

Original Article

2D:4D ratios predict hand grip strength (but not hand grip endurance) in men (but not in women)

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Abstract

In humans, the ratio of the second digit to the fourth digit — the 2D:4D ratio — is a sexually dimorphic trait (men, on average, exhibit lower 2D:4D ratios than do women) that is influenced by prenatal testosterone exposure, but not by circulating testosterone levels in adulthood. Consequently, 2D:4D ratios are commonly used as indirect measures of prenatal testosterone exposure. Many studies have examined the associations of 2D:4D ratios with sexually dimorphic adaptations that are thought to be influenced by such exposure, including physical prowess. The existing literature, however, remains unclear as to (1) whether 2D:4D ratios are more closely linked to strength or to endurance; and (2) whether 2D:4D ratios are linked with physical prowess for both men and women. In 100 men and 122 women, the relationship of 2D:4D ratios with maximum voluntary contraction (MVC) scores (hand grip strength) and maximum endurance time (MET) scores (local muscular endurance) using a hand dynamometer was examined. Controlling for age, height, weight, and average digit length, we found that 2D:4D ratios significantly predicted MVC scores in men, but not in women. 2D:4D ratios did not significantly predict MET scores for either sex. These results suggest that prenatal testosterone exposure in this sample is significantly related to hand grip strength in men, but not in women (and to local muscular endurance in neither sex), and, therefore, that strength, rather than local muscular endurance, potentially drives the relationship between 2D:4D ratios and physical prowess.

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1. Introduction

In many species, sex hormones play a vital role in cognitive and physiological sexual differentiation (Berenbaum & Beltz, 2011). In human males, the sex hormone testosterone is synthesized and released by the testes in utero (Clarnette, Sugita, & Hutson, 1997; Migeon & Wisniewski, 1998). During gestation, the brain undergoes rapid development and exposure to testosterone permanently organizes the structure of the brain in a way that influences, for example, aggression, spatial abilities, interests, gender identity, and sexual orientation (Berenbaum & Beltz, 2011). Prenatal exposure to testosterone also appears to contribute to the well-established sex difference in the ratio of the second digit to the fourth digit: the 2D:4D ratio (Manning, Scutt, Wilson,

& Lewis-Jones, 1998; Manning, 2011, 2002). Men reliably exhibit smaller 2D:4D ratios than do women (e.g., Phelps, 1952) and according to one review, no studies have yielded evidence for smaller 2D:4D ratios in women (Peters, Mackenzie, & Bryden, 2002). McIntyre, Ellison, Lieberman, Demerath, and Towne (2005) explored 2D:4D measurements in adults and concluded that adults' 2D:4D ratios are reliable approximations of the prenatal influence of testosterone. Likewise, Hönekopp, Bartholdt, Beier, and Liebert (2007) found that 2D:4D ratios are not associated with adult hormone levels.

Other findings lend credence to the claim that the 2D:4D ratio reflects intrauterine exposure to testosterone (and, perhaps also, increased sensitivity to testosterone via intrauterine regulation of testosterone receptors). In rats, elevated prenatal exposure to testosterone appears to yield lower 2D:4D ratios (Talarovicová, Krsková, & Blazeková, 2009), and in mice, the ratio of androgen to estrogen exposure appears to influence 2D:4D ratios (Zheng & Cohn, 2011). In humans, Lutchmaya, Baron-Cohen, Raggatt,

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Knickmeyer, and Manning (2004) found a negative association of the ratio of testosterone to estradiol in amniotic fluid (controlling for sex) with 2D:4D ratios at age 2, such that high testosterone-to-estradiol ratios were associated with smaller 2D:4D ratios. Furthermore, Brown, Hines, Fane, and Breedlove (2002) and Ökten, Kalyoncu, and Yariş (2002) found smaller 2D:4D ratios in patients with congenital adrenal hyperplasia, a disease marked by overexposure to androgens in utero and subsequent hypermasculinization of many features (but cf. Buck, Williams, Hughes, & Acerini, 2003). Additionally, sensitivity to testosterone appears to be related to the number of CAG repeats in the androgen receptor gene (Chamberlain, Driver, & Miesfeld, 1994). Manning, Bundred, Newton, and Flanagan (2003) and Butovskaya, Vasilyev, Lazebny, Burkova, Kulikov, Mabulla, Shibalev, and Ryskov (2012) found that males with more CAG repeats had larger 2D:4D ratios, and Knickmeyer, Woolson, Hamer, Konneker, and Gilmore (2011) found that the interaction of salivary testosterone and CAG repeats predicted 2D:4D ratios (but cf. Hampson & Sankar, 2012; Hurd, Vaillancourt, & Dinsdale, 2011; Loehlin, Medland, & Martin, 2012). Similarly, men with complete androgen insensitivity syndrome, who are unable to respond to androgen exposure, exhibit larger 2D:4D ratios than men who are sensitive to androgen exposure (Berenbaum, Bryk, Nowak, Quigley, & Moffat, 2009). Finally, van Anders, Vernon, and Wilbur (2006) found that females with a same-sex dizygotic twin had larger 2D:4D ratios than did females with an opposite-sex dizygotic twin, suggesting that the presence of a male twin exposes the female co-twin to higher levels of testosterone, thereby resulting in smaller 2D:4D ratios for females developing in the presence of male co-twins than for females developing in the presence of female co-twins (but cf. Medland, Loehlin, & Martin, 2008).

Based on the evidence that smaller 2D:4D ratios result from prenatal exposure to high levels of testosterone, many studies have correlated sexually dimorphic characteristics that are also thought to be influenced by prenatal exposure to testosterone with 2D:4D ratios. For example, smaller 2D:4D ratios have been associated with males' perceived dominance (Neave, Laing, Fink, & Manning, 2003), self-reported physical aggression towards sexual competitors (Cousins, Fugère, & Franklin, 2009), self-reported number of sexual partners (Hönekopp, Voracek, & Manning, 2006) and self-reported sensation-seeking (Fink, Neave, Laughton, & Manning, 2006; Fink, Thanzami, Seydel, & Manning, 2006). These results suggest that intrauterine exposure to testosterone influences sexually selected adaptations that play a role in male intrasexual competition. Studies have also evaluated the associations of 2D:4D ratios with measures of strength and endurance (Fink, Neave, et al., 2006; Fink, Thanzami, et al., 2006; Gallup, White, & Gallup, 2007; Hönekopp & Schuster, 2010; van Anders, 2007). The findings of these studies have been mixed, however: Fink, Neave, et al. (2006) and Fink, Thanzami, et al. (2006) found a significant negative correlation

of 2D:4D ratios and strength in German and Mizos men, but Gallup et al. (2007) did not find this correlation in US college men or women, and van Anders (2007) did not find this correlation in Canadian women.

Hönekopp and Schuster (2010) conducted a meta-analytic review of 25 previously published studies and found that 2D:4D ratios were significantly negatively correlated with physical prowess ($r \approx -0.26$, $p < .001$) and that sex was not a significant moderator ($p = .143$) of this association. Furthermore, in an attempt to determine which aspects of physical prowess drive the relationship of 2D:4D ratios with physical prowess (i.e., strength, endurance, or both), they reviewed five studies pertaining specifically to the association between 2D:4D ratios and running performance. They found that running distance was a significant moderator ($p = .00008$) of the association between 2D:4D ratios and running performance such that 2D:4D ratios were a stronger predictor of running performance as running distance increased. They also found that the apparent moderation by running distance of the association of 2D:4D ratios with running performance did not differ across the sexes ($p = .186$). On this basis, Hönekopp and Schuster (2010) concluded that the relationship of 2D:4D ratios with physical prowess is not moderated by sex and that the relationship between 2D:4D ratios and physical prowess is driven by the effects of 2D:4D ratios on cardio-respiratory endurance. This is an interesting speculation; however, four limitations in the existing literature remain to be addressed.

First, of the 25 studies that Hönekopp and Schuster (2010) reviewed, only two studies included both male and female participants, and only three of the studies involving female participants measured physical prowess with a behavioral measure (one used running speed in a one-mile race, a second used a gym-based fitness test, and a third used hand grip strength). Thus, the existing database on the links between 2D:4D and women's physical prowess is actually quite sparse, which necessarily limited Hönekopp and Schuster's (2010) statistical power for meta-analytically detecting sex differences in the associations of 2D:4D ratios with various measures of physical prowess. Second, the conclusion that endurance, rather than strength, is the component of physical prowess that drives the association between 2D:4D ratios and physical prowess is supported only by meta-analytic synthesis; no studies included in the meta-analysis itself examined both strength and endurance in the same participant samples. Third, in the meta-analytic synthesis, only cardio-respiratory endurance was used as a measure of endurance, whereas no measures of local muscular endurance were used. To determine whether strength or endurance drives the relationship between physical prowess and 2D:4D ratios, measuring the strength and endurance of the same muscle groups (grip flexors), using the same apparatus (in our case, a hand dynamometer), in both men and women in the same participant sample would potentially be enlightening. Fourth, not all of the studies included in the meta-analysis controlled for participants' age, height, weight and other measures that might

confound the relationships of 2D:4D ratios with strength and endurance. In the present study, we evaluated both hand grip strength and local muscular endurance (hand grip measures are valid indicators of upper body strength and endurance; Bohannon, 1998, 2004) in a study of 222 men and women. We also statistically controlled for age, height, weight, and average digit length (we controlled for average digit length on the premise that hand length and span are associated with grip strength; Li, Hewson, Duchêne, & Hogrel, 2010; Macdermid, Fehr, & Lindsay, 2002).

2. Methods

2.1. Participants

Participants were 222 students who were enrolled in an introductory psychology course at the University of Miami. The sample included 122 women aged 17–48 (mean=19.33, S.D.=3.16) and 100 men aged 18–23 (mean=19.12, S.D.=1.11). Participants were excluded if they reported any history of Reynaud's syndrome, cardiovascular disorder, fainting, seizures, or frostbite, or any current fractures, open cuts, or open sores on their hands or arms. Experimenters were certified to conduct human subjects research and obtained written documentation of informed consent from all participants. Participants received US\$7.00 and a small amount of credit toward a research familiarization requirement in their courses. This study was approved by the University of Miami's Institutional Review Board.

2.2. Procedure

In a single laboratory session, we measured both strength and endurance via a hand grip dynamometer. Participants completed the maximum voluntary contraction (MVC) task first and then completed two trials to estimate maximum endurance time (MET). Experimenters were male and female undergraduate research assistants at the University of Miami. To obtain a measure of MVC of the grip flexors (Little & Johnson, 1986), which measures hand grip strength in kilograms, participants were asked to sit comfortably in a chair with their backs straight, knees bent, and feet flat on the floor. They were then asked to (1) place their elbows on the table (shoulder width apart), (2) place their dominant forearm on the table in a prone position, and (3) place their non-dominant forearm on the table in a supine position. Next, participants were instructed to hold the dynamometer with their dominant hand palm up and to squeeze the dynamometer with their non-dominant hand palm down (with the dynamometer directly in front of them). The dynamometer was set at 2 in., and participants were asked to squeeze the dynamometer as hard as possible and to hold it for 3 s. Experimenters began timing with a stop watch when the maximum grip strength was reached and experimenters asked participants to stop squeezing when 3 s had passed.

After participants completed the MVC task, they were told that they would have a brief rest before they completed the first MET trial. To obtain MET (Little & Johnson, 1986), which measures local muscular endurance, participants were asked to sit and place their hands as described above and then to squeeze the dynamometer at 70% of their MVC and hold it for as long as possible. Experimenters began timing when participants reached 70% of their MVC, and they stopped timing when participants' grip dropped below 70% of their MVC. Then, participants were asked to repeat the MET task, although they were not told about the second MET trial until after they had completed the first (to prevent participants from conserving their strength during the first trial). After the second MET trial, participants completed a questionnaire including items pertaining to their sex and age (height and weight were obtained prior to the study).

Next, to measure 2D:4D, experimenters drew two dots on participants' dominant hands with a washable cosmetic pencil — one in the center of the crease between the 2D and the palm, the other in the center of the crease between the 4D and the palm (measures of physical prowess are reliably associated with both the left and right 2D:4D ratio with no difference between hands, so we used dominant hands only for statistical control; Hönekopp & Schuster, 2010). Experimenters then demonstrated how participants should position their hands to be photocopied. Participants were asked to place their dominant hands on the glass without exerting pressure, without hyperextending their fingers, and with all four digits parallel and together. Participants' hands were covered with a blue piece of material to provide contrast between the outline of the hand and the paper. Then, participants were asked to lift their hands off the glass and replace it as described above for a second photocopy. Participants were then debriefed and paid.

Hand photocopies were evaluated by three research assistants independently. The lengths of participants' second and fourth digits were measured in inches to the nearest 16th of an inch and recorded to the fourth decimal place. Digits were measured from the center of the cosmetic pencil dot to the tip of the digit (not including fingernails). A mean of the measurements from the first photocopy and the second photocopy was calculated. The 2D mean of both photocopies was divided by the 4D mean of both photocopies to create a 2D:4D ratio for each participant. Agreement among all three raters' 2D:4D ratio estimates was acceptable: Cronbach's α for the three 2D:4D ratio measurements was 0.94, and the single-measure intraclass correlation coefficient (using a two-way mixed model and an absolute agreement definition) representing agreement among raters was 0.84.

3. Results

3.1. Sex differences

Replicating the well-established sex difference in 2D:4D ratios (e.g., Phelps, 1952), results showed that men had lower

Table 1

Means, standard errors and sex differences in 2D:4D ratios, maximum voluntary contraction scores, log-transformed maximum endurance time scores, age, height, weight, and average digit length

Variable	Females			Males			<i>t</i>	<i>df</i>	<i>p</i>	95% CI		<i>d</i>
	<i>n</i>	Mean	S.E.	<i>n</i>	Mean	S.E.				LL	UL	
2D:4D Ratio	122	0.98	0.0033	100	0.96	0.0032	3.81	220	<.001	0.01	0.03	0.52
Maximum voluntary contraction (kg)	122	22.18	0.53	98	36.97	0.87	-14.45	164	<.001	-16.82	-12.77	2.00
Maximum endurance time 1 ^a	122	2.81	0.05	99	3.00	0.06	-2.39	219	.018	-0.34	-0.03	0.32
Maximum endurance time 2 ^a	121	2.52	0.06	99	2.68	0.07	-1.83	218	.069	-0.34	0.01	0.23
Mean maximum endurance time ^a	122	2.66	0.05	99	2.84	0.06	-2.36	219	.019	-0.33	-0.03	0.32
Age	120	19.33	0.29	97	19.12	0.11	0.65	154	.517	-0.41	0.81	0.09
Height (cm)	108	162.31	0.95	82	177.92	0.96	-11.38	188	<.001	-18.31	-12.90	1.68
Weight (kg)	110	59.36	1.21	82	76.66	1.25	-9.80	190	<.001	-20.78	-13.82	1.44
Average digit length (cm)	122	6.81	0.04	100	7.33	0.42	-8.99	220	<.001	-0.63	-0.40	1.21

CI=Confidence interval; LL=lower limit; UL=upper limit; *d*=standardized mean difference between the sexes (with positive scores indicating larger mean values for men).

^a Log transformed.

2D:4D ratios than did women. Men also had longer mean 2D and 4D lengths than did women. Men on average had higher MVC (kg) scores than did women. The skewness and kurtosis of the first MET (seconds) scores were 1.69 and 1.18, respectively, and the skewness and kurtosis of the second MET scores were 1.18 and 1.46, respectively, so the MET data were transformed via logarithmic transformation to better approximate normal distributions. Men had longer log-transformed MET scores on the first trial and (with marginal statistical significance) on the second trial than did women on the first trial and on the second trial. Men also had higher log-transformed mean MET scores than did women (see Table 1 for means, standard errors and sex differences in 2D:4D ratios, MVC, log-transformed METs, age, height, weight, and average digit length).

3.2. Correlations among dependent variables

MVC scores were not significantly correlated with the first or second trial MET scores, but the first trial MET scores were correlated with the second trial MET scores ($r=0.62, p<.001$). Because the MET scores on the first and second trial were so highly correlated, we used the log-transformed mean of the MET scores on the first and second trial in subsequent analyses.

Table 2

Results of regression of maximum voluntary contraction on sex, 2D:4D ratios, experimenter sex, and their interactions

Variable	<i>B</i>	S.E. <i>B</i>	β	<i>t</i>	<i>p</i>
Constant	21.97	1.01		21.66	<.001
Sex	14.00	1.51	0.68	9.26	<.001
2D:4D Ratio	-15.71	27.00	-0.05	-0.58	.56
Experimenter sex	17.29	36.18	0.83	0.48	.63
Sex*2D:4D Ratio	-105.78	43.81	-0.23	-2.41	.02
Sex*Experimenter sex	-63.72	55.97	-2.66	-1.14	.26
2D:4D Ratio*Experimenter sex	-17.18	37.01	-0.80	-0.46	.64
Sex*2D:4D Ratio*Experimenter sex	65.20	57.91	2.62	1.13	.26

$R^2=0.56, F(7, 212)=37.77, p<.001$.

3.3. Ethnic differences

Of the participants who reported their ethnicity, one participant identified as American Indian or Alaskan Native, 24 participants identified as Asian, none identified as Native Hawaiian or Pacific Islander, 14 identified as Black or African American, 135 identified as White, 20 identified as more than one race, and 23 identified as another race. Although effects of ethnicity on 2D:4D ratios have been reported in the literature (Knickmeyer et al., 2011; Manning, 2002; Manning et al., 2000; Manning, Stewart, Bundred, & Trivers, 2004), we found no differences in the 2D:4D ratios of participants who identified as Asian, Black or African American, White, more than one race, or another race (the American Indian or Alaskan Native group was excluded from this analysis because only one participant identified as American Indian or Alaskan Native) [analysis of variance: $F(4,211)=0.13, p=.97$].

3.4. Effect of experimenter sex

Based on previous evidence that 2D:4D ratios are associated with responses to a laboratory task after exposure to “sex-related cues” (Van den Bergh & Dewitte,

Table 3

Results of regression of log-transformed mean maximum endurance time on sex, 2D:4D ratios, experimenter sex, and their interactions

Variable	<i>B</i>	S.E. <i>B</i>	β	<i>t</i>	<i>p</i>
Constant	2.66	0.08		32.63	<.001
Sex	0.27	0.12	0.24	2.26	.02
2D:4D Ratio	-0.56	2.17	-0.03	-0.26	.80
Experimenter sex	0.63	2.90	0.56	0.22	.83
Sex*2D:4D Ratio	4.81	3.52	0.19	1.37	.17
Sex*Experimenter sex	0.82	4.49	0.62	0.18	.86
2D:4D Ratio*Experimenter sex	-0.63	2.97	-0.54	-0.21	.83
Sex*2D:4D Ratio*Experimenter sex	-0.97	4.65	-0.71	-0.21	.83

$R^2=0.05, F(7,217)=1.62, p=.13$.

2006) and that 2D:4D ratios appear to modify the effects of administered testosterone (van Honk et al., 2011), it is possible that an interaction effect of sex, 2D:4D ratio, and experimenter sex on MVC and MET scores may exist such that men with lower 2D:4D ratios tested by female experimenters exhibited higher MVC or MET scores. However, when we simultaneously regressed our dependent variables (MVC and MET scores) on a dummy-coded variable representing participant sex (0=female; 1=male), a dummy-coded variable representing experimenter sex (0=female; 1=male), a mean-centered measure of 2D:4D ratios (which we computed by removing the sample mean from each participant's 2D:4D ratio), and the product-term interactions that resulted from multiplying these variables, we did not find significant three-way interactions of sex, 2D:4D ratios and experimenter sex on scores (see Tables 2 and 3). Thus, we concluded that lower male 2D:4D ratios were not associated with higher scores after exposure to female experimenters in particular. Thus, experimenter sex was subsequently ignored in further analyses.

3.5. Effect of handedness

Based on evidence that the magnitude of the sex difference in 2D:4D ratios is greater in the right than in the left hand (Hönekopp & Watson, 2010), we simultaneously regressed MVC and MET scores on the dummy-coded variable representing participant sex, the mean-centered measure of 2D:4D ratios, a dummy-coded variable representing handedness (0=right; 1=left), and the product-term interactions that resulted from multiplying these variables. We did not find a significant three-way interaction of sex, handedness and 2D:4D ratios (see Tables 4 and 5), so we analyzed data from both right- and left-handed subjects together.

3.6. Regressing MVC and MET scores on 2D:4D ratios, sex, and the interaction of 2D:4D ratios and sex

We conducted multiple regressions to evaluate whether strength, endurance, or both contribute to the association of 2D:4D ratios with physical prowess in men and women. In each regression, we simultaneously regressed one of two

Table 4

Results of regression of maximum voluntary contraction on sex, 2D:4D ratios, handedness, and their interactions

Variable	<i>B</i>	S.E. <i>B</i>	β	<i>t</i>	<i>p</i>
Constant	22.27	0.71		31.41	<.001
Sex	13.91	1.06	0.68	13.14	<.001
2D:4D Ratio	-28.47	20.16	-0.10	-1.41	.16
Handedness	-1.87	46.64	-0.06	-0.04	.97
Sex*2D:4D Ratio	-74.35	30.92	-0.16	-2.40	.02
Sex*Handedness	-76.25	74.58	-1.71	-1.02	.31
2D:4D Ratio*Handedness	4.04	47.89	0.13	0.08	.93
Sex*2D:4D Ratio*Handedness	74.88	77.20	1.61	0.97	.33

$R^2=0.56$, $F(7,209)=37.42$, $p<.001$.

Table 5

Results of regression of log-transformed mean maximum endurance time on sex, 2D:4D ratios, experimenter sex, and their interactions

Variable	<i>B</i>	S.E. <i>B</i>	β	<i>T</i>	<i>p</i>
Constant	2.69	0.06		46.99	<.001
Sex	0.17	0.09	0.15	2.02	.04
2D:4D Ratio	-1.31	1.63	-0.08	-0.81	.42
Handedness	-2.24	3.77	-1.36	-0.59	.55
Sex*2D:4D Ratio	5.72	2.50	0.22	2.29	.02
Sex*Handedness	10.70	6.02	4.30	1.78	.08
2D:4D Ratio*Handedness	2.18	3.87	1.28	0.56	.57
Sex*2D:4D Ratio*Handedness	-10.77	6.23	-4.16	-1.73	.09

$R^2=0.07$, $F(7, 210)=2.14$, $p=.04$.

dependent variables (MVC and MET scores) on the dummy-coded variable representing participant sex, the mean-centered measure of 2D:4D ratios, and the product-term interaction that resulted from multiplying these two variables.

Jointly, sex, 2D:4D ratios, and their interaction predicted significant variance in MVC scores (see Table 6). Sex and the interaction between sex and 2D:4D ratios were significant predictors of MVC scores, whereas 2D:4D ratios were not a significant predictor of MVC scores (see Table 6). To explore the interaction of sex and 2D:4D ratios on MVC scores, we ran separate univariate regressions of MVC scores on 2D:4D ratios for men and women. 2D:4D ratios were significant predictors of MVC scores for men [$R^2=0.12$, $F(1,97)=13.38$, $p<.001$], but not for women [$R^2=0.02$, $F(1,121)=2.86$, $p=.09$], suggesting that men (but not women) who had had more intrauterine exposure to testosterone were physically stronger than men who had had less intrauterine exposure to testosterone (see Figs. 1 and 2). When age, height, weight, and average digit length were added as predictors of MVC scores, 2D:4D ratios were still a significant predictor of male [$R^2=0.18$, $F(5,73)=3.19$, $p=.01$], and not female [$R^2=0.05$, $F(5,101)=0.97$, $p=.44$], MVC scores, suggesting that age, height, weight, and average digit length do not confound the relationship between 2D:4D ratios and MVC scores.

Jointly, sex, 2D:4D ratios, and their interaction predicted significant variance in MET scores (see Table 7). Even so, whereas sex was a significant predictor of MET scores, neither the 2D:4D ratios nor the interaction of sex and 2D:4D ratios emerged as a statistically significant predictor of MET scores (see Table 7). To illustrate, we ran separate univariate regressions of MET scores on 2D:4D scores for

Table 6

Results of regression of maximum voluntary contraction on sex, 2D:4D ratios, and their interaction

Variable	<i>B</i>	S.E. <i>B</i>	β	<i>t</i>	<i>p</i>
Constant	22.38	0.65		34.64	<.001
Sex	13.67	0.98	0.66	13.97	<.001
2D:4D Ratio	-25.81	18.21	-0.09	-1.42	.158
Sex*2D:4D Ratio	-67.06	28.32	-0.14	-2.37	.019

$R^2=0.55$, $F(3,219)=88.56$, $p<.001$.

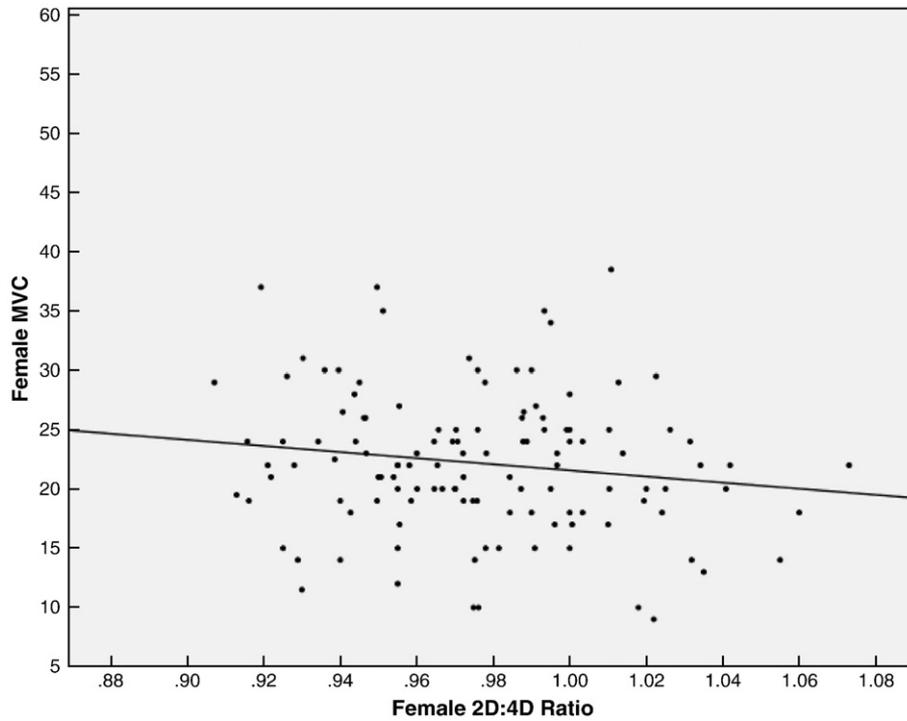


Fig. 1. Relationship between female maximum voluntary contraction scores and 2D:4D ratios.

men and women. 2D:4D ratios were not significant predictors of MET scores for men [$R^2=0.03$, $F(1,97)=3.07$, $p=.08$] or for women [$R^2<0.01$, $F(1,120)=0.45$, $p=.50$], suggesting that neither men nor women who had had more intrauterine exposure to testosterone exhibited greater

local muscular endurance than men or women who had had less intrauterine exposure to testosterone (see Figs. 3 and 4). When age, height, weight, and average digit length were added as predictors of MET scores, 2D:4D ratios were still not a significant predictor of male [$R^2=0.34$,

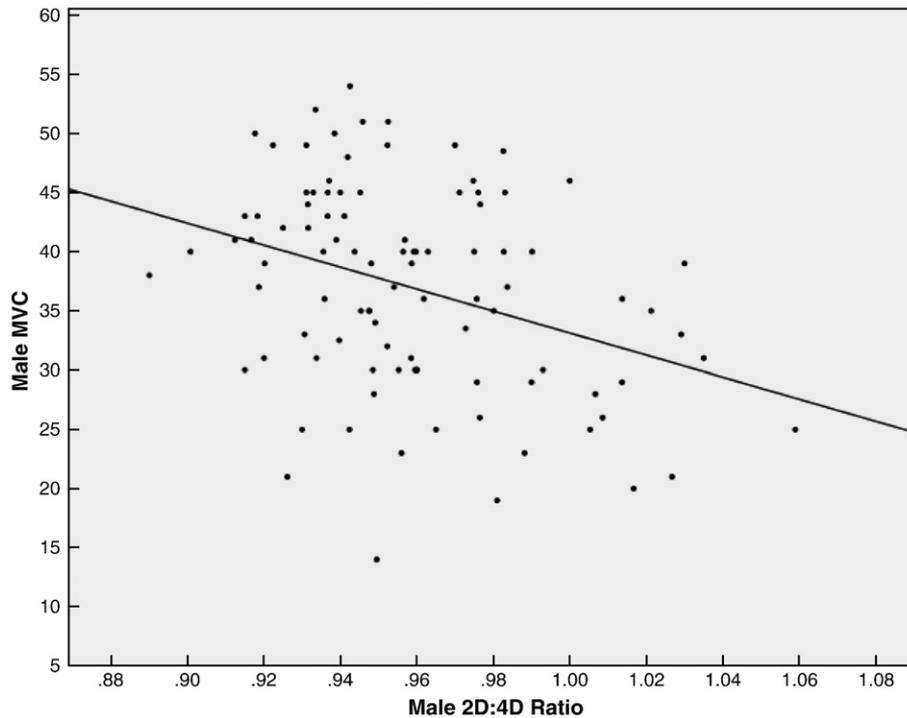


Fig. 2. Relationship between male maximum voluntary contraction scores and 2D:4D ratios.

Table 7

Results of regression of log-transformed mean maximum endurance time on sex, 2D:4D ratios, and their interaction

Variable	<i>B</i>	S.E. <i>B</i>	β	<i>t</i>	<i>p</i>
Constant	2.67	0.05		51.57	<.001
Sex	0.20	0.08	0.18	2.60	.01
2D:4D Ratio	-0.92	1.46	-0.06	-0.63	.528
Sex*2D:4D Ratio	4.18	2.27	0.16	1.84	.067

$R^2=0.04$, $F(3,220)=3.17$, $p=.03$.

$F(5,74)=1.98$, $p=.09$] or female [$R^2=0.05$, $F(5,101)=1.09$, $p=.37$] MET scores.

4. Discussion

Our data support the hypothesis that prenatal exposure to testosterone, as measured by 2D:4D ratios, influences a sexually dimorphic, performance-based measure of hand grip strength (as measured by MVC scores) for men, but not for women. Specifically, 2D:4D ratios were negatively associated with men's MVC scores, but not women's. Our data do not support the hypothesis that prenatal exposure to testosterone (measured by 2D:4D ratios) influences men's or women's local muscular endurance (as measured by MET scores at 70% of participants' MVC scores). We conclude on this basis that it is strength, rather than local muscular endurance (as measured by hand dynamometer), that is

responsible for the relationships between 2D:4D ratios and physical prowess that have been uncovered in previous research (Hönekopp & Schuster, 2010). We conclude furthermore that the association of prenatal exposure to testosterone (as indexed by 2D:4D ratios) and strength pertains only to men, and not to women. Importantly, the statistical associations we discovered here were obtained even when controlling for age, height, weight, and average digit length, which suggests that it may be prenatal exposure to testosterone per se, rather than other common strength-related variables with which it might be vulnerable to confounding, that is responsible for the associations we found here.

Our results, and our interpretations of them, come with three caveats. First, with respect to our method for assessing local muscular endurance, participants were asked to perform two MET trials soon after the MVC trial. It is possible that an association of 2D:4D with local muscular endurance might have been uncovered had we had allowed a longer amount of time to elapse between the estimation of MVC scores and the estimation of MET scores. Second, it is worth pointing out that our research evaluated hand grip-based measures of strength and local muscular endurance, so our conclusions might not pertain to measures of strength and endurance obtained with other muscle groups, or to other forms of endurance (e.g., cardio-respiratory endurance, as in Hönekopp & Schuster, 2010). Third, our sample was limited to university students. In the future, it would be useful to examine these associations in other groups of participants.

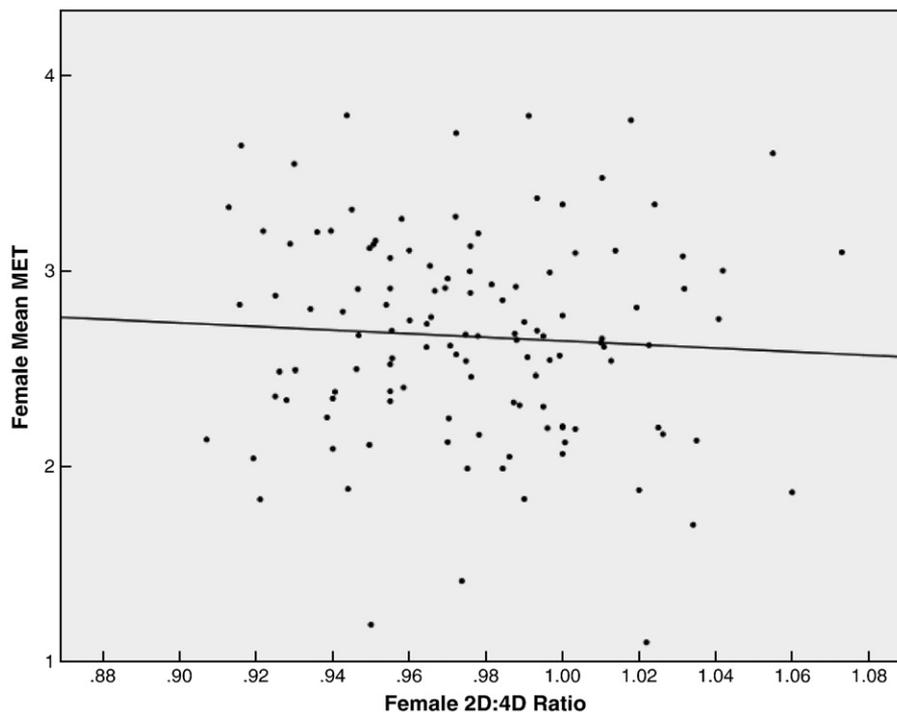


Fig. 3. Relationship between female log-transformed mean maximum endurance time scores and 2D:4D ratios.

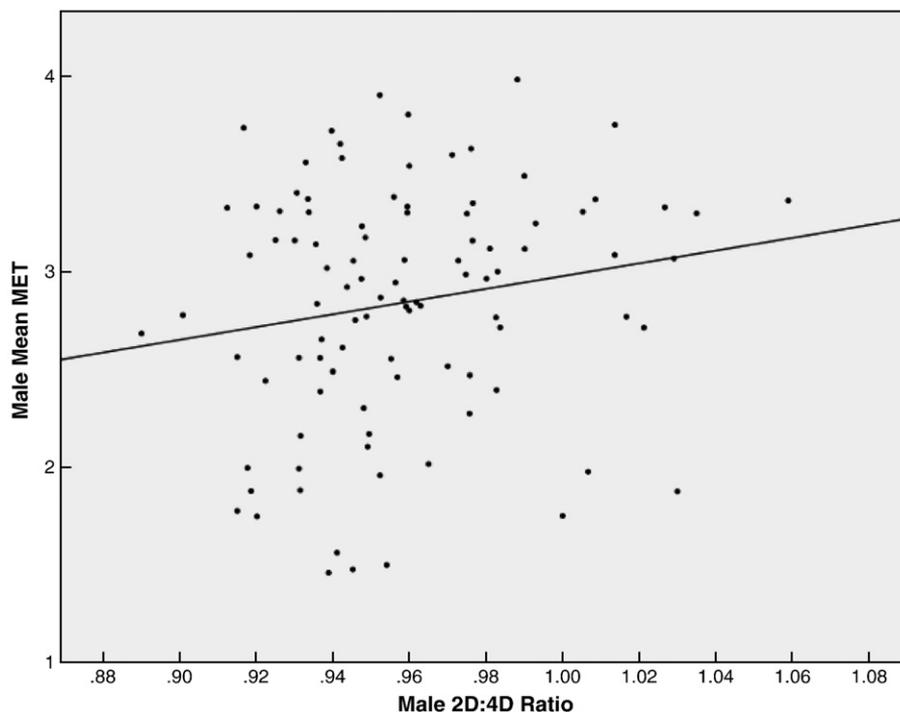


Fig. 4. Relationship between male log-transformed mean maximum endurance time scores and 2D:4D ratios.

Sexual selection leads to cognitive and physiological adaptations that are well designed for promoting success in both intrasexual and intersexual competition (e.g., Bateman, 1948; Buss & Schmitt, 1993; Geary, 2006; Geary, 2010). Physical prowess is, no doubt, part of this evolutionary heritage, because men with high degrees of strength at their disposal are better able to compete with other men for reproductive access to females and for control of the resources females require for effective parental care (Geary, 2010; Sell, Tooby, & Cosmides, 2009). Clarifying results from previous work (Hönekopp & Schuster, 2010), our findings suggest that prenatal exposure to testosterone is part of the proximate physiology that generates these male-specific adaptations in men (but not in women) by way of its organizational effects on males (but not on females) during intrauterine development — and that it does so by increasing not men's local muscular endurance, but rather, their strength per se.

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References

- Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, 2, 349–368. Retrieved from <http://www4.nau.edu/shustercourses/BIO%20698/Literature/Bateman1948.pdf>.
- Berenbaum, S. A., & Beltz, A. M. (2011). Sexual differentiation of human behavior: effects of prenatal and pubertal organizational hormones. *Frontiers in Neuroendocrinology*, 32, 183–200. <http://dx.doi.org/10.1016/j.yfrne.2011.03.001> Elsevier Inc.
- Berenbaum, S. A., Bryk, K. K., Nowak, N., Quigley, C. A., & Moffat, S. (2009). Fingers as a marker of prenatal androgen exposure. *Endocrinology*, 150(11), 5119–5124. <http://dx.doi.org/10.1210/en.2009-0774>.
- Bohannon, R. W. (1998). Hand-grip dynamometry provides a valid indication of upper extremity strength impairment in home care patients. *Journal of Hand Therapy*, 11, 258–260. [http://dx.doi.org/10.1016/S0894-1130\(98\)80021-5](http://dx.doi.org/10.1016/S0894-1130(98)80021-5) Hanley & Belfus, Inc.
- Bohannon, R. W. (2004). Adequacy of hand-grip dynamometry for characterizing upper limb strength after stroke. *Isokinetics and Exercise Science*, 12, 263–265.
- 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. <http://dx.doi.org/10.1006/hbeh.2002.1830>.
- 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(5), 976–979. <http://dx.doi.org/10.1093/humrep/deg198>.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: an evolutionary perspective of human mating. *Psychological Review*, 100(2), 204–232.
- Butovskaya, M. L., Vasilyev, V. A., Lazebny, O. E., Burkova, V. N., Kulikov, A. M., Mabulla, A., Shibalev, D. V., & Ryskov, A. P. (2012). Aggression, digit ratio, and variation in the androgen receptor, serotonin transporter, and dopamine D4 receptor genes in African foragers: the Hadza. *Behavior Genetics*, 647–662. <http://dx.doi.org/10.1007/s10519-012-9533-2>.
- Chamberlain, N. L., Driver, E. D., & Miesfeld, R. L. (1994). The length and location of CAG trinucleotide repeats in the androgen receptor N-terminal domain affect transactivation function. *Nucleic Acids Research*, 22(15), 3181–3186. Retrieved from <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=310294&tool=pmcentrez&rendertype=abstract>.

- Clarnette, T. D., Sugita, Y., & Hutson, J. M. (1997). Genital anomalies in human and animal models reveal the mechanisms and hormones governing testicular descent. *British Journal of Urology*, *79*(1), 99–12. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9043507>.
- Cousins, A. J., Fugère, M. A., & Franklin, M. (2009). Digit ratio (2D:4D), mate guarding, and physical aggression in dating couples. *Personality and Individual Differences*, *46*, 709–713, <http://dx.doi.org/10.1016/j.paid.2009.01.029> Elsevier Ltd.
- Fink, B., Neave, N., Laughton, K., & Manning, J. T. (2006). Second to fourth digit ratio and sensation seeking. *Personality and Individual Differences*, *41*, 1253–1262, <http://dx.doi.org/10.1016/j.paid.2006.05.002>.
- Fink, B., Thanzami, V., Seydel, H., & Manning, J. T. (2006). Digit ratio and hand-grip strength in German and Mizos men: cross-cultural evidence for an organizing effect of prenatal testosterone on strength. *American Journal of Human Biology*, *18*, 776–782. <http://onlinelibrary.wiley.com/doi/10.1002/ajhb.20549/pdf>.
- Gallup, A. C., White, D. D., & Gallup, G. G. (2007). Handgrip strength predicts sexual behavior, body morphology, and aggression in male college students. *Evolution and Human Behavior*, *28*(6), 423–429, <http://dx.doi.org/10.1016/j.evolhumbehav.2007.07.001>.
- Geary, D. C. (2006). Sexual selection and the evolution of human sex differences. *Psychological Topics*, *15*(2), 203–238.
- Geary, D. C. (2010). *Male, female: The evolution of human sex differences* (2nd ed.). Washington, DC: American Psychological Association.
- Hampson, E., & Sankar, J. S. (2012). Re-examining the Manning hypothesis: androgen receptor polymorphism and the 2D:4D digit ratio. *Evolution and Human Behavior*, in press, <http://dx.doi.org/10.1016/j.evolhumbehav.2012.02.003> Elsevier Inc.
- Hönekopp, J., Bartholdt, L., Beier, L., & Liebert, A. (2007). Second to fourth digit length ratio (2D:4D) and adult sex hormone levels: new data and a meta-analytic review. *Psychoneuroendocrinology*, *32*(4), 313–321, <http://dx.doi.org/10.1016/j.psyneuen.2007.01.007>.
- Hönekopp, J., & Schuster, M. (2010). A meta-analysis on 2D:4D and athletic prowess: substantial relationships but neither hand out-predicts the other. *Personality and Individual Differences*, *48*, 4–0, <http://dx.doi.org/10.1016/j.paid.2009.08.009> Elsevier Ltd.
- Hönekopp, J., Voracek, M., & Manning, J. T. (2006). 2nd to 4th digit ratio (2D:4D) and number of sex partners: evidence for effects of prenatal testosterone in men. *Psychoneuroendocrinology*, *31*, 30–37, <http://dx.doi.org/10.1016/j.psyneuen.2005.05.009>.
- Hönekopp, J., & Watson, S. (2010). Meta-analysis of digit ratio 2D:4D shows greater sex difference in the right hand. *American Journal of Human Biology*, *22*(5), 619–630, <http://dx.doi.org/10.1002/ajhb.21054>.
- Hurd, P. L., Vaillancourt, K. L., & Dinsdale, N. L. (2011). Aggression, digit ratio and variation in androgen receptor and monoamine oxidase A genes in men. *Behavior Genetics*, *41*(4), 543–556, <http://dx.doi.org/10.1007/s10519-010-9404-7>.
- Knickmeyer, R. C., Woolson, S., Hamer, R. M., Konneker, T., & Gilmore, J. (2011). 2D:4D ratios in the first 2 years of life: stability and relation to testosterone exposure and sensitivity. *Hormones and Behavior*, *60*(3), 256–263, <http://dx.doi.org/10.1016/j.yhbeh.2011.05.009> Elsevier Inc.
- Li, K., Hewson, D. J., Duchêne, J., & Hogrel, J. -Y. (2010). Predicting maximal grip strength using hand circumference. *Manual Therapy*, *15*, 579–585, <http://dx.doi.org/10.1016/j.math.2010.06.010>.
- Little, M. A., & Johnson, B. R. (1986). Grip strength, muscle fatigue, and body composition in nomadic Turkana pastoralists. *American Journal of Physical Anthropology*, *69*, 335–344, <http://dx.doi.org/10.1002/ajpa.1330690306>.
- Loehlin, J. C., Medland, S. E., & Martin, N. G. (2012). Is CAG sequence length in the androgen receptor gene correlated with finger-length ratio? *Personality and Individual Differences*, *52*(2), 224–227, <http://dx.doi.org/10.1016/j.paid.2011.09.009> Elsevier Ltd.
- Lutchmaya, S., Baron-Cohen, S., Raggatt, P., Knickmeyer, R., & Manning, J. (2004). 2nd to 4th digit ratios, fetal testosterone and estradiol. *Early Human Development*, *77*, 23–28, <http://dx.doi.org/10.1016/j.earlhumdev.2003.12.002>.
- Macdermid, J. C., Fehr, L., & Lindsay, K. (2002). The effect of physical factors on grip strength and dexterity. *British Journal of Hand Therapy*, *7*(4), 112–118.
- Manning, J. T. (2002). *Digit ratio: A pointer to fertility, behavior, and health*. New Brunswick: Rutgers University Press.
- Manning, J. T. (2011). Resolving the role of prenatal sex steroids in the development of digit ratio. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(39), 16143–16144, <http://dx.doi.org/10.1073/pnas.1113312108>.
- Manning, J. T., Barley, L., Walton, J., Lewis-Jones, D. I., Trivers, R. I., & Singh, D., et al. (2000). The 2nd:4th digit ratio, sexual dimorphism, population differences, and reproductive success. Evidence for sexually antagonistic genes? *Hormones and Behavior*, *21*(3), 163–183. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10828555>.
- Manning, J. T., Bundred, P. E., Newton, D. J., & Flanagan, B. F. (2003). The second to fourth digit ratio and variation in the androgen receptor gene. *Evolution and Human Behavior*, *24*, 399–405, [http://dx.doi.org/10.1016/S1090-5138\(03\)00052-7](http://dx.doi.org/10.1016/S1090-5138(03)00052-7).
- 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 (Oxford, England)*, *13*(11), 3000–3004. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9853845>.
- Manning, J. T., Stewart, A., Bundred, P. E., & Trivers, R. L. (2004). Sex and ethnic differences in 2nd to 4th digit ratio of children. *Early Human Development*, *80*(2), 161–168, <http://dx.doi.org/10.1016/j.earlhumdev.2004.06.004>.
- McIntyre, M. H., Ellison, P. T., Lieberman, D. E., Demerath, E., & Towne, B. (2005). The development of sex differences in digital formula from infancy in the Fels Longitudinal Study. *Proceedings of the Royal Society B*, *272*, 1473–1479, <http://dx.doi.org/10.1098/rspb.2005.3100>.
- Medland, S. E., Loehlin, J. C., & Martin, N. G. (2008). No effects of prenatal hormone transfer on digit ratio in a large sample of same- and opposite-sex dizygotic twins. *Personality and Individual Differences*, *44*(5), 1225–1234, <http://dx.doi.org/10.1016/j.paid.2007.11.017>.
- Migeon, C. J., & Wisniewski, A. B. (1998). Sexual differentiation: From genes to gender. *Hormone Research*, *50*, 245–251.
- Neave, N., Laing, S., Fink, B., & Manning, J. T. (2003). Second to fourth digit ratio, testosterone and perceived male dominance. *Proceedings Biological Sciences/The Royal Society*, *270*, 2167–2172, <http://dx.doi.org/10.1098/rspb.2003.2502>.
- Ökten, A., Kalyoncu, M., & Yariş, 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. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12441204>.
- Peters, M., Mackenzie, K., & Bryden, P. (2002). Finger length and distal finger extent patterns in humans. *American Journal of Physical Anthropology*, *117*, 209–217, <http://dx.doi.org/10.1002/ajpa.10029>.
- Phelps, V. R. (1952). Relative index finger length as a sex-influenced trait in man. *American Journal of Human Genetics*, *4*, 72–89. Retrieved from <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1716436&tool=pmcentrez&rendertype=abstract>.
- Sell, A., Tooby, J., & Cosmides, L. (2009). Formidability and the logic of human anger. *Proceedings of the National Academy of Sciences*, *106*(35), 15073–15078, <http://dx.doi.org/10.1073/pnas.0904312106>.
- Talarovicová, A., Krsková, L., & Blazeková, J. (2009). Testosterone enhancement during pregnancy influences the 2D:4D ratio and open field motor activity of rat siblings in adulthood. *Hormones and Behavior*, *55*(1), 235–239, <http://dx.doi.org/10.1016/j.yhbeh.2008.10.010> Elsevier Inc.
- van Anders, S. M. (2007). Grip strength and digit ratios are not correlated in women. *American Journal of Human Biology*, *19*, 437–439, <http://dx.doi.org/10.1002/ajhb>.
- van Anders, S. M., Vernon, P. A., & Wilbur, C. J. (2006). Finger-length ratios show evidence of prenatal hormone-transfer between opposite-sex twins. *Hormones and Behavior*, *49*, 315–319, <http://dx.doi.org/10.1016/j.yhbeh.2005.08.003>.

- Van den Bergh, B., & Dewitte, S. (2006). Digit ratio (2D:4D) moderates the impact of sexual cues on men's decisions in ultimatum games. *Proceedings of the Royal Society B*, 273(1597), 2091–2095, <http://dx.doi.org/10.1098/rspb.2006.3550>.
- van Honk, J., Schutter, D. J., Bos, P. A., Kruijt, A. -W., Lentjes, E. G., & Baron-Cohen, S. (2011). Testosterone administration impairs cognitive empathy in women depending on second-to-fourth digit ratio. *Proceedings of the National Academy of Sciences of the United States of America*, 108(8), 3448–3452, <http://dx.doi.org/10.1073/pnas.10118911108>.
- Zheng, Z., & Cohn, M. J. (2011). Developmental basis of sexually dimorphic digit ratios. *Proceedings of the National Academy of Sciences of the United States of America*, 108(39), 16289–16294, <http://dx.doi.org/10.1073/pnas.1108312108>.