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Digit ratio (2D:4D) and its behavioral correlates in infant rhesus macaques (*Macaca mulatta*)

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Abstract

2D:4D ratios are typically lower in adult human males than females and are linked to numerous sex-differentiated behaviors. 2D:4D ratios are considered an indicator of prenatal androgen exposure; if so, children's 2D:4D ratios would arguably be even better indicators of prenatal androgen exposure since children have experienced fewer postnatal influences than adults. However, sex differences in 2D:4D ratios as well as associations between 2D:4D ratios and sex-typed behaviors in children have been inconsistent. Several studies also report sex differences and behavioral correlates of 2D:4D ratios in adult non-human primates, but little is known about 2D:4D ratios in infant non-human primates. This study examined sex differences in 2D:4D ratios over the first month of life, and associations with behavioral outcomes at 12–24 weeks of age, in $N = 304$ infant rhesus macaques. An increase in 2D:4D ratios over the first month of life was found, as well as associations with aggression and play behaviors, but no sex differences in 2D:4D ratios were observed. These results highlight the need for future developmental studies of 2D:4D ratios in order to determine not only their stability and predictive value, but also to discern the mechanism connecting prenatal androgen exposure, 2D:4D ratios, and behavioral outcomes.

KEYWORDS

aggression, digit ratio, infant, play, sex differences

1 | INTRODUCTION

The ratio between index (2D) and ring (4D) finger lengths is generally lower in men than in women, and this difference is more pronounced on the right hand than the left hand (Hönekopp & Watson, 2010). 2D:4D ratios have been correlated with a number of behavioral outcomes including, for example, aggression (Turanovic, Pratt, & Piquero, 2017), mental rotation abilities (Alexander & Son, 2007), athletic abilities (Hönekopp & Schuster, 2010), reproductive success in men (Klimek, Galbarczyk, Nenko, Alvarado, & Jasienska, 2014), and number of sexual partners in men (Hönekopp, Voracek, & Manning, 2006). These sex-typed behavioral patterns have led to

the suggestion that 2D:4D ratios may correlate with testosterone levels in adults (Manning, Scutt, Wilson, & Lewis-Jones, 1998; but see also Hönekopp, Bartholdt, Beier, & Liebert, 2007) and prenatally with androgen exposure in utero (Lutchmaya, Baron-Cohen, Raggatt, Knickmeyer, & Manning, 2004; but see also Ventura, Gomes, Pita, Neto, & Taylor, 2013). Evidence from mice suggests that androgens and estrogens differentially regulate the genes that cause growth of the fourth digit (Zheng & Cohn, 2011). Thus, 2D:4D ratios may be a convenient marker of prenatal androgen exposure that appears to affect behavioral outcomes across the life span; however, the exact mechanism connecting prenatal androgen exposure, digit development, and behavioral outcomes remains unknown.

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The majority of 2D:4D ratio studies have been conducted in adult populations; less is known about the development of 2D:4D ratios and their behavioral outcomes during infancy and childhood. While some data support the idea that the sex difference in 2D:4D ratios is observable starting at 18–24 months old (Manning et al., 1998; Saenz & Alexander, 2013; Williams, Greenhalgh, & Manning, 2003; Wong & Hines, 2016), some investigators have found it even in fetuses (Galís, Ten Broek, van Dongen, & Wijnaendts, 2010), consistent with the idea that prenatal androgen exposure is involved. On the other hand, several studies have failed to find any sex differences in 2D:4D ratios in infants (Alexander, Wilcox, & Farmer, 2009; Knickmeyer, Woolson, Hamer, Konneker, & Gilmore, 2011; Lutchmaya et al., 2004). There is also evidence that 2D:4D ratios change during development, in particular that they become larger throughout childhood (McIntyre, Ellison, Lieberman, Demerath, & Towne, 2005; Trivers, Manning, & Jacobson, 2006; Williams et al., 2003; Wong & Hines, 2016), suggesting that both pre- and postnatal developmental processes are involved in the determination of the 2D:4D ratio sex difference. However, in the absence of clearly controlled experimental manipulations, unravelling the biological mechanisms of 2D:4D ratios and their behavioral associations has been challenging.

To resolve this issue, investigators have taken to examining 2D:4D ratios in animal models. Due to their anatomical, physiological, and behavioral closeness to humans, primates are of particular interest as a model. While not all primate species show a sex difference in 2D:4D ratios, non-pair-bonded species with high levels of intrasexual competition exhibit the human pattern of adult males' 2D:4D ratio being lower than females' (Nelson & Shultz, 2010). Rhesus macaques (*Macaca mulatta*), who fall into this category (but see Baxter et al., 2018, for evidence suggesting that rhesus macaques display the opposite pattern to humans), experience a rise in testosterone in the first few months postpartum (Robinson & Bridson, 1979), similar to humans (Prince, 2001), and male fetuses are exposed to higher levels of androgens than female fetuses in utero – even though they do not experience a distinct peak in mid-gestation as humans do (Ellinwood, Brenner, Hess, & Resko, 1980). Behaviorally, low 2D:4D ratios have been associated with higher rank in female rhesus macaques (Nelson, Hoffman, Gerald, & Shultz, 2010), who tend to show higher levels of aggression towards conspecifics than low ranking females (Westergaard et al., 2003). However, little is known about the development of 2D:4D ratio in rhesus macaques, whether digit ratios remain stable across development or tend to increase as in humans, or whether infant 2D:4D ratios are predictive of behavioral outcomes.

This study sought to address this issue by measuring finger lengths in infant rhesus macaques. Infants were measured on two occasions, at age day 14 and day 30, which allowed the examination of developmental stability of 2D:4D ratios over a short window of time. In addition, infants were observed at ages 12–24 weeks for sex-typed behavior (social play, aggression). Due to their similarity to humans, infants were expected to show a sex difference in 2D:4D ratios early in life, and for ratios to increase with age. Moreover,

2D:4D ratios were expected to correlate with behavioral outcomes, with lower ratios being associated with higher levels of social play and aggression.

2 | METHODS

2.1 | Subjects

All data were collected at the Laboratory of Comparative Ethology, Eunice Kennedy Shriver National Institute of Child Health and Human Development in Poolesville, MD between 2007 and 2016. Fingers lengths were measured from a total of 304 monkeys (147 female). 235 monkeys (114 female) were measured at age day 14 (D14) and 216 monkeys (100 female) were measured at age day 30 (D30), including 147 monkeys (67 female) for which measurements were obtained on both days.

One hundred and sixty-one infants were reared by their mothers and lived in social groups comprised of one adult male, 8–12 adult females, and 2–6 infants of similar age. Social groups were housed in indoor-outdoor enclosures measuring 2.44 × 3.05 × 2.21 m indoors and 2.44 × 3.0 × 2.44 m outdoors, and enriched with wood chips, multiple perches, swings, and other enrichment devices. Monkeys were fed Purina High Protein Monkey Chow (#5054) and supplemental fruit and other foraging materials such as peanuts or sunflower seeds twice daily. Water was available ad libitum.

One hundred and forty-three infants were separated from their mothers on the day they were born (typically by 8a.m.), and were reared in a nursery facility for ongoing, unrelated studies. Infants were individually housed in incubators (51 × 38 × 43 cm) for the first two weeks of life and in metal cages (61 × 61 × 76 cm) thereafter. All housing arrangements contained an inanimate fleece surrogate, loose pieces of fleece fabric, and various plush, plastic, and rubber toys. For the first month of life, infants could see and hear, but not physically contact, other infants of similar age. Human caretakers were present for 13 hr each day and interacted with infants every 2 hr for feeding and cleaning purposes. Infants were bottle fed Similac formula and as they became older, were offered water ad libitum. Starting at 16 days of age, infants were given Purina High Protein Monkey Chow (#5054) and at 2 months old, daily enrichment consisting of fruit, seeds or nuts. For unrelated studies, infants were assigned to one of two rearing conditions when the youngest infant of the group turned 36 days: 75 infants were reared with three to four peers (i.e., peer-reared); 68 infants were reared with their surrogate (i.e., surrogate-reared) and were given 2-hr play sessions with three to four peers each weekday. While surrogate-reared infants retained their surrogate for the duration of the study, peer-reared infants were initially given one surrogate per infant but when each infant turned four months of age, a surrogate was removed from the cage. Play sessions for surrogate-reared infants were conducted in a 71 × 81 × 152 cm cage enriched with toys, hanging surrogates, fleece blankets, and a water bottle. The sex distribution in peer groups and play groups was balanced

as much as possible, usually two males and two females per group. For further details see Simpson, Miller, Ferrari, Suomi, & Paukner, 2016.

2.2 | Procedure

2.2.1 | Finger measurements

On days 14 and 30 ± 2 , all infants underwent a standardized neonatal assessment of neurological and behavioral development (Schneider & Suomi, 1992). At the end of the c. 30-min assessment, infants were chemically restraint with 10 mg/kg ketamine IM in order to collect biological samples. At the end of sample collection, fingers were measured with a digital Vernier caliper to the nearest 0.01 mm. Measurements on all four fingers of each hand were obtained by measuring from the crease closest to the palm of the hand to the tip of the finger. When possible, a second experimenter collected the same measurements immediately afterwards for reliability (see below for further details). If infants showed signs of recovery from restraint, such as starting to flex fingers, no measurements were collected. After full recovery, infants were transported back to their home cage or reunited with their mothers in their home enclosure.

2.2.2 | Behavioral observations

Data were collected by seven observers, who were blind to the aim of the study. Each observer was first trained by an established observer until there was inter-observer agreement across all behavioral scores of at least 85% over five sessions (ICC, $p < .05$). Nursery-reared infants were scored twice a week, once in the morning and once in the afternoon, for 5 min intervals using behavioral software (JWatcher, <http://www.jwatcher.ucla.edu/>). An established ethogram of 22 behaviors was used to capture infants' behavior in their home cage (for peer-reared infants) or during play sessions (for surrogate-reared infants). Behavioral observations occurred at least 30 min after the start of a play session for surrogate-reared infants or any other manipulation/testing of peer-reared infants. Coded behaviors included duration of five self-directed behaviors (e.g., self-groom, scratch), duration of 15 states (e.g., locomotion, sleep), and frequency of two events (spasm, vocalization).

The durations of two known sexually differentiated behaviors were summarized between infant ages 12–24 weeks:

PLAY: Performance of any play behavior including: initiating play by "play face", non-aggressive chasing, tagging, swatting, bobbing, biting, pulling, lunging, mouthing, wrestling (rough and tumble), and receiving play from another animal. Past research has indicated that infant males show higher levels of play behavior than females (Harlow, 1965).

AGGRESSION: Initiation of aggressive behaviors, such as biting, hair pulling, aggressive chases, threats, hitting, or slapping. Past research has indicated that infant males show higher levels of aggression than females (Bernstein & Ehardt, 1985; Harlow, 1965).

2.3 | Reliability analysis

One hundred and forty-three monkeys were measured by a second experimenter on D14 (60.9%) and 131 monkeys on D30 (60.7%). To assess reliability of measurements, Cronbach's alpha was calculated for each finger, which ranged from 0.813 to 0.910. Intraclass correlation coefficients (r_1) were also calculated for each finger, which ranged between .813 and .907. These reliability analyses indicate that there were no directional biases between measurements, and the mean for each finger measurement (where available) was used for further analyses. Individual values that deviated for more than 2.5 standard deviations above or below the mean were trimmed prior to analyses.

3 | RESULTS

3.1 | Finger lengths

There were no differences between mother-reared and nursery-reared infants in finger lengths (all $ps > .05$). Males were significantly larger at birth than females (female: $M = 483.59$ g, $SD = 77.52$, males: $M = 505.59$ g, $SD = 77.39$, $t(300) = 2.463$, $p = .014$). Birth weight also significantly correlated with finger lengths on both D14 and D30 (all $ps < .001$). However, there was no statistically significant difference between males and females with regards to finger lengths ($ps > .05$).

As expected, fingers were longer on D30 compared to D14 (Table 1). To evaluate if there was a difference in the rate of growth for each finger, a repeated measures ANOVA using males ($N = 75$) and females ($N = 60$) for which measurements were obtained on both D14 and D30 on the difference score between D30 and D14 showed a main effect for finger ($F(3, 399) = 3.217$, $p = .023$, partial $\eta^2 = 0.024$), but no effect for or interaction with infant sex (both $p > .05$). Post hoc comparisons suggest that 5D shows significantly less growth between D14 and D30 than the other fingers (mean growth: 2D = 0.44 mm, 3D = 0.42 mm, 4D = 0.37 mm, 5D = 0.25 mm; ps : 2D–5D = .004, 3D–5D = .016, 4D–5D = .080), and no differences between 2D, 3D, and 4D growth (all $ps > .05$).

3.2 | 2D:4D ratios

To assess whether mean 2D:4D ratios changed across time, a repeated-measures ANOVA with age (D14, D30) and hand (left, right) as within-subject factor showed a main effect for age ($F(1, 137) = 4.23$, $p = .042$, $\eta p^2 = .030$), but no effect for hand ($F(1, 137) = 3.46$, $p = .065$, $\eta p^2 = .025$). 2D:4D ratios tended to be larger at D30 ($M = 0.818 \pm 0.003$) compared to D14 ($M = 0.813 \pm 0.002$). 2D:4D ratios were weakly to moderately correlated between the left hand and the right hand on D14 ($r = .17$, $p = .009$) and on D30 ($r = .401$, $p < .001$).

On D14, Females showed a larger 2D:4D ratio right hand than males ($M = 0.8105 \pm 0.038$ vs. 0.8101 ± 0.036), but smaller 2D:4D ratios left hand ($M = 0.8135 \pm 0.036$ vs. $M = 0.8156 \pm 0.030$) and on both

TABLE 1 Descriptive statistics of fingers lengths (in mm) \pm SEM

	2nd Digit right	3rd Digit right	4th Digit right	5th Digit right	2nd Digit left	3rd Digit left	4th Digit left	5th Digit left
Female D14	18.57 \pm 0.12	23.50 \pm 0.16	22.90 \pm 0.16	18.80 \pm 0.13	18.76 \pm 0.12	23.61 \pm 0.15	23.00 \pm 0.14	18.56 \pm 0.14
Male D14	18.56 \pm 0.11	23.62 \pm 0.13	22.94 \pm 0.14	18.66 \pm 0.13	18.72 \pm 0.10	23.47 \pm 0.13	22.95 \pm 0.13	18.39 \pm 0.13
Female D30	19.15 \pm 0.14	24.27 \pm 0.15	23.56 \pm 0.13	19.20 \pm 0.13	19.34 \pm 0.12	24.21 \pm 0.16	23.65 \pm 0.15	19.01 \pm 0.14
Male D30	19.01 \pm 0.13	23.95 \pm 0.15	23.31 \pm 0.14	19.08 \pm 0.12	19.18 \pm 0.11	24.05 \pm 0.14	23.34 \pm 0.15	18.80 \pm 0.13

Note: Finger lengths were measured on both right and left hands at age 14 days (top 2 rows) and age 30 days (bottom 2 rows) for male and female infants.

hands on D30 (right hand: $M = 0.8146 \pm 0.041$ vs. $M = 0.8149 \pm 0.039$; left hand: $M = 0.8169 \pm 0.036$ vs. $M = 0.8206 \pm 0.031$). There were no significant differences between male and female 2D:4D ratios for either hand or either time point (independent sample *t* tests, all p s > .05; Figure 1). The D14 and D30 values were weakly but significantly correlated with each other (right hand: $r = .299$, $p < .001$; left hand: $r = .205$, $p = .015$), with the D14 ratios explaining about 7% of the variation in the D30 ratios (right hand: $r^2 = .089$, left hand $r^2 = .042$).

3.3 | Behavioral observations

Preliminary analyses revealed a significance difference in aggression between male and female infants ($F(1, 135) = 5.204$, $p = .024$, partial $\eta^2 = 0.037$), but no effect of rearing ($p = .098$). Males showed significantly more aggressive behavior than females ($M = 0.069 \pm 0.014$ vs. $M = 0.021 \pm 0.015$). For play behavior, there was a significant effect for rearing ($F(1, 135) = 20.893$, $p < .001$, partial $\eta^2 = 0.134$), a significant effect for infant sex ($F(1, 135) = 5.737$, $p = .018$, partial $\eta^2 = 0.041$) as well as a significant interaction between rearing and infant sex ($F(1, 135) = 4.474$, $p = .036$, partial $\eta^2 = 0.032$). While peer-reared males ($M = 13.981 \pm 2.829$) showed comparable levels of play to peer-reared females ($M = 13.115 \pm 3.307$, $p = .843$), surrogate-reared males ($M = 34.651 \pm 3.106$) played significantly more than surrogate-reared females ($M = 20.707 \pm 3.106$, $p = .002$).

To examine the relationship between 2D:4D ratios and behavior, male and female infants were analyzed separately. A multiple regression model with 2D:4D ratios (left hand/right hand, D14/D30) entered first into the model and rearing (peer, surrogate) entered second. For females, entry of 2D:4D ratios alone did not yield a significant prediction equation ($F(4, 24) = 1.11$, $p = .38$). For males, 2D:4D ratios significantly predicted aggression ($F(4, 36) = 3.35$, $p = .021$, $r^2 = 29.5\%$) with rearing not increasing fit of the model (F change test, $F(1, 31) = 0.163$, $p = .689$). Only right hand 2D:4D ratio on D14 was a significant predictor, with lower 2D:4D ratios predicting higher levels of aggression ($\beta = -.442$, $t = -2.869$, $p = .007$). Similar analyses for play behavior yielded a significant prediction equation in females based on 2D:4D ratios alone ($F(4, 24) = 3.565$, $p = .024$, $r^2 = 41.6\%$) and significantly better model fit when rearing was added (F change test, $F(1, 19) = 7.61$, $p = .013$, $r^2 = 58.3\%$). Both peer-rearing ($\beta = .513$, $t = 2.759$, $p = .013$) and 2D:4D ratio left hand on D30 ($\beta = -.406$, $t = -2.623$, $p = .013$) were negatively associated with play, meaning that peer-rearing decreased play behavior

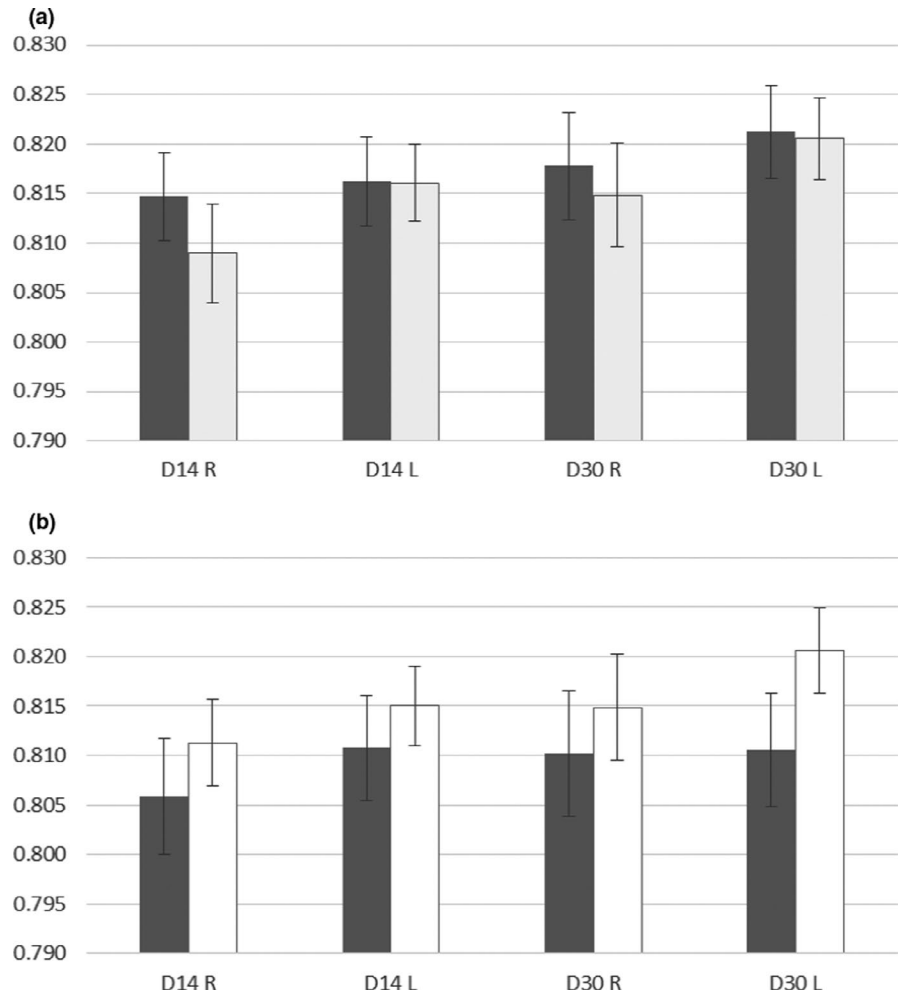
compared to surrogate-rearing, and that smaller 2D:4D ratios on the left hand at D30 were associated with more play. For male infants, 2D:4D ratios alone did not render a significant model ($F(4, 36) = 0.561$, $p = .692$) but addition of rearing significantly improved model fit (F change test, $F(1, 31) = 26.74$, $p < .001$, $r^2 = 49.8\%$). Only rearing significantly predicted play behavior with surrogate-reared males playing more than peer-reared males ($\beta = -.716$, $t = -5.171$, $p < .001$).

4 | DISCUSSION

This study aimed to describe potential sex differences in 2D:4D ratio in infant rhesus macaques and to investigate the relationship between 2D:4D ratio and behavioral outcomes. Basic descriptions of finger lengths confirmed growth between day 14 and day 30 of life. A small increase in 2D:4D ratio was also observed between days 14 and 30, suggesting that, similar to humans, 2D:4D ratios are not fixed at birth but may change throughout development (e.g., McIntyre et al., 2005). Interestingly, when compared to adult values (e.g., Nelson & Shultz, 2010), it appears that 2D:4D ratios may develop differently in males and females: in order to reach adult values, male 2D:4D ratio would have to decrease after D30, whereas female 2D:4D ratio would have to continue to increase. Interactions with left/right hand, perhaps dependent on handedness (Manning & Peters, 2009), may also occur but would require further investigations, including how postnatal androgen surges may relate to the accentuation and stabilization of 2D:4D ratios (Ventura et al., 2013).

Similar to some studies with human infants (Alexander et al., 2009; Knickmeyer et al., 2011; Lutchmaya et al., 2004) and primate infants (Frye, Rapaport, Melber, Sears, & Tardif, 2019; Nelson & Voracek, 2010), this study failed to find any sex differences in 2D:4D ratios in the first month of rhesus macaque infants' life. One possibility for this negative finding is a potential lack of power in this study. However, using data reported by Nelson and Shultz (2010) on a large sample of adult rhesus macaques ($N = 295$) to estimate effect size and assuming power of 0.8, the required sample size for this study is 226 subjects, which was achieved for D14 ($N = 230$) and approached for D30 ($N = 210$). Thus, lack of power is an unlikely explanation for the obtained negative results. Another possible issue could be difficulties in measuring the small fingers of infants in a reliable manner, thereby introducing additional noise into the data. However, as shown, overall reliability of measurements was good,

FIGURE 1 Average 2D:4D ratios for mother-reared infants (a) and nursery-reared infants (b). Bars depict ratios at age 14 days (D14) and age 30 days (D30) from infants' left (L) and right (R) hands. Gray bars indicate females and white bars indicate males; error bars represent SEMs



and finger growth between day 14 and day 30 was evident, suggesting the collected data fulfilled basic requirements of scientific rigor. Some human studies have found sex differences in 2D:4D ratios prenatally (Galis et al., 2010) and in newborns (Ventura et al., 2013), and macaques are thought to develop approximately 4× faster than human infants (Wallen, 2005). In this study, infants' fingers were measured at an age that was before the end of the postnatal testosterone surge in males at 2–3 months old (Mann et al., 1984), which might significantly affect finger growth and 2D:4D ratio development. Thus, future studies should consider investigations of 2D:4D ratios over longer periods, spanning time periods before and after this testosterone surge, to determine at which point in development 2D:4D ratios start to show reliable sex differences.

As expected, sex differences were observed in both aggression and play behavior, with play behavior also showing rearing effects. This finding is consistent with previous studies that reported play behavior being affected by rearing condition (Champoux, Shannon, Airoso, & Suomi, 1999). It is thought that whereas peer-reared infants form an attachment to each other, inhibiting play behavior, surrogate-reared infants form an attachment to their inanimate surrogate, leaving them free to engage in species-normative play when peers are available (Champoux et al., 1999). While play durations were reduced for all peer-reared infants, male

peer-reared monkeys were especially affected, suggesting that males are particularly vulnerable in this regard. Therefore, rearing was controlled in subsequent analyses of 2D:4D ratios and play. Results show that associations of both aggression and play with neonatal 2D:4D ratios are inconsistent. Aggression was associated only with males and 2D:4D ratios measured on D14 on the right hand, and play behavior was associated only with females and 2D:4D ratios measured on D30 on the left hand. However, both of these associations were in the predicted direction with lower 2D:4D ratios predicting higher male-typical behaviors. A human study investigating 2D:4D ratios and play and toy preferences in 2- to 3.5-year-old children similarly showed inconsistent relationships between 2D:4D ratios and sex-typed play behaviors (Wong & Hines, 2016). While this study has some unique strengths, including a replication over a 2-week period to evaluate developmental change in 2D:4D ratios, it nonetheless failed to find a sex difference in 2D:4D ratios itself, which may have impacted any associations with behavioral outcomes.

In conclusion, the question of the mechanism underpinning prenatal androgen exposure, 2D:4D ratios, and behavioral outcomes remains a priority for future investigations, which is likely to involve a combination of genetic (e.g., Gobrogge, Breedlove, & Klump, 2008; Nelson & Voracek, 2010) and other developmental factors (Voracek

& Dressler, 2009; Wallen, 2009). Identification of this mechanism may also help to clear up any potential links between 2D:4D ratios and developmental (e.g., Asperger's syndrome; Manning, Baron-Cohen, Wheelwright, & Sanders, 2001) and mental (e.g., anxiety and depression; Evardone & Alexander, 2009; McHenry, Carrier, Hull, & Kabbaj, 2014) disorders, for which a validated monkey model would be particularly useful.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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