Since January 2020 Elsevier has created a COVID-19 resource centre with free information in English and Mandarin on the novel coronavirus COVID-19. The COVID-19 resource centre is hosted on Elsevier Connect, the company's public news and information website.

Elsevier hereby grants permission to make all its COVID-19-related research that is available on the COVID-19 resource centre - including this research content - immediately available in PubMed Central and other publicly funded repositories, such as the WHO COVID database with rights for unrestricted research re-use and analyses in any form or by any means with acknowledgement of the original source. These permissions are granted for free by Elsevier for as long as the COVID-19 resource centre remains active.

Early Human Development 149 (2020) 105138

Contents lists available at ScienceDirect

Early Human Development

journal homepage: www.elsevier.com/locate/earlhumdev

Second-to-fourth digit ratio and facial shape in Buryats of Southern Siberia

Victoria V. Rostovtseva[a,*], Anna A. Mezentseva[b], Sonja Windhager[c], Marina L. Butovskaya[a,d]

[a] Institute of Ethnology and Anthropology, Russian Academy of Sciences, Leninskiy pr-t 32a, Moscow 119334, Russia
[b] Department of Ethnology, Lomonosov Moscow State University, Lomonosovskiy pr-t 27/4, Moscow 119192, Russia
[c] Department of Evolutionary Anthropology, University of Vienna, Althanstrasse 14, Vienna 1090, Austria
[d] National Research University Higher School of Economics, Myasnitskaya str. 20, Moscow 101000, Russia

ARTICLE INFO

Keywords:
2D:4D
Digit ratio
Prenatal hormones
Sexual dimorphism
Facial shape
Testosterone

ABSTRACT

Background: The 2nd-to-4th digit ratio (2D:4D) is a putative predictor of a prenatal exposure to sex hormones. 2D:4D is sexually dimorphic (males < females). Studies, linking digit ratio and full facial shapes among Europeans, show that a low 2D:4D is associated with a set of male-specific facial features. Buryats – Mongolian people from Southern Siberia – demonstrate a different pattern of facial sexual dimorphism than Europeans (narrower and more vertically elongated faces in men as opposed to women).

Aim: The aim of the present study was to investigate the association between facial shape and the 2D:4D in comparison to the pattern of facial sexual dimorphism in Buryats.

Subjects: Buryats: 88 men and 80 women aged 20 ± 2 years.

Outcome measures: To assess relationship between facial shape and 2D:4D we used a geometric morphometric approach based on standardized full-face frontal photographs and direct measurements of the digit lengths among right-handed individuals.

Results: The results revealed that 2D:4D was associated with facial morphology in Buryat men, and to a lesser extent in women. Narrower faces, elongated in the vertical direction, and a narrower lower facial outline, were characteristic of Buryat men with low 2D:4D ratios, which corresponded to the male-like facial shapes in Buryats.

Conclusions: In Europeans, such facial features were reported for men with a high 2D:4D, which corresponded more to female-like European facial shapes. Hence, our results show that sex-specific morphogenesis in humans is multidirectional, and that digit ratio is capable of predicting sex-specific facial traits even in populations with differing sexually-dimorphic morphology.

1. Introduction

During the last decades, the 2nd-to-4th digits ratio (2D:4D) has been extensively studied as a putative predictor of a prenatal exposure to sex hormones in humans [1–4]. Sexual dimorphism of digit ratios is found across a majority of vertebrates starting from amphibians [5,6], although it is not unidirectional in all species [7,8]. For many human populations, the 2D:4D has been reported to be sexually dimorphic (with higher values in women) [9–13], which occurs as early as at the 9th week of gestation [14,15]. The Leydig cells, which are responsible for production of testosterone (T), start functioning in human male fetuses from the 8th week of gestation [16], suggesting that an increase in T concentration during early prenatal development can be associated with sex-specific digit morphogenesis. Part of the mechanisms underlying an impact of prenatal androgen/estrogen exposure on the formation of differences in the 2nd and 4th digit lengths has already been experimentally revealed in mice [17]. This, along with studies linking the development of digits and gonads [18], and with androgen receptor sensitivity [19], suggests 2D:4D to be a fine potential predictor of exposure to sex hormones *in utero*. The role of the 2D:4D as a marker is also supported by numerous studies reporting its association with sex-specific morphology and behavior in humans [10,20–26] (although see [27–29] for criticism).

Human facial morphology is also subjected to considerable sex differences, with men on average having more robust faces: a relatively lower forehead, an (at least slightly) higher facial width-to-height ratio (fWHR), and larger lower face [23,27–37]. One of the reasons for this is also the exposure to gonadal hormones [23,26,37–42].

Surprisingly, research on the 2D:4D ratio in combination with facial morphology are very rare. Few comprehensive studies, linking digit

* Corresponding author.
E-mail address: victoria.v.rostovtseva@gmail.com (V.V. Rostovtseva).

https://doi.org/10.1016/j.earlhumdev.2020.105138
Received 21 June 2020; Received in revised form 8 July 2020; Accepted 14 July 2020
0378-3782/ © 2020 Elsevier B.V. All rights reserved.

ratio and full facial shapes among representatives of European populations [23,26,43], have demonstrated that a low 2D:4D (a typically male trait) shows association with a set of population-specific male facial features, but with an admixture of some other, unrelated to chromosomal sex, patterns [23]. The association between 2D:4D and facial shape was also reported to be especially pronounced in men [23]. Another study, also focusing on a full-facial shape analysis among Europeans, has revealed that male-specific facial traits occur in boys even prior to puberty, and are negatively associated with the 2D:4D ratio [25].

Sex-specific facial morphology may be subjected to population differences. A number of studies provide evidence that, leastways, such differences occur between European and Asian populations. Primary differences are located in such facial areas as the lower face, which in Europeans tend to demonstrate higher widths in men, and in Asians – in women [23,29,32,34,35,44,45], nose, and lip shapes [35,44,46]. Therefore, it is of special interest to explore whether the association between 2D:4D and facial morphology in different populations corresponds to the observed variation in facial sexual dimorphism.

Buryats – Mongolian people of Southern Siberia – may be considered as a population of interest for comparison with Europeans. According to the previous studies, sexual dimorphism in facial parameters of Buryats are similar to that reported for other Asian populations (higher relative lower facial width, and thinner upper lips in females), but also has a distinctive feature, such as a lower fWHR in men [44,47–49]. These facial parameters distinguish representatives of the Buryat population from European subjects, studied earlier with regard to association between 2D:4D ratio and facial shape [22,25,26,43]. Assuming that 2D:4D is related to prenatal androgenization, we hypothesized that the expression of more male-specific facial traits in Buryats will be associated with lower digit ratios in both sexes. At the same time, this association is expected to demonstrate a partly reversed pattern compared to Europeans, which is in line with the observed differences in the facial sexual dimorphism patterns. Of course, none of this precludes additional effects of post-pubertal steroid action on the adult sexual dimorphism.

To test this hypothesis, we conducted a study among modern Buryats, investigating association between 2D:4D ratio and full facial shape using geometric morphometrics. This is, to our knowledge, the first study to address this issue in Siberian (and Mongolian) populations.

2. Materials and methods

Participants of our study were 187 Buryats (88 female, 99 male) – representatives of a Mongolian population living in Southern Siberia (Baikal Lake area). Participants were aged 20 ± 2 years (from 17 to 25 years, with two male outliers, who were 16 and 28 years of age). No significant sex differences in age were observed. All of the participants were residents of Ulan-Ude – the capital of Buryatia. All of them (with two exceptions) were students of different specialities (natural and social sciences, engineering, and arts) represented in approximately equal proportions. The body mass index of the participants was within the normal range (men: 22.06 ± 2.66 kg/m^2; women: 21.50 ± 2.48 kg/m^2; [50,51]).

The 2nd and 4th digit lengths were measured directly [3,22] using an electronic caliper with a precision of 0.01 mm. Each participant's digits were measured twice, and the mean value of two measurements was used for further analysis. The Intraclass Correlation Coefficient (ICC; [52]) between two measurements (two-way mixed model, absolute agreement, single measurement) was 0.99 ($p < 0.001$). In the current study, we focused on the right-hand digit ratio, as it has been previously reported to show a stronger relationship with sex-specific traits [3,11,17,53]. Only self-reported right-handed participants were selected for the analysis, since they were the majority, and it is known that handedness, as a presumable consequence of specific cerebral lateralization, may be associated with exposure to prenatal sex hormones [54–57]. Therefore, the final sample consisted of 168 individuals (80 women, 88 men). Participants had no congenital or acquired damage to the hand or fingers on the right hand.

The facial morphology was analyzed using geometric morphometrics [58] based on standardized facial photographs. Participants had no congenital or acquired facial deformations. Each participant was photographed in full-face, with a neutral facial expression, sitting on a fixed chair, with a natural head position (Frankfort horizontal plane). The camera was positioned at eyes' height. The distance between camera and participant was 170 cm. Every photograph included a scale bar (in cm). Seventy-one digital landmarks and semi-landmarks [45] were placed on each photograph using tpsDig2 2.17 [59]. To test for inter-rater agreement, the manual landmark digitization was made by two independent observers on 40 randomly selected photographs (20 male and 20 female faces). According to the ICC estimates (based on single measurement, absolute agreement, two-way mixed-effects model), the inter-observer agreement was almost perfect (ICC = 0.98, $p < 0.001$). The method was deemed reliable enough to proceed with manual digitalization of landmarks by one of the observers. The facial configurations were standardized for position, orientation and scale using a Generalized Procrustes superimposition, which was performed iteratively together with the sliding of the semi-landmarks in tpsRelw 1.67 [59]. In addition, the facial shape information was symmetrized in Mathematica 11 [60]. Thereafter, the facial shape coordinates were regressed upon sex of the participants (male, female) and the 2D:4D ratio using tpsRegr 1.45 [59]. To test for statistical significance permutation tests with 10,000 permutations were used [61]. Visualization of facial shape differences was realized with thin-plate deformation grids using tpsRegr 1.45 [59]. Geometric morphometric morphs' visualization was conducted by unwarping and averaging the images in tpsSuper 2.04 [45,59].

3. Results

Within the given age range, there was no significant effect of age on male facial shape variation (var. expl. < 1%, $p = 0.524$), and a weak trend was detected only in women (var. expl. 2.43%, $p = 0.063$). Also there was no association between age and 2D:4D, neither in men ($R^2 < 0.001$, $p = 0.968$), nor in women ($R^2 < 0.001$, $p = 0.889$). Female Buryats generally had higher digit ratios on the right hand (0.96 ± 0.03), than male Buryats (0.95 ± 0.03), but the difference was not statistically significant (Student's *t*-test: $t = -0.590$, $p = 0.556$). To test for possible allometric effects, which suggest a negative relationship between 2D:4D and general finger lengths (as well as general hand size) [62–64], we have regressed 2D:4D ratio upon mean digits length (sum of the lengths for 2nd and 4th digits divided by two). Linear regression analysis for the whole sample (Beta = 0.029, $R^2 = 0.001$, $p = 0.705$), as well as for men (Beta = 0.033, $R^2 = 0.001$, $p = 0.762$), and women (Beta = 0.118, $R^2 = 0.014$, $p = 0.298$) separately did not reveal any significant associations. Hence, lower 2D:4D ratios in our study were not associated with longer digits, which do not support the allometry hypothesis.

To assess sexual dimorphism in facial shape, we regressed facial shape coordinates upon the sex of participants. A permutation test revealed significant differences in facial shape between right-handed men and women (var. expl. 20%; $p < 0.001$). Fig. 1a displays the average female and male faces with an exaggeration factor of 2.5 (to facilitate visual perception of the observed differences). Next, we regressed the facial shape coordinates upon 2D:4D of the right hand, for men and women separately. In terms of facial shape variation, the permutation test revealed a significant association only for men (N = 88, var. expl. 3%, $p = 0.036$), whereas 2D:4D did not significantly contribute to female facial variation(N = 80, var. expl. < 1%, $p = 0.773$). Still, the correlation between facial shape scores and 2D:4D was significant in both sexes (men: $r = 0.36$, $p = 0.0005$; women: $r = 0.27$, $p = 0.017$),

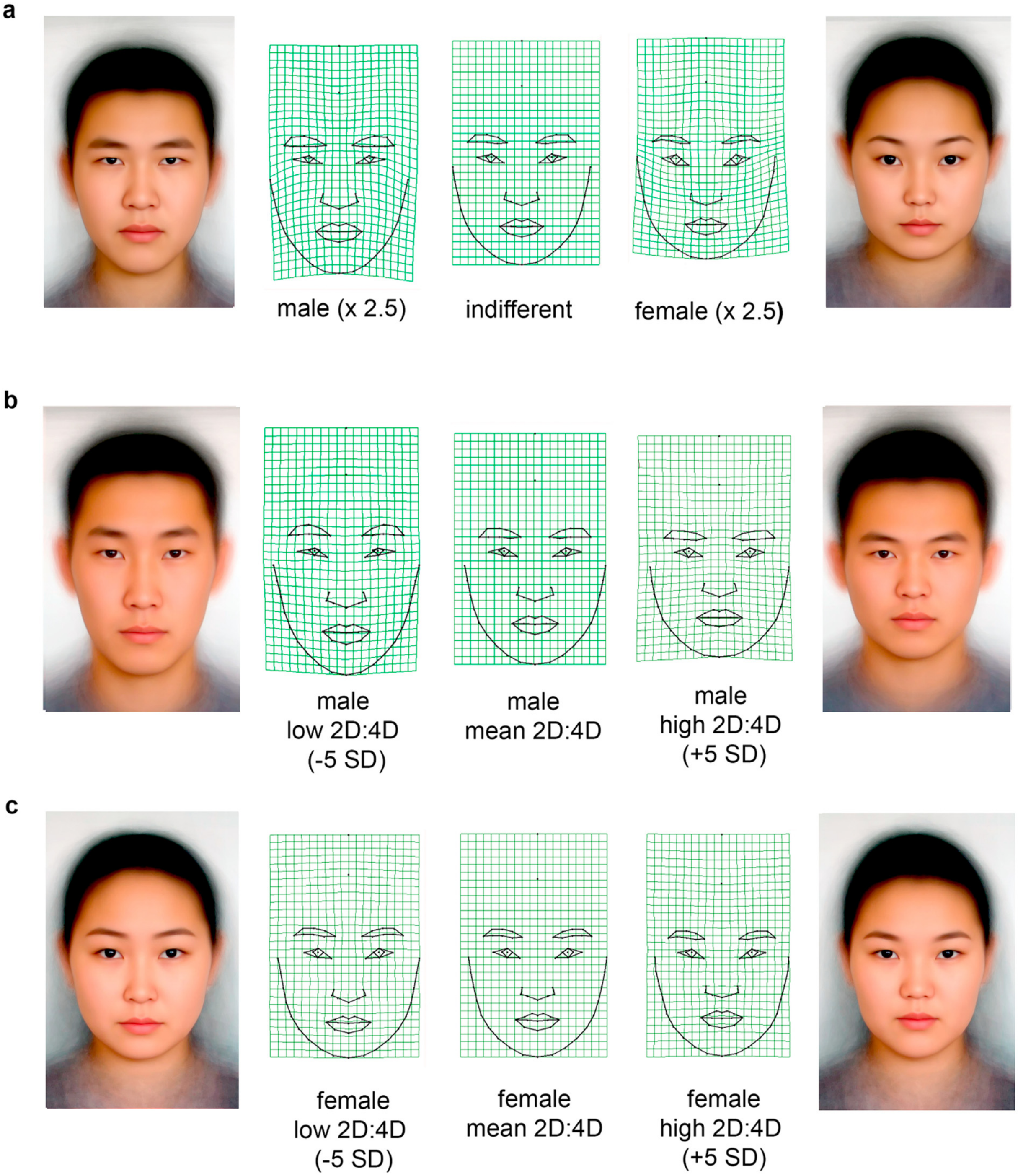

Fig. 1. Sexual dimorphism in the facial shape of right-handed Buryats (a), and facial shape differences associated with the 2D:4D ratio of the right hand, a putative proxy for prenatal androgen exposure, for male (b) and female (c) Buryats.
(a) Sex differences are statistically significant (N = 168; var. expl. 20%; $p < 0.001$) and exaggerated by a factor of 2.5. (b) Association between facial shape and 2D:4D in men and (c) in women. The average face here is deformed towards ± 5 standard deviations of 2D:4D from that mean.

which means that there is a weak, but significant association between facial shape and 2D:4D in both sexes. Fig. 1 displays the effect of the 2D:4D on facial shape within each sex, exaggerated to +/− 5 SD from the male (Fig. 1b) and the female (Fig. 1c) averages, respectively. The amount of exaggeration was chosen arbitrarily to facilitate visual perception of shape differences.

According to the deformation grids displayed in Fig. 1b, lower 2D:4D ratios (which presumably indicate a high level of prenatal androgenization) in men were associated with male-related facial features (Fig. 1a), such as a relatively narrower face with larger general height in the vertical plane, a relatively narrower lower face (in the area of the bigonial breadth), and narrower eyes fissures. At the same time higher 2D:4D ratios (low prenatal androgenization) in men were associated with some characteristics typical of women in that population. However, not all of the sex-specific morphometric traits corresponded to the variation in facial shape explained by the 2D:4D ratio in men. Namely, such parameters are the distance between the eyes and eyebrows as well as relative forehead height, which are distinctive features for men and women, but remained unaffected or demonstrated a reverse pattern when seen as a function of 2D:4D ratios. Thus, the main differences associated with 2D:4D are located in the mid- and lower part of the male face (in the craniofacial segment), whereas the area of the frontal bone (including forehead and the eyebrow region) did not show differences in expected direction. In women with higher 2D:4D ratios, the relatively wider spacing of eyebrows and eyes reflect the female pattern, whereas the relatively more massive chin region and lower hairline do not fit the other patterns. The diminutiveness of shape changes even if presented for ± 5 SD supports the comparably weak relationship between 2D:4D and facial shape in women.

4. Discussion

Our study demonstrated that 2D:4D ratio, as a putative proxy for prenatal androgen exposure, is associated with male facial morphology, which has also been previously reported for other populations [23,25,26,43]. However, a comparison of our results with the results of these studies shows that the pattern of facial sexual dimorphism, and accordingly the shape pattern of the association with 2D:4D differs between populations. Generally narrower faces, elongated in the vertical direction, and particularly a narrower lower facial outline, were characteristic of men (and boys) of European origin with high 2D:4D ratios. This in turn at least partly corresponded to the female-like facial shapes in that population (Europeans). At the same time, low 2D:4D ratios in those studies were characteristic of men with relatively wider faces (especially in the lower face), which corresponds to male-related features in Europeans [23,29]. Still, in our study of Buryats (Mongolian origin) the pattern was somewhat reversed, which at the same time corresponded to the general direction of facial sexual dimorphism in Buryats (Fig. 1a). Part of the sex-specific facial traits was not associated with the male 2D:4D pattern both in our study, and in the studies by our colleagues conducted in Europe [23,26]. This indicates the existence of further mechanisms for sex-specific facial morphogenesis, such as the impact of sex hormone exposure on later stages of ontogenesis (perinatal [37], pubertal hormones [42]), allometric effects [65], genetics [66,67], and sexual selection [36,68–71]) to result in the observable pattern of sexual dimorphism in young adulthood. The lack of association between 2D:4D and some facial regions might cause null results in studies where only some discrete indexes or incomplete facial shapes are considered. We suppose that this could be one of the reasons for null association between 2D:4D and facial shape reported by Whitehouse and colleagues [37], who run the analysis based on 21 facial landmarks (and no information on the full-face outline and visible eye shape). With regard to the study by Whitehouse and others it is also important to note, that the lack of association between T concentrations in umbilical cord upon delivery and the 2D:4D ratios, which has been also reported by several studies earlier [72,73], cannot evidence that 2D:4D is a poor predictor of prenatal androgenization. The reason is that umbilical cord method deals with the level of hormones in the perinatal period, when T is significantly decreased compared to early prenatal levels [74]. Whitehouse and colleagues [37] obtained relatively large correlation coefficients between perinatal hormone levels and adult facial scores (from a discriminant function analysis of adult sex differences based on a number of facial distances). It remains to be determined whether the perinatal hormonal effects replicate in studies like ours, where facial shape is studied more holistically by preserving the geometry of the morphological structures, and independently of absolute size differences. The lack of a significant association of facial shape variation and 2D:4D in women is in line with the findings of Fink and colleagues [23] for European faces. In sum, our results suggest that, if 2D:4D ratios can be considered as a marker of prenatal androgenization, the impact of prenatal hormones can at least partly explain the male-specific morphogenesis characteristic of a particular population. Our findings also indicate that population homogeneity of studied subjects should be strictly enforced in research dealing with androgen exposure and its consequences, to avoid false null or contradictive results.

Funding

VR, AM, MB were supported by the Russian Science Foundation, grant 18-18-00075. SW was supported by the Austrian Science Fund, FWF, P29397 and the Young Investigator Award of the Faculty of Life Sciences, University of Vienna.

Conflict of interest statement

None declared.

CRediT authorship contribution statement

Victoria V. Rostovtseva: Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Validation, Writing - original draft, Writing - review & editing.**Anna A. Mezentseva:**Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing - review & editing.**Sonja Windhager:**Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Supervision, Visualization, Writing - review & editing.**Marina L. Butovskaya:**Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing - review & editing.

Acknowledgments

The authors are grateful to East-Siberian State Institute of Culture for assistance in organizing the study in Buryatia, and to Philipp Gunz and Philipp Mitteroecker for sharing their Mathematica code.

References

[1] S.M. Breedlove, Minireview: organizational hypothesis: instances of the fingerpost, Endocrinology 151 (9) (2010) 4116–4122, https://doi.org/10.1210/en.2010-0041.

[2] J. Hönekopp, L. Bartholdt, L. Beier, A. Liebert, Second to fourth digit length ratio (2D:4D) and adult sex hormone levels: new data and a meta-analytic review, Psychoneuroendocrinology 32 (4) (2007) 313–321, https://doi.org/10.1016/j.psyneuen.2007.01.007.

[3] J.T. Manning, D. Scutt, J. Wilson, D.I. Lewis-Jones, The ratio of 2nd to 4th digit length: a predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen, Hum. Reprod. 13 (11) (1998) 3000–3004, https://doi.org/10.1093/humrep/13.11.3000.

[4] J. Manning, L. Kilduff, C. Cook, B. Crewther, B. Fink, Digit ratio (2D:4D): a biomarker for prenatal sex steroids and adult sex steroids in challenge situations, Front. Endocrinol. 5 (2014), https://doi.org/10.3389/fendo.2014.00009.

[5] M.P. Lombardo, P.A. Thorpe, B.M. Brown, K. Sian, Digit ratio in birds, Anat. Rec. 291 (12) (2008) 1611–1618, https://doi.org/10.1002/ar.20769.

[6] G.V. Direnzo, J.L. Stynoski, Patterns of second-to-fourth digit length ratios (2D:4D) in two species of frogs and two species of lizards at La Selva, Costa Rica, Anat. Rec. 295 (4) (2012) 597–603, https://doi.org/10.1002/ar.22411.

[7] A.D. Abbott, R.J. Colman, R. Tiefenthaler, D.A. Dumesic, D.H. Abbott, Early-to-mid gestation fetal testosterone increases right hand 2D:4D finger length ratio in polycystic ovary syndrome-like monkeys, PLoS One 7 (8) (2012) e42372, , https://doi.org/10.1371/journal.pone.0042372.

[8] A. Baxter, E.K. Wood, P. Jarman, A.N. Cameron, J.P. Capitanio, J.D. Higley, Sex differences in rhesus monkeys' digit ratio (2D:4D ratio) and its association with maternal social dominance rank, Front. Behav. Neurosci. 12 (2018), https://doi.org/10.3389/fnbeh.2018.00213.

[9] M. Butovskaya, J. Fedenok, V. Burkova, J. Manning, Sex differences in 2D:4D and aggression in children and adolescents from five regions of Russia, Am. J. Phys. Anthrop. 152 (1) (2013) 130–139, https://doi.org/10.1002/ajpa.22337.

[10] M. Butovskaya, V. Burkova, D. Karelin, B. Fink, Digit ratio (2D:4D), aggression, and dominance in the Hadza and the Datoga of Tanzania, Am. J. Hum. Biol. 27 (5) (2015) 620–627, https://doi.org/10.1002/ajhb.22718.

[11] J. Hönekopp, S. Watson, Meta-analysis of digit ratio 2D:4D shows greater sex difference in the right hand, Am. J. Hum. Biol. 22 (5) (2010) 619–630, https://doi.org/10.1002/ajhb.21054.

[12] J.T. Manning, L. Barley, J. Walton, D.I. Lewis-Jones, R.L. Trivers, D. Singh, et al., The 2nd:4th digit ratio, sexual dimorphism, population differences, and reproductive success, Evol. Hum. Behav. 21 (3) (2000) 163–183, https://doi.org/10.1016/S1090-5138(00)00029-5.

[13] J.T. Manning, B. Fink, Understanding COVID-19: digit ratio (2D: 4D) and sex differences in national case fatality rates, Early Hum. Dev. (2020) 105074.

[14] F. Galis, C.M.A. Ten Broek, S. Van Dongen, L.C.D. Wijnaendts, Sexual dimorphism in the prenatal digit ratio (2D:4D), Arch. Sex. Behav. 39 (1) (2009) 57–62, https://doi.org/10.1007/s10508-009-9485-7.

[15] M.A. Malas, S. Dogan, E. HilalEvcil, K. Desdicioglu, Fetal development of the hand, digits and digit ratio (2D:4D), Early Hum. Dev. 82 (7) (2006) 469–475, https://doi.org/10.1016/j.earlhumdev.2005.12.002.
[16] V.W.K. Lee, H.G. Burger, Pituitary testicular axis during pubertal development, in: D.M. de Kretser, H.G. Burger, B. Hudson (Eds.), The Pituitary and Testis. Monographs on Endocrinology, 25 Springer, Berlin, Heidelberg, 1983, pp. 44–70, , https://doi.org/10.1007/978-3-642-81912-4_3.
[17] Z. Zheng, M.J. Cohn, Developmental basis of sexually dimorphic digit ratios, PNAS USA 108 (39) (2011) 16289–16294, https://doi.org/10.1073/pnas.1108312108.
[18] A.J. Lawrance-Owen, G. Bargary, J.M. Bosten, P.T. Goodbourn, R.E. Hogg, J.D. Mollon, Genetic association suggests that SMOC1 mediates between prenatal sex hormones and digit ratio, Hum. Genet. 132 (4) (2012) 415–421, https://doi.org/10.1007/s00439-012-1259-y.
[19] N.M. Warrington, E. Shevroja, G. Hemani, P.G. Hysi, Y. Jiang, A. Auton, et al., Genome-wide association study identifies nine novel loci for 2D:4D finger ratio, a putative retrospective biomarker of testosterone exposure in utero, Hum. Mol. Genet. 27 (11) (2018) 2025–2038, https://doi.org/10.1093/hmg/ddy121.
[20] B. Auyeung, S. Baron-Cohen, E. Ashwin, R. Knickmeyer, K. Taylor, G. Hackett, M. Hines, Fetal testosterone predicts sexually differentiated childhood behavior in girls and in boys, Psychol. Sci. 20 (2) (2009) 144–148, https://doi.org/10.1111/j.1467-9280.2009.02279.x.
[21] B. Fink, N. Neave, J.T. Manning, Second to fourth digit ratio, body mass index, waist-to-hip ratio, and waist-to-chest ratio: their relationships in heterosexual men and women, Ann. Hum. Biol. 30 (6) (2003) 728–738, https://doi.org/10.1080/03014460310001620153.
[22] B. Fink, J.T. Manning, N. Neave, Second to fourth digit ratio and the 'big five' personality factors, Pers. Individ. Differ. 37 (3) (2004) 495–503, https://doi.org/10.1016/j.paid.2003.09.018.
[23] B. Fink, K. Grammer, P. Mitteroecker, P. Gunz, K. Schaefer, F.L. Bookstein, J. Manning, Second to fourth digit ratio and face shape, P. Roy. Soc. B-Biol. Sci. 272 (1576) (2005) 1995–2001, https://doi.org/10.1098/rspb.2005.3179.
[24] M. Hines, Sex-related variation in human behavior and the brain, Trends Cogn. Sci. 14 (10) (2010) 448–456, https://doi.org/10.1016/j.tics.2010.07.005.
[25] K. Meindl, S. Windhager, B. Wallner, K. Schaefer, Second-to-fourth digit ratio and facial shape in boys: the lower the digit ratio, the more robust the face, P. Roy. Soc. B-Biol. Sci. 279 (1737) (2012) 2457–2463, https://doi.org/10.1098/rspb.2011.2351.
[26] K. Schaefer, B. Fink, P. Mitteroecker, N. Neave, F.L. Bookstein, Visualizing facial shape regression upon 2nd to 4th digit ratio and testosterone, Coll. Antropol 29 (2) (2005) 415–419.
[27] L. Bigoni, J. Velemínská, J. Brůžek, Three-dimensional geometric morphometric analysis of cranio-facial sexual dimorphism in a Central European sample of known sex, Homo 61 (1) (2010) 16–32, https://doi.org/10.1016/j.jchb.2009.09.004.
[28] M.L. Butovskaya, S. Windhager, D. Karelin, A. Mezentseva, K. Schaefer, B. Fink, Associations of physical strength with facial shape in an African pastoralist society, the Maasai of northern Tanzania, PLoS One 13 (5) (2018) e0197738, , https://doi.org/10.1371/journal.pone.0197738.
[29] L.G. Farkas, M.J. Katic, C.R. Forrest, International anthropometric study of facial morphology in various ethnic groups/races, J. Craniofac. Surg. 16 (4) (2005) 615–646, https://doi.org/10.1097/01.scs.0000171847.58031.9e.
[30] M. Coquerelle, F.L. Bookstein, J. Braga, D.J. Halazonetis, G.W. Weber, P. Mitteroecker, Sexual dimorphism of the human mandible and its association with dental development, Am. J. Phys. Anthropol. 145 (2) (2011) 192–202, https://doi.org/10.1002/ajpa.21485.
[31] S.N. Geniole, T.F. Denson, B.J. Dixson, J.M. Carré, C.M. McCormick, Evidence from meta-analyses of the facial width-to-height ratio as an evolved cue of threat, PLoS One 10 (7) (2015) e0132726, , https://doi.org/10.1371/journal.pone.0132726.
[32] K. Kasai, L.C. Richards, T. Brown, Comparative study of craniofacial morphology in Japanese and Australian aboriginal populations, Hum. Biol. 65 (5) (1993) 821–834.
[33] R.S.S. Kramer, Sexual dimorphism of facial width-to-height ratio in human skulls and faces: a meta-analytical approach, Evol. Hum. Behav. 38 (3) (2017) 414–420, https://doi.org/10.1016/j.evolhumbehav.2016.12.002.
[34] Y. Liu, C.H. Kau, L. Talbert, F. Pan, Three-dimensional analysis of facial morphology, J. Craniofac. Surg. 25 (5) (2014) 1890–1894, https://doi.org/10.1097/01.SCS.0000436677.51573.a6.
[35] C. Tanikawa, E. Zere, K. Takada, Sexual dimorphism in the facial morphology of adult humans: a three-dimensional analysis, Homo 67 (1) (2016) 23–49, https://doi.org/10.1016/j.jchb.2015.10.001.
[36] E.M. Weston, A.E. Friday, P. Liò, Biometric evidence that sexual selection has shaped the Hominin face, PLoS One 2 (8) (2007) e710, https://doi.org/10.1371/journal.pone.0000710.
[37] A.J. Whitehouse, S.Z. Gilani, F. Shafait, A. Mian, D.W. Tan, M.T. Maybery, et al., Prenatal testosterone exposure is related to sexually dimorphic facial morphology in adulthood, Proc. Roy. Soc. B-Biol. Sci. 282 (1816) (2015) 20151351, https://doi.org/10.1098/rspb.2015.1351.
[38] C.W. Bardin, J.F. Catterall, Testosterone: a major determinant of extragenital sexual dimorphism, Science 211 (4488) (1981) 1285–1294.
[39] C.E. Lefevre, G.J. Lewis, D.I. Perrett, L. Penke, Telling facial metrics: facial width is associated with testosterone levels in men, Evol. Hum. Behav. 34 (4) (2013) 273–279, https://doi.org/10.1016/j.evolhumbehav.2013.03.005.
[40] M.J. Law Smith, D.I. Perrett, B.C. Jones, R.E. Cornwell, F.R. Moore, D.R. Feinberg, et al., Facial appearance is a cue to oestrogen levels in women, Proc. Roy. Soc. B-Biol. Sci. 273 (1583) (2006) 135–140, https://doi.org/10.1098/rspb.2005.3296.
[41] K. Marečková, M.M. Chakravarty, C. Lawrence, G. Leonard, D. Perusse, M. Perron, et al., Identifying craniofacial features associated with prenatal exposure to androgens and testing their relationship with brain development, Brain Struct. Funct. 220 (6) (2015) 3233–3244, https://doi.org/10.1007/s00429-014-0852-3.
[42] A. Verdonck, M. Gaethofs, C. Carels, F. de Zegher, Effect of low-dose testosterone treatment on craniofacial growth in boys with delayed puberty, Eur. J. Orthod. 21 (2) (1999) 137–143, https://doi.org/10.1093/ejo/21.2.137.
[43] S.M. Weinberg, T.E. Parsons, Z.D. Raffensperger, M.L. Marazita, Prenatal sex hormones, digit ratio, and face shape in adult males, Orthod. Craniofac. Res. 18 (1) (2014) 21–26, https://doi.org/10.1111/ocr.12055.
[44] V.V. Rostovtseva, A.A. Mezentseva, S. Windhager, M.L. Butovskaya, Sexual dimorphism in facial shape of modern Buryats of southern Siberia, Am. J. Hum. Biol. (2020) e23458, https://doi.org/10.1002/ajhb.23458.
[45] S. Windhager, K. Schaefer, B. Fink, Geometric morphometrics of male facial shape in relation to physical strength and perceived attractiveness, dominance, and masculinity, Am. J. Hum. Biol. 23 (6) (2011) 805–814, https://doi.org/10.1002/ajhb.21219.
[46] R.J. Hennessy, A. Kinsella, J.L. Waddington, 3D laser surface scanning and geometric morphometric analysis of craniofacial shape as an index of cerebro-craniofacial morphogenesis: initial application to sexual dimorphism, Biol. Psychiatry 51 (6) (2002) 507–514, https://doi.org/10.1016/S0006-3223(01)01327-0.
[47] V.P. Alexeev, I.I. Gohman, Antropologiya Aziatskoj Chasti SSSR [Anthropology of the Asian Part of the USSR], Nauka, Moscow, 1984.
[48] T.S. Balueva, E.V. Veselovskaya, Novyj kompleks antropologicheskih priznakov v plasticheskoj rekonstrukcii [a new complex of anthropological traits in plastic reconstruction], Sovetskaya etnografiya 3 (1989) 48–59.
[49] N.N. Mamonova, Kochevniki Zabajkal'ya IX-XIII vv. Po dannym paleoantropologii [Transbaikal nomads of IX-XIII cent. According to the paleoanthropological data], Antropologicheskij sbornik 1 (1961) 207–225.
[50] A. Kozlov, G. Vershubsky, M. Kozlova, Indigenous peoples of northern Russia: anthropology and health, Int. J. Circumpolar Health 66 (sup1) (2007) 1–184, https://doi.org/10.1080/22423982.2007.11864604B.
[51] World Health Organization, 2020. Mean body mass index, Available from: https://www.who.int/gho/ncd/risk_factors/bmi_text/en/[accessed 04.06.2020].
[52] T.K. Koo, M.Y. Li, A guideline of selecting and reporting intraclass correlation coefficients for reliability research, J. Chiropr. Med. 15 (2) (2016) 155–163, https://doi.org/10.1016/j.jcm.2016.02.012.
[53] J.T. Manning, Digit Ratio: A Pointer to Fertility, Behavior, and Health, Rutgers University Press, New Brunswick, 2002.
[54] T. Beking, R.H. Geuze, T.G.G. Groothuis, Investigating effects of steroid hormones on lateralization of brain and behavior, in: L. Rogers, G. Vallortigara (Eds.), Lateralized Brain Functions. Neuromethods, 122 Human Press, New York, 2017, pp. 633–666, , https://doi.org/10.1007/978-1-4939-6725-4_20.
[55] T. Beking, R.H. Geuze, M. van Faassen, I.P. Kema, B.P.C. Kreukels, T.G.G. Groothuis, Prenatal and pubertal testosterone affect brain lateralization, Psychoneuroendocrinology 88 (2018) 78–91, https://doi.org/10.1016/j.psyneuen.2017.10.027.
[56] C.C.C. Cohen-Bendahan, J.K. Buitelaar, S.H.M. van Goozen, P.T. Cohen-Kettenis, Prenatal exposure to testosterone and functional cerebral lateralization: a study in same-sex and opposite-sex twin girls, Psychoneuroendocrinology 29 (7) (2004) 911–916, https://doi.org/10.1016/j.psyneuen.2003.07.001.
[57] G.M. Grimshaw, M.P. Bryden, J.-A.K. Finegan, Relations between prenatal testosterone and cerebral lateralization in children, Neuropsychology 9 (1) (1995) 68–79, https://doi.org/10.1037/0894-4105.9.1.68.
[58] F.L. Bookstein, Morphometric Tools for Landmark Data: Geometry and Biology, Cambridge University Press, New York, 1991.
[59] F. Rohlf, The tps series of software, Hystrix, the Italian Journal of Mammalogy 26 (1) (2015) 1–4, https://doi.org/10.4404/hystrix-26.1-11264.
[60] P. Mitteroecker, P. Gunz, Advances in geometric morphometrics, Evol. Biol. 36 (2) (2009) 235–247, https://doi.org/10.1007/s11692-009-9055-x.
[61] P. Good, Permutation Tests: A Practical Guide to Resampling Methods for Testing Hypotheses, Springer, New York, 2000.
[62] W. Forstmeier, Avoiding misinterpretation of regression lines in allometry: is sexual dimorphism in digit ratio spurious? BioRxiv 298786 (2018), https://doi.org/10.1101/298786.
[63] L. Kratochvíl, J. Flegr, Differences in the 2nd to 4th digit length ratio in humans reflect shifts along the common allometric line, Biol. Lett. 5 (5) (2009) 643–646, https://doi.org/10.1098/rsbl.2009.0346.
[64] L. Lolli, A.M. Batterham, L. Kratochvíl, J. Flegr, K.L. Weston, G. Atkinson, A comprehensive allometric analysis of 2nd digit length to 4th digit length in humans, P. Roy. Soc. B-Biol. Sci. 284 (1857) (2017) 20170356, , https://doi.org/10.1098/rspb.2017.0356.
[65] P. Mitteroecker, P. Gunz, S. Windhager, K. Schaefer, A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology, Hystrix, the Italian Journal of Mammalogy 24 (1) (2013) 59–66, https://doi.org/10.4404/hystrix-24.1-6369.
[66] F. Liu, F. van der Lijn, C. Schurmann, G. Zhu, M.M. Chakravarty, P.G. Hysi, et al., A genome-wide association study identifies five loci influencing facial morphology in Europeans, PLoS Genet. 8 (9) (2012) e1002932, , https://doi.org/10.1371/journal.pgen.1002932.
[67] S. Richmond, L.J. Howe, S. Lewis, E. Stergiakouli, A. Zhurov, Facial genetics: a brief overview, Front. Genet. 9 (2018) 462, https://doi.org/10.3389/fgene.2018.00462.
[68] T.R. Clarkson, M.J. Sidari, R. Sains, M. Alexander, M. Harrison, V. Mefodeva, et al., A multivariate analysis of women's mating strategies and sexual selection on men's facial morphology, Roy. Soc. Open Sci. 7 (1) (2020) 191209, https://doi.org/10.1098/rsos.191209.
[69] C. Darwin, The Descent of Man, and Selection in Relation to Sex, Murray, London, 1871.
[70] D. Jones, C.L. Brace, W. Jankowiak, K.N. Laland, L.E. Musselman, J.H. Langlois,

et al., Sexual selection, physical attractiveness, and facial neoteny: cross-cultural evidence and implications [and comments and reply], Curr. Anthropol. 36 (5) (1995) 723–748, https://doi.org/10.1086/204427.

[71] Perrett, D.I., Lee, K.J., Penton-Voak, I., Rowland, D.A., Yoshikawa, S., Burt, D.M., et al. Effects of sexual dimorphism on facial attractiveness, Nature 394(6696) (1998) 884–887. https://doi: https://doi.org/10.1038/29772.

[72] M. Hickey, D.A. Doherty, R. Hart, R.J. Norman, E. Mattes, H.C. Atkinson, et al., Maternal and umbilical cord androgen concentrations do not predict digit ratio (2D:4D) in girls: a prospective cohort study, Psychoneuroendocrinology 35 (8) (2010) 1235–1244, https://doi.org/10.1016/j.psyneuen.2010.02.013.

[73] L.P. Hollier, J.A. Keelan, E.S. Jamnadass, M.T. Maybery, M. Hickey, A.J. Whitehouse, Adult digit ratio (2D:4D) is not related to umbilical cord androgen or estrogen concentrations, their ratios or net bioactivity, Early Hum. Dev. 91 (2) (2015) 111–117, https://doi.org/10.1016/j.earlhumdev.2014.12.011.

[74] J. Codesal, J. Regadera, M. Nista, J. Regadera-Sejas, R. Paniagua, Involution of human fetal leydigcells: animmunohistochemical, ultrastructural and quantitative study, J. Anat. 172 (1990) 103–114.