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Digit length ratios predict reactive aggression in women, but not in men

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Abstract

Considerable evidence suggests that digit length and dermatoglyphic asymmetry patterns in the hand are affected by early exposure to androgens. Because androgens play an important role in sexual differentiation of morphological and behavioral traits, digit length patterns often display sex differences. When present, sex differences in digit lengths are more pronounced on the right side as compared to the left side. Moreover, the ratio of the second to fourth digit length (2D:4D) in the right hand is inversely correlated with testosterone (T) in men. Because T is implicated in agonistic behavior, 2D:4D may be used as a marker of androgen exposure and subsequent behavioral variation in adulthood. Consequently, we investigated the relationships among 2D:4D, directional asymmetry of 2D:4D (left hand 2D:4D minus right hand 2D:4D) as a variant of T, and human reactive aggression. One hundred young men (n = 51) and women (n = 49) participated in our experiments (mean age = 20.1 years). Participants called two noncompliant confederates to solicit donations for a fictitious charity organization and selected follow-up letters after the calls. The force exerted when hanging up the phone and the "tone" of the follow-up letters were used to assess reactive aggression. High aggression scores were associated with high directional asymmetry of 2D:4D and masculinized (low) right hand 2D:4D, only in females and under high provocation. Directional asymmetry of 2D:4D was positively correlated with T in males (pooled data, n = 97). Taken together, these data confirm the predominantly right-sided influence of androgens on digit length and suggest that digit length ratios may be associated with female reactive aggression when sufficient provocation is present.
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Keywords: 2D:4D; Digit length ratio; Directional asymmetry; Lateralization; Aggression; Anger; Provocation; Androgens; Testosterone; Sex differences

Introduction

The disproportionate length of human fingers has generated much interest among researchers. The lengths of the second digit (2D) and fourth digit (4D) have received the greatest attention, because of the noted sex differences (reviewed in Peters et al., 2002). The distal extent of 4D with respect to the middle finger is relatively greater than that of 2D in most males, whereas the pattern remains unspecified in females (Peters et al., 2002). The sex differences have generally been tested by expressing the pattern as 2D to 4D ratio (2D:4D). According to this formulation, males have lower 2D:4D compared to females in most populations (Manning et al., 2000a, Manning et al., 1998; Peters et al., 2002), whereas no sex difference has been reported in others (reviewed in Manning, 2002). Curiously, when sex differences are noted, they are generally larger for the right hand than the left in humans (McFadden and Shubel, 2002; Williams et al., 2000) and baboons (McFadden and Bracht, 2003). Right-rear paws in mice are also sexually dimorphic with lower 2D:4D in males compared to females (Brown et al., 2002a). Prenatal androgens may play a role in digit length patterns because most mammalian sex differences are androgen dependent (Brown et al., 2002a,c), and digit length rankings and bone-to-bone proportions during human embryonic and fetal development are comparable to those in adulthood (Garn et al., 1975). Furthermore, studies with rodents have indicated that the neuroanatomical asymmetries favoring the right-

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hand side are generally observed in males and can be largely attributed to the action of the sex steroid hormone, testosterone (T) (reviewed in Wisniewski, 1998). The timing of 2D:4D differentiation, presumably as a result of androgen exposure, remains inconclusive. In one study, adult T was negatively correlated with 2D:4D in the right hand (cf. Manning et al., 1998), suggesting that T can have activational effects on the 2D:4D relationship.

A variety of behaviors that are either sexually dimorphic or ascribed to the actions of sex steroids also correlate with 2D:4D (reviewed in Manning, 2002). For example, significant associations have been reported between 2D:4D and sexual orientation and/or preference (Brown et al., 2002b; Lippa, 2003; Rahman and Wilson, 2003; Robinson and Manning, 2000; Williams et al., 2000), lateralization of hand performance (Manning et al., 2000b), and autism (Manning et al., 2001). Furthermore, low (masculinized) 2D:4D is linked to hyperactivity in girls (Williams et al., 2003), spatial navigation skills (Csatho et al., 2001), sensation seeking, and lack of inhibitions in adult women (Austin et al., 2002). Aggressive behavior is relevant to 2D:4D research, because it is sexually dimorphic. In a variety of species, including humans, males are typically more overtly aggressive than females (van Goozen et al., 1995). Sex differences in agonistic behavior are largely attributed to the actions of sex steroids, especially those of T. To our knowledge, however, no previous studies have reported any associations between 2D:4D and aggression. Accordingly, we examined the relationship between digit length ratio and human reactive aggression. Reactive aggression was operationally defined as an angry-like response to frustration (goal blocking), provocation, or threat (Berkowitz, 1989). We hypothesized that low 2D:4D, especially in the right hand would be positively correlated with aggression. Lateralization of 2D:4D was also tested through its association with adult T. Specifically, we predicted an asymmetrical influence of adult T concentrations on the right and left hand digit ratios as previously suggested (Brown et al., 2002a,b), as well as a significant association between lateralization of 2D:4D and aggression.

Materials and methods

Study sample

Participants were part of a larger study that investigated the associations among nondirectional variations from perfect symmetry in bilateral morphological traits, testosterone, and aggression. One hundred (49 female, 51 male; mean age = 20.1 years) college students at the Ohio State University participated for course credit. The results of this experiment have been reported elsewhere (Benderlioglu et al., 2004). Here, new indices were constructed with the second and fourth digit lengths, and, T, age, handedness, height, and weight were used as control variables for further analyses. The associations among digit length indices and aggression have not been previously reported.

Experiments

In Phase I of the study, participants were informed that they were part of a research project that investigated the effects of circulating hormones on behavior and on tissue components of the body. The second and fourth digit lengths were measured to the nearest 0.01 mm with a digital caliper on the ventral surface of the hand from the basal crease of the digits to the tip. Each participant was measured twice. Injuries were noted, and broken digits or digits with injuries that occurred within the past 6 months were omitted. A mixed model two-way ANOVA (side × individual) with repeated measurements on each side showed negligible measurement error, that is, between-side variance was greater than the error (2nd digit $F_{[1,99]} = 5.51$, $P < 0.0001$; 4th digit $F_{[1,99]} = 9.48$, $P < 0.0001$). The two measurements were then averaged to construct digit length ratios and directional asymmetries.

2D:4D

The digit ratio was obtained by dividing the second digit length to that of the fourth in the right (R2D:4D) and left (L2D:4D) hands (Manning et al., 1998).

Directional asymmetry of the digit ratios

A separate directional assymetry (DA) index to express lateralization of the R2D:4D and L2D:4D was also prepared by subtracting L2D:4D from R2D:4D (Brown et al., 2002a; Rahman and Wilson, 2003). According to this index, positive values of DA would indicate a more male typical, low 2D:4D in the right hand compared to the left hand. Negative values of DA would in turn display the opposite pattern.

Handedness

Participants completed a slightly revised version of the "Waterloo Handedness Questionnaire-Revised" (WHQ-R) (Elias et al., 1998) that excluded open-ended questions. Accordingly, questions on hand preference consisted of 38 scaled items to assess self-reported hand preference and performance. Responses of (a) left always, (b) left usually, (c) equal, (d) right usually, (e) right always were scored from −2 to 2, with equal being scored as 0.

Testosterone (T)

Upon completion of the questionnaires and digit measurements, saliva samples were collected from consenting participants. Salivary measurements offer advantages for behavioral research because they are noninvasive. Salivary

testosterone represents a biologically active fraction (free) of testosterone. Participants were instructed to rinse their mouth with water 15–20 min before collection. We collected 5–7 ml saliva in a polyethylene tube from participants chewing sugar free bubblegum, which has no cross reactivity with free T radioimmunoassay (RIA) (Dabbs, 1991). Samples were frozen at −80°C until assayed. All samples were analyzed in a single RIA using a Coat-A-Count kit for Total Testosterone (Diagnostics Products, Los Angeles, CA). All T samples were collected between 10:30 and 17:30 to control generally for diurnal variation in T. This time period is consistent with the significantly lower variability in T concentrations compared to those in the early morning and late evening (Dabbs, 1990; Diver et al., 2003). We also introduced the time of the day as a factor in the statistical analyses to further test whether sample collection time had a significant effect on the dependent measures. The results were not significant (P's > 0.05).

Other variables

Data on sex, age, height, and weight of the participants were also collected during the study.

Aggression measures

The details of the experimental conditions and aggression measures have been previously reported (Benderlioglu et al., 2004). Briefly, participants were invited to join the second phase of the study that purported to measure persuasive ability. In this phase, they were asked to raise money for a fictitious charity organization. The participants were informed about a relationship between the pitch of the voice and persuasive ability. Both male and females were led to believe that they scored high in T which lowers the pitch of the voice hence they should be able to convey messages more assertively. Also, they were promised two free tickets to a local movie theater if they were able to obtain any donations. Participants called two male confederates, who both refused to donate.

The confederates were uninformed about the conditions of the experiment. The first calls were placed under 'low provocation' conditions where the first confederate appeared to be amenable to charity donations. He did not challenge the caller and declared to be persuaded by the worthiness of the donation. However, he cited lack of money as a reason not to contribute. The second calls were placed under 'high provocation' conditions where the second confederate was confrontational; he challenged the caller and the worthiness of the donation.

The force applied when hanging up the telephone was an indicator of aggression. Force was measured by a balance plate (Bertec Co., Columbus, OH) built into the desk where the participants placed the calls. Participants were alone when they placed and terminated the calls. Therefore, the force measured served as a reliable indicator of emotional arousal because of "minimal sanctions against slamming it" (Kulik and Brown, 1979).

After these two unsuccessful calls, the participants were asked to send prepared follow-up letters to the confederates on behalf of the fictitious charity organization. They were told that no identification, such as name and signature should be included. They made the choice of cover letters in a discreet manner so that the experimenter was not aware of which letters were chosen. The tone of the letters carried three main themes. The first had a self-effacing tone, that is, apologizing for "the imposition on your time." The second was assertive, but neither self-effacing nor outwardly aggressive ". . .at a time when assistance is critical, rejection is often received." The third was outwardly aggressive "you are performing a disservice to the community." (Kulik and Brown, 1979). The letters were coded as 0, 1, and 2 to reflect aggression scores. The experimental conditions involving the charity organization, follow-up letters, and balance plate were adapted from a previous study (Kulik and Brown, 1979).

After choosing the letters, a second saliva sample was collected. Participants were subsequently debriefed and the real purpose of the study was revealed, including all conditions involving deception. Debriefings indicated that none of the subjects was aware of the real conditions of the study and none had suspected the authenticity of the charity organization. An independent judge, who was uninformed about the experimental hypotheses or conditions, evaluated taped conversations between the participants and confederates. In her evaluation, most participants were rated as "frustrated/upset" or "angry" after the calls in an overall assessment. This assessment was based on such cues as "slamming down the phone", use of profanity, and other emotionally charged words and sentences.

Statistical analyses

All statistical analyses were performed with standard statistical software, SAS version 8.2 (SAS Institute, NC). Weight, height, age, handedness, and saliva testosterone measurements served as control variables, where appropriate. Accordingly, the reported correlation coefficients depict relationships between dependent and main exploratory variables, whereas the effect of the controls has been partialled out (i.e., partial r). It should also be noted that DA, R2D:4D, L2D:4D, and aggression associations were investigated while T was held constant. Because of the previously reported significant relationship between 2D:4D and adult free T (i.e., Manning et al., 1998), a dependency between predictor variables may occur, leading to multicollinearity. However, our previous study (Benderlioglu et al., 2004) upon which the current analyses are based found a significant correlation between high reactive aggression and high T in both males and females. Digit ratios largely tap a presumable organizational effect of early androgen exposure that permanently alters morphology and neural organization

of the brain. In contrast, adult free T concentrations are more likely to tap an activational effect of sex steroids on behavior that is temporary. Because there is no evidence linking prenatal T to adult T in humans, inclusion of these two variables in the same analyses is appropriate and unlikely to result in multicollinearity. Preliminary analyses pertaining to the current sample also yielded no significant correlations between digit ratios and T in neither males nor females (P's > 0.05). Furthermore, tests of multicollinearity showed no significant signs of dependency of the parameters (VIFs < 1.4).

Results

A one-way repeated-measures ANOVA with phase of the experiment as the single factor showed a nonsignificant decrease in T after frustration both for males and females (P's > 0.05). Therefore, we performed our analyses on T samples obtained in the neutral condition (Phase I).

Sex differences in digit lengths

A two-way ANOVA with sex between subject and side within subject factors showed no sex differences in digit ratios for either side of the hand (P's > 0.05).

Digit ratios and T

There were no significant correlations between T and digit ratios (P's > 0.05). These nonsignificant results may be due to our small sample size. To raise the power of our analyses, we pooled our sample with a previous study (Benderlioglu and Nelson, 2004). The experimental protocol involving the digit length measurements and collection of saliva samples was exactly the same as that of the Phase I experiment in the current study. Similarly, this second study population consisted of young college students of comparable age (Avr Age: 20.47; SEM: 0.14; N = 174). The pooling resulted in a sample of 97 males and 77 females that covered all available data on digit lengths and T. The new analyses, which have not been previously reported elsewhere, yielded significant results only for males. Specifically, high T concentrations were associated with increased DA in males (Beta = 0.21, P = 0.0451, age, height controlled). (Fig. 1). That is, R2D:4D displayed a more masculinized pattern compared to L2D:4D with increasing T concentrations.

Digit length ratios and aggression

Multiple regression analyses showed that DA in females was significantly associated with reactive aggression in the high provocation condition as measured by force (Beta = 0.50; P = 0.0060, age, weight, T, handedness controlled). (Fig. 2). The overall aggression model was also significant (P = 0.0117, R^2 = 20.4). In addition, masculinized, low R2D:4D was correlated with high reactive aggression as measured by letters in females under high provocation (Beta = −0.46; P = 0.0045; T, age controlled). A closer investigation of the relationship between R2D:4D and verbal aggression in Fig. 3 revealed potential influential cases, however. That is, three females with the lowest R2D:4D were also among those with the highest verbal aggression scores. We therefore excluded these females from our analyses. The results remained statistically significant (Beta = −0.40, P = 0.0114). We also validated these results with Grubbs' (1969) test for the three female potential outliers. Grubb's test confirmed our findings that neither these data points nor any others were influential in the analyses (P > 0.05).

Discussion

The current study investigated the associations among digit length ratios and aggression in young human adults. We also examined whether adult T concentrations are

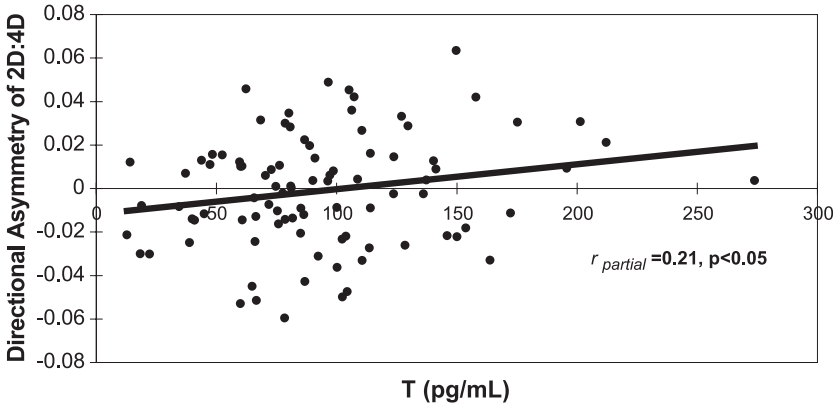

Fig. 1. Testosterone and male digit length ratios. Directional asymmetry (DA) of 2D:4D increased along with T concentrations only in males in the pooled sample (Benderlioglu and Nelson, 2004) (the effects of height and age have been partialled out).

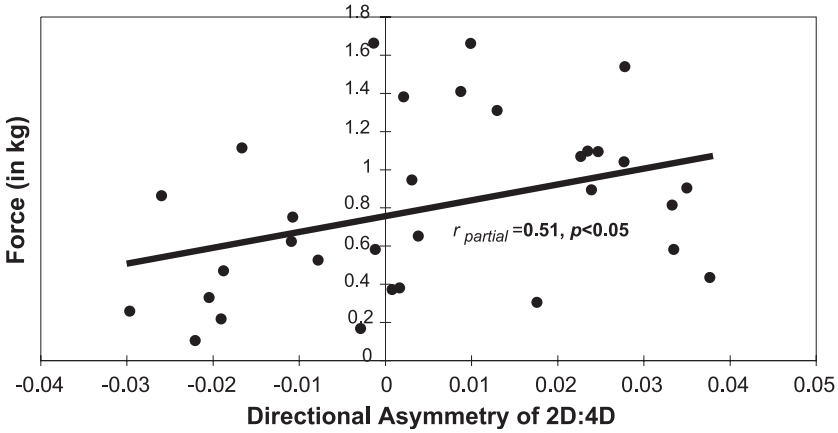

Fig. 2. Digit ratio and female reactive aggression as measured by force. In females, high aggression scores were associated with typical male (lower) 2D:4D in the right hand compared to the left under high provocation.

related to lateralization of 2D:4D. Our results indicate that male directional asymmetry (DA) increased as T concentrations increased confirming the predominantly right side effect of T on digit lengths.

The positive correlation between T and DA in the current study and previously reported relationship between T and masculinized R2D:4D in males (Manning et al., 1998) suggested that digit ratios could be used as a proxy to test the behavioral outcome of possessing a male-typical digit pattern in females. There is considerable evidence suggesting that prenatal T in typical (Hines et al., 2002) and clinical (Berenbaum and Hines, 1992; Dittmann et al., 1990; Ehrhardt and Baker, 1974; Ehrhardt et al., 1968; Fane et al., 2001; Slijper, 1984) populations is associated with masculinized and/or defeminized behavior in females. In contrast, previous studies of men produced inconsistent results. Males who had been prenatally exposed to high concentrations of androgens either do not generally differ from other males in sex-typical behavior (Collaer and Hines, 1995; Hines et al., 2002), display less male-typical (Hines and Kaufman, 1994; Slijper, 1984), or more masculinized childhood behavior (Ehrhardt and Baker, 1974). In contrast to these findings on men, our results confirmed and extended the previous studies on women and showed significant associations among male-typical digit length ratios and reactive aggression only in women. Specifically, high aggression scores as measured by force were associated with typical male (lower) 2D:4D in the right hand compared to the left in highly provoked females. Also, masculinized, low 2D:4D in the right hand was correlated with high reactive aggression as measured by letters under high provocation, again, only in females. These results suggest that male-typical morphology in certain characters in women may be associated with elevated anger arousal. The degree to which a character is masculinized, and its differential effects on behavior require further investigation for males; for example, the source of circulating androgens during ontogeny and adulthood varies according to sex. The lack of significant association in males may also represent a “ceiling effect”. Because males are exposed

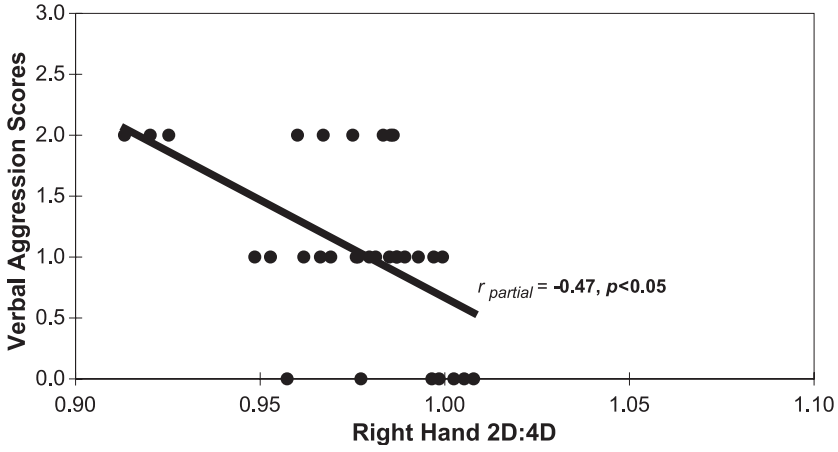

Fig. 3. Digit ratio and female reactive aggression as measured by letters. In females, masculinized, low 2D:4D in the right hand was correlated with high reactive aggression as measured by letters under high provocation.

to higher concentrations of prenatal androgens than females, hormonal variability in males during ontogeny exists against a background of high T (Hines et al., 2002). Therefore, all males might have received sufficient androgens to elicit aggression in a more uniform manner compared to females and independent measures were not able to detect individual variation in male reactive aggression. Comparative longitudinal studies with animals where exogenous androgen exposure can be manipulated, and with clinical samples where endogenous androgen concentrations markedly differ from those of typical populations may help understand the null effect of masculinized 2D:4D on aggression in males.

Variation in digit length ratios and patterns is generally attributed to prenatal androgen exposure (Brown et al., 2002a,b; Manning, 2002; Manning et al., 1998). An "experiment of nature" provides support for this hypothesis. Females with congenital adrenal hyperplasia (CAH) display more masculinized 2D:4D in the right hand compared to that of the unaffected females (Brown et al., 2002c). Because androgen concentrations are generally normalized at birth in both CAH males and females, this morphological difference is attributed to the unusually high concentrations of circulating androgens during fetal life (Brown et al., 2002c). Although prenatal androgen exposure and the subsequent male-typical digit length pattern remain a viable hypothesis, an important limitation prevents us to draw direct conclusions for our study. That is, there is no evidence that links adult T to prenatal T in human populations. Therefore, the observed associations among DA and T in males, and, DA, R2D:4D, and reactive aggression in females cannot be attributed to prenatal androgen exposure.

Furthermore, our study did not find any sex differences in digit length patterns. Although some studies reported significant sexual dimorphism, there is a substantial overlap between male and female digit length ratios, and some studies found no sex differences (reviewed in Manning, 2002). Our sample size was relatively small and consisted of young college students which may not be representative of the overall population to tap actual sex differences. It should also be noted that the presence of sexual dimorphism in digit ratios appears to be neither a necessary nor a sufficient condition for the observed significant associations between 2D:4D and sexually dimorphic traits. Previous studies where no sex differences were reported, but significant associations between 2D:4D and sex-related traits, such as autism (Manning et al., 2001) and sensation seeking (Austin et al., 2002) were found, support this proposition. Similarly, one study reported null findings between 2D:4D and sex-related domains, such as mental rotation performance, despite the presence of sexual dimorphism in digit length ratios in the expected direction (Coolican and Peters, 2003). Additional research with large and truly representative samples is needed to explore this phenomenon.

Why is the right hand more susceptible to the influence of adult T (i.e., Manning et al., 1998 and the current study)? The actions of sex steroids may produce brain asymmetries both in form and function that may pertain to this association (Brown et al., 2002a). Specifically, morphological, physiological, and functional studies across species demonstrate that hemispheric asymmetries vary in accordance with sex, gonadectomy, hormone replacement, and natural fluctuations of sex steroids (reviewed in Wisniewski, 1998). When neuroanatomical asymmetries in the brain favor the right-hand side, this effect is observed generally in both human and nonhuman males, and largely attributed to T in rodent models (Wisniewski, 1998). Therefore, the primarily right-sided influence of T on digit length patterns may indicate asymmetrical effects of T on tissues outside of the central nervous system (Brown et al., 2002a).

Developmental origins of the influence of androgens on finger length patterns require further investigation. First, to our knowledge, no study has investigated the associations among androgens and digit patterns in different age groups, including children. Such an association, or lack of thereof, would suggest that digit length proportions are variable (or fixed) throughout life span. Studies on age and variation in digit morphology also produced mixed results (Garn et al., 1975; Harris et al., 1992; Manning et al., 1998; Williams et al., 2003). Additional research is needed to conclusively establish the age-dependent patterns of 2D:4D while taking into account the actions of androgens across life span. This would be especially useful given the role of sex steroids on bone formation and resorption during ontogeny and adulthood.

In summary, individual differences in female reactive aggression under high provocation can be partially attributed to the male-typical patterning of the second and fourth digits in adulthood. Although adult T concentrations appear to be related, developmental origins of the relationship between T and digit size are yet to be established. Future research would benefit from employing longitudinal studies while carefully controlling for mechanical demands on hands, physical activity, and age-dependent fluctuations in sex-steroid hormones. Animal models would also be informative by manipulating the amount of circulating fetal androgens across experimental and control groups, and observing the subsequent behavioral and morphological changes.

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References

Austin, E.J., Manning, J.T., McInroy, K., Mathews, E., 2002. A preliminary investigation of the associations between personality, cognitive ability and digit ratio. Pers. Individ. Differ. 33, 1115–1124.

Benderlioglu, Z., Nelson, R.J., 2004. Season of birth and fluctuating asymmetry. Am. J. Hum. Biol. 16, 298–310.

Benderlioglu, Z., Sciulli, P.W., Nelson, R.J., 2004. Fluctuating asymmetry predicts human reactive aggression. Am. J. Hum. Biol. 16, 458–469.

Berenbaum, S.A., Hines, M., 1992. Early androgens are related to childhood sex-typed toy preferences. Psychol. Sci. 3, 203–206.

Berkowitz, L., 1989. Frustration–aggression hypothesis: examination and reformulation. Psychol. Bull. 106, 59–73.

Brown, W.M., Finn, C.J., Breedlove, S.M., 2002a. Sexual dimorphism in digit-length ratios of laboratory mice. Anat. Rec. 267, 231–234.

Brown, W.M., Finn, C.J., Cooke, B.M., Breedlove, S.M., 2002b. Differences in finger length ratios between self-identified "butch" and "femme" lesbians. Arch. Sex. Behav. 31, 123–127.

Brown, W.M., Hines, M., Fane, B.A., Breedlove, S.M., 2002c. Masculinized finger length patterns in human males and females with congenital adrenal hyperplasia. Horm. Behav. 42, 380–386.

Collaer, M.L., Hines, M., 1995. Human behavioral sex-differences—A role for gonadal-hormones during early development. Psychol. Bull. 118, 55–107.

Coolican, J., Peters, M., 2003. Sexual dimorphism in the 2D/4D ratio and its relation to mental rotation performance. Evol. Hum. Behav. 24, 179–183.

Csatho, A., Osvath, A., Karadi, K., Bicsak, T., Manning, J., Kallai, J., 2001. Spatial navigation related to the ratio of second to fourth digit length in women. Learn. Individ. Differ. 13, 239–249.

Dabbs, J.M., 1990. Salivary testosterone measurements: reliability across hours, days, and weeks. Physiol. Behav. 48, 83–86.

Dabbs, J.M., 1991. Salivary testosterone measurements—Collecting, storing, and mailing. Physiol. Behav. 49, 815–817.

Dittmann, R.W., Kappes, M.H., Kappes, M.E., Borger, D., Stegner, H., Willig, R.H., Wallis, H., 1990. Congenital adrenal-hyperplasia .1. Gender-related behavior and attitudes in female-patients and sisters. Psychoneuroendocrinology 15, 401–420.

Diver, M.J., Imtiaz, K.E., Ahmad, A.M., Vora, J.P., Fraser, W.D., 2003. Diurnal rhythms of serum total, free and bioavailable testosterone and of SHBG in middle-aged men compared with those in young men. Clin. Endocrinol. 58, 710–717.

Ehrhardt, A.A., Baker, S.W., 1974. Fetal androgens, human central nervous system differentiation, and behavior sex differences. In: Friedman, R.C., R.M., van de Wiele, R.L. (Eds.), Sex Differences in Behavior. Wiley, New York, pp. 33–52.

Ehrhardt, A.A., Epstein, R., Money, J., 1968. Fetal androgens and female gender identity in the early-treated adrenogenital syndrome. Johns Hopkins Med. J. 122, 160–167.

Elias, L.J., Bryden, M.P., Bulman-Fleming, M.B., 1998. Footedness is a better predictor than is handedness of emotional lateralization. Neuropsychologia 36, 37–43.

Fane, B.A., Brook, C., Hines, M., 2001. Gender role behavior and targeting abilities in children with congenital adrenal hyperplasia (CAH). Horm. Behav. 39, 331.

Garn, S.M., Burdi, A.R., Babler, W.J., Stinson, S., 1975. Early prenatal attainment of adult metacarpal–phalangeal rankings and proportions. Am. J. Phys. Anthropol. 43, 327–332.

Grubbs, F.E., 1969. Procedures for detecting outlying observations in samples. Technometrics 11, 1–21.

Harris, E.F., Aksharanugraha, K., Behrents, R.G., 1992. Metacarpophalangeal length changes in humans during adulthood: a longitudinal study. Am. J. Phys. Anthropol. 87, 263–275.

Hines, M., Kaufman, F.R., 1994. Androgen and the development of human sex-typical behavior: rough-and-tumble play and sex of preferred playmates in children with congenital adrenal hyperplasia (CAH). Child Dev. 65, 1042–1053.

Hines, M., Golombok, S., Rust, J., Johnston, K.J., Golding, J., 2002. Testosterone during pregnancy and gender role behavior of preschool children: a longitudinal, population study. Child Dev. 73, 1678–1687.

Kulik, J.A., Brown, R., 1979. Frustration, attribution of blame, and aggression. J. Exp. Soc. Psychol. 15, 183–194.

Lippa, R.A., 2003. Are 2d:4d finger-length ratios related to sexual orientation? Yes for men, no for women. J. Pers. Soc. Psychol. 85, 179–188.

Manning, J.T., 2002. Digit Ratio: A Pointer To Fertility, Behavior, and Health. Rutgers Univ. Press, New Jersey.

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. Hum. Reprod. 13, 3000–3004.

Manning, J.T., Barley, L., Walton, J., Lewis-Jones, D.I., Trivers, R.L., Singh, D., Thornhill, R., Rohde, P., Bereczkei, T., Henzi, P., Soler, M., Szwed, A., 2000a. The 2nd:4th digit ratio, sexual dimorphism, population differences, and reproductive success. Evidence for sexually antagonistic genes? Evol. Hum. Behav. 21, 163–183.

Manning, J.T., Trivers, R.L., Thornhill, R., Singh, D., 2000b. The 2nd:4th digit ratio and asymmetry of hand performance in Jamaican children. Laterality 5, 121–132.

Manning, J.T., Baron-Cohen, S., Wheelwright, S., Sanders, G., 2001. The 2nd to 4th digit ratio and autism. Dev. Med. Child Neurol. 43, 160–164.

McFadden, D., Bracht, M.S., 2003. The relative lengths and weights of metacarpals and metatarsals in baboons (*Papio hamadryas*). Horm. Behav. 43, 347–355.

McFadden, D., Shubel, E., 2002. Relative lengths of fingers and toes in human males and females. Horm. Behav. 42, 492–500.

Peters, M., Mackenzie, K., Bryden, P., 2002. Finger length and distal finger extent patterns in humans. Am. J. Phys. Anthropol. 117, 209–217.

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

Robinson, S.J., Manning, J.T., 2000. The ratio of 2nd to 4th digit length and male homosexuality. Evol. Hum. Behav. 21, 333–345.

Slijper, F.M., 1984. Androgens and gender role behaviour in girls with congenital adrenal hyperplasia (CAH). Prog. Brain Res. 61, 417–422.

van Goozen, S.H.M., Cohen-Kettenis, P.T., Gooren, L.J.G., Frijda, N.H., van de Poll, N.E., 1995. Gender differences in behaviour: activating effects of cross-sex hormones. Psychoneuroendocrinology 20, 343–363.

Williams, T.J., Pepitone, M.E., Christensen, S.E., Cooke, B.M., Huberman, A.D., Breedlove, N.J., Breedlove, T.J., Jordan, C.L., Breedlove, S.M., 2000. Finger-length ratios and sexual orientation. Nature 404, 455–456.

Williams, J.H., Greenhalgh, K.D., Manning, J.T., 2003. Second to fourth finger ratio and possible precursors of developmental psychopathology in preschool children. Early Hum. Dev. 72, 57–65.

Wisniewski, A.B., 1998. Sexually-dimorphic patterns of cortical asymmetry and the role for sex steroid hormones in determining cortical patterns of lateralization. Psychoneuroendocrinology 23, 519–547.