



Personality and facial morphology: Links to assertiveness and neuroticism in capuchins (*Sapajus [Cebus] apella*)



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ABSTRACT

Personality has important links to health, social status, and life history outcomes (e.g. longevity and reproductive success). Human facial morphology appears to signal aspects of one's personality to others, raising questions about the evolutionary origins of such associations (e.g. signals of mate quality). Studies in non-human primates may help to achieve this goal: for instance, facial width-to-height ratio (fWHR) in the male face has been associated with dominance not only in humans but also in capuchin monkeys. Here we test the association of personality (assertiveness, openness, attentiveness, neuroticism, and sociability) with fWHR, face width/lower-face height, and lower face/face height ratio in 64 capuchins (*Sapajus apella*). In a structural model of personality and facial metrics, fWHR was associated with assertiveness, while lower face/face height ratio was associated with neuroticism (*erratic vs. stable behaviour*) and attentiveness (*helpfulness vs. distractibility*). Facial morphology thus appears to associate with three personality domains, which may act as a signal of status in capuchins.

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1. Introduction

Human personality is associated with differences in important behaviours, ranging from work (Ferguson, Heckman, & Corr, 2011) to well-being (Weiss, Bates, & Luciano, 2008). Research into the biological and evolutionary origins of personality may be of value in understanding these associations. One approach is the examination of links between individual differences in facial structure and behaviour (Plavcan, 2012; Plavcan, Vanschaik, & Kappeler, 1995; Weston, Friday, Johnstone, & Schrenk, 2004), including personality (e.g. Kramer & Ward, 2010; Penton-Voak, Pound, Little, & Perrett, 2006). For instance, facial width-to-height ratio (fWHR: the ratio of the bizygomatic-width to upper face height: see Fig. 1) shows links to dominance-like traits (Carré & McCormick, 2008) though not all studies have found these to be significant (Deaner et al., 2012; Özener, 2012). fWHR has also been associated with achievement striving (Lewis, Lefevre, & Bates, 2012), and with deception and untrustworthiness (Haselhuhn & Wong, 2012; Stirrat & Perrett, 2010).

Recently, links between personality and facial phenotype have been reported by Lefevre et al. (submitted for publication) in a non-human species, the brown capuchin monkey (*Sapajus apella*). Similar to humans, capuchin fWHR predicted individual differences in assertive behaviour and alpha status. Such findings therefore suggest that comparative studies between humans and non-human primates may shed light on the biological and evolutionary basis of appearance-personality associations.

Here we extend this initial work with the same population of capuchins. Because both personality and facial morphology are multi-dimensional, we assessed two additional measures of facial morphology, previously found to be sexually dimorphic in humans (Penton-Voak et al., 2001), but not previously assessed in non-human primates. Second, we moved beyond the single personality trait of assertiveness available to Lefevre et al. to include the full five domains of the Hominoid Personality Questionnaire (Weiss et al., 2009) assessed in capuchins (Morton et al., 2013).

The two new facial metrics assessed were lower face/face height, and face width/lower face height (see Fig. 1). Unlike fWHR (which shows species-specific differences in sexual dimorphism: Kramer, Jones, & Ward, 2012; Lefevre et al., 2012; Özener, 2012), both face width/lower face height and lower face/face height are

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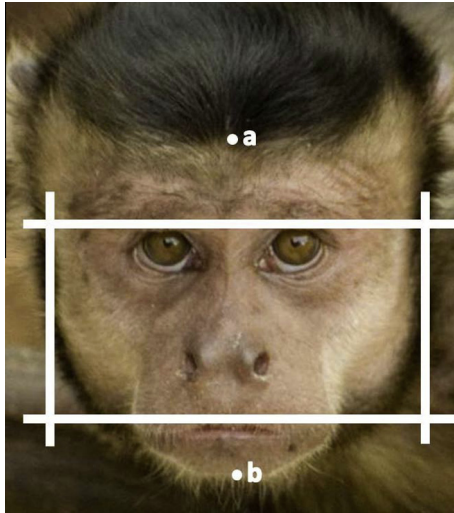


Fig. 1. Measures and measuring points used for morphometric calculations. *Note:* Horizontal lines show the distance between the upper lip and highest point of the eyelids (upper face height), vertical lines show the bizygomatic width. fWHR was calculated as width divided by height using these spans. Face width/lower face height was calculated as the bizygomatic width divided by the distance between the highest point of the eyelids and the lowest point of the chin (marked “b”). Lower face/face height was calculated as the distance between the highest point of the eyelids and the lowest point of the chin divided by the length of the whole face (a–b).

reliably sexually dimorphic in humans (Lefevre et al., 2012; Penton-Voak et al., 2001). Human face width/lower face height is correlated with fWHR, whereas lower face/face height may be independent of fWHR (Lefevre et al., 2012), and the two are weakly inversely correlated (Penton-Voak et al. (2001)). We used a broad assessment of personality – the Hominoid Personality Questionnaire (Weiss et al., 2009), assessing five personality domains in capuchins: Assertiveness (identified by item loadings on *Bullying/Aggressive vs. Gentle/Cautious*); Openness (*Inventive/Inquisitive vs. Quitting*); Attentiveness (*helpfulness vs. distractibility*); Neuroticism (*erratic vs. stable behaviour*), and Sociability (*Affectionate, Friendly vs. Solitary/Depressed*) (Morton et al., 2013).

Given the evidence for an association between fWHR and assertiveness, and the relative independence of assertiveness from other dimensions of personality (Morton et al., 2013), we predicted that assertiveness would remain as the key indicator of fWHR, even after controlling for other personality variables. Secondly, we wished to establish whether the two additional facial metrics discussed above are sexually dimorphic in capuchins. Penton-Voak et al. (2001) reported that lower face/face height was inversely correlated ($r = -0.32$) with face width/lower face height in humans. We therefore tested the association of the two new facial metrics to personality, and whether these were independent predictors or shared variance of personality traits. To our knowledge, neither has been tested for association with personality in either humans or non-human primates. We tentatively predicted that, like fWHR, face width/lower face height would be associated with assertiveness in capuchins based on its shared dependence on face width. The possible links of lower face/face height to personality are unclear, and thus were not specified ahead of analysis.

2. Method

2.1. Sample

The sample consisted of 64 individuals of *Sapajus* recruited across three sites. 6 females (mean age 8.2 ± 4.0 years) and 10

males (mean age 11.4 ± 13.4 years) were recruited from the Living Links to Human Evolution Research Centre, University of St Andrews, Edinburgh Zoo (Macdonald & Whiten, 2011). The Language Research Center, Georgia State University provided 13 females (mean age 15.3 ± 11.8 years) and 9 males (mean age 10.9 ± 5.8 years). Finally 10 females (mean age 12.8 ± 9.2 years) and 16 males (mean age 6.6 ± 4.5 years) were recruited from the Laboratory of Comparative Ethology at the National Institute of Health. The study was non-invasive, approved by local ethics committees, and complied with the 2012 regulations of the Association for the Study of Animal Behaviour.

2.2. Facial measures

Measures were based on frontal facial photographs. Prior to measurement, photographs were horizontally aligned and scaled according to inter-pupillary distance (using the Psychomorph software package; <http://users.aber.ac.uk/bpt/jpsychomorph> (Tiddeman, Perrett, & Burt, 2001)). fWHR was then computed as the ratio of bizygomatic-width (maximum horizontal distance from the left to the right facial boundary) to upper face height (vertical distance from the mid-point of the upper lip to the highest point of the eyelids; see Fig. 1). Lower face/face height and face width/lower face height (Penton-Voak et al., 2001) were calculated as shown in Fig. 1. Measurement reliability was good (ICC = .86) based on a subset of photographs ($N = 18$) measured twice. In addition, measures from several photographs per individual (mean = 4.69, SD = 2.44) were averaged in order to maximise the signal to noise ratio. All images were taken within 1 calendar year, thus controlling for longitudinal changes.

2.3. Personality measures

The personality ratings were collected for each animal individually using the Hominoid Personality Questionnaire (Weiss et al., 2009). This 54-item measure has been validated in chimpanzees (*Pan troglodytes*) (Weiss et al., 2009), orang-utans (*Pongo spp.*) (Weiss, King, & Perkins, 2006), rhesus macaques (*Macaca mulatta*) (Weiss, Adams, Widdig, & Gerald, 2011), and brown capuchin monkeys (Morton et al., 2013). The items consist of adjective markers, accompanied by one to three short behavioural descriptions. For example, the item *Fearful* is described as “Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.” Items are scored on a 7-point Likert scale ranging from 1: display either total absence or negligible amounts of the trait, to 7: display extremely large amounts of the traits.

All personality data used in this study are described fully in Morton et al. (2013). Briefly, ratings were collected for 127 monkeys. Between one and seven raters, each familiar with the monkeys, conducted the ratings, and to maintain independence of scoring were asked not to discuss their ratings with other raters. Inter-rater reliability was calculated for all monkeys with two or

Table 1
Means (and standard deviations) for personality dimensions and facial metrics.

Trait	Female	Male
Assertiveness	3.79 (1.13)	3.88 (0.93)
Openness	4.03 (0.69)	4.40 (0.69)
Sociability	4.74 (0.67)	4.74 (0.72)
Attentiveness	4.68 (0.65)	4.79 (0.54)
Neuroticism	4.0 (0.61)	4.10 (0.53)
fWHR	2.14 (0.14)	2.20 (0.17)
Face width/lower face height	1.41 (0.08)	1.45 (0.09)
Lower face/face height	0.75 (0.04)	0.74 (0.04)

Table 2Table of zero-order correlations among all personality and face variables. $N = 64$ for all cells.

	Attentiveness	Neuroticism	Assertiveness	Openness	Sociability	Lower face/face height	fWHR	Face width/lower face height
Attentiveness	1.00	−0.53	0.02	0.14	0.54	−0.31	0.14	0.17
Neuroticism	−0.53	1.00	0.00	0.34	−0.40	0.18	−0.19	−0.25
Assertiveness	0.02	0.00	1.00	0.08	0.22	−0.04	0.52	0.27
Openness	0.14	0.34	0.08	1.00	0.34	−0.35	−0.03	−0.19
Sociability	0.54	−0.40	0.22	0.34	1.00	−0.22	0.22	0.07
Lower face/face height	−0.31	0.18	−0.04	−0.35	−0.22	1.00	0.02	−0.11
fWHR	0.14	−0.19	0.52	−0.03	0.22	0.02	1.00	0.45
Face width/lower face height	0.17	−0.25	0.27	−0.19	0.07	−0.11	0.45	1.00

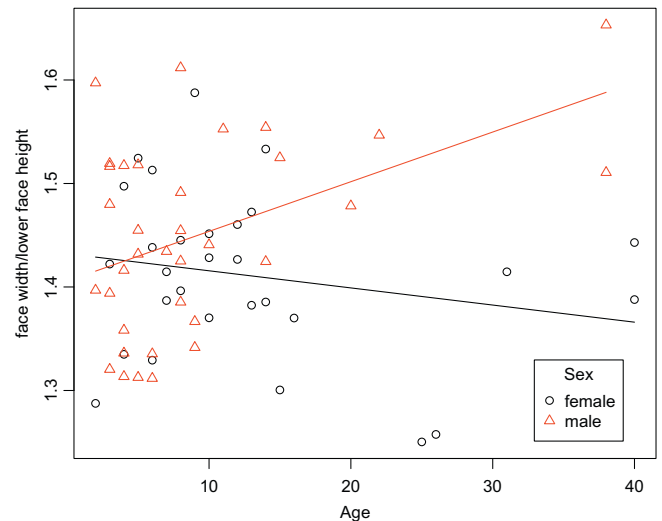
more raters ($n = 121$). Reliability of items are reported in Morton et al. (2013). For the whole sample, the number of components to extract was determined using parallel analysis. Five components – assertiveness, openness, attentiveness, neuroticism, and sociability – were extracted using Principal Components Analysis (see component descriptions above). Personality scores for the current sample were based on this analysis; all but 3 monkeys in our sample were rated by two or more raters. Each factor was validated against observations of behaviour within monkey's social groups, and to how individuals responded to cognitive testing (Morton et al., 2013; Morton, Lee, & Buchanan-smith, 2013). Inter-rater reliabilities and behavioural validation support personality ratings as valid measures of primate personality, and refute arguments of anthropomorphism (Weiss et al., 2009).

3. Results

Descriptive statistics for the measured variables, and correlations among the personality dimensions and facial metrics, are shown in Tables 1 and 2 respectively. We found a strong association between the two width-based measures (fWHR and face width/lower face height; $r = .45$, $p < .001$), suggesting they share variance and may both be linked to assertiveness. Lower face/face height was independent of both fWHR ($r = .02$, $p = .90$) and face width/lower face height ($r = -0.11$, $p = .11$).

We first examined associations of fWHR to personality traits besides assertiveness. A regression model was constructed with fWHR as the dependent variable and entering all five personality traits – openness, neuroticism, attentiveness, assertiveness and sociability – as independent variables with covariates of age, age², sex, age × sex (See Table 3). This model was significant ($F(9,54) = 6.66$, $p < .001$, adjusted $R^2 = 0.45$) and replicated the previously reported significant age × sex interaction ($F(1,54) = 14.36$, $p < .001$) and the association of fWHR with assertiveness ($F(1,54) = 12.71$, $p < .001$). However, no other personality dimensions approached significance for association with fWHR (see Table 3).

We next examined associations between the two new facial metrics and personality using identical regression models to those

**Fig. 2.** Linear fits of age against face width/lower face height, separately for each sex.

used for fWHR above (See Table 3). For face width/lower face height (full model: $F(9,54) = 3.15$, $p < .001$, adjusted $R^2 = 0.23$) a significant age × sex interaction was found ($F(1, 54) = 5.87$, $p = .02$), with sex differences increasing across the life span (see Fig. 2). These findings of significant sex differences in face width/lower face height are compatible with data from humans, in which face width/lower face height is also dimorphic (Penton-Voak et al., 2001). To explicitly test the sexual dimorphism of this trait, models not including personality were also run. Face width/lower face height showed both a main effect of sex ($F(1,59) = 4.09$, $p = 0.047$), and a significant age × sex interaction ($F(1,59) = 8.39$, $p = 0.005$), with males and females showing higher and lower ratios with age, respectively (Fig. 2).

Assertiveness (but no other personality dimension) showed a significant association with face width/lower face height ($F(1,54) = 6.47$, $p = .014$). This association, however, did not appear to account for additional unique variance in assertiveness over and

Table 3Regression of fWHR and face width/lower face height on demographic variables and personality ($n = 64$).

	fWHR				face width/lower face height			
	Est.	SE	<i>t</i>	<i>P</i> -value	Est.	SE	<i>t</i>	<i>P</i> -value
Age	0.004	0.008	0.557	0.579	−0.013	0.005	−2.493	0.016
Sex	−0.069	0.049	−1.405	0.166	−0.021	0.033	−0.638	0.526
Age ²	−0.000	0.000	−1.796	0.078	0.000	0.000	2.002	0.050
Assertiveness	0.058	0.016	3.566	<0.001	0.028	0.011	2.543	0.014
Openness	−0.008	0.032	−0.244	0.808	−0.039	0.022	−1.822	0.074
Neuroticism	−0.053	0.041	−1.297	0.200	−0.038	0.027	−1.404	0.166
Sociability	0.018	0.032	0.576	0.567	−0.018	0.021	−0.866	0.390
Attentiveness	−0.039	0.039	−1.098	0.277	0.006	0.024	0.267	0.791
Age × Sex	0.013	0.004	3.789	<0.001	0.006	0.002	2.422	0.019

above fWHR: adding fWHR to the model rendered the association of face width/lower face height with assertiveness non-significant ($F(1, 53) = 2.12, p = .151$). This finding suggests that face width/lower face height taps the same underlying biological variance that relates fWHR to assertiveness in capuchins.

Turning to lower face/face height, we again examined associations with personality using regression models with lower face/face height as the dependent variable, covariates of age, age², and sex and independent predictors of assertiveness, openness, attentiveness, neuroticism and sociability as conducted above for the width-based metrics (full model: $F(9, 54) = 2.85, p = .008$, adjusted $R^2 = 0.21$). There was a significant effect of age ($F(1, 54) = 6.01, p = .017$), but no significant evidence for sexual dimorphism (i.e., no effects of sex or age \times sex interaction: see Table 3). This lack of dimorphism was confirmed in a simpler model containing just age, with age² and age \times sex as predictors: Lower face/face height increased with age ($F(1, 59) = 4.33, p = 0.04$) but showed no sex or age \times sex effects ($p = 0.63$ and 0.75 respectively). In humans, both neuroticism (Costa & McCrae, 1992) and lower face/face height are dimorphic (Penton-Voak et al., 2001). We thus tested for dimorphism in neuroticism in the present sample of capuchins, but found it to be non-dimorphic ($F(1, 62) = 0.56, p = 0.45$).

Examining associations of lower face/face height with personality, associations were found with both neuroticism and attentiveness. Higher neuroticism was associated with greater lower face/face height ratios ($F(1, 54) = 6.25, p = .015$, see Fig. 3). However, depending on the order of entry into the model, both attentiveness and neuroticism showed links to lower face/face height. Because of this potential association with two simultaneous personality outcomes, we utilised structural equation modelling (SEM) to produce an integrated model of fWHR and lower face/face height with assertiveness, neuroticism and attentiveness.

SEM allows a test of the hypothesis that the association of lower face/face height is best modelled, either as being specific to one or other of these traits (with the apparent association to both traits simply reflecting covariance among the traits in this sample); or, by contrast, that lower face/face height influences both neuroticism and attentiveness, thus accounting in part for their overlapping behavioural elements (see Fig. 4). Simultaneously we can examine the impact of fWHR, its links to lower face, and their joint impact on assertiveness. Our base model is shown in Fig. 4. This fit well ($\chi^2(6) = 7.11, RMSEA = 0.054, CFI = 0.981, TLI = 0.968$), indicat-

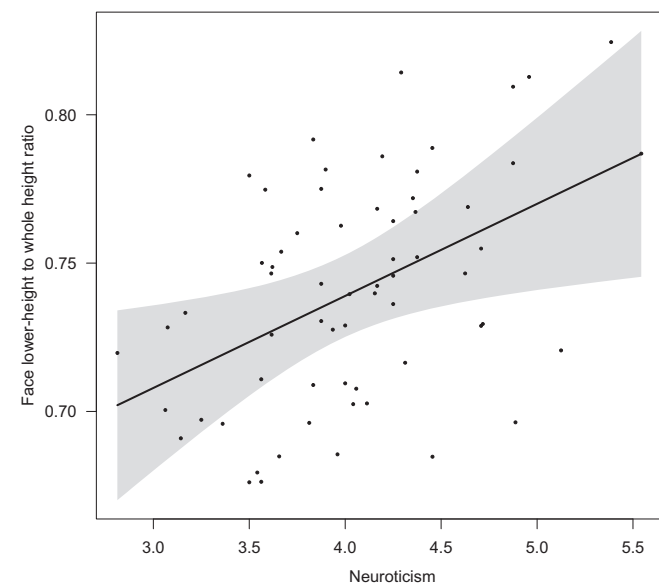


Fig. 3. Regression plot of lower face/face height against Neuroticism.

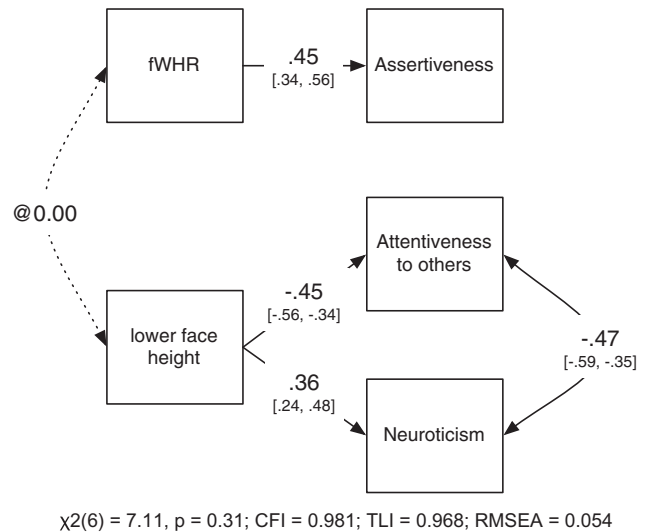


Fig. 4. Structural equation model predicting Assertiveness, Attentiveness to others, and Neuroticism from fWHR and lower face/face height. Note: Standardized path coefficients shown [95% confidence intervals in brackets]. Model fit was good according to CFI, TLI, and RMSEA.

ing that the width and height based facial measures are well accounted for as separate (uncorrelated) influences on the three personality traits. Dropping the path from lower face/face height to either attentiveness or to neuroticism reduced model fit significantly ($\chi^2(1) = 14.39, p = .0001$ and $\chi^2(1) = 6.59, p = .0034$, respectively). Lower face/face height, then, appears to directly influence both attentiveness and neuroticism.

4. Discussion

We tested the association of three facial metrics with five personality dimensions in 64 capuchins (*Sapajus apella*). fWHR and face width/lower face height associated with assertiveness even after controlling for the other four personality dimensions, with fWHR accounting for this association. In contrast, a higher ratio of lower face/face height (i.e., relatively longer lower face) was significantly associated with higher neuroticism and lower attentiveness scores. The results suggest that facial morphology reliably reflects three major personality domains: assertiveness, attentiveness and neuroticism, via two uncorrelated morphological ratio measures.

The present study extends the previously reported association of relative facial width to assertiveness (Lefevre et al., submitted for publication) by examining the full spectrum of personality and an additional width-linked facial feature: face width/lower face height. To our knowledge, the association of face width/lower face height with assertiveness per se has not been evaluated in any primate species (including humans). Unlike human fWHR (Kramer et al., 2012; Lefevre et al., 2012; Özener, 2012), face width/lower face height is sexually dimorphic in humans (Penton-Voak et al., 2001) with women showing higher ratios than men. In the present sample we also found dimorphism of face width/lower face height, however males showed higher ratios than females, a difference that increased with age. The association with assertiveness shown here, then, suggests that it would be informative to assess the relationship of face width/lower face height to behaviour in large human samples of both sexes, perhaps controlling for neuroticism, which was linked to face height.

The question of why these three facial metrics relate to assertiveness, attentiveness, and neuroticism is open. Given the paucity

of literature on this issue, we speculate that a common factor is a link to status and leadership traits (Lilienfeld et al., 2012). Work in humans has suggested that status is best conceived of as two orthogonal dimensions based, respectively, on coercion and pro-social competence (Henrich & Gil-White, 2001). The association of face-width metrics with a more aggression-linked capacity for dominance clearly fits with links of FWHR to testosterone (Lefevre, Lewis, Perrett, & Penke, 2013; Penton-Voak & Chen, 2004), and thus fits the coercion profile. Consistent with the interpretation that traits associated with lower face/face height share links to pro-social competence, the two traits linked to lower face/face height (neuroticism and attentiveness) are both associated with vigilance and with attention span in cognitive testing. The association with lower face/face height, then, may be driven primarily by the markers these two traits share, namely vigilance and attention span (Morton et al., 2013). Such attentive behaviour appears to confer status not by aggression, but via a “policing” role associated with reduced time in play and increased time in vigilant attention (Flack, Girvan, de Waal, & Krakauer, 2006). Thus lower face/face height may be linked to this second, social, form of status. Such pro-social monitoring status, shown here to relate to lower face/face height ratio, may presage the prestige-earning dimension of status found in humans (Henrich & Gil-White, 2001).

In seeking human personality dimensions compatible with “policing”, the most likely candidate would appear to be the HEXACO Honesty-humility dimension which is based on duty, caution, and being self-effacing (Ashton & Lee, 2007). It would be valuable to test links of lower face/face height ratio in humans to Honesty-humility and to ratings of admiration in others. A similar dimension – ‘Equable’ – has been reported in rhesus macaques, which, like attentiveness, is associated with reduced play (Weinstein, Capitano, & Gosling, 2008). It would thus be useful to examine face morphological links in rhesus macaques.

Openness and sociability were unrelated to any of the facial metrics. In capuchins, openness is related to task participation and learning performance, while sociability is related to social contact and alert behaviour (Morton et al., 2013; Morton, Lee, & Buchanan-Smith, 2013). The present findings suggest that, at least in capuchins, openness and sociability play a role in sociality and cognition, but independently of status drive or achievement. In addition, and in distinction to human research, we did not find sexual dimorphism for neuroticism or for lower face/face height ratios in capuchins. Both these traits are dimorphic in humans (Del Giudice, Booth, & Irwing, 2012; Penton-Voak et al., 2001). Sexual dimorphism for personality may, then, be linked to dimorphism in morphology, with these dimorphisms varying across species under distinct social and sexual selection pressures. Addressing species differences in social structure, cognition and behaviour may help to establish what determines species-specific personality traits, and why they are associated with facial morphology.

In summary, these results shed light on biomarkers of personality, and on personality differences across species. It would benefit to have sufficient power to explore in more detail the significant sex-specific age growth in capuchin facial metrics, as well as to examine effects of location and body weight in relation to these findings. Additional studies examining the lower face/face height metric in other species would be valuable, and may shed light on the origins of status effects on well-being and emotional traits linked to status in humans (Wood, Boyce, Moore, & Brown, 2012).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.paid.2013.10.008>.

References

- Ashton, M. C., & Lee, K. (2007). Empirical, theoretical, and practical advantages of the HEXACO model of personality structure. *Personality and Social Psychology Review*, 11(2), 150–166 [doi: 10.1177/1088868306294907].
- Carré, J. M., & McCormick, C. M. (2008). In your face: Facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. *Proceedings Biological Sciences/The Royal Society*, 275(1651), 2651–2656 [doi: 10.1098/rspb.2008.0873].
- Costa, P. T., Jr., & McCrae, R. R. (1992). *Revised NEO personality inventory-professional manual*. Florida: Psychological Assessment Resources Inc.
- Deaner, R. O., Geary, D. C., Puts, D. A., Ham, S. A., Kruger, J., Fles, E., et al. (2012). A sex difference in the predisposition for physical competition: Males play sports much more than females even in the contemporary US. *PLoS One*, 7(11), e49168 [doi: 10.1371/journal.pone.0049168].
- Del Giudice, M., Booth, T., & Irwing, P. (2012). The distance between Mars and Venus: Measuring global sex differences in personality. *PLoS One*, 7(1), e29265. <http://dx.doi.org/10.1371/journal.pone.0029265>.
- Ferguson, E., Heckman, J. J., & Corr, P. (2011). Personality and economics: Overview and proposed framework. *Personality and Individual Differences*, 51(3), 201–209 [doi: 10.1016/j.paid.2011.03.030].
- Flack, J. C., Girvan, M., de Waal, F. B., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, 439(7075), 426–429. <http://dx.doi.org/10.1038/nature04326>.
- Haselhuhn, M. P., & Wong, E. M. (2012). Bad to the bone: facial structure predicts unethical behaviour. *Proceedings Biological Sciences/The Royal Society*, 279(1728), 571–576 [doi: 10.1098/rspb.2011.1193].
- Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22(3), 165–196 [doi: S109051380000714].
- Kramer, R. S., Jones, A. L., & Ward, R. (2012). A lack of sexual dimorphism in width-to-height ratio in white European faces using 2D photographs, 3D scans, and anthropometry. *PLoS One*, 7(8), e42705. <http://dx.doi.org/10.1371/journal.pone.0042705>.
- Kramer, R. S., & Ward, R. (2010). Internal facial features are signals of personality and health. *Quarterly Journal of Experimental Psychology*, 63(11), 2273–2287. <http://dx.doi.org/10.1080/17470211003770912>.
- Lefevre, C. E., Lewis, G. J., Bates, T. C., Dzhelyova, M., Coetzee, V., Deary, I. J., et al. (2012). No evidence for sexual dimorphism of facial width-to-height ratio in four large adult samples. *Evolution and Human Behavior*, 33(6), 623–627. <http://dx.doi.org/10.1016/j.evolhumbehav.2012.03.002>.
- Lefevre, C. E., Lewis, G. J., Perrett, D. I., & Penke, L. (2013). Telling facial metrics: Facial width is associated with testosterone levels in men. *Evolution and Human Behavior*, 34(4), 273–279. <http://dx.doi.org/10.1016/j.evolhumbehav.2013.03.005>.
- Lefevre, C. E., Wilson, V. A. D., Morton, F. B., Brosnan, S. F., Paukner, A., & Bates, T. C. (submitted for publication). Facial width-to-height ratio predicts dominance in capuchin monkeys. *PLoS One*.
- Lewis, G. J., Lefevre, C. E., & Bates, T. C. (2012). Facial width-to-height ratio predicts achievement drive in US presidents. *Personality and Individual Differences*, 52(7), 855–857. <http://dx.doi.org/10.1016/j.paid.2011.12.030>.
- Lilienfeld, S. O., Waldman, I. D., Landfield, K., Watts, A. L., Rubenzer, S., & Faschingbauer, T. R. (2012). Fearless dominance and the US presidency: Implications of psychopathic personality traits for successful and unsuccessful political leadership. *Journal of Personality and Social Psychology*, 103(3), 489–505. <http://dx.doi.org/10.1037/a0029392>.
- Macdonald, C., & Whiten, A. (2011). The living links to human evolution research centre in edinburgh zoo: A new endeavour in collaboration. *International Zoo Yearbook*, 45, 7–17.
- Morton, F. B., Lee, P. C., & Buchanan-Smith, H. M. (2013). Taking personality selection bias seriously in animal cognition research: A case study in capuchin monkeys (*Sapajus apella*). *Animal Cognition*, 16(4), 677–684. <http://dx.doi.org/10.1007/s10071-013-0603-5>.
- Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S., Thierry, B., Paukner, A., et al. (2013). Personality structure in brown capuchin monkeys (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp.*), and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology*, 127(3), 282–298. <http://dx.doi.org/10.1037/a0031723>.
- Özener, B. (2012). Facial width-to-height ratio in a Turkish population is not sexually dimorphic and is unrelated to aggressive behavior. *Evolution and Human Behavior*, 33(3), 169–173. <http://dx.doi.org/10.1016/j.evolhumbehav.2011.08.001>.

- Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior*, 25(4), 229–241.
- Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., et al. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society B-Biological Sciences*, 268(1476), 1617–1623 [doi:10.1098/rspb.2001.1703].
- Penton-Voak, I. S., Pound, N., Little, A. C., & Perrett, D. I. (2006). Personality judgments from natural and composite facial images: More evidence for a kernel of truth in social perception. *Social Cognition*, 24(5), 607–640.
- Plavcan, J. M. (2012). Sexual size dimorphism, canine dimorphism, and male–male competition in primates where do humans fit in? *Human Nature*, 23(1), 45–67. <http://dx.doi.org/10.1007/S12110-012-9130-3>.
- Plavcan, J. M., Vanschaik, C. P., & Kappeler, P. M. (1995). Competition, coalitions and canine size in primates. *Journal of Human Evolution*, 28(3), 245–276 [doi:10.1006/jhev.1995.1019].
- Stirrat, M., & Perrett, D. I. (2010). Valid facial cues to cooperation and trust: Male facial width and trustworthiness. *Psychological Science*, 21(3), 349–354. <http://dx.doi.org/10.1177/0956797610362647>.
- Tiddeman, B. P., Perrett, D. I., & Burt, D. M. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications*, 21, 42–50.
- Weinstein, T. R., Capitanio, J. P., & Gosling, S. D. (2008). Personality in animals. In O. P. John, R. W. Robins, & L. A. Pervin (Eds.), *Handbook of personality* (3rd ed., pp. 328–348). NY: Guilford.
- Weiss, A., Adams, M. J., Widdig, A., & Gerald, M. S. (2011). Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. [Research Support, N.I.H., Extramural]. *Journal of Comparative Psychology*, 125(1), 72–83. <http://dx.doi.org/10.1037/a0021187>.
- Weiss, A., Bates, T. C., & Luciano, M. (2008). Happiness is a personal(ity) thing: The genetics of personality and well-being in a representative sample. *Psychological Science*, 19(3), 205–210. <http://dx.doi.org/10.1111/j.1467-9280.2008.02068.x>.
- Weiss, A., Inoue-Murayama, M., Hong, K. W., Inoue, E., Udono, T., Ochiai, T., et al. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology*, 71(4), 283–292. <http://dx.doi.org/10.1002/ajp.20649>.
- Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology*, 90(3), 501–511. <http://dx.doi.org/10.1037/0022-3514.90.3.501>.
- Weston, E. M., Friday, A. E., Johnstone, R. A., & Schrenk, F. (2004). Wide faces or large canines? The attractive versus the aggressive primate. [Comparative Study Research Support, Non-U.S. Gov't]. *Proceedings Biological Sciences/The Royal Society*, 271 Suppl 6, S416–419. doi: 10.1098/rsbl.2004.0203.
- Wood, A. M., Boyce, C. J., Moore, S. C., & Brown, G. D. A. (2012). An evolutionary based social rank explanation of why low income predicts mental distress: A 17 year cohort study of 30,000 people. *Journal of Affective Disorders*, 136, 882–888.