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Sex hormones and finger length What does 2D:4D indicate?

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Abstract

Much recent research has focused on the ratio of the lengths of the second to fourth manual digits (2D:4D) as a predictor of the degree of expression of sexually dimorphic and other sex-hormone-mediated traits. However, published findings are often contradictory or subject to various methodological problems. In the present study, we reassessed the relationships among three measures of 2D:4D (left hand, right hand, and mean) and several variables previously claimed to be related to 2D:4D, including sexual orientation, spatial ability, status, physical prowess, and components of reproductive success. In addition, we examined the relationship between 2D:4D measures and several other traits whose expression is thought to be related to sex hormones, including voice pitch, sociosexuality, mating success, and fluctuating asymmetry. 2D:4D measures showed highly significant sex differences, as did spatial ability, sociosexuality, components of reproductive and mating success, and fluctuating asymmetry. However, out of 57 correlations, 2D:4D correlated significantly in the predicted direction only with sexual orientation (for both sexes) and only for left hand 2D:4D. We discuss the recent 2D:4D literature in light of these findings and consider their implications for understanding the timing of developmental events.

Keywords: 2D:4D; 2D/4D; Androgens; Digit length; Digit ratio; Sex differences; Sex hormones; Testosterone

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1. Introduction

The ratio of the lengths of the second and fourth manual digits (2D:4D) reliably differs by sex, with males having a lower 2D:4D (Manning, Scutt, Wilson, & Lewis-Jones, 1998). This sex difference exists in 2-year-old children (Manning et al., 1998) and may be established prenatally by the 13th or 14th week postconception (Garn, Burdi, Babler, & Stinson, 1975; Phelps, 1952). The same sex difference has also been reported for at least one other mammal (Brown, Finn, & Breedlove, 2002) and one bird (Burley & Foster, 2004). Because of its early emergence, sexual dimorphism in 2D:4D is thought to be influenced by, and hence to reflect, prenatal sex hormone regimes. In particular, high prenatal androgens, low prenatal estrogens, or both, may produce a low (masculine) 2D:4D (Manning et al., 1998). These assumptions are partially supported by studies of males and females with congenital adrenal hyperplasia (CAH), a condition characterized by the overproduction of prenatal androgens. Brown, Hines, Fane, and Breedlove (2002) and Okten, Kalyoncu, and Yaris (2002) offer evidence that CAH is associated with lower (more masculine) 2D:4D in both sexes, although the effect was not consistently observed in both hands. However, Buck, Williams, Hughes, and Acerini (2003) examined 2D:4D using radiographs of the left hand of control boys and girls, and girls with CAH (approximately 70 subjects per group). While they found the usual sex difference, they found no difference in 2D:4D between control girls and those with CAH.

For any trait affected by androgens, development depends not only on hormone levels but also on the activity of the androgen receptor (AR) molecule. In humans and other primates there is considerable allelic diversity in the AR gene, particularly as regards the number of CAG repeats in the N-terminal domain. Sensitivity to testosterone appears to be inversely proportional to the number of CAG repeats (Chamberlain, Driver, & Miesfeld, 1994; Kazemi-Esfarjani, Trifiro, & Pinski, 1995). Building on this datum, Manning, Bundred, Newton, and Flanagan (2003) demonstrated that in a sample of 50 men, right 2D:4D was positively correlated with the number of CAG repeats: Relatively androgen-insensitive men had higher (less masculine) right 2D:4D.

Jamison, Meier, and Campbell (1993) suggested that prenatal sex hormone levels correlate with adult levels, and Manning et al. (1998) were able to demonstrate that right 2D:4D correlates negatively with adult testosterone levels in men. Lumping both sexes of adults, positive correlations were also observed between 2D:4D and estrogen levels (right hand), prolactin levels (right hand), and luteinizing hormone levels (both hands). Unfortunately, this analytical approach could yield spurious results due to sex differences in both hormone levels and 2D:4D. Manning et al. presented no data relating testosterone levels to 2D:4D in adult women. More recently, Neave, Laing, Fink, and Manning (2003) reported that neither right nor left 2D:4D was significantly related to current salivary testosterone levels in undergraduate men.

These reports have stimulated considerable research on the relationship between 2D:4D and various traits putatively linked to sex hormones. The results of these studies have been mixed (see Table 1). While some authors report significant correlations between 2D:4D and such diverse traits as fertility, sexual attitudes and orientation, status, and cognitive abilities, attempts at replication by other authors have often failed. Some failures to replicate may be due to

Table 1
Summary of previously tested phenotypic correlations with 2D:4D

Domain/Trait	Correlation of trait with 2D:4D: Sign	Comments	Reference
Prenatal hormones			
CAH	–	Girls, both hands	Okten et al. (2002)
	–	Boys, right hand only	Okten et al. (2002)
	–	Girls, right hand only	Brown et al. (2002)
	–	Boys, left hand only	Brown et al. (2002)
	0	Only left hand evaluated	Buck et al. (2003)
Maternal WHR	–	Sexes combined	Manning et al. (1998)
Otoacoustic emissions	+	Left side, homosexual men only; but no correction for 24 tests	McFadden and Shubel (2003)
Current hormones			
Testosterone	–	Men sampled from infertility clinic	Manning et al. (1998)
	0	Men, both hands	Neave et al. (2003)
Estrogen	+	Sexes combined	Manning et al. (1998)
Luteinizing hormone	+	Sexes combined, right hand only	Manning et al. (1998)
Progesterone	+	Sexes combined, right hand only	Manning et al. (1998)
WHR	–	Women, right hand only	Manning et al. (2000)
	0	Men	Manning et al. (2000)
Fertility			
Sperm count	–	Right hand only	Manning et al. (1998)
Ejaculate quality	0	Four variables including sperm count	Firman et al. (2003)
Reproductive success	–	Men, four of seven samples not significant	Manning et al. (2000)
	+	Women, five of eight samples not significant	Manning et al. (2000)
Offspring sex ratio	–	Effect significant only when ethnicity is controlled	Manning et al. (2002)
Sexual orientation and identity			
Homosexuality	–	Men, left hand only; bisexuals lower than both homosexuals and controls	Robinson and Manning (2000)
	–	Men, both hands	Rahman and Wilson (2003)
	–	Women, both hands	Rahman and Wilson (2003)
	–	Women, right hand only	McFadden and Shubel (2002)
	+	Men, left hand only	McFadden and Shubel (2002)
	–	Women, right hand only	Williams et al. (2000)
	0	Men	Williams et al. (2000)
	–	Twins discordant for homosexuality	Hall and Love (2003)
Sex role identity	–	"Butch" lower than "femme" lesbians	Brown et al. (2002)
	–	Bem Sex Role Inventory	Csathó et al. (2003)
Health			
Autism	–	Parents and sibs also lower than controls	Manning et al. (2001)
Breast cancer	+	Age-of-onset effect, right hand only	Manning and Leinster (2001)
Myocardial infarction	+	Age-of-onset effect, right hand only	Manning (2002)

Table 1 (*continued*)

Domain/Trait	Correlation of trait with 2D:4D		Reference
	Sign	Comments	
Health			
Fetal growth	+	Placental weight	Ronalds, Phillips, Godfrey, and Manning (2002)
	–	Neonatal crown–heel length	Ronalds et al. (2002)
Vigor			
Soccer ability	–	League players vs. controls	Manning and Taylor (2001)
Athletic ability	–	Right hand only	Manning and Taylor (2001)
Running speed	–	800 and 1500 m, right hand only	Manning (2002)
Cognitive abilities and personality			
Spatial ability	0	Men, water-level task	Manning (2002)
	–	Men, MRT, unusual scoring method	Manning (2002)
	–	Women, latency to problem solution	Csathó et al. (2003)
	+	Women, spatial recall	Csathó et al. (2003)
	–	Men, MRT, unspecified scoring method	Manning (2002)
	0	Women, MRT, unspecified scoring method	Manning (2002)
	0	Men, MRT, large sample	Coolican and Peters (2003)
	0	Women, MRT, large sample	Coolican and Peters (2003)
Verbal fluency	+	Men, Varley Test (semantic fluency)	Manning (2002)
	0	Women, Varley Test (semantic fluency)	Manning (2002)
	0	Men, FAS Test (phonological fluency)	Manning (2002)
	0	Women, FAS Test (phonological fluency)	Manning (2002)
Musical ability	–	Men, symphony members vs. controls	Sluming and Manning (2000)
	0	Women, symphony members vs. controls	Sluming and Manning (2000)
Left handedness	–	Right hand only	Manning et al. (2000)
Psychoticism	–	Sexes combined, average of both hands	Austin, Manning, McInroy, and Mathews (2002)
Neuroticism	+	Sexes combined, average of both hands	Austin et al. (2002)
Sensation seeking	–	Women	Austin et al. (2002)
	0	Men	Austin et al. (2002)
Depression	0	Men	(Martin 1999)
	0	Women	Martin et al. (1999)
Appearance			
Attractiveness	0	Men	Neave et al. (2003)
Masculinity	–	Men	Neave et al. (2003)
Height	0	Men	Neave et al. (2003)
Status			
SES	+	Men, right hand only	Manning (2002)
	0	Women	Manning (2002)
Dominance	–	Men	Neave et al. (2003)

+ = significant positive correlation; – = significant negative correlation; 0 = no significant relationship; MRT = mental rotations test; for dichotomous traits (e.g., CAH) correlation indicates direction of change in 2D:4D when trait is present.

variation in methodology. Indeed, most positive results (with the exception of sexual orientation) have derived from a single laboratory. However, the positive results are not as compelling as they might be for two reasons. First, digit ratio has been operationalized at least four different ways: left 2D:4D, right 2D:4D, mean 2D:4D, and the difference between right and left 2D:4D (called D_{r-1}). Other measures such as 4D/height have been used as well (Martin, Manning & Downick 1999). This use of multiple predictor variables within a single study greatly increases the risk of Type I error (i.e., concluding that a relationship exists where none does). Second, the examination of a large number of possible phenotypic correlates of fetal hormone regimes within a study likewise expands the risk of Type I error. For example, Austin, Manning, McInroy, and Mathews (2002) assessed the relationship between 2D:4D and 18 abilities and personality dimensions, for each sex and for the sexes combined. Of the 56 (3×18) resulting correlations, 2 were significant (see their Table 2), and these two are not fully independent because one is a subscale of the other. These facts suggest a cautious approach to claims of a relationship between 2D:4D and particular aspects of the phenotype. Some, but not all, of these studies have used corrections (e.g., Bonferroni) for multiple comparisons.

As Table 1 shows, many reported relationships are restricted to one sex, sexual orientation, or hand. Moreover, there are puzzling inconsistencies. For example, spatial ability is sexually dimorphic and, on both experimental and clinical evidence, appears linked to the ontogenetic effects of sex hormones (Gaulin, 1995; Kimura & Hampson, 1993). For example, hyper-androgenized females with CAH exhibit elevated spatial ability compared to matched controls (Hampson, Rovet, & Altmann, 1998; Perlman, 1973; Resnick, Berenbaum, Gottesman, & Bouchard, 1986), whereas hypoandrogenized females with Turner's syndrome exhibit a specific cognitive deficit in the area of spatial problem solving (Buchsbaum & Henkin, 1980; Rovet & Netley, 1982). Against this coherent background of research on spatial ability, the 2D:4D data are less patterned. The study of spatial navigation by Csathó et al. (2003) used a testing arena designed to be an analogue of the Morris water-maze (Morris, 1981). The Morris water maze reliably yields a male advantage (measured as shorter latencies to problem solution), but Csathó et al. found that shorter (more masculine) 2D:4D was significantly associated with *longer* solution latencies. Manning (2002) found no relationship between 2D:4D and performance on the Water-Level task, another spatial task that typically yields a male advantage. The Mental-Rotation Test (Shepard & Metzler, 1971; Vandenberg & Kuse, 1978) produces the largest sex difference of any spatial task, and Manning does report that male (but not female) performance is negatively correlated with 2D:4D. However, with large samples of men and women, Coolican and Peters (2003) found no such relationship in either sex, nor did Austin et al. (2002).

At least for males, the sexual orientation data are also inconsistent. Rahman and Wilson (2003) found that both sexes of homosexuals have masculinized 2D:4D compared to same-sex heterosexuals. McFadden and Shubel (2002) agree regarding females but found that male homosexuals had *feminized* 2D:4D, whereas Williams et al. (2000) found no significant relationship between 2D:4D and male sexual orientation. Finally, Robinson and Manning (2000) found that the 2D:4D measures of male homosexuals were significantly masculinized, but that those of bisexual men were even more so. These relationships are far from clear at present.

1.1. The present research

In the two studies reported here, we reassessed the relationship between 2D:4D and several variables previously claimed to be related to 2D:4D (see Table 1), including sexual orientation, spatial ability, status, physical prowess, and components of reproductive success. In addition we examined the relationship between 2D:4D and several other traits whose expression is thought to be related to sex hormones, including voice pitch, sociosexuality, mating success, and fluctuating asymmetry (FA).

Low voice pitch is a male secondary sex characteristic whose pubertal development depends on elevated testosterone (T) levels (Beckford et al., 1985; Hollien, 1960; Hollien, Green, & Massey, 1994). Voice pitch continues to correlate negatively with salivary T levels in young adult men (Dabbs & Mallinger, 1999) and decreases with androgen treatment (Need et al., 1993). Thus, voice pitch indicates postnatal (pubertal and current) androgen levels.

Sociosexuality is a dimension of personality that indexes interest in casual or uncommitted sex. Sociosexuality is thought to differentiate separately within sex, such that high androgen and high estrogen levels lead to high sociosexuality for males and females, respectively (Mikach & Bailey, 1999). Like sociosexuality, the behaviors that lead to mating success are believed to differentiate separately within sex, such that high androgen and high estrogen lead to high mating success in males and females, respectively (Mikach & Bailey, 1999).

Sluming and Manning (2000) found a significant relationship between 2D:4D and musical ability. Because musical ability may be an honest signal of male genetic quality (Miller, 2000), Manning (2002) suggested that, in addition to signaling fertility, 2D:4D may also be a reliable signal of genetic quality. Fluctuating asymmetry (FA; Van Valen, 1962) is probably the most widely employed proxy measure of underlying genetic quality (Gangestad & Thornhill, 1997, 1999; Møller 1997; Møller & Thornhill, 1997a, 1997b).

2. Methods

Subjects were 230 male and 120 female undergraduates between the ages of 18 and 30 recruited from the psychology subject pool at the University of Pittsburgh. Subjects participated in one of two studies approved by the governing human subjects committee. To maximize our ability to detect relationships between 2D:4D and other aspects of the phenotype, we did not use Bonferroni correction of P values.

2.1. Study 1

One hundred eleven self-reported heterosexual males (mean age 18.9, standard deviation = 1.2) participated in the first study. After signing a consent form that outlined the experimental procedure, each subject was seated at a computer monitor and given a combination headphone/headset microphone and a short written passage. The experimenter's recorded voice instructed the subject to read the passage aloud, ostensibly as a test of the recording equipment. The subject was then told that he would be competing with a male in another room for a lunch date with a woman in a third room, a protocol similar to that of Simpson, Gangestad, Christensen, and Leck (1999). In actuality, the male competitor was audio recorded, and the female was video recorded. The subject's voice was recorded as he (1) read the passage aloud ("baseline" recording), (2) described himself to the female ("courtship" recording), and (3) described why other men might respect or admire him to his competitor ("competitive" recording). From their consent forms subjects were aware of the upcoming "dating game" when they made their baseline recording; thus this knowledge may have influenced acoustic parameters of their voices. After this dating game scenario, each subject was given a questionnaire designed to assess social and physical dominance, sociosexuality, sexual interest in the potential date, and previous mating success.

2.1.1. Voice pitch

Average *fundamental frequency* (F_0), the acoustic parameter most closely related to pitch, was later measured for each participant's three recordings using the voice analysis software program, Praat.

2.1.2. Social and physical dominance

Dominance entails access to rewards, such as mates and resources, that is not typically challenged by others. In most animals, dominance is largely a matter of intimidation through threats of aggression. In humans, dominance may also be achieved through skillful leadership and persuasion (Henrich & Gil-White, 2001). Thus, dominance may result from the ability to utilize physical force (*physical dominance*) or from leadership ability and prestige (*social dominance*).

Social and physical dominance were assessed via self-ratings. Following Mazur and Booth (1998), subjects were instructed that "a [socially] dominant person tells other people what to do, is respected, influential, and often a leader; while submissive people are not influential or assertive and are usually directed by others." Subjects were then asked to rate their own dominance/submissiveness on a 6-point scale. To measure physical dominance, subjects were asked about their level of agreement with the following statement: "If you got in a fistfight with an average undergraduate male, you would probably win." Subjects were also asked to rate the social and physical dominance of their competitor. Because every subject was exposed to the same competitor, a subject's rating of his competitor could be used as a baseline from which to evaluate his self-rating. The difference between a subject's rating of his own dominance and his rating of his competitor's dominance is here referred to as *relative* (social or physical) *dominance*.

2.1.3. Sociosexuality and sexual interest

According to the sociosexuality orientation inventory (SOI) developed by Simpson and Gangestad (1991), sociosexuality is measured by the subject's level of agreement or disagreement with a series of statements (e.g., "It is better not to have sexual relations until you are married") The statements are counterbalanced by polarity, such that for some items agreement indicates high sociosexuality, whereas for others disagreement does so. The inventory is scored by first inverting the choices of the reverse-polarity items, assigning values for "strongly disagree" through "strongly agree" and then summing these values over all items. Low scores on the sociosexuality inventory indicate low interest in uncommitted sex. Subjects were asked to respond to a 12-item sociosexuality questionnaire. Also, as a measure of general interest in courtship, subjects were asked about their level of interest in going on a date with the (video recorded) woman who interviewed them.

2.1.4. Mating success

Mating success is a function of copulatory frequency with fertile partners. In this study, mating success was measured in two ways: number of potential conceptions and number of sex partners.

2.1.4.1. Number of potential conceptions: males. Mating success was first evaluated by estimating the number of conceptions that would likely result from a particular copulatory pattern in the absence of contraception. The number of potential conceptions (NPC; Pérusse, 1993) was calculated according to the equation

$$\mathrm{NPC} = \sum_{m=1}^{n} (1 - 0.97^{p_m}) \tag{1}$$

where the exponents $p_1 \ldots p_n$ represent the number of coital acts with partners $1 \ldots n$, respectively. The constant 0.97 represents the probability that a single unprotected copulatory act, at a random time during the female's ovulatory cycle, will fail to result in a conception. This constant is derived empirically from the fertility research of Bongaarts and Potter (1983) and Leridon (1977). Thus, 0.97^p is the probability that p copulatory acts will fail to produce a conception, and therefore $1-0.97^p$ is the chance that p copulatory acts *will* produce a conception. The NPC calculation simply sums this quantity across sexual partners. NPC was calculated for subjects during the past year because the NPC calculation assumes that each female mate can conceive only once—a reasonable assumption over a single year.

2.1.4.2. Number of sex partners. Although number of sexual partners is an important component of male mating success, it is not perfectly correlated with NPC. This occurs because males who have had sex with many women may nonetheless have low NPC scores if they copulated few times with each partner. The number of sexual partners each subject had in the past year was therefore used as a measure of desire for and ability to obtain multiple sex partners. We chose an interval of 1 year (a) to ensure some variance, (b) to maximize recall accuracy, and (c) for comparability with other research (e.g., Faurie, Pontier, & Raymond, 2004) in the field.

2.1.5. Digit lengths and fluctuating asymmetry

After each subject completed this questionnaire, measurements and hand photocopies were obtained for assessing 2D:4D and FA. Each subject's wrists were measured at their maximum diameter, alternating left and right until each wrist had been measured twice. The correlation between repeated measurements was $r=.985$ for the left wrist and $r=.982$ for the right. Next, each subject's hands were photocopied, alternating left and right until each hand had been photocopied twice. Second through fifth digit lengths were later measured from these photocopies using a digital caliper accurate to 0.01 mm. Each digit was measured from tip to basal crease, and measurements from the two photocopies were averaged to obtain a final length measurement for each digit. Ten percent of digit lengths were remeasured from photocopies to assess intrameasurer reliability. Correlations between repeated measurements ranged from $r=.990$ to .998.

Four measures of 2D:4D were calculated from measurements of digit lengths. These included right 2D:4D, left 2D:4D, average 2D:4D, and the difference between right and left 2D:4D (D_{r-l}).

The asymmetry of each trait (wrists and four digits) was calculated as the absolute difference between left and right sides, divided by the average of the left and right measurements for the trait. A composite measure of fluctuating asymmetry was obtained by averaging the asymmetries of all five traits. Thus, total FA was obtained via the formula

$$FA = \frac{\sum_{i=1}^{5} \frac{|L_i - R_i|}{(L_i + R_i)/2}}{5} \tag{2}$$

where L and R represent left and right measurements of trait i. Traits that subjects reported having injured were discarded, and FA measurements from the remaining traits were averaged.

2.2. Study 2

One hundred nineteen male and 120 female subjects participated in this study. Palmar surfaces of each subject's hands were photocopied, and second and fourth digit lengths were later measured from these photocopies to be used in calculating FA and 2D:4D (see above). Unlike Study 1, FA was calculated only for the second and fourth digits. The average FA of these two traits alone is here referred to as $FA_{2,4}$ to distinguish it from FA of the five traits measured in Study 1, referred to simply as FA.

Over 10% of the sample (30 subjects) was remeasured for assessing intrameasurer reliability. Correlations between first and second measurements ranged from $r=.990$ to .996.

2.2.1. Mental rotation ability

The original paper-and-pencil version of the Vandenburg and Kuse (1978) mental rotation test was administered to subjects, who were given 7 min to complete the task. This task consists of 20 items, each with two correct and two incorrect choices, and is conventionally scored as correct minus incorrect to adjust for guessing. When scored in this way, the MRT yields a reliable sex difference of approximately .7 standard deviation (Linn & Petersen, 1985; Rosenthal & Rubin, 1982).

2.2.2. Mating success and sexual orientation

Following the mental rotation test, subjects completed the 12-item sociosexuality questionnaire described in Study 1 and answered a short sexual history questionnaire, which yielded the data necessary for calculating NPC and number of sexual partners in the past year (see above) and for assessing sexual orientation. Subjects were asked about their sexual orientation using a 5-point scale ranging from 1 (*exclusive sexual interest in members of the opposite sex*) to 5 (*exclusive sexual interest in members of the same sex*). Subjects who answered 1 or 2 on this scale were considered heterosexual, while those who answered 4 or 5 were considered homosexual.

2.2.3. Number of potential conceptions: females

Because the NPCs of females and males are differentially affected by sex with multiple partners, NPC was calculated differently for the two sexes. If .97 is the probability that a single unprotected copulatory act, at a random time during a female's ovulatory cycle, will fail to result in a conception, then a female's probability of conception can be estimated by the equation

$$\mathrm{NPC} = 1 - .97^{k} \tag{3}$$

where k is her total number of copulatory acts since her last conception. In this study, values for k were derived by summing the numbers of copulations each female reported for each of her mates.

2.3. Statistical analysis

Data from Study 1 and Study 2 were lumped wherever methods were identical in order to increase our statistical power to detect any 2D:4D relationships. One-tailed statistical tests were used when directional (i.e., masculine/feminine) predictions could be made. This included all correlations and sex differences, with the exceptions of sex differences in $FA_{2,4}$, partner number, and NPC, which were analyzed using two-tailed t tests (see Discussion).

3. Results

3.1. Sex differences

The various 2D:4D measures and the candidate correlates of 2D:4D (mental-rotation performance, partner number, NPC, sociosexuality, and $FA_{2,4}$) were first analyzed for sex differences using t tests. (Table 2).

Significant sex differences were found for all measures of 2D:4D ($6.21 \leq t \leq 7.23$; $P < .0001$), except D_{r-l} (the difference between right and left 2D:4D), which did not differ

Table 2
Sex differences

	Females		Males			
	Mean	N	Mean	N	t value	P value
MRT	13.5	120	20.0	119	−5.15	<.0001
No. of partners	2.08	120	1.57	222	2.19	.015[a]
NPC	.480	120	.369	219	2.47	.014[a]
Sociosexuality	2.75	120	3.77	229	−9.66	<.0001
Left 2D:4D	.979	120	.955	218	6.21	<.0001
Right 2D:4D	.974	120	.949	220	7.00	<.0001
Mean 2D:4D	.977	120	.951	213	7.23	<.0001
D_{r-1}	.005	120	.001	214	.610	.271
$FA_{2,4}$	.022	120	.018	213	2.97	.004[a]

[a] Two-tailed P value.

significantly between the sexes (t = 0.610, P = .271). This result agrees with that of Manning et al. (2000), who found no significant sex difference in D_{r-1} in a sample of 567 males and 661 females from seven populations. Thus, D_{r-1} is unlikely to be a reliable marker for prenatal sex hormone regimes and will not be examined here as an independent variable.

All dependent variables showed significant sex differences. Male scores on the mental rotation test (20.0 ± 0.921) were significantly higher than those for females (13.5 ± 0.901) (t = − 5.15, P < .0001), whereas females had significantly lower sociosexuality scores (t = −9.66, P < .0001), indicating lower interest in casual sex than males, they reported having had significantly more sexual partners in the past year (t = 2.19, two-tailed P = .030) and had significantly higher NPC scores (t = 2.47, two-tailed P = .028). Females also had significantly higher $FA_{2,4}$ than did males (t = 2.97, two-tailed P = .004).

3.2. Correlations with 2D:4D among females

Sexual orientation was significantly related to left 2D:4D (r = −.161, P = .040) and marginally significantly related to mean 2D:4D (r = −.143, P = .061) (Table 3). 2D:4D (left, right, and mean) did not significantly predict female NPCs, number of sex partners in the past year, sociosexuality, or $FA_{2,4}$ (F tests), although left 2D:4D was almost significantly related to $FA_{2,4}$ (r = .146, P = .060). However, females with higher (more feminine) left and mean 2D:4D had significantly better MRT scores (r = .157 and 0.167, P = .043 and .034, respectively), and right 2D:4D was marginally significantly related (r = .147, P = .054) to MRT score in the same, unexpected direction (Table 3).

3.3. Correlations with 2D:4D among males

Male sexual orientation was significantly related to left 2D:4D (r = −.125, P = .034) (Table 4). Among the (self-identified heterosexual) males from Study 1, no 2D:4D measure was significantly related to courtship-, competitive-, or baseline-voice pitch; relative social

Table 3
Correlations between digit ratio and other measures in women

	Left 2D:4D			Right 2D:4D			Mean 2D:4D		
	N	*r*	*P*	*N*	*r*	*P*	*N*	*r*	*P*
MRT	120	.157	.043	120	.147	.054	120	.167	.034
No. of partners	120	−.044	.316	120	.075	.207	120	−.064	.244
NPC	120	−.003	.487	120	−.068	.230	120	−.037	.344
Sociosexuality	120	.134	.073	120	−.042	.326	120	.057	.269
Sexual orientation	120	−.161	.040	120	−.095	.152	120	−.143	.061
$FA_{2,4}$	120	.146	.056	120	.021	.411	120	.093	.155

or physical dominance; interest in the female interviewer; or FA. Among all male participants, MRT, NPC; number of sex partners in the past year, and $FA_{2,4}$ were not significantly related to any measure of 2D:4D. However, left 2D:4D was significantly related to sociosexuality ($r = .127$, $P = .031$) and mean 2D:4D was marginally significantly related ($r = .093$, $P = .088$) to sociosexuality (Table 4). On the possibility that spatial ability is curvilinearly related to androgen dosage in men (Hines et al., 2003) we also tested for a quadratic relationship between 2D:4D and MRT performance. This relationship was nonsignificant for left, right, and mean 2D:4D (F=0.49, 0.98, and 0.93, respectively, all n.s.).

3.4. Factor analysis

Factor analysis offers another analytical approach to examining relationships among these various phenotypic measures. Those traits subject to similar control mechanisms should

Table 4
Correlations between digit ratio and other measures in men

	Left 2D:4D			Right 2D:4D			Mean 2D:4D		
	N	*r*	*P*	*N*	*r*	*P*	*N*	*r*	*P*
MRT	119	.013	.446	119	−.091	.162	119	−.042	.324
No. of partners	211	.014	.420	212	−.062	.186	206	−.001	.497
NPC	207	−.039	.290	209	−.023	.368	202	−.008	.458
Sociosexuality	218	.127	.031	219	.013	.424	213	.093	.088
Sexual orientation	217	−.125	.034	219	.020	.385	212	−.061	.187
Interest in female	98	.035	.383	100	.050	.408	93	.044	.338
Relative social dominance	99	−.019	.271	101	−.097	.273	94	−.061	.259
Relative physical dominance	98	.139	.114	100	.052	.323	93	.110	.146
Baseline F_0	99	.048	.493	101	.037	.300	94	.047	.325
Courtship F_0	99	.032	.415	101	.026	.367	94	.032	.380
Competitive F_0	99	.037	.357	101	.062	.265	94	.054	.302
FA	99	.032	.340	101	−.029	.312	94	.002	.493
$FA_{2,4}$	213	.051	.482	213	−.044	.250	213	.004	.316

cluster together. To maximize the data available for analysis, three separate varimax-rotated factor analyses were performed: one for the Study 1 participants, and one for each sex of participant in Study 2. Each yielded four or five factors and explained approximately 75% of the variance.

In each of these analyses, the three digit-ratio variables loaded heavily onto a single factor, and no other variables loaded heavily onto that same factor. In general, the other obvious constructs each loaded onto a single factor. For example, in Study 1, the three F_0 variables loaded onto one factor. Sociosexuality, number of sex partners in the past year, and NPC loaded together. MRT score formed a separate factor, except in females, where it clustered with $FA_{2,4}$.

4. Discussion

The significant sex differences in 2D:4D found in this study support the role of sex hormones in the development of digit lengths. Sex differences in mental rotation performance and sociosexuality were also highly significant in the predicted directions. Interestingly, number of sex partners, number of potential conceptions, and $FA_{2,4}$, showed significant sex differences, as well, with females exceeding males for all three variables.

NPC and number of mates should exhibit no sex difference in a population with an unbiased sex ratio. This is because every time a female conceives or has heterosexual intercourse, a male does as well. On the other hand, given females' apparent underreporting of their sexual activity and/or males' overreporting (Baker & Bellis, 1995), one might predict the opposite of our findings. Three nonmutually exclusive explanations for these results suggest themselves: First, copulations with females may be concentrated among a few males who largely escape detection in a sample of this size, while copulations with males may be more evenly distributed among females (but see Baker & Bellis, 1995, for the reverse prediction). Second, because females sexually mature earlier and undergo menopause, their sexual activity may be concentrated earlier in life than is the sexual activity of males. Finally, females in their late teens and early twenties are expected to be more attractive as mates than are males of the same age (e.g., Buss & Schmitt, 1989). Thus, females in this age group may engage disproportionately in sex with older (more desirable) males.

Another interesting and unexpected finding was a sex difference in $FA_{2,4}$. Across many vertebrate species, males are more parasitized than are females, perhaps because of males' riskier behavior or higher circulating levels of the immunosuppressant hormone, testosterone (Zuk & McKean, 1996). All else being equal, higher parasitic infection rates in males should cause greater FA in males, but the reverse was found. Greater levels of FA in women than in men have also been found in dermatoglyphics (Arrieta et al., 1995; Micles & Kobyliansky, 1991) and dentition (Mizoguchi, 1988), although Perzigian (1977) and Townsend (1981) found no sex difference in levels of dental FA. Though not the focus of the present research, the observed sex differences in sexual activity and FA are intriguing and await replication and further investigation.

With respect to the main focus of the present research, our results suggest that the usefulness of 2D:4D as a predictor of other sex-hormone-mediated traits is limited. The 18 female correlations, 6 (Traits)$\times$3 (Measures) of 2D:4D, produced only three significant results, and the 39 total male correlations, 13 (Traits)$\times$3 (Measures) of 2D:4D, produced only two significant results at the .05 level. Of the three significant female correlations, two were counter to the predicted direction. Lower (more masculine) 2D:4D measures were expected to correlate with higher MRT scores in females, but the reverse was found. Likewise, one of the two significant male correlations was counter to expectation; males with higher (more feminine) 2D:4D ratios reported higher sociosexuality scores (greater interest in casual sex). Thus, only 2 correlations out of 57 were significant in the predicted direction. These indicated a link between sexual orientation and left 2D:4D that was manifested in both sexes. Additionally, factor analysis revealed that 2D:4D measures did not cluster with other measured traits.

The question arises: How can 2D:4D be a valid predictor of sex hormone levels and yet be unrelated to so many traits that also depend on sex hormones for their development? The answer may involve developmental timing. Sex hormone levels fluctuate substantially during human growth and development, and various sexually dimorphic traits differentiate at different times. Thus, traits that differentiate under the same hormonal influences may nonetheless be uncorrelated in their expression if they differ in developmental timing. Indeed, our factor analyses indicate that most of these sexually dimorphic traits do not cluster together. Although Manning et al. (1998) found a significant correlation between 2D:4D and adult androgen levels, their finding was limited to males, and the only attempt at replication of which we are aware (Neave et al., 2003) failed. If this result turns out to be spurious, then 2D:4D may indicate little more than sex hormone levels at the time when 2D:4D differentiates sexually.

One of the most robust correlates of 2D:4D is sexual orientation. Several independent laboratories have noted such a relationship, both for male sexual orientation (Rahman & Wilson, 2003; Robinson & Manning, 2000) and, more consistently, for female sexual orientation (Brown, Finn, Cooke, & Breedlove, 2002; Hall & Love, 2003; McFadden & Schubel, 2002; Rahman & Wilson, 2003). The present study supports these findings.

On the other hand, spatial ability does not appear to correlate reliably with 2D:4D (Austin et al., 2002; Coolican & Peters, 2003; this study) and yet probably differentiates sexually under the influence of the same hormones affecting sexual orientation. This suggests that 2D:4D and sexual partner preference differentiate sexually at similar times, but that their developmental timing does not coincide with the sexual differentiation of spatial ability. Abnormal fluctuations in fetal sex hormone levels (due to maternal hormonal fluctuations or factors intrinsic to the developing fetus) may primarily affect traits that differentiate sexually around the time of the fluctuations. Because CAH girls are exposed to consistently higher androgen levels prenatally, they tend to be masculinized for many traits that sexually differentiate prenatally. Thus, CAH girls exhibit masculinized spatial abilities, sexual orientation, childhood play patterns (Berenbaum, 1999), and 2D:4D.

In conclusion, 2D:4D may be statistically unrelated to the expression of many sex-hormone-dependent traits because (1) the timing of sexual differentiation in these traits differs from the timing of 2D:4D sexual differentiation and (2) individual differences in sex hormone regimes during 2D:4D sexual differentiation are statistically unrelated to individual differences in sex hormone regimes during sexual differentiation in these other traits.

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