range	.041	.050	.053	.065	.034	.048	.044	.044	.034	.032	.031	.048
	N	115	117	68	109	116	118	68	109	115	117	68	109
Berkeley													
	Median	.0137[b]	.0108[b]	.0204[b]	.0136[b]	.0082	.0073	.0082	.0041[c]	–	–	–	–
	Range	.038	.031	.041	.049	.027	.033	.018	.027	–	–	–	–
	N	18	18	11	29	64	44	26	53	–	–	–	–

Ht = Heterosexual, Hm = Homosexual

[a] Two-Way ANOVA $F(1, 407)$ sexual orientation = 4.91, $p = .027$

[b] Two-Way ANOVA, $F(1, 72)$ sex = 4.18, $p = .045$

[c] Non-normal and skewed right

Table 4 FA in second and fourth digits after adjustment for trait size and DA

Data source	Statistic	Trait											
		2D				4D				2D + 4D			
		Men		Women		Men		Women		Men		Women	
		Hm	Ht	Hm	Ht	Hm	Ht	Hm	Ht	Hm	Ht	Hm	Ht
Berkeley													
	Median	.0108[a,b]	.0135[a,b]	.0159	.0132[b]	.0122[b]	.0132[b]	.0148[b]	.0164[b]	.0133[b]	.0155[b]	.0157	.0145[b]
	Range	.057	.055	.057	.054	.052	.052	.050	.064	.048	.032	.052	.054
	N	189	91	80	116	193	92	81	113	186	89	76	112
Pittsburgh													
	Median	–	.0151[b]	–	.0138[b]	–	.0165[b]	–	.0197[b]	–	.0157	–	.0171[b]
	Range	–	.061	–	.072	–	.049	–	.067	–	.051	–	.057
	N	–	108	–	103	–	106	–	104	–	106	–	103

Ht = Heterosexual, Hm = Homosexual

[a] Sexual orientation difference, M–W $U = 7309.5$, $p = .042$

[b] Non-normal and skewed right

When we adjusted these data for DA, and included only individuals who reported themselves as exclusively heterosexual (Group B participants), there was no longer a significant difference in digit FA between the sexes (Table 4).

2D:4D Ratios and Digit Asymmetry

Berkeley Data

Within each of the four study groups, some individuals had rightward second digit asymmetry, i.e., longer right digits, and some had leftward asymmetry. Presumably, these differences in DA represent different growth programs that are shared in varying degrees across sexes and sexual orientations. Previous studies of 2D:4D have not examined these two subpopulations separately. They may represent discrete subpopulations with qualitatively different responses to growth signals. Here, we examined digit ratios after separating the individuals in the sex and sexual orientation groups according to their DA. We compared heterosexual men and women who had either leftward asymmetry (digit longer on the left) or rightward asymmetry in both digits. The Berkeley data showed statistically significant sexual dimorphism of the 2D:4D ratio even with relatively small sample sizes, when the participants had leftward DA in both digits (Fig. 3a; (right hand $t(39) = 2.49$, $p = .017$; left hand $t(39) = 2.99$, $p = .0047$)). In contrast, when the participants had rightward DA, there was no statistically significant sexual dimorphism in their digit ratios (Fig. 3b; right hand $t(36) = 1.32$, ns; left hand $t(36) = 1.51$, ns). Closer inspection shows that, among heterosexual women, laterality of the two digits was not a factor in their digit ratios, i.e., their digit ratios were the same regardless of whether they had rightward or leftward DA. Heterosexual men, in contrast, had digit ratios in both hands that varied as a function of their asymmetry. Those men with leftward asymmetry had lower ratios than their rightward counterparts (two-way ANOVA of hand and laterality, $F(1, 78 = 5.48$, $p = .022$), i.e., leftward males have moved away from the female pattern.

Homosexuals of both sexes who had rightward asymmetry in both digits had the same 2D:4D ratios as their heterosexual counterparts (Fig. 3b). A different picture emerged when we examined sexual orientation groups with leftward DA (Fig. 3a). Here, homosexuals differed from heterosexuals (Right Hand two-way ANOVA, $F(1, 89 = 6.51$; $p = .0122$) and Left Hand, $F(1, 89 = 8.25$; $p = .0051$)). Leftward asymmetry in homosexual women was associated with a lower 2D:4D ratio compared to homosexual women with rightward asymmetry (Right hand, $t_{(33)} = 2.41$, $p = .021$). In contrast, homosexual men with leftward asymmetry had the same 2D:4D ratios as their rightward asymmetry peers. The sexual orientation differences observed here among leftward asymmetry groups reflected asymmetry-dependent difference in the 2D:4D ratios of homosexual women and heterosexual men, whereas the 2D:4D ratios were not asymmetry dependent in either heterosexual women or homosexual men.

Pittsburgh Data

Group A men (Fig. 4a) showed a pattern of 2D:4D ratios similar to that in the Berkeley data. The 2D:4D ratio of those Group A men, in which both digits showed leftward DA,

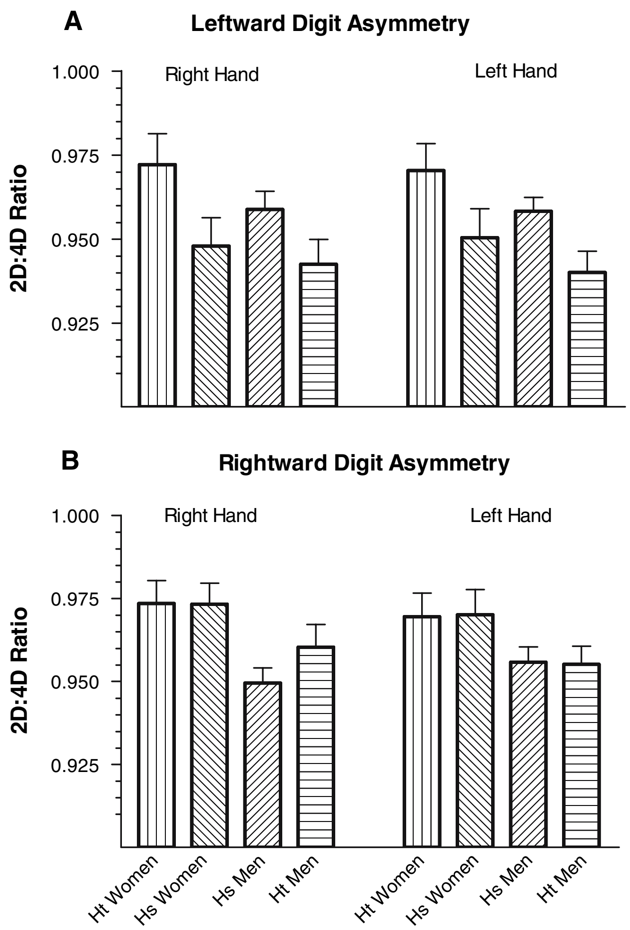

Fig. 3 2D:4D ratios in heterosexual (Ht) and homosexual (Hm) men and women from the Berkeley dataset. Leftward asymmetry includes those participants who had both second and fourth digits longer on the left hand and correspondingly, in rightward asymmetry, these participants had second and fourth digits longer on the right hand

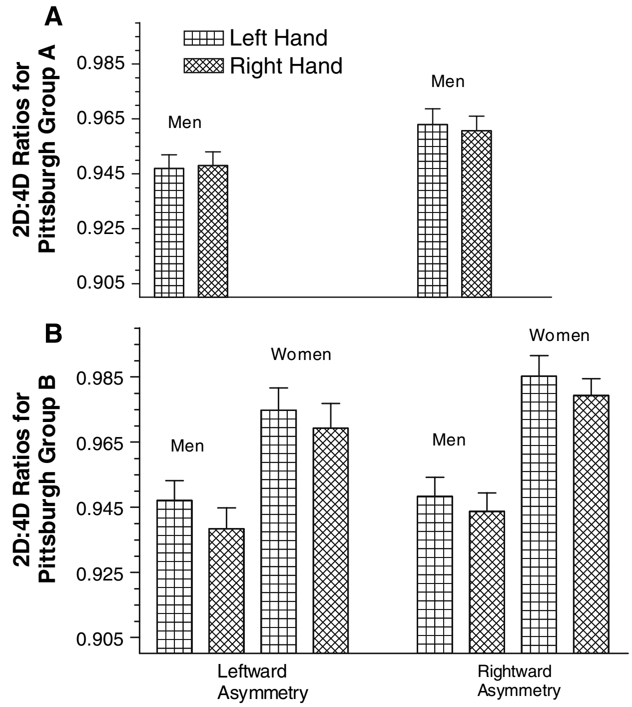

Fig. 4 2D:4D ratios in heterosexual men and women from the Pittsburgh data subsets. In each pair of columns, the legend indicates what hand the ratios are from. Leftward asymmetry includes those participants who had both second and fourth digits longer on the left hand and correspondingly, in rightward asymmetry, these participants had the second and fourth digits longer on the right hand

was significantly lower than the 2D:4D ratio of those men with rightward DA (two-way ANOVA of hand side and laterality; $F(1, 83) = 6.46$, $p = .013$.

In contrast, in Group B (Fig. 4b), there was no significant relationship between DA and 2D:4D ratios in either sex. However, there was a significant effect of laterality if Groups A and B were combined (three-way ANOVA of sex, hand side, and laterality; $F(1, 292 = 4.77$, $p = .030$), and there was a significant sexual dimorphism among the heterosexuals in Group B with men having a mean of .94 vs. .97 for women (three-way ANOVA of sex, laterality and hand), $F(1, 206) = 49.3$, $p < .0001$.

Relationship of Putative Steroid Markers to FA in Homosexual Men

We hypothesized that homosexual men who have had similar sex steroid exposure to that of heterosexual men might have increased FA as the principal etiological factor in their atypical sexual orientation. Assuming that long-bone-to-stature ratios are directly related to amount of early steroid exposure, we divided the homosexual men in the multi-site data into quartiles based on their arm:stature ratio. Then, we compared the mean unadjusted FA for those individuals in the top and bottom quartiles. Homosexual men in the top quartile had ratios in the heterosexual male range. The FA of hand width (M $FA_{bottom\ quartile} = 1.13$ mm (SEM = .188); M $FA_{top\ quartile} = 1.18$ mm (SEM = .155)) and of hand length did not differ between the top and bottom quartiles of the arm:stature ratio distribution. We did the same procedure for two other ratios that are proxy measures of steroid exposure: the hand length:stature ratio and the leg:stature ratio (data not shown). A three-way ANOVA with proxy measures, asymmetry traits, and proxy quartiles as factors indicated that those homosexual men with highest steroid exposure did not differ from those with the lowest steroid exposure in terms of FA, ($F(1, 335) = 1.40$, ns.

Relationship of Anatomical Laterality to Handedness

Hand use may be a factor in the frequency of leftward and rightward DA and in the degree of the asymmetry. Heterosexual men and women in the Berkeley data were examined in terms of the relative frequency of right-handed (RH) and of non-right-handed (NRH) individuals in groups, that had rightward second digit asymmetry and that had leftward second digit asymmetry. Using the Fisher's Exact Test, we repeated the same analysis with the fourth digit and with hand width. Only in the second digit of women was there a significant relationship between handedness and anatomical laterality ($p = .003$). Within the group of 33 women with leftward DA in the second digit, nine were NRH, whereas within the group of 60 women with rightward DA, only one was NRH. This effect was much weaker in men and not statistically significant. Fourth digit DA was not significantly related to handedness in either sex. Hand width DA was also not related to handedness, but this may be due to the relatively small sample size.

Discussion

There are three important findings in our study. The first was that a large part of the variance in 2D:4D ratios was a function of DA. The variable and inconsistent differences between the sexes and between sexual orientations in the 2D:4D ratio (for a review, see McFadden et al., 2006) may be due partly to variation in the number of individuals with leftward digit laterality in the sampled populations. Separating individuals according to the DA of both of these digits revealed that those who had rightward DA had relatively similar 2D:4D ratios regardless of their sex or sexual orientation (Fig. 3). The sex difference was absent for Berkeley groups with rightward DA (although it might have been statistically significant in a larger sample). This picture changed substantially when one examined people with leftward DA in these two digits: sexual orientation differences appeared and the sexual dimorphism in 2D:4D was statistically significant. However, the change was due to variation in only two of the four groups: heterosexual men and homosexual women. These two groups had different digit ratios depending on whether they had leftward DA or rightward DA in these digits. In contrast, the digit ratios in homosexual men and heterosexual women were not significantly affected by laterality. The pattern in the Pittsburgh data was less clear, with heterosexual men showing laterality-dependent 2D:4D ratios in one group of men, but not the other group.

It is not clear why laterality differentially affected digit ratios in the groups with male partner preference but not in the groups with female partner preference. Martin and Nguyen (2004) have shown greater long bone growth in heterosexual men and homosexual women and argued that this results from exposure to greater levels of sex steroids developmentally. Correspondingly, one possible explanation for the lower 2D:4D ratios in those leftward groups with a female partner preference is that perinatal androgen causes either increased growth of the fourth digit or decreased growth of the second digit, either of which would lead to a lower ratio. Examination of the present data supports only the latter explanation, because the drop in the 2D:4D ratio in the leftward group was not related to an elongated fourth digit but rather to a shorter second digit. Factors causing leftward laterality may interfere in some way with second digit growth or timing of growth termination. Geschwind and Galaburda (1985) suggested that testosterone might act on the brain by selectively slowing the growth of some sites, thus allowing other expanding brain structures to assume a contralateral advantage. Such an explanation could also account for these data, especially if the second and fourth digits on each hand are thought of as developing contralateral to each other

Another possible explanation for the differences in digit growth which might account for the observed variation in 2D:4D ratios is timing of puberty. Heterosexual women reach puberty before heterosexual men. Blanchard and Bogaert (1996) have pointed out that the timing of puberty may differ in homosexuals and heterosexuals, and that homosexual men may reach puberty sooner than heterosexual men; however, in a comparison of multiple indicators of puberty in homosexuals and heterosexuals, Savin-Williams and Ream (2006) found no acceleration, but rather a delay in puberty among gay men. Puberty signals a rise in estrogen level that eventually causes the termination of long bone growth (Grumbach & Auchus, 1999). Sex differences in long bone growth with adult women having relatively shorter legs and arms may be the result of earlier puberty in girls. Differences in puberty onset might also explain the shorter second digit in the leftward heterosexual men, if leftward digit asymmetry is associated with earlier puberty, but would not explain why the fourth digit length does not change in leftward DA. Sappington and Topolski (2005) found a significant interaction among sex, handedness, and age of pubertal onset in math scores in a sample of college students; however, their data indicate that left-handed individuals were less likely to have early puberty than right-handed individuals. Additional studies are needed to clarify these questions.

The second important finding was that laterality was present in several bilateral anatomical traits of the hand and that it varied with sex and sexual orientation (Table 2). What factors dictate this laterality are not clear, but the fact that the extent and frequency of DA in the second and fourth digits differed between men and women suggests sex steroids as one possible factor. DA was observed in each of the four hand variables that we measured in the current study in at least one, and sometimes in all, of the four sex/sexual orientation groups. Some traits were more likely to show DA than others, with hand width being lateralized in all groups, whereas hand length was lateralized only in heterosexual women. In none of the four variables was a preponderance of heterosexual women lateralized to the left, whereas men showed leftward DA for some traits, suggesting that rightward laterality is the result when perinatal androgen levels are low, and that androgen exposure raises the probability of leftward asymmetry. Like heterosexual men, homosexual women had significantly less rightward DA in hand width than heterosexual women and, unlike heterosexual women, did not have rightward DA in hand length. This is consistent with arguments that homosexual orientation in women is due, in part, to elevated androgen levels during early development (Martin & Baum, 1986). However, if androgen exposure were the only factor to cause leftward laterality, we would not expect to see approximately 38% of heterosexual men with rightward second digit DA and approximately 35% of heterosexual women with leftward second digit DA (Table 2). Another factor besides steroids that could determine laterality is usage. One might anticipate that the side with greatest usage would be larger, and we did find evidence that this was true for the second digit where the average DA in NRH individuals who have leftward asymmetry in the second digit is about .3 mm or 25% greater than that of RH individuals with leftward DA. However, this "usage effect" is weaker in the fourth digit, and furthermore, many individuals with rightward digit DA are NRH. Rasmussen and Milner (1977) have reported a similar relationship between handedness and laterality of language in the cortex where left handed individuals are more likely than RH individuals to have language lateralized to the right temporal cortex.

Hall and Kimura (1994) reported that women and homosexual men were more likely to have a leftward laterality in finger ridges when compared to heterosexual men. Micle and Kobyliansky (1988) did not find a sex difference in ridge count DA, and Dittmar (1998) found a difference in only one of the five finger pairs. Furthermore, Mustanski et al. (2002) were not able to replicate either the sex effect or the sexual orientation effect on laterality that Hall and Kimura had found. Our findings, while not involving dermal ridges, are relevant to these findings, because these studies are all concerned with whether and how prenatal steroid exposure might account for the diversity in observed morphological and behavioral patterns. Unlike the dermatoglyphic results of Hall and Kimura (1994), in our study heterosexual women and homosexual men had opposite DA in second digit length, i.e., heterosexual women had predominately rightward DA and homosexual men had leftward DA. Dittmar (1998) correlated asymmetry levels in ridge count from different digit pairs and found that the asymmetry in one digit usually did not predict the asymmetry in its neighbors. We found significant positive correlations between hand width and hand length DA in heterosexuals but not in homosexuals, and we found positive correlations between second and fourth digit DA in one of our datasets (Pittsburgh) but not the other (Berkeley). Taken together, these findings suggest that laterality in the hand is not a unitary phenomenon with a single cause, and that it is unlikely to be caused by simple differences in sex steroid exposure. It seems more likely that local control of growth in relation to demands put on the hand by environmental stresses and ethnic differences in response to growth signals may play a larger role in the diversity of DA in hand traits. This is particularly worth considering in light of the findings of Harris, Aksharanugraha, and Behrents (1992). Their data indicated that the distal phalanges may continue to grow in adulthood and that the metacarpals appear to decrease in length as one ages, and these things happen differentially in the two sexes.

The third important finding of this study was that homosexuals had lower FA in hand traits than heterosexuals, which contradicts the theory that increased developmental instability is a cause of atypical sexual orientation. Our FA analysis was done with adjustment for trait size, with adjustment for DA, and with non-parametric statistics for non-normally distributed groups. In second digit FA, we found that homosexual men had significantly *lower* FA than heterosexual men. In composite hand width and length FA, homosexuals also had lower FA than heterosexuals. Furthermore, looking at FA in homosexual men that were in the upper quartile of several morphometric ratios, i.e., in the range of heterosexual men, provided no indication that developmental instability is a factor in those cases were sex steroid exposure was apparently adequate to masculinize skeletal ratios. If the lower FA results in homosexuals can be replicated in other studies and traits, it might suggest the existence of some positive fitness components that could play a role in balancing selection and maintenance of homosexuality in a population.

Palmer and Strobeck (1986, 2003) have illuminated the common pitfalls in analyses of FA. Foremost among the potential methodological errors is the failure to compare normally distributed samples and the failure to account for DA. Also, failure to account for differences in trait size may bias the composite FA. Unfortunately, the published studies comparing FA in homosexuals and heterosexuals have not taken these factors into account (Green & Young, 2000; Mustanski et al., 2002; Rahman, 2005a; Rahman & Wilson, 2003). If one sample group is normally distributed and the other is not, there may be apparent FA differences where none exist, or vice versa. Rahman and Wilson (2003) examined FA of second and fourth digits in a sample of 240 individuals divided equally among heterosexual and homosexual men and women. They found no significant differences between these groups in FA of either digit or of the combined composite, and they also found no significant differences in the normality in the total sample. However, they estimated normality by using a one-sample *t*-test, rather than a test designed to detect differences in normality (e.g., the Kolmogorov–Smirnov test). They also applied the test to the entire sample rather than separately to the groups being compared. As a result, they may have missed potential trait differences in DA and in skewness between these groups. Our data indicate that these group and trait differences do exist. It seems likely that the magnitude of these differences in DA would bias any estimate of FA that fails to account for them. Similarly, the results of Rahman (2005a)—who examined traditional anthropometric measures of FA in heterosexuals and homosexuals (width and length of ears, width of wrists, ankles and feet as well as finger lengths)—may be flawed because the composite FA included traits (second and fourth digits) that are likely to be skewed differentially in their sex/sexual orientation groups and because an incorrect test was used to test normality.

In conclusion, morphological variation and laterality in the hand are associated with the sex of the individual and with the factors that may cause sexual orientation. Since sex steroids are a significant factor in both bone growth stimulation during late childhood and in growth termination during adolescence, the differences seen between heterosexuals and homosexuals in DA and FA suggest an underlying difference either in exposure to sex steroids or in sensitivity to sex steroids in these groups. The complexity of the interaction between sensitive periods, hormone levels, and tissue specific response makes cause and effect difficult to ascertain. Prospective studies are needed to clarify these relationships.

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References

Barden, H. S. (1980). Fluctuating dental asymmetry: A measure of developmental instability in Down syndrome. *American Journal of Physical Anthropology, 52*, 169–173.

Blanchard, R., & Bogaert, A. F. (1996). Homosexuality in men and number of older brothers. *American Journal of Psychiatry, 153*, 27–31.

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.

Buck, J. J., Williams, R. M., Hughes, I. A., & Acerini, C. L. (2003). In-utero androgen exposure and 2nd to 4th digit length ratio-comparisons between healthy controls and females with classical congenital adrenal hyperplasia. *Human Reproduction, 18*, 976–979.

Diehl, K., & Martin, J. T. (2006). Fluctuating asymmetry in Hispanic type II diabetics [Abstract]. *Journal of Investigative Medicine, 54*(Suppl. 1), S122.

Dittmar, M. (1998). Finger ridge count asymmetry and diversity in Andean Indians and interpopulation comparisons. *American Journal of Physical Anthropology, 105*, 377–393.

Geschwind, N., & Galaburda, A. M. (1985). Cerebral lateralization. Biological mechanisms, associations, and pathology: III. A hypothesis and a program for research. *Archives of Neurology, 42*, 634–654.

Graham, J. H., Emlen, J. M., Freeman, D. C., Leamy, L. J., & Kieser, J. A. (1998). Directional asymmetry and the measurement of developmental instability. *Biological Journal of the Linnean Society, 64*, 1–16.

Green, R., & Young, R. (2000). Fingerprint asymmetry in male and female transsexuals. *Personality and Individual Differences, 29*, 933–942.

Grumbach, M. M., & Auchus, R. J. (1999). Estrogen: Consequences and implications of human mutations in synthesis and action. *Journal of Clinical Endocrinology and Metabolism, 84*, 4677–4694.

Gualtieri, T., & Hicks, R. (1985). An immunoreactive theory of selective male affliction. *Behavioral and Brain Sciences, 8*, 427–441.

Hall, J. A., & Kimura, D. (1994). Dermatoglyphic asymmetry and sexual orientation in men. *Behavioral Neuroscience, 108*, 1203–1206.

Harris, E. F., Aksharanugraha, K., & Behrents, R. G. (1992). Metacarpophalangeal length changes in humans during adulthood: A longitudinal study. *American Journal of Physical Anthropology, 87*, 263–275.

Harrison, G. A., Weiner, J. S., Tanner, J. M., & Barnicot, N. A. (1964). *Human biology: An introduction to human evolution, variation, and growth*. New York: Oxford University Press.

Kieser, J. A., Groeneveld, H. T., & Da Silva, P. C. (1997). Dental asymmetry, maternal obesity, and smoking. *American Journal of Physical Anthropology, 102*, 133–139.

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.

Lippa, R. A. (2003). Handedness, sexual orientation, and gender-related personality traits in men and women. *Archives of Sexual Behavior, 32*, 103–114.

Malas, M. A., Dogan, S., Evcil, E. H., & Desdicioglu, K. (2006). Fetal development of the hand, digits and digit ratio (2D:4D). *Early Human Development, 82*, 469–475.

Manning, J. T. (2002). *Digit ratio: A pointer to fertility, behavior and health*. New Brunswick, NJ: Rutgers University Press.

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.

Maresh, M. M. (1955). Linear growth of long bones of extremities from infancy through adolescence. *American Journal of Diseases of Children, 89*, 725–742.

Martin, J. T., & Baum, M. J. (1986). Neonatal exposure of female ferrets to testosterone alters sociosexual preferences in adulthood. *Psychoneuroendocrinology, 11*, 167–176.

Martin, J. T., & Nguyen, D. H. (2004). Anthropometric analysis of homosexuals and heterosexuals: Implications for early hormone exposure. *Hormones and Behavior, 45*, 31–39.

McCormick, C. M., & Witelson, S. F. (1994). Functional cerebral asymmetry and sexual orientation in men and women. *Behavioral Neuroscience, 108*, 525–531.

McCormick, C. M., Witelson, S. F., & Kingstone, E. (1990). Left-handedness in homosexual men and women: Neuroendocrine implications. *Psychoneuroendocrinology, 15*, 69–76.

McFadden, D., Loehlin, J. C., Breedlove, S. M., Lippa, R. A., Manning, J. T., & Rahman, Q. (2006). A reanalysis of five studies on sexual orientation and the relative length of index and ring fingers. *Archives of Sexual Behavior, 34*, 341–356.

Micle, S., & Kobyliansky, E. (1988). Sex differences in the intraindividual diversity of finger dermatoglyphics: Pattern types and ridge counts. *Human Biology, 60*, 123–134.

Milne, B., Belsky, J., Poulton, R., Thomson, W., Caspi, A., & Kieser, J. (2003). Fluctuating asymmetry and physical health among young adults. *Evolution and Human Behavior, 24*, 53–63.

Mustanski, B. S., Bailey, J. M., & Kaspar, S. (2002). Dermatoglyphics, handedness, sex, and sexual orientation. *Archives of Sexual Behavior, 31*, 113–122.

Okten, A., Kalyoncu, 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.

Palmer, A. R., & Strobeck, C. (1986). Fluctuating asymmetry: Measurement, analysis, patterns. *Annual Review of Ecology and Systematics, 17*, 391–421.

Palmer, A. R., & Strobeck, C. (2003). Fluctuating asymmetry analysis revisited. In M. Polak (Ed.), *Developmental instability (DI): Causes and consequences* (pp. 279–319). Oxford: Oxford University Press.

Peretz, B., Ever-Hadani, P., Casamassimo, P., Eidelman, E., Shellhart, C., & Hagerman, R. (1988). Crown size asymmetry in males with fra (X) or Martin-Bell syndrome. *American Journal of Medical Genetics, 30*, 185–190.

Phelps, V. R. (1952). Relative index finger length as a sex-influenced trait in man. *American Journal of Human Genetics, 4*, 72–89.

Putz, D., Gaulin, S., Sporter, R., & McBurney, D. (2004). Sex hormones and finger length what does 2D:4D indicate? *Evolution and Human Behavior, 25*, 182–199.

Rahman, Q. (2005a). Fluctuating asymmetry, 2nd to 4th finger length ratios and human sexual orientation. *Psychoneuroendocrinology, 30*, 382–391.

Rahman, Q. (2005b). The neurodevelopment of human sexual orientation. *Neuroscience and Biobehavioral Review, 29*, 1057–1066.

Rahman, Q., & Wilson, G. D. (2003). Sexual orientation and the 2nd to 4th finger length ratio: Evidence for organizing effects of sex hormones or developmental instability? *Psychoneuroendocrinology, 28*, 288–303.

Rasmussen, T., & Milner, B. (1977). The role of early left-brain injury in determining lateralization of cerebral speech functions. *Annals of the New York Academy of Science, 299*, 355–369.

Sappington, J., & Topolski, R. (2005). Math performance as a function of sex, laterality, and age of pubertal onset. *Laterality, 10*, 369–379.

Savin-Williams, R. C., & Ream, G. L. (2006). Pubertal onset and sexual orientation in an adolescent national probability sample. *Archives of Sexual Behavior, 35*, 279–286.

Thornhill, R., & Gangestad, S. (2006). Facial sexual dimorphism, developmental stability and susceptibility to disease in men and women. *Evolution and Human Behavior, 27*, 131–144.

Thornhill, R., & Moller, A. (1997). Developmental stability, disease and medicine. *Biological Reviews, 72*, 497–548.

Weinberg, S. M., Scott, N. M., Neiswanger, K., Marazita, M. L. (2005). Intraobserver error associated with measurements of the hand. *American Journal of Human Biology, 17*, 368–371.

Williams, T. J., Pepitone, M. E., Christensen, S. E., Cooke, B. M., Huberman, A. D., Breedlove, N. J., et al. (2000). Finger-length ratios and sexual orientation. *Nature, 404*, 455–456.