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Original Article

# Digit Ratio (2D:4D), Aggression, and Testosterone in Men Exposed to an Aggressive Video Stimulus

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**Abstract:** The relative lengths of the 2$^{nd}$ and 4$^{th}$ digits (2D:4D) is a negative biomarker for prenatal testosterone, and low 2D:4D may be associated with aggression. However, the evidence for a 2D:4D-aggression association is mixed. Here we test the hypothesis that 2D:4D is robustly linked to aggression in "challenge" situations in which testosterone is increased. Participants were exposed to an aggressive video and a control video. Aggression was measured after each video and salivary free testosterone levels before and after each video. Compared to the control video, the aggressive video was associated with raised aggression responses and a marginally significant increase in testosterone. Left 2D:4D was negatively correlated with aggression after the aggressive video and the strength of the correlation was higher in those participants who showed the greatest increases in testosterone. Left 2D:4D was also negatively correlated to the difference between aggression scores in the aggressive and control conditions. The control video did not influence testosterone concentrations and there were no associations between 2D:4D and aggression. We conclude that 2D:4D moderates the impact of an aggressive stimulus on aggression, such that an increase in testosterone resulting from a "challenge" is associated with a negative correlation between 2D:4D and aggression.

**Keywords:** 2D:4D, prenatal testosterone, testosterone, aggressive video

## Introduction

The relative lengths of the 2nd and 4th digits (2D:4D) is a sexually dimorphic trait in which males tend to have longer 4th digits relative to 2nd digits than do females (Manning, Scutt, Wilson, and Lewis-Jones, 1998). It has been hypothesized that 2D:4D is a biomarker for prenatal testosterone (PT) and prenatal estrogen (PE) such that 2D:4D is negatively correlated to PT and positively correlated to PE (Manning, 2002, 2011; Manning et al., 1998). The evidence for this hypothesis has been reported in both correlational and experimental studies. With regard to the former, individuals with congenital adrenal hyperplasia (a trait associated with high prenatal androgen) tend to have low "masculinized" 2D:4D (for meta-analysis, see Hönekopp and Watson, 2010). In contrast, Klinefelter's men (individuals with XXY sex chromosomes), who have low prenatal testosterone, show high "feminized" 2D:4D (Manning et al., 2013). In addition, XY individuals who are partly or completely insensitive to androgen have mean 2D:4D that is similar to that of females (Berenbaum, Bryk, Nowak, Quigley, and Moffat, 2009). With regard to experimental evidence, in rodents the administration of *in utero* testosterone or the blocking of estrogen receptors has been shown to lower 2D:4D, whereas administration of estrogen or blocking androgen receptors increases 2D:4D (Talarovicova, Krskova, and Blazekova, 2009; Zheng and Cohn, 2011). Further examination of these and related data suggests that 2D:4D is fixed in a narrow prenatal window of development and is linked to the activation of "skeletogenic" genes by sex steroids. The skeletogenic genes, some 20 in number, have multiple additional functions which include the morphogenesis of the reproductive organs and the brain (Lawrance-Owen, Bargary, Bosten, Goodbourn, and Hogg, 2013; Zheng and Cohn, 2011)

These findings provide compelling evidence that 2D:4D is negatively related to PT and positively related to PE, such that it reflects both sensitivity to sex steroids and the concentration of prenatal sex steroids (Manning, 2011). However, there remains a debate on whether small gradations in 2D:4D are closely correlated to individual levels of PT and PE. For instance, Hampson and Sankar (2012) suggested that the correlation between 2D:4D and sensitivity to testosterone is not substantial, whereas Van Honk and colleagues have reported that very small gradations in 2D:4D strongly moderates the influence of experimentally-administered testosterone on empathy (van Honk et al., 2011), co-operation (van Honk, Montoya, Bos, van Vugt, and Terburg, 2012), and moral judgments (Montoya et al., 2013) in women. To our knowledge, no experiment has been undertaken to examine the relationship between 2D:4D and aggression in men and, in particular, whether this relationship may be explained by fluctuating testosterone levels.

Aggression in humans is strongly sex dependent, such that men tend to show more same-sex physical aggression compared to women (e.g., Campbell and Muncer, 2008). Therefore, this would suggest that 2D:4D is negatively related to physical aggression. However, such a relationship is controversial. The first examination of the association reported that 2D:4D did not correlate with aggression (Austin, Manning, McInroy, and Mathews, 2002). Subsequent studies have reported both significant and non-significant findings in links between 2D:4D and aggression. For example, Hurd, Vaillancourt, and Dinsdale (2011) found a significant negative relationship between 2D:4D and physical aggression in a sample of Canadian men, but Butovskaya et al. (2012) reported no association between 2D:4D and physical aggression in a sample of Hadza men. A recent meta-analysis (Hönekopp and Watson, 2011) has not resolved these differences, reporting only a small but significant, negative relationship between 2D:4D and aggression in men ($r$ = -0.06). These discrepancies in the literature concerning 2D:4D and aggression in men may be resolved, to some extent, if aggression is influenced by testosterone induced by an aggressive challenge and such influence is additionally moderated by 2D:4D.

There is evidence for an aggression-testosterone-2D:4D link in the presence of a challenge. Millet and Dewitte (2007) reported no relationship between 2D:4D and physical or provoked aggression in a sample of 45 men, but a significant negative correlation with both physical and provoked aggression, and 2D:4D was noted immediately after exposure to an aggressive video. Although testosterone was not measured in this study, there are reports of increases in testosterone after watching an aggressive video clip (e.g., Cook and Crewther, 2012; also see Millet, 2010 for general discussion of the link between aggressive stimuli and testosterone production), which, in turn, may influence the expression of such behaviors as aggression. Furthermore, a study of Italian football players in "Series A" showed low 2D:4D and high testosterone were linked to the number of fouls during games (Perciavalle et al., 2013). This correlation is to be expected if low 2D:4D predicts high physical aggression during the challenge of a competitive game of football. Therefore, studies that address any association between 2D:4D and aggression would benefit from experimentally manipulating testosterone levels using a "challenge" stimulus such as an aggressive video.

In this study, we examined the relationship between 2D:4D, testosterone responsiveness, and provoked aggression in men in relation to an aggressive video stimulus. We manipulated testosterone levels by exposing the participants to an aggressive challenge video and also a control video. Aggression was measured after each video and free testosterone was measured before and after exposure to each video. Our working hypothesis was that the aggressive video would raise testosterone levels and, in this context, 2D:4D would be negatively related to aggression. In contrast, we expected testosterone would not be raised by the control video and, in this context, 2D:4D would not be associated with aggression.

## Materials and Methods

We broadly followed the protocol of Millet and Dewitte (2007) and considered their measure of provoked aggression as the outcome variable.

### *Participants*

Participants were recruited from male students and staff of a UK University. The sample (as in Millet and Dewitte, 2007) comprised 45 Caucasian men with a mean age of 24.27 ($SD$ = 7.72) years. Most participants were from the UK. Each participant had the protocols explained to them and signed informed consent before the study commenced. Ethical approval was provided by a local University Ethics Committee.

*Protocols*

A randomized experimental study with a cross-over design was used to address the study's hypotheses. All participants were assessed between the hours of 10am and 4pm, with subsequent assessments made at the same time of day for each individual. After arriving at the testing facility, each participant was asked to provide a saliva sample and was then exposed to either an aggressive video (a rugby haka plus rugby tackles) or a control video (a blank screen), both of which had a duration of 4 minutes. A haka is a ritualized display which is a traditional war dance or challenge of the Maori people. It is performed before national New Zealand rugby matches. Our recent work demonstrated an acute rise in free testosterone levels with this type of aggressive stimulus (Cook and Crewther, 2012). We checked the effectiveness of the manipulation in each participant by asking: (i) "To what extent has physical aggression been shown in the video?" and (ii) "How aggressive does this video look in general?" Both questions were scored out of 100 for effectiveness (0 = not effective; 100 = highly effective). A second saliva sample was collected 15 minutes after exposure to the video to coincide with the testosterone surges reported elsewhere (Cook and Crewther, 2012). Due to experimental constraints, the videos were shown on a large video screen and presented to participants in small groups (1-4). There were no interactions between participants while watching the video footage, or during the short period after, to ensure minimal effects of the social environment on the hormonal and behaviour measures. The aggressive video was watched without any sound.

After viewing the aggressive or control video, the participants were presented with five situations from the aggression provocation questionnaire used by Millet and Dewitte (2007). For each situation, participants were asked to rate on a five-point Likert scale (1 being lowest, 5 being highest) how angry, irritated, and frustrated they would feel in each situation. The testing procedure was repeated, after a period of approximately one week, when the participant was exposed to whichever video they previously had not seen.

*2D:4D assessment*

At the completion of the first video exposure, the ventral surface of the participant's hands was photocopied. In order to minimize possible distortion of the fingertips by pressure on the glass plate of the photocopier, all participants were asked to gently place their hand on the glass plate. All photocopies were checked to ensure the finger tips were not flattened and that the finger creases were clearly displayed. Measurement of finger length was from the finger crease proximal to the palm to the tip of the finger using vernier calipers measuring to 0.01 mm (Manning et al., 1998).

*Saliva collection and hormone analysis*

Saliva was collected by passive drool into sterile containers, approximately 2 ml over a timed collection period of 2 minutes. The samples were subsequently stored at -30° C until assay. After thawing and centrifugation (2000 rpm x 10 minutes), the saliva samples were analyzed in duplicate for testosterone concentrations using commercial kits (Salimetrics LLC, USA) and the manufacturers' guidelines. The minimum detection limit for the T assay was 6.1 pg/ml, with inter-assay coefficients of variation (CV) of < 9.7%.

## Results

The repeatability (ICC) of the first and second measurement of 2D:4D was high and significant for both hands (right hand: $ICC = 0.93$, $F = 26.82$, $p = 0.0001$; left hand: $ICC = 0.93$, $F = 28.58$, $p = 0.0001$). Therefore, the between-individual differences in 2D:4D were significantly greater than measurement error. Mean 2D:4D was calculated for right (0.949 [0.021]) and left (0.953 [0.027]) hands and used in subsequent analyses.

Considering the manipulation, we calculated a mean of the two manipulation checks. Ratings for aggressive content were high for the aggressive video (79.87[11.67]) and very low for the control video (0.91 [1.55]). The difference was significant, $t(45) = 43.58$, $p = 0.0001$.

With regard to the aggression provocation questionnaire, we calculated a composite score for provoked aggressive tendency after the aggressive video and after the control video (PAT: aggressive video condition $PAT_{aggress} = 60.09$ [5.52]; control $PAT_{control} = 54.52$ [9.41]). The former was significantly higher than the latter, $t(45) = 5.61$, $p = 0.0003$.

Considering the testosterone levels associated with the aggressive video, mean testosterone was higher after the video (156.92 [59.45] pg/ml) in comparison to before the video (144.63 [51.11] pg/ml). The magnitude of the increase (12.30 pg/ml) was marginally significant (one-sample *t*-test mean set at zero, $t = 1.81$, $p = 0.08$).

In contrast to the aggressive video, the testosterone levels associated with the control video were slightly higher before (166.73 [72.13] pg/ml) compared to after the video (163.27 [60.13] pg/ml). The magnitude of the change was not significant (one-sample *t*-test mean set at zero, $t = 0.59$, $p = 0.56$).

### *Manipulation effects and provoked aggression tendency*

The perceived magnitude of aggression reported in the manipulation check did not correlate with $PAT_{aggress}$ ($r = 0.19$, $p = 0.21$). Also the difference between the manipulation score for the aggressive and control conditions did not correlate with the difference in $PAT_{aggress}$ - $PAT_{control}$ ($r = 0.02$, $p = 0.88$).

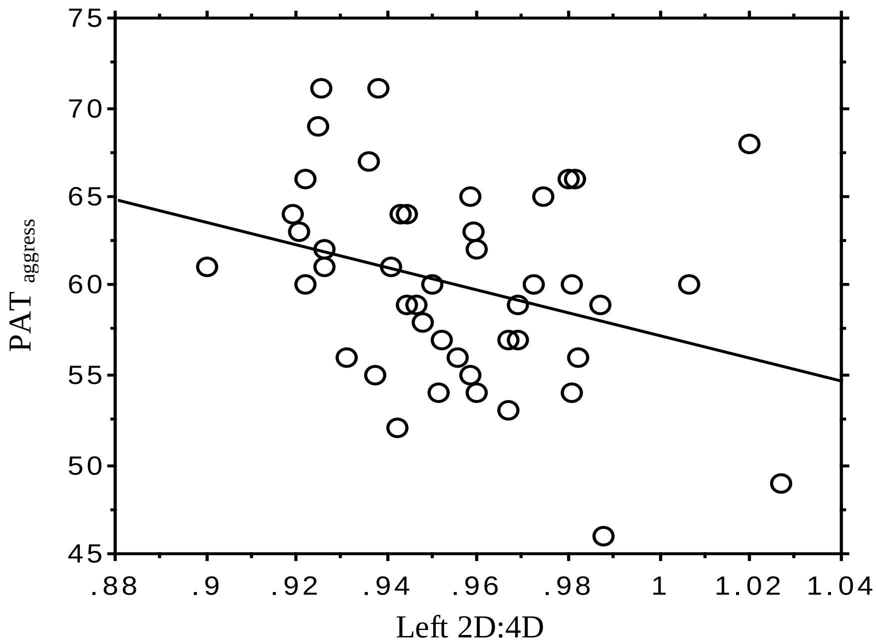
### *Digit ratio, testosterone and provoked aggression tendency*

With regard to the aggressive video condition, 2D:4D was negatively related to $PAT_{aggress}$, and this was significant for left 2D:4D ($r = -0.31$, $p = 0.04$; see Figure 1) but not right 2D:4D ($r = -0.23$, $p = 0.13$). We checked this finding by applying a more conservative test for correlation, i.e., the Spearman correlation test, and again found a significant association for left 2D:4D ($r_s = -0.32$, $z = 2.13$, $p = 0.03$) but not right 2D:4D ($r_s = -0.22$, $z = 1.46$, $p = 0.14$). There were no associations between testosterone and $PAT_{aggress}$ (testosterone before video: $r = 0.08$, $p = 0.59$; testosterone after video: $r = 0.001$, $p = 0.99$; testosterone after video – testosterone before video: $r = 0.02$, $p = 0.88$).

We considered the relationship between left 2D:4D, $PAT_{aggress}$, and testosterone further by performing a multiple regression analysis with dependent variable $PAT_{aggress}$ and independent variables left 2D:4D, change in testosterone (testosterone after video – testosterone before video), and the interaction between left 2D:4D and change in testosterone. We found that left 2D:4D was no longer significantly related to $PAT_{aggress}$

($b$ = -37.03, $t$ = 1.21, $p$ = 0.24). However, the change in testosterone was now positively related to $PAT_{aggress}$ ($b$ = 1.68, $t$ = 2.24, $p$ = 0.03), and there was a significant negative relationship for left 2D:4D*change in testosterone ($b$ = -1.77, $t$ = 2.25, $p$ = 0.03). For right 2D:4D, there was no significant relationship with $PAT_{aggress}$ ($b$ = -55.74, $t$ = 1.38, $p$ = 0.18), change in testosterone ($b$ = 0.45, $t$ = 0.37, $p$ = 0.72), or the interaction right 2D:4D*change in testosterone ($b$ = -0.48, $t$ = 0.37, $p$ = 0.71).

**Figure 1.** The relationship between left 2D:4D and $PAT_{aggress}$ in 45 men




In order to focus on the interaction left 2D:4D*change in testosterone, we calculated a median split in the magnitude of the testosterone change (low: $n$ = 22, mean change = -19.50 [25.42] pg/ml; high: $n$ = 23, mean change = 42.71[39.50] pg/ml). The relationship between left 2D:4D and $PAT_{aggress}$ in the low change group was positive and weak ($r$ = 0.11, $p$ = 0.61), but in the high change group it was a strong and significant negative association ($r$ = -0.53, $p$ = 0.009; see Figure 2). A similar pattern was found using a Spearman correlation test (low change: $r_s$ = -0.09, $z$ = 0.04, $p$ = 0.97; high change: $r_s$ = -0.50, $z$ = 2.34, $p$ = 0.02). Considering the control video condition, correlations between 2D:4D and $PAT_{control}$ tended to be positive but non-significant (left 2D:4D: $r$ = 0.12, $p$ = 0.46; right 2D:4D: $r$ = 0.18, $p$ = 0.26). With regard to testosterone, there were no significant associations with $PAT_{control}$ (testosterone before video: $r$ = 0.01, $p$ = 0.51; testosterone after video: $r$ = 0.03, $p$ = 0.85; testosterone after video – testosterone before video: $r$ = -0.14, $p$ = 0.36).

With regard to comparisons between the aggressive and control video conditions, considering differences between $PAT_{aggress}$ and $PAT_{control}$, left 2D:4D was negatively and significantly correlated with $PAT_{aggress}$-$PAT_{control}$ ($r$ = -0.36, $p$ = 0.02; see Figure 3), and right 2D:4D was negatively but non-significantly correlated with $PAT_{aggress}$-$PAT_{control}$ ($r$ = -

0.26, $p$ = 0.09). In this instance, Spearman correlation tests showed that both left 2D:4D and right 2D:4D were significantly negatively related to $PAT_{aggress}$-$PAT_{control}$ (left 2D:4D: $r_s$ = -0.34, $z$ = 2.26, $p$ = 0.02; right 2D:4D: $r_s$ = -0.37, $z$ = 2.41, $p$ = 0.02).

**Figure 2.** The relationships between left 2D:4D and $PAT_{aggress}$ in men showing high change in testosterone after viewing the aggressive video, $n$ = 23

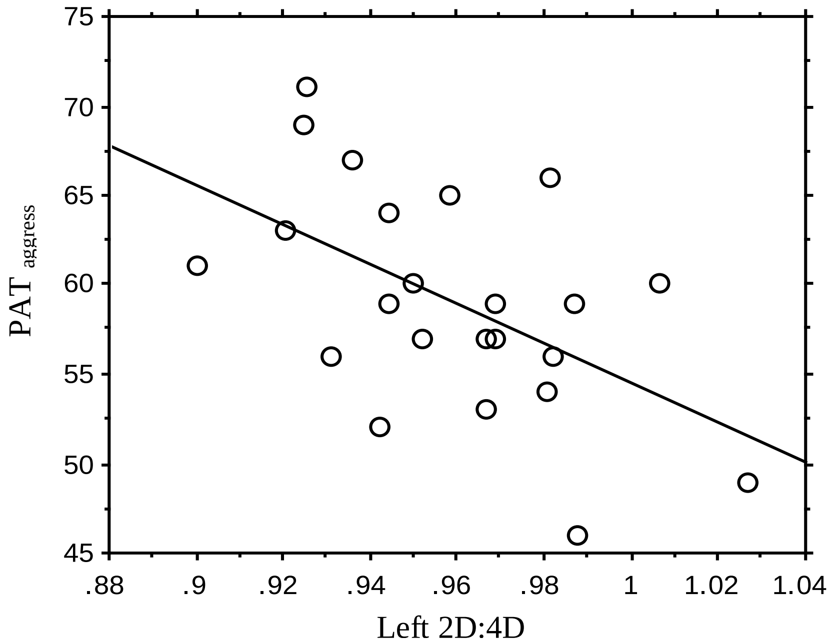
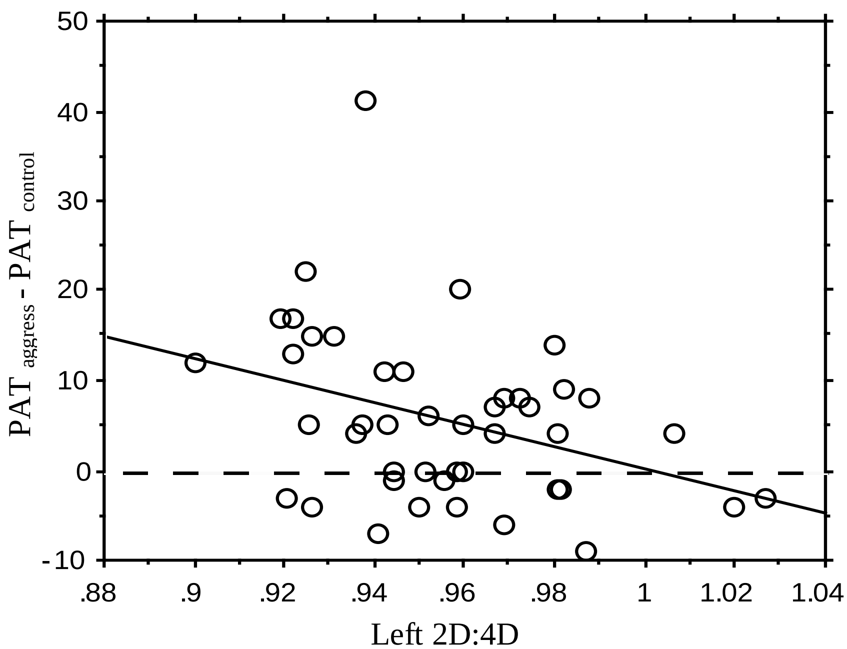



**Figure 3.** The relationships between left 2D:4D and PATaggress - PATcontrol in 45 men



## Discussion

This study gave the following key results: (i) With regard to the aggressive video, this was associated with a marginally significant increase in testosterone levels. In addition, aggression levels were significantly greater after the aggressive video compared to after the control video (i.e., $PAT_{aggress} > PAT_{control}$). Left 2D:4D was significantly and negatively correlated to $PAT_{aggress}$ (product-moment and Spearman correlations). A multiple regression showed testosterone increase was positively related to $PAT_{aggress}$ and there was a significant interaction of left 2D:4D*change in testosterone. Considering a median split of testosterone change, we found that among individuals with increased testosterone there was a strong negative correlation between left 2D:4D and $PAT_{aggress}$ (product-moment and Spearman correlations) (ii) The control video did not have any impact on testosterone levels. There were no significant correlations between left and right 2D:4D and $PAT_{control}$. (iii) Considering differences between the aggressive and control conditions, left 2D:4D (product-moment and Spearman correlations) and right 2D:4D (Spearman correlation only) correlated negatively with the difference between $PAT_{aggress}$ and $PAT_{control}$.

Our results replicate those of Millet and Dewitte (2007), in that we found a significant negative correlation between 2D:4D and aggression after an aggressive stimulus. The effect was related to an increase in testosterone concentrations, insofar as it was greatest in the sub-group that showed the greatest increase in testosterone. This suggests that low 2D:4D men are likely to show high aggression in conditions of challenge (such as aggressive encounters, including aggressive sports), which is consistent with the challenge hypothesis. Most of the significant associations we found were for left 2D:4D. In general, 2D:4D correlations with target traits tend to be strongest for right 2D:4D. However, for links with sports performance the left 2D:4D is of equal importance (Hönekopp and Schuster, 2010). Performance in sports involves a challenge which may be similar to an aggressive situation. This may explain the link with left 2D:4D and aggression in our findings. There was no correlation between 2D:4D and aggression after the control video. This suggests that in the absence of an aggressive challenge a low 2D:4D is not a strong biomarker for aggression. Thus, with regard to the relationship between 2D:4D and aggression, it is possible to see negative or null correlations, as have been reported by Hurd et al. (2010) and Butovskaya et al. (2012). The former is likely if most of the study participants have recently been exposed to a challenge, whereas the latter is likely if there was no preceding challenge in most participants.

The finding of a link between low 2D:4D and aggression in challenge conditions may be explained by two underlying mechanisms:

Firstly: *2D:4D and sensitivity to testosterone*. Low 2D:4D is thought to be a marker for testosterone levels in the fetus and also sensitivity to testosterone in the fetus and adult. Therefore, a spike in testosterone may lead to an increase in aggression, and this would be particularly seen in low 2D:4D men. Is low 2D:4D linked to high sensitivity to testosterone? Sensitivity to testosterone is partly dependent on allelic variation in the androgen receptor gene (AR). Within the terminal domain of the AR is a polymorphic region with a variable number of CAG repeats. Low CAGn is associated with high sensitivity to testosterone. Therefore, spikes in testosterone may elicit a greater effect in those individuals with low CAGn, and in men with low 2D:4D if the latter is linked to low CAGn. However, the correlational evidence for a link between low 2D:4D and low CAGn is mixed. The prediction is that 2D:4D is positively correlated with CAGn. With regard to studies of aggression, a positive association between 2D:4D and CAGn was found for left hand 2D:4D (significant, $p = 0.01$) and right hand 2D:4D (marginally significant, $p = 0.08$) by Butovskaya et al. (2012), but not by Hurd et al. (2011). Regarding general population samples, Manning, Bundred, Newton, and Flanagan (2003) reported a significant positive relationship between right 2D:4D ($p = 0.04$) and right-left 2D:4D ($p = 0.01$) and CAGn in men. Loehlin, Medland, and Martin (2012) failed to replicate this, but did report a significant positive relationship between left 2D:4D and CAGn ($p = 0.04$) in women. Knickmeyer, Woolson, Hamer, Konneker, and Gilmore (2011), as well as Hampson and Sankar (2012), reported no association between low 2D:4D and low CAGn. However, the former found that high neonatal testosterone levels plus low CAGn in infants together predicted low 2D:4D, whereas the latter reported no interaction between testosterone and CAGn in adults. Finally, Folland, McCauley, Phypers, Hanson, and Mastana (2012) reported positive but non-significant associations between 2D:4D and CAGn in left and right hands. It is important to note that all these studies are correlational in nature. However, three experimental studies have shown that 2D:4D is a marker for subtle variations in sensitivity to testosterone, with the digit ratio found to be a strong modulator of the effect of administered testosterone on empathy (van Honk et al., 2011), cooperation (van Honk et al., 2012), and moral judgments (Montoya et al., 2013).

Secondly: *2D:4D, challenge and testosterone production*. There is little evidence to support the view that 2D:4D is correlated with circulating levels of testosterone in general population samples (e.g., Muller et al., 2011). However, 2D:4D may predict testosterone production immediately after a "challenge." For example, Kilduff et al. (2013) have reported that low right 2D:4D (relative to left 2D:4D) predicts high testosterone production after a physical challenge (a repeated sprint test). In the sporting domain, there have been a number of reports of links between low 2D:4D and high performance in men (e.g., football: Manning and Taylor, 2001; rowing: Longman, Stock, and Wells, 2011; rugby: Bennett, Manning, Cook, and Kilduff, 2010). We suggest that under challenge, men with low 2D:4D show a combination of sensitivity to testosterone and a tendency to produce high levels of testosterone. This combination may underlie the behavioral and physiological attributes (such as high aggression and VO2max; see Hill, Simpson, Millet, Manning, and Kilduff, 2012) associated with sports success. Further work may show that, under challenge, 2D:4D is a powerful predictor of abilities that are useful in aggressive and sports contests and dominance behaviors. These may include visuo-spatial perception and judgment of the emotional state of opponents.

In conclusion, we have found an aggressive video was associated with raised aggression responses and marginally significant increases in testosterone. Left hand 2D:4D was negatively correlated with aggression after the aggressive video and this correlation was stronger in those participants with the highest increase in testosterone. Left 2D:4D was also negatively correlated to the difference between aggression scores in the aggressive and control conditions, such that participants with high aggression in the former compared to the latter also had low 2D:4D. We conclude that 2D:4D moderates the impact of an aggressive stimulus on aggression, such that an increase in testosterone is associated with a negative correlation between 2D:4D and aggression.

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## References

Austin, E. J., Manning, J. T., McInroy, K., and Mathews, E. (2002). A preliminary investigation of the associations between personality, cognitive ability and digit ratio. *Personality and Individual Differences, 33,* 1115-1124.

Bennett, M., Manning, J. T., Cook, C. J., and Kilduff, L. P. (2010). Digit ratio (2D:4D) and performance in elite rugby players. *Journal Sports Sciences*, *28*, 1415-1421.

Berenbaum, S. A., Bryk, K. K., Nowak, N., Quigley, C. A., and Moffat, S. (2009). Fingers as a marker of prenatal androgen exposure. *Endocrinology, 150*, 4819-4822.

Butovskaya, M. L., Vasilyev, V. A., Lazebny, O. E., Burkova, V. N., Kulikov, A. M., Mabulla, A., . . . 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*, *42*, 647-662.

Campbell, A., and Muncer, S. (2008). Intent to harm or injure? Gender and the expression of anger. *Aggressive Behaviour, 34*, 282-93.

Cook, C. J., and Crewther, B. T. (2012). Changes in salivary testosterone concentrations and subsequent voluntary squat performance following the presentation of short video clips. *Hormones and Behavior, 61*, 17-22.

Folland, J. P., McCauley, T. M., Phypers, C., Hanson, B., and Mastana, S. S. (2012). Relationship of 2D:4D finger ratio with muscle strength, testosterone, and androgen receptor CAG repeat genotype. *American Journal Physical Anthropology, 149*, 81-87.

Hampson, E., and Sankar J. S. (2012). Re-examining the Manning hypothesis: Androgen receptor polymorphism and the 2D:4D ratio. *Evolution and Human Behavior*, *33*, 557-561.

Hill, R., Simpson, B., Millet, G., Manning, J. T., and Kilduff, L. (2012). Right-left digit ratio (2D:4D) and maximal oxygen uptake. *Journal of Sports Sciences*, *30*, 129-134.

Hönekopp, J., and Schuster, M. (2010). A meta-analysis on 2D:4D and athletic prowess: Substantial relationships but neither hand outpredicts the other. *Personality and Individual Differences, 48,* 4-10.

Hönekopp, J., and Watson, S. (2010). Meta-analysis of digit ratio 2D:4D shows greater sex difference in the right hand. *American Journal Human Biology, 22*, 619-630.

Hönekopp, J., and Watson S. (2011). Meta-analysis of the relationship between digit-ratio 2D:4D, and aggression. *Personality and Individual Differences*, *51*, 381-386.

Hurd, P. L., Vaillancourt, K. L., and Dinsdale, N. L. (2010). Aggression, digit ratio and variation in androgen receptor and monoamine oxidase *a* genes in men. *Behavior*

*Genetics, 41*, 543-556.

Kilduff, L., Cook, C. J., Bennett, M., Crewther, B., Bracken, R. M., Manning, J. (2013). Right-left digit ratio (2D:4D) predicts free testosterone levels associated with a physical challenge. *Journal of Sports Sciences*, *31*, 677-683.

Knickmeyer, R. C., Woolson, S., Hamer, R. M., Konneker, T., and Gilmore, J. H. (2011). 2D:4D ratios in the first 2 years of life: Stability and relation to testosterone exposure and sensitivity. *Hormones and Behavior*, *60*, 256-263.

Lawrance-Owen, A. J., Bargary, G., Bosten, J. M., Goodbourn, P. T., and Hogg, R. E. (2013). Genetic association suggests that SMOC1 mediates between prenatal sex hormones and digit ratio. *Human Genetics*, *132*, 415-421.

Loehlin, J. C., Medland, S. E., and Martin N. G. (2012). Is CAG sequence length in the androgen receptor gene correlated with finger-length ratio? *Personality and Individual Differences, 52*, 224-227.

Longman, D., Stock, J. T., and Wells, J. C. (2011). Digit ratio (2D:4D) and rowing ergometer performance in males and females. *American Journal Physical Anthropology, 144*, 337-341.

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 USA, 108*, 16143-16144.

Manning, J. T., Bundred, P. E., Newton, D. J., and Flanagan, B. F. (2003) The second to fourth digit ratio and variation in the androgen receptor gene. *Evolution and Human Behavior, 24*, 399-405.

Manning, J.T., Kilduff, L.P., Trivers, R. (2013). Digit ratio (2D:4D) in Klinefelter's syndrome. *Andrology*, 1, 94-99.

Manning, J. T., Scutt, D., Wilson, J., and 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, 13*, 3000-3004.

Manning, J. T., and Taylor, R. P. (2001). Second to fourth digit ratio and male ability in sport: Implications for sexual selection in humans. *Evolution and Human Behavior, 22*, 61-69.

Millet, K. (2010). An inter-actionist perspective on the relation between 2D:4D and behaviour: An overview of (moderated) relationships between 2D:4D and economic decision making. *Personality and Individual Differences, 51*, 397-401.

Millet, K., and Dewitte, S. (2007). Digit ratio (2D:4D) moderates the impact of an aggressive music video on aggression. *Personality and Individual Differences, 43*, 289-294.

Montoya, E. R., Terburg, D., Bos, P. A., Will, G. J., Buskens, V., Raub, W., and van Honk, J. (2013). Testosterone administration modulates moral judgements depending on second-to-fourth digit ratio. *Psychoneuroendocrinology, 38*, 1362-1369.

Muller, D. C., Giles, G. G., Bassett, J., Morris, H. A., Manning, J. T., Hopper, J. L., . . . Severi, G. (2011). Second to fourth digit ratio (2D: 4D) and concentrations of circulating sex hormones in adulthood. *Reproductive Biology and Endocrinology, 9*, 57.

Perciavalle, V., Corrado, D. D., Petralia, M. C., Gurrisi, L., Massimino, S., and Coco, M. (2013). The second-to-fourth digit ratio correlates with aggressive behaviour in professional soccer players. *Molecular Medicine Reports, 7*, 1733-1738.

Talarovicova, A., Krskova, L., and Blazekova, L. (2009). Testosterone enhancement during pregnancy influences the 2D:4D ratio and open field motor activity of rat siblings in adulthood. *Hormones and Behavior*, *55*, 235-239.

Van Honk, J., Montoya, E. R., Bos, P. A., van Vugt, M., and Terburg D. (2012). New evidence on testosterone and cooperation. *Nature, 485*, E4-E5.

Van Honk, J., Schutter, D. J., Bos, P. A., Kruijt, A-W., Lentjes, E. G., and 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 USA*, *108*, 3448-3452.

Zheng, Z., and Cohn, M. J. (2011). Developmental basis of sexually dimorphic digit ratios. *Proceedings of the National Academy of Sciences USA*, *108*, 16289-16294.