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Bonobos have a more human-like second-to-fourth finger length ratio (2D:4D) than chimpanzees: a hypothesized indication of lower prenatal androgens

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ABSTRACT

The ratio of the second-to-fourth finger lengths (2D:4D) has been proposed as an indicator of prenatal sex differentiation. However, 2D:4D has not been studied in the closest living human relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). We report the results from 79 chimpanzees and 39 bonobos of both sexes, including infants, juveniles, and adults. We observed the expected sex difference in 2D:4D, and substantially higher, more human-like, 2D:4D in bonobos than chimpanzees. Previous research indicates that sex differences in 2D:4D result from differences in prenatal sex hormone levels. We hypothesize that the species difference in 2D:4D between bonobos and chimpanzees suggests a possible role for early exposure to sex hormones in the development of behavioral differences between the two species.

Introduction

Humans have two closest living relatives: the well-known chimpanzee (*Pan troglodytes*) and the less well-known bonobo (*Pan paniscus*) (Won and Hey, 2005). Bonobos have a relatively female-dominated social system compared to the more male-dominated chimpanzee social system (Kano, 1992; de Waal and Lanting, 1997), and have been presented as a serious challenge to the reconstruction of the behavior of the last common *Pan-Homo* ancestor (Parish and de Waal, 2000). Paleoanthropologists have attempted to use morphological evidence to reconstruct behavioral patterns based largely on functional and mechanical considerations. For example, patterns of anatomical sex dimorphism in living and fossil species have been linked evolutionarily to variation in mating systems, based on the principle that these anatomical features play a role in sex-specific reproductive effort (Plavcan, 2000). Evidence about the developmental processes yielding sex and species differences further contributes to interpreting their behavioral or functional implications. In the case of differences between chimpanzees and bonobos, prior research has focused on the possible role of heterochrony, especially paedomorphosis (Shea, 1983a,b; Shea and Groves, 1987; Lieberman et al., 2007), which has been further linked to reduced levels of aggression toward conspecifics (Wrangham and Pilbeam, 2001).

Some of the differences observed between chimpanzees and bonobos may be mediated by species differences in patterns of reproductive development and exposure to sex hormones. Relative to chimpanzees, adult bonobos show reduced sex dimorphism in both body size (Zihlman and Cramer, 1978) and the canine teeth (Begun and Deane, 2005). In addition, adult testosterone levels of male bonobos are lower than those of adult chimpanzees (Sannen et al., 2003). While sex dimorphism in body size in *Pan* arises largely, but not entirely, during puberty (Leigh and Shea, 1996; Smith and Leigh, 1998), canine dimorphism arises mostly prior to puberty as a result of bimaturism (Schwartz et al., 2001). The timing and ontogenetic processes resulting in body size and canine sex dimorphism appear to vary across primates, and even within the hominoids (Leigh and Shea, 1996; Schwartz et al., 2001; Leigh et al., 2005). We hypothesized that the differences in both social behavior and sex dimorphism that distinguish chimpanzees and bonobos also arise in part due to prenatal androgens, implying a potential role for endocrine system changes in the evolution of chimpanzees and humans.

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To date, there is no direct evidence about fetal production of androgens, or their effects, in the genus *Pan*. In humans and some other species, the basic pattern of fetal hormone production has been characterized by drawing blood from aborted fetuses at different gestation lengths. Venipuncture of *living* fetuses for direct measurement of blood hormones is technically difficult and dangerous, but steroid hormones diffuse into amniotic fluid, allowing the use of amniocentesis samples for the study of fetal hormone production. That said, to our knowledge, endocrine studies of neither aborted nor living chimpanzee or bonobo fetuses have been conducted, and would likely be infeasible and/or unethical. A feasible alternative approach to studying effects of fetal hormones would contribute to a better understanding of the evolutionary developmental processes leading to the substantial variation in sex dimorphism observed in three closely related species: humans, chimpanzees, and bonobos.

The ratio of the length of the second digit (index finger) to the fourth digit (ring finger), 2D:4D, is higher in human females than males, and has been proposed as an inverse marker for prenatal androgens (Manning et al., 1998; Manning, 2002; McIntyre, 2006). Several techniques have been used to measure digit ratios, including direct skin surface measurements from flexion creases, measurement of photocopies or digital images, and measurement of bone lengths from radiographs or skeletal material (Manning, 2002). While it seems likely that prenatal or infant androgens play some role in the development of observed sex differences in human 2D:4D, other, as yet unknown factors also contribute to substantial variation in 2D:4D between human populations, complicating the interpretation of results. In addition to population differences, there is a slight and much smaller tendency for 2D:4D to increase with age in young children. This change is clearer in longitudinal samples than in cross-sectional studies (Manning et al., 1998, 2004; McIntyre et al., 2005, 2006).

Similar kinds of analyses based on skin surface measurements in chimpanzees and bonobos have not been previously reported. Provided that 2D:4D is a useful marker for early hormone action in humans, would the measure be similarly useful in the genus *Pan*? The limited evidence about non-human hominoid sex differences in 2D:4D come from a study of collections of chimpanzee and gorilla metacarpals, which found sex differences analogous to those found in human metacarpals. In humans, the sex difference in metacarpal 2D:4D is smaller in magnitude, but correlated with the sex differences observed in finger length 2D:4D (Robertson et al., 2008). Previously studied mammalian taxa include baboons (McFadden and Bracht, 2003; Roney et al., 2004), and mice (Brown et al., 2002; Leoni et al., 2005; Hurd and Wahlsten, 2006; Hurd et al., 2008; Manno, 2008). Other taxa include birds (Burley and Foster, 2004;Saino et al., 2007; Dreiss et al., 2008), reptiles (Chang et al., 2006; Rubolini et al., 2006; Lombardo and Thorpe, 2008), and amphibians (Chang, 2008). Lack of predicted sex differences in 2D:4D are unsurprising, particularly in the case of diapsids, for example, given that these taxa lack a postnatal surge in male testosterone production (Corbier et al. 1992a,b). It has been suggested that the usual sex difference in diapsid 2D:4D may also be opposite that in synapsids (Chang, 2008).

In the absence of direct measurements of early sex hormones in chimpanzees, bonobos, and humans, a comparison of 2D:4D may be informative regarding factors that govern profound variation in dimorphism and behavior in this group. In particular, we predicted that bonobos would show a lower *sex difference* in 2D:4D than chimpanzees. This finding suggests either early hypo-masculinization of males, hyper-masculinization of females, or both. Such differences in the magnitude of the sex difference among closely-related species are likely to be associated with variation in early sexual differentiation and not other factors.

Methods

During routine annual medical examinations, we used a Canon CanoScan LIDE200 photo scanner to take digital images of the left and right hands of 97 chimpanzees living at the Tchimpounga chimpanzee sanctuary in the Republic of the Congo and 44 bonobos living at the Lola ya Bonobo bonobo sanctuary in the Democratic Republic of the Congo. To allow for lateral comparisons, only individuals for whom 2D:4D could be measured on both hands were included in this analysis. One or both of the scanned images could not be measured from 18 chimpanzees and 5 bonobos. The reasons for our inability to measure these individuals included either obvious injury to one or more fingers or poor scan quality, most often resulting from an inability to fully extend the fingers against the scanner glass. Finger lengths were measured from the most proximal flexion crease to tip, as in humans. We calculated left-hand 2D:4D, right-hand 2D:4D, and the difference (right minus left 2D:4D).

A second coder used the same methodology to independently re-measure a randomly selected 20% of the hands using the Adobe Photoshop ruler tool. We assessed reliability in 2D:4D measures by calculating intraclass correlations (ICC) in this subsample. Right-hand 2D:4D showed acceptable reliability, similar to what has been reported for human 2D:4D ($ICC = 0.886$). The reliability for left-hand 2D:4D was somewhat lower ($ICC = 0.709$), but this was largely due to a single disagreement about the position of a proximal flexion crease ($ICC = 0.833$, with case excluded).

Approximate age was known for all 39 bonobos and for 70 of 79 chimpanzees included in our analyses. Age class was known for the remaining 9 chimpanzees and converted into approximate age for the purpose of this analysis. Included subjects from both species ranged in age from 2 to 22 years old (bonobos: 11 infants, 20 juveniles, 8 adults; chimpanzees: 19 infants, 33 juveniles, 27 adults). Left- and right-hand 2D:4D were analyzed separately.

As 2D:4D has been shown to increase with age in young human children (Manning et al., 1998, 2004; McIntyre et al., 2005, 2006), we employed ANOVA and general linear models to test for sex, species, and sex-by-species interactions, while also simultaneously considering effects of age and interactions between age and the other effects of interest. We used a significant sex-by-species interaction in the expected direction of effect, to test for reduced sex dimorphism in bonobos. The initial general linear model included terms for sex, species, and age as a continuous variable, with all interaction terms. We reduced models in a stepwise manner, with removal of terms in order of highest p-value, until only significant terms remained. Main effects reported in the results are after removal of all interaction terms. The use of a general linear model may be inappropriate where the dependent variable is not normally distributed. However, 2D:4D was found to be quite normally distributed in the combined sample of bonobos and chimpanzees (left hand: Kolmogorov-Smirnov $Z = 0.569$, $p = 0.903$, right hand: $Z = 0.641$, $p = 0.806$).

This research was conducted while the principal investigator (BH) was on faculty at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. The welfare of animals involved in this study was protected following standards applicable in Germany.

Results

Mean digit ratio measures by species and sex are shown in Table 1. The main effect of sex on 2D:4D was detected in both the right hand, $F(1,118) = 5.52$, $p = 0.020$, and the left, $F(1,118) = 4.23$, $p = 0.042$. Contrary to our hypothesis, the ANOVA showed no significant sex-by-species interaction in either the left or right

Table 1
Means and standard deviations (SD) of age and 2D:4D digit ratio measures in chimpanzees and bonobos by sex.

	Chimpanzee Female $N = 40$	Chimpanzee Male $N = 39$	Bonobo Female $N = 12$	Bonobo Male $N = 27$
Age (years)	11.2 SD: 5.3	10.6 SD: 5.1	8.8 SD: 4.2	7.8 SD: 4.2
Left 2D:4D	0.918 SD: 0.031	0.906 SD: 0.038	0.956 SD: 0.032	0.940 SD: 0.034
Right 2D:4D	0.909 SD: 0.035	0.897 SD: 0.044	0.952 SD: 0.028	0.927 SD: 0.029
Right – Left 2D:4D	−0.009 SD: 0.026	−0.009 SD: 0.034	−0.004 SD: 0.026	−0.014 SD: 0.035

hand. These results indicate that chimpanzees and bonobos show similar magnitudes of sex difference in 2D:4D. We also observed a large main effect of species on both right-hand 2D:4D, $F(1,118) = 22.99$, $p < 0.001$, and left-hand 2D:4D, $F(1,118) = 28.01$, $p < 0.001$, with bonobos showing higher 2D:4D than chimpanzees.

We further considered models including age as a continuous variable. Contrary to our hypothesis, results showed no significant sex-by-species interaction in either the left or right hand (Fig. 1). The main effect of sex on 2D:4D was detected in both the right hand, $F(1,118) = 5.52$, $p = 0.020$, partial $\eta^2 = 0.046$, and the left hand, $F(1,118) = 4.23$, $p = 0.042$, partial $\eta^2 = 0.036$. We also observed an unanticipated significant difference in the age-related change in 2D:4D by sex, with males showing a more negative slope, $F(1,118) = 7.32$, $p = 0.008$. This difference is present only in chimpanzees (Fig. 1), but the 3-way interaction among sex, species, and age did not reach statistical significance, $F(1,118) = 1.85$, $p = 0.176$, possibly owing to lack of power. Moreover, we also observed a large main effect of species on both right-hand 2D:4D, $F(1,118) = 22.99$, $p < 0.001$, partial $\eta^2 = 0.167$, and left-hand 2D:4D, $F(1,118) = 28.01$, $p < 0.001$, partial $\eta^2 = 0.196$, with bonobos showing higher 2D:4D than chimpanzees. Figure 1 displays sex and species differences in right- and left-hand 2D:4D. No significant effects were detected for the difference of right- from left-hand 2D:4D.

Discussion

Mean sex differences in the 2D:4D of chimpanzees and bonobos appear roughly comparable to those of humans (Manning et al., 2000). However, chimpanzees show evidence for a substantial increase in sex differences with age, a pattern observed only weakly in humans and only at young ages (McIntyre et al., 2005). As this was a cross-sectional study, the reasons for the interaction of sex differences with age are unclear. It appears that, in young individuals, chimpanzees show, if anything, a *smaller* sex difference in 2D:4D than do bonobos. These results, therefore, do not suggest that bonobo males are relatively hypo-masculinized in early development compared to chimpanzee males (or, conversely, that bonobo females are hyper-masculinized).

We did, however, observe that means for bonobos closely approached human population means (Manning et al., 2000), while means for chimpanzees were significantly lower (i.e., more "masculine"). Based on information from metacarpals (McFadden and Bracht, 2005), it is likely that average 2D:4D values of gorillas are even lower than those of chimpanzees. There are a number of plausible explanations for species differences in 2D:4D, which may be unrelated to reproductive development, and, in general, species differences in single measures are difficult to interpret due to the confounding effects of many simultaneous differences between species (Garland and Adolph, 1994).

Two plausible alternative explanations for species differences in 2D:4D are that they might result either as adaptations for differences in function or indirectly from differences in body proportions, rather than as a result of differences in reproductive development. For example, species differences in 2D:4D could, in principle, be biomechanical adaptations supporting different behavioral repertoires. However, the relative lengths of the second and fourth digital rays are not thought to play a functional role in locomotion (Napier, 1980). Inouye (1992, 1994, 1999) did not detect significant differences among bonobos, chimpanzees, and gorillas in the use of the second relative to fourth fingers for knuckle walking. Alternatively, species may differ in body proportions for

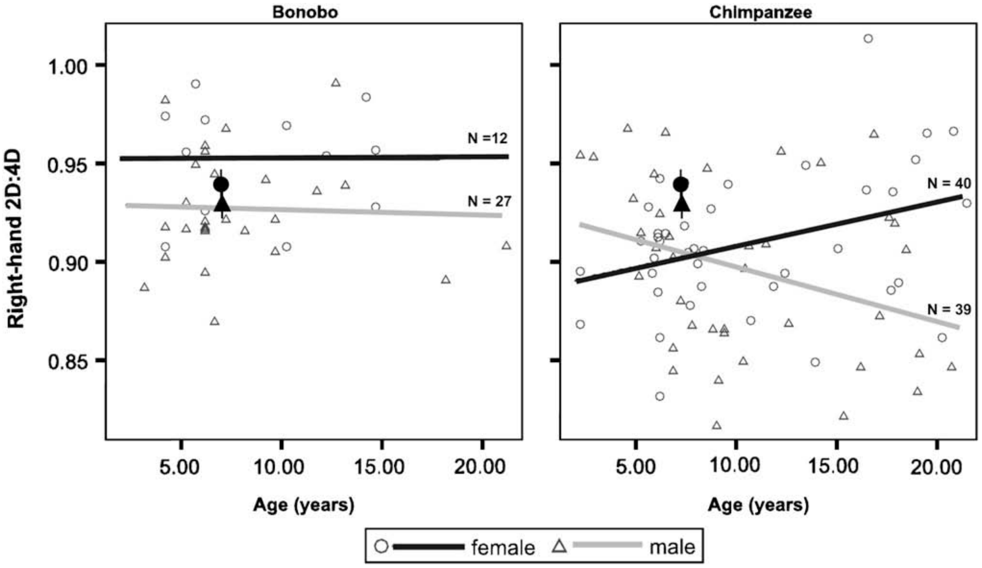

Fig. 1. Plot of the ratio of second-to-fourth digits (2D:4D) on the right hands of bonobos and chimpanzees by age with regression lines from a general linear model. The sexes are plotted separately, with samples sizes shown at the right end of each regression line. The slopes of the lines for chimpanzee females ($p = 0.028$) and males ($p = 0.047$) differ significantly from zero. Mean 2D:4D, measured using a similar technique, from a sample of 7.5 year-old human females (large, filled circle) and males (large, filled triangle) are also indicated, with 95% confidence intervals (Manning et al., 2000). These do not differ significantly from bonobo means obtained in this study, but do differ from chimpanzee means (males: $t = 3.9$, $df = 70.0$, $p < 0.001$, females: $t = 4.7$, $df = 70.5$, $p < 0.001$).

reasons unrelated to direct function by way of variable homeobox gene activation, which influences a number of body proportions simultaneously (Reno et al., 2008). Nevertheless, one would expect chimpanzees and bonobos to show similar patterns of homeobox activation relative to humans, and therefore similar finger length ratios, given that humans engage in substantially different patterns of locomotion and object manipulation (Reno et al., 2008). As such, the difference between chimpanzees and bonobos, and relative similarity between bonobos and humans, remains notable, and perhaps worthy of further study.

Alternatively, the differences between chimpanzees and bonobos may, in fact, indicate differences in reproductive development. If so, our results suggest that the notable species differences in social systems, and also in levels of tolerance toward, and potential for cooperation with, conspecifics (Hare et al., 2007) may be associated with reduced masculinization of both male and female bonobos. This phenomenon would be analogous to reports that human population differences in 2D:4D are closely associated with the level of polygyny, and therefore male-male competition (Manning, 2008). Following this logic, we would predict that gibbons (*Hylobates* sps.) would have a 2D:4D that is even higher than bonobos, while those of orangutans (*Pongo* sps.) and gorillas (*Gorilla gorilla*) would be at least as low as chimpanzees, with some evidence from metacarpals already suggesting the latter (McFadden and Bracht, 2005). Recent evidence from humans also shows that low 2D:4D is associated with delayed (i.e., more male-like) pubertal onset (Matchock, 2008). It is interesting to note that comparisons of bonobo and chimpanzee female ages at pubertal onset have demonstrated a trend toward earlier onset in bonobos, though not significantly so in the necessarily small samples included in these studies (De Lathouwers and Van Elsacker, 2005).

Whether differences in 2D:4D among chimpanzees, bonobos, and humans result from divergent functional adaptations, indirectly from differences in body proportions, or from differences in reproductive development, it seems clear that 2D:4D contains information about the ontogeny of sex and species differences in the genera *Pan* and *Homo*, and with further research, may aid in the reconstruction of the common ancestor, and identification of key developmental changes that occurred over the course of human evolution. If 2D:4D is ultimately found to be associated with endocrinological variation and not functional variation, it would provide a unique tool for studying primate ontogeny. Anatomical measures that provide insight into the physiological underpinnings of development provide interesting complements to those focused on function *per se*. Future research should focus on the association between 2D:4D and other traits, anatomical or behavioral, that have been shown to vary among bonobos, chimpanzees, and humans.

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