A cross-cultural study of sex-typicality and averageness: Correlation between

frontal and lateral measures of human faces

Running head: Association between frontal and profile facial shapes

by

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Abstract

Objectives: Facial averageness and sexual dimorphism are extensively studied attractiveness markers,

which are viewed as possible indicators of biological quality. Both are complex morphological traits

and both can be easily assessed from frontal and lateral projection of a human face. Interestingly,

examination of mutual relations between the frontal and lateral dimensions of these markers has so far

received little attention in published research.

Methods: In our cross-cultural study, we used geometric morphometric data from male and female

faces from Brazil, Cameroon, Colombia, and the Czech Republic, and analysed correlations between

frontal and lateral measurements of averageness and degree of maleness/femaleness, i.e. individual

variation in features that characterize sexual dimorphism. We also analysed whether the association

between frontal and lateral measurements differs in men and women.

Results: In general, our results showed a moderate correlation in sexually dimorphic features between

lateral and frontal facial configuration in both sexes, while frontal and lateral facial averageness was

moderately correlated only in women. This pattern was less consistent when individual populations

were analysed separately.

Conclusions: Referring to the multiple signalling theory, we propose that especially in women,

lateral/frontal correlations support a hypothesis of redundancy of information provided by the frontal

and lateral dimension of a given facial attractiveness marker. The absence of a significant correlation

in male facial averageness suggests that frontal and lateral averageness may convey different

information about an individual.

Keywords: human faces, facial averageness and sexual dimorphism, frontal and lateral projections,

geometric morphometrics, multiple signalling theory

1. INTRODUCTION

Comprehensive research of the role of human face in mate choice led to the identification of several physical markers of facial attractiveness. Two well-known examples of such markers are averageness and sex-typicality (Kościński, 2008; Little, Jones, & DeBruine, 2011; Rhodes, 2006; Thornhill & Gangestad, 1999).

Averageness refers to facial morphology that is biometrically average in a given population (Little et al., 2011; Rhodes, 2006). It has been proposed that average faces are seen as attractive because averageness reflects certain aspects of mate quality, such as heterozygosity, which is in turn related to higher immunocompetence and disease resistance (Gangestad & Buss, 1993; Grammer & Thornhill, 1994; Thornhill & Gangestad, 1993). While the existence of a common genetic component for averageness and attractiveness is still a matter of discussion (Lee et al., 2016; Lie, Rhodes, & Simmons, 2008), the notion of a link between averageness and actual health is supported by some published research (Rhodes et al., 2001; Thornhill & Møller, 1997; Zebrowitz & Rhodes, 2004).

Sex-typicality or, in other words, sexual dimorphism in human faces develops especially during puberty due to the influence of androgens and oestrogens (Enlow, 1990; Farkas, 1988; Tanner, 1989). High levels of testosterone are linked to the development of typically male (i.e., masculine) secondary sexual facial characteristics, such as large jawbones, prominent cheekbones, robust eyebrow ridges, and generally longer and more protruding facial bones. Conversely, the absence of masculinity markers, accompanied by increased size of the lips and thin and receding cheeks, are attributed to a high oestrogen to testosterone ratio and are characteristic of feminine facial morphology (Little et al., 2011; Mydlová, Dupej, Koudelová, & Velemínská, 2015; Rhodes, 2006; Thornhill & Møller, 1997; Verdonck, Gaethofs, Carels, & de Zegher, 1999). Several empirical studies confirm the link between sex-specific facial shapes and steroid hormones in both sexes (Law Smith et al., 2006; Penton-Voak & Chen, 2004; Verdonck et al., 1999). Sexually dimorphic, feminine facial shapes are preferred in female faces because femininity may indicate sexual maturity and a high female reproductive capacity (Gangestad & Scheyd, 2005; Kościński, 2007; Little et al., 2011; Rhodes, 2006). Association between attractiveness and sexual dimorphism in male faces is more complex because in men, both masculine

and feminine faces can be preferred (Kościński, 2007; Little et al., 2011; Rhodes, 2006). Several

interpretations of aesthetic preference for male sexually dimorphic facial characteristics have been

proposed. Firstly, since fully developed sexually dimorphic facial shapes indicate sexual maturity,

sexual dimorphism may indicate the ability to produce offspring (Rhodes, 2006; Thornhill & Møller,

1997). Secondly, it has been proposed that highly dimorphic faces advertise immunocompetence:

since high levels of male sex hormones are considered detrimental to the immune system, only high-

quality individuals can afford to bear the costs of conspicuous sexual ornaments (Folstad & Karter,

1992; Thornhill & Møller, 1997; Wedekind & Folstad, 1994; Zahavi, 1975, but see also Scott, Clark,

Boothroyd, & Penton-Voak, 2013 for a discussion of the immunocompetence handicap hypothesis).

And finally, exaggerated sexual dimorphism in faces may serve as a cue for personality. For instance,

high masculinity in male faces has been associated with higher levels of dominance, aggressiveness,

and dishonesty, as well as lower levels of emotionality, warmth, cooperativeness, and parenting

abilities (Perrett et al., 1998; Scott et al., 2013). The perception of such anti-social traits may direct

women's preferences towards more feminine male faces (Perrett et al., 1998). Interestingly,

preferences for facial sexual dimorphism in both male and female faces may also reflect the recently

evolved information-processing mechanisms operating in urbanised and highly populated

environments (Scott et al., 2013).

Both facial averageness and secondary sexual characteristics are attractiveness markers that

can be easily assessed in facial profiles, but it should be noted that research of facial beauty rarely

focuses on lateral facial morphology (Kościński, 2009). Nonetheless, results from several studies of

averageness of facial profiles are analogous to the results of en-face investigations and they do show

that mathematically average profiles are attractive (Spyropoulos & Halazonetis, 2001; Valentine,

Darling, & Donnelly, 2004; Valenzano, Mennucci, Tartarelli, & Cellerino, 2006). Moreover,

numerous studies of facial profiles carried out within aesthetic medicine and orthodontics found that

morphological deviations from average profile shapes (i.e. orthognathic profiles with biometrically

normal proportions) lower the perceived facial attractiveness (e.g. Gautam, Shashikalakumari, & Garg,

2013; Hönn, Dietz, Eiselt, & Göz, 2008; Johnston et al., 2005; Soh, Chew, & Wong, 2007;

Türkkahraman & Gökalp, 2004). Similarly, research results on the attractiveness of facial profile

sexual dimorphism are also in line with some findings of studies of en-face facial morphology. In

particular, higher femininity of both male and female facial profiles was found to be associated with

higher facial attractiveness (Swaddle & Reierson, 2002; Valenzano et al., 2006) and, at least in men,

also with lower perceived dominance (Swaddle & Reierson, 2002).

The agreement between results obtained by en-face and facial profile studies implies that

lateral and frontal measures of averageness and sexual dimorphism should be correlated. Such a view

corresponds with anatomical and developmental analyses which show that horizontal, vertical, and

anteroposterior craniofacial dimensions are interrelated (Enlow, 1990). On the other hand, faces are

complex and multi-trait body parts that cannot be studied as one developmentally homogenous

structure. Indeed, the morphogenesis of particular facial characteristics is subjected to genetic,

epigenetic, environmental, and even functional influences (Claes et al., 2014; Enlow, 1990;

Hallgrimsson, Mio, Marcucio, & Spritz, 2014; Liu et al., 2012). Multilevel interactions between these

factors result in a considerable morphological diversity of particular facial features and faces as a

whole (Enlow, 1990; Hallgrimsson et al., 2014). At least in theory, therefore, measurements of

seemingly identical qualities from frontal and lateral perspective could be uncorrelated or correlate

only weakly. In fact, a three-dimensional computer tomography study of human skulls had shown that

mutual relations between the size of different facial structures can be complex, and a straightforward

anticipation of correlation between traits dimensions is not necessarily justified (Wang, Otsuka,

Akimoto, & Sato, 2013).

To our best knowledge, only one study analysed directly the association between frontal and

lateral markers of facial attractiveness, such as averageness and sexual dimorphism. Using frontal and

lateral facial photographs of the same individual and applying geometric morphometric to analyse

facial morphology, Danel, Dziedzic-Danel, and Kleisner (2016) found that neither individual

expression of frontal averageness nor frontal sexually dimorphic traits are correlated with their lateral

counterparts. The absence of statistically significant correlations between frontal and lateral

measurements was found in both male and female faces. However, the sample of facial pictures used

by Danel et al. (2016) was relatively small and limited only to one population, namely adult

Caucasians of Polish origin. These shortcomings, jointly with the absence of other studies on

interrelations between frontal and lateral markers of facial attractiveness, do not allow for a

generalization the findings of Danel et al. (2016) or an extrapolation of this study's conclusions to

different populations.

In the current study, we address the abovementioned limitations and replicate Danel's et al.

(2016) study using a larger and more ethnically diverse sample, which includes participants from the

Czech Republic (Europe), Cameroon (Africa), and two South American countries: Brazil and

Colombia. More specifically, we analyse correlations between frontal and lateral measures of

averageness and individual expression of sexually dimorphic traits in these four different populations

from different parts of the world. We started by testing whether frontal and lateral views provide

redundant cues about an individual's sex-typicality and averageness. If so, the individual expression of

averageness and level of sexual dimorphism (maleness/ femaleness) should be closely correlated. Then

we examined whether the association between frontal and lateral measurements differs in male and

female faces.

2. METHODS

2.1 Ethics statement

These particular studies were approved by the Institutional Review Board of Charles University,

Faculty of Science (for the data collection in Brazil – 2011/7, for the data collection in Cameroon and

the Czech Republic – 2014/10) and the Institutional Committee on Research Ethics, El Bosque

University (for the data collection in Colombia – 2016/2). All participants provided a written informed

consent prior to participating in the study. Morphometric data of frontal and lateral images were

analysed anonymously.

2.2 Facial photographs

We used facial frontal and lateral portraits of 100 Brazilians (51 women: Mean Age±SD = 24.1±4.9,

range 18–35; 49 men: Mean Age±SD = 23.29±3.63, range 18–32), 102 Cameroonians (51 women:

Mean Age±SD = 24.92±8.4, range: 17–54; 52 men: Mean Age±SD = 23.75±5.49, range 17–44), 98

Colombians (49 women: Mean Age±SD = 21.5±3.29, range 18–33; 49 men: Mean Age±SD = 20.1±

1.71, range 18–27), and 191 Czechs (139 women: Mean Age±SD = 21.45±2.51, range 18–34; 52 men:

Mean Age±SD = 23.06±4.45, range 19–39). Due to a possible laterality of human facial morphology

(Danel & Pawlowski, 2007; Farkas & Cheung, 1981; Simmons, Rhodes, Peters, & Koehler, 2004), we

decided to use always the same, namely left, facial profile. Although facial photographs were collected

by different authors, they followed a standardised procedure (Třebický, Fialová, Kleisner, & Havlíček,

2016). As stated above, our dataset is highly ethnically diverse, since it includes individuals from one

European, one African, and two ethnically mixed South American countries.

2.3 Geometric morphometrics

We determined 72 landmarks (including 36 semilandmarks) on frontal facial portraits and

and 21 landmarks (including 6 semilandmarks) on profile images. Landmarks are corresponding

locations that can be anatomically or geometrically defined in all objects in the sample. While

landmarks reflect homologous structures and locations on faces of different individuals,

semilandmarks denote curves and outlines. For landmark and semilandmarks locations on frontal and

lateral facial images, see Danel et al. (2016).

Facial frontal and profile configurations of landmarks were superimposed by a generalised

Procrustes analysis (GPA) using the 'gpagen' function implemented in the geomorph package in R

(Adams & Otárola-Castillo, 2013). GPA standardized the size of the objects and removed rotational

and translational effects in order to minimize distances between homologous landmarks. The 'gpagen'

function was also used to align sliding semilandmarks by means on the minimum bending energy

criterion.

For each set of faces we run separate GPA and computed the mean configuration (consensus).

The Procrustes distances between the consesus and each configuration in the set was computed and

used as a measure of individual averageness A higher facial averageness score thus indicates closer

proximity of a configuration to the mean shape.

To assess the level of individual expression of facial traits responsible for sexual shape

dimorphism (SShD), i.e., the degree of maleness/femaleness as suggested by Mitteorecker et al.

(2015), we determined the position of an individual facial shape along the axis between male and

female mean shapes (Mitteroecker et al., 2015; Valenzano et al., 2006). This position can be

numerically expressed by continuous scores of ordination constrained by sex, i.e., by projecting

individual facial configurations onto the vector between the average female and male face.

2.4 Statistical analysis

Since the individual scores of facial metrics did not meet the statistical requirement for normal

distribution, we performed correlational analyses using nonparametric methods. Relationships

between frontal and lateral facial configurations were investigated using Kendall's Tau correlation

coefficient for measurements of both averageness and sexual shape dimorphism. Comparisons of

correlation coefficients obtained for a pooled sample of men and women were carried out using

Fisher's transformation for Kendall's Tau coefficients according to Walker (2003) and Zar (1999). All

these tests are two-tailed.

3. RESULTS

Correlations between frontal and lateral facial shapes for averageness and individual expression of

sexually dimorphic traits (maleness/femaleness) are summarised in Table 1. When shape coordinates

for all samples were pooled together across countries but separately for men and women, averageness

showed a significant frontal/lateral association only in women (Fig 1). A formal comparison of sex

differences in the correlation coefficients confirmed that the association between frontal and lateral

facial averageness is significantly stronger in women than in men ($Z = 4.11$, $p < .0001$).

Table 1. Kendall's Tau correlations between frontal and lateral facial configuration for averageness (AVRGN) and the degree individual expression of traits associated with sexual shape dimorphism (SShD).

SAMPLE	SEX	AVRGN	SShD	N
ALL	women	.275**	.200**	290
	men	.042	.202**	201
Brazil	women	.126	.194*	51
	men	.064	.092	49
Cameroon	women	.220*	.154	51
	men	-.035	.071	51
Colombia	women	.143	.197*	49
	men	.022	.224*	49
Czech Republic	women	.206**	.260**	139
	men	.015	.101	52

* p-value ≤ .05   ** p-value ≤ .001

On the other hand, the association between frontal and lateral individual expression of sexual shape dimorphism was significant in the pooled samples of both men and women (Fig 1). The strength of the correlation was comparable for both women and men, and difference between the correlations was not statistically significant (Z = -0.04, p = .971).

Figure 1. Scatterplots showing pooled data separately for men and women. Upper panel

shows correlations between frontal and lateral values of averageness (i.e., the distance of each

specimen from the Procrustes mean configuration). Lower panel demonstrates the association

between individual scores of sexual shape dimorphism (SShD) computed for frontal and lateral

configurations.

When samples were analysed separately, it turned out that Brazilian women display a

significant frontal-lateral correlation for femaleness but not for averageness. Conversely, analysis of

the sample of Cameroonian women showed a significant frontal-lateral correlation for averageness but

not for femaleness. In the Colombian women, neither frontal-lateral averageness nor measures of

femaleness were significantly correlated. In Czech women, frontal configurations were significantly

correlated with profiles in both averageness and femaleness.

In the male samples, the correlation coefficient for frontal and lateral maleness reached

significant levels only in the Colombian men. In the other populations, the association between frontal

and lateral facial configurations was not statistically significant.

In general, female faces showed a higher degree of correlation between frontal and lateral

configuration for both averageness and individual expression of sexually dimorphic shape features

than men. An exception was the Colombian sample, where correlation coefficients for measures of

sexual shape dimorphism was higher for men than for women.

4. DICUSSION

Using data from four populations from different parts of the world, we examined whether profile and

lateral configurations correlate in individual expression of averageness and sexually dimorphic

characteristics of facial shape (maleness and femaleness). In general, we found that individual

expression of profile and frontal sexual dimorphism is moderately correlated in both men and women.

The strength of these associations does not differ between men and women. Correlations between

frontal and lateral averageness did, however, reveal some profound differences between the sexes:

while in women, averageness of enfaces was significantly associated with averageness of profiles, no

such correlation was found in men.

Analyses performed separately for particular populations showed a similar trend but the

association was significant only in some cases: while frontal and lateral averageness were significantly

correlated in Czech and Cameroonian women (and not related in other groups), frontal and lateral

measures of sexual shape dimorphism were significantly associated in Czech and Brazilian women

and in Colombian men. The observed absence of homogenous pattern in particular samples might be

due to the relatively small sample sizes of the particular analysed populations.

The current results, which show significant correlations between frontal and lateral facial

configurations, are in line with ontogenetic analyses indicating that various facial structures are

developmentally interrelated (Enlow, 1990). Our results are also in agreement with facial

attractiveness studies which show that frontal and lateral facial averageness and sexual dimorphism

may exert congruent effects on the facial beauty of individuals (Swaddle & Reierson, 2002; Valentine

et al., 2004; Valenzano et al., 2006).

Nonetheless, it should be noted that the correlations found in our study are at most moderate.

This indicates that the spatial development of complex facial configurations, such as frontal and lateral

facial averageness (e.g. Claes & Shriver, 2014; Enlow, 1990; Hallgrimsson et al., 2014; Liu et al.,

2012), may be influenced by various factors. A possible explanation of the only moderate correlations

between lateral and frontal facial structures might be that faces show a higher phenotypic variation and

lower between-trait correlation that other parts of the human body. It has been proposed that this

morphological diversity could be the consequence of human sociality and selection pressures on

identity signalling facilitated by facial recognition in complex social systems (Sheehan et al., 2014).

However, even if individual recognition and discrimination does play a role in the

development of highly variable and loosely related frontal and lateral facial morphology, it does not

explain why these correlations are generally weaker in men than in women. We propose that these sex

differences between women and men may reflect differences in the information conveyed by male and

female faces. Previous studies of multimodal signalling show that vocal and facial attractiveness are

often correlated in women (Feinberg et al., 2005; Penton-Voak et al., 2001), while in men the evidence

is more ambiguous (Lander, 2008; Oguchi & Kikuchi, 1997; Saxton, Burriss, Murray, Rowland, &

Roberts, 2009; Saxton, Caryl, & Roberts, 2006; Valentová, Roberts, & Havlícek, 2013; Wells,

Baguley, Sergeant, & Dunn, 2013). Faces are not multimodal but unimodal entities which depend

solely on visual perception. Nevertheless, even unimodal objects, such as faces, can still carry multiple

signals which can be either redundant or non-redundant. While redundant signals bear identical

information, in non-redundant signals, different components covey different information (Johnstone &

Grafen, 1992; Partan & Marler, 2005; Schluter & Price, 1993). A stronger correlation between frontal

and lateral structures should point to signal redundancy, while weak or no correlation may indicate a

disparity of information carried by the relevant features. According to our results regarding

averageness, it seems that female faces may carry more redundant signals since in women, lateral and

frontal structures are more closely correlated. Male faces, on the other hand, show no correlation

between frontal and lateral averageness, which may indicate that the two aspects of the overall facial

morphology convey different messages.

Differences between the sexes in frontal-lateral correlation in averageness can be explained by

the fact that female faces are under a strong intersexual and intrasexual selection pressure for physical

attractiveness (Buss et al., 1989; Fisher, 2004; Hatfield & Sprecher, 1995; Li, Bailey, Kenrick, &

Linsenmeier, 2002). Because faces closer to the average are commonly seen as more attractive (Little

et al., 2011), information provided by women's frontal facial structures may be further reinforced if

the profile morphology is also closer to an average shape. In men, however, selection pressure on their

facial morphology is weaker, because other modalities – such as voice pitch, social status, career

prospects, and access to resources – determine the overall mate value of the individual and affect

women's preferences (Buss et al., 1989; Feingold, 1992; Hatfield & Sprecher, 1995; Li et al., 2002;

Saxton, Mackey, McCarty, & Neave, 2016). A lower correlation between frontal and lateral measures

of facial averageness in men may imply that the two facets of averageness carry non-redundant

information (possibly due to lower selection pressure on averageness of male faces). In the case of

sexual shape dimorphism, frontal morphology correlates with lateral in both sexes, which suggests a

redundancy of information conveyed by profile and lateral facial configurations. This could be

because sexual dimorphism is an important facial cue in both sexes, and facial features associated with

sex-typicality are under intersexual and/or intrasexual selection pressure in both men and women

(Fink, Klappauf, Brewer, & Shackelford, 2014; Puts, 2010; Scott et al., 2013).

Multiple signalling theory, which predicts that depending on the redundant and non-redundant

character of a signal the same or different information can be conveyed by different features (Wells,

Dunn, Sergeant, & Davies, 2009), offers an appropriate framework to interpret the presence or absence

of correlations observed in the current study. Our study did not, however, test any explicit hypotheses

which could be derived from this general theory. Future research could address this issue by, for

instance, investigating whether the qualities of individuals predicted based on frontal images are in

agreement with analogous assessments made on the basis of facial profiles. As in the current

examination, implementation of such studies in cross-cultural settings may also provide a broader and

more universal perspective on factors which might influence the appearance and perception of various

facial cues.

As for limitations, our sample sizes for men and women in particular populations were

relatively small. Simple sample size estimations show that an adequate sample size for identification

of a significant association of Kendall's Tau = .15 (equivalent of r = .23; Gilpin, 1993; Walker, 2003),

with statistical power of $1 - \beta = .90$, should be over n = 190 (Hulley, Cummings, Browner, Grady, &

Newman, 2013). Such numbers of men and women were obtained when data from the four

populations were pooled together, which also implies that results from the separate populations should

be interpreted with a degree of caution. Furthermore, in this study only left profile pictures were taken.

Faces are not, however, perfectly bilateral (Danel & Pawlowski, 2007; Farkas & Cheung, 1981;

Simmons et al., 2004), and analyses of correlations between frontal and lateral faces should therefore

be replicated also with right profiles.

In conclusion, the current cross-cultural study examined interrelations between frontal and

lateral configurations of averageness and sexual shape dimorphism, two commonly accepted markers

of facial attractiveness. Results show that measures of frontal and lateral shape dimorphism are

moderately correlated in both men and women. A similar moderate correlation was observed in frontal

and lateral facial averageness in women but not in men. The framework provided by multiple

signalling theory may help explain the observed interrelations, but further research focused

specifically on the redundant and non-redundant signalling roles of traits associated with lateral and

frontal averageness and sexual shape dimorphism is needed.

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AUTHOR CONTRIBUTION

DD and KK analyzed the data and drafted the manuscript. DD and KK designed the study, and

directed implementation and data collection. JVL , ORS, JDL, MACV and KK collected the data.

JVL, ORS, JDL, and MACV edited the manuscript for intellectual content and provided critical

comments on the manuscript.

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REFERENCES

Adams, D. C., & Otárola-Castillo, E. (2013). geomorph: an r package for the collection and analysis of

geometric morphometric shape data. *Methods in Ecology and Evolution*, *4*(4), 393–399. doi:

10.1111/2041-210X.12035

Buss, D. M., Darwin, C., Lacaita, C. C., Murray, J., Tatham, R. G., Darwin, C., … Matthews, S.

(1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures.

Behavioral and Brain Sciences, *12*(1), 1-49. doi: 10.1017/S0140525X00023992

Claes, P., Liberton, D. K., Daniels, K., Rosana, K. M., Quillen, E. E., Pearson, L. N., … Shriver, M.

D. (2014). Modeling 3D facial shape from DNA. *PLoS Genetics*, *10*(3), e1004224. doi:

10.1371/journal.pgen.1004224

Claes, P., & Shriver, M. D. (2014). Establishing a multidisciplinary context for modeling 3D facial

shape from DNA. *PLoS Genetics*, *10*(11), e1004725. doi: 10.1371/journal.pgen.1004725

Danel, D. P., Dziedzic-Danel, A., & Kleisner, K. (2016). Does age difference really matter? Facial

markers of biological quality and age difference between husband and wife. *HOMO - Journal of*

Comparative Human Biology, *67*(4), 337–347. doi:10.1016/j.jchb.2016.05.002

Danel, D., & Pawlowski, B. (2007). Eye-mouth-eye angle as a good indicator of face masculinization,

asymmetry, and attractiveness (Homo sapiens). *Journal of Comparative Psychology*, *121*(2), 221–225.

doi:10.1016/j.jchb.2016.05.002

Enlow, D. H. (1990). *Facial Growth* (3rd ed.). Philadelphia: W.B. Saunders.

Farkas, L. G. (1988). Age- and sex-related changes in facial proportions. In L. G. Farkas & I. R.

Munro (Eds.), *Anthropometric Proportions in Medicine* (pp. 29–56). Springfield, IL: Thomas.

Farkas, L. G., & Cheung, G. (1981). Facial asymmetry in healthy North American Caucasians. An

anthropometrical study. *The Angle Orthodontist*, *51*(1), 70–7. doi:10.1043/0003-

3219(1981)051<0070:FAIHNA>2.0.CO;2

Feinberg, D. R., Jones, B. C., DeBruine, L. M., Moore, F. R., Law Smith, M. J., Cornwell, R. E., …

Perrett, D. I. (2005). The voice and face of woman: One ornament that signals quality? *Evolution and*

Human Behavior, *26*(5), 398–408. doi: 10.1016/j.evolhumbehav.2005.04.001

Feingold, A. (1992). Gender differences in mate selection preferences: a test of the parental investment

model. *Psychological Bulletin*, *112*(1), 125–139. doi: 10.1037/0033-2909.112.1.125

Fink, B., Klappauf, D., Brewer, G., & Shackelford, T. K. (2014). Female physical characteristics and

intra-sexual competition in women. *Personality and Individual Differences, 58*, 138-141. doi:

10.1016/j.paid.2013.10.015

Fisher, M. L. (2004). Female intrasexual competition decreases female facial attractiveness.

Proceedings. Biological Sciences, (Suppl 5), S283-285. doi: 10.1098/rsbl.2004.0160

Folstad, I., & Karter, A. J. (1992). Parasites, Bright Males, and the Immunocompetence Handicap. *The*

American Naturalist, *139*(3), 603–622. doi:10.1086/285346

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology*

and Sociobiology, *14*(2), 89–96. doi:10.1016/0162-3095(93)90009-7

Gangestad, S. W., & Scheyd, G. J. (2005). The evolution of human physical attractiveness. *Annual*

Review of Anthropology, *34*(1), 523–548. doi:10.1016/j.evolhumbehav.2004.04.003

Gautam, G., Shashikalakumari, V., & Garg, G. (2013). Facial attractiveness influenced by lower face

vertical proportions and mandibular prominence. *Orthodontic Waves*, *72*(1), 30–35. doi:

10.1016/j.odw.2012.11.002

Gilpin, A. R. (1993). Table for Conversion of Kendall'S Tau to Spearman'S Rho Within the Context

of Measures of Magnitude of Effect for Meta-Analysis. *Educational and Psychological Measurement*,

53(1), 87–92. doi: 10.1177/0013164493053001007

Grammer, K., & Thornhill, R. (1994). Human (Homo sapiens) facial attractiveness and sexual

selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, *108*(3), 233–

242. doi:10.1037/0735-7036.108.3.233

Hallgrimsson, B., Mio, W., Marcucio, R. S., & Spritz, R. (2014). Let's face it--complex traits are just

not that simple. *PLoS Genetics*, *10*(11), e1004724. doi:10.1371/journal.pgen.1004724

Hatfield, E., & Sprecher, S. (1995). Men's and Women's Preferences in Marital Partners in the United

States, Russia, and Japan. *Journal of Cross-Cultural Psychology*, *26*(6), 728–750. doi:

10.1177/002202219502600613

Hönn, M., Dietz, K., Eiselt, M.-L., & Göz, G. (2008). Attractiveness of facial profiles as rated by

individuals with different levels of education. *Journal of Orofacial Orthopedics*, *69*(1), 20–30. doi:

10.1007/s00056-008-0735-4

Hulley, S. B., Cummings, S. R., Browner, W. S., Grady, D. G., & Newman, T. B. (2013). *Designing*

clinical research: an epidemiologic approach (4th ed.). Philadelphia, PA: Lippincott Williams &

Wilkins.

Johnston, D. J., Hunt, O., Johnston, C. D., Burden, D. J., Stevenson, M., & Hepper, P. (2005). The

influence of lower face vertical proportion on facial attractiveness. *European Journal of Orthodontics*,

27(4), 349–54. doi: 10.1093/ejo/cji023

Johnstone, R. A., & Grafen, A. (1992). Error-Prone Signalling. *Proceedings of the Royal Society B:*

Biological Sciences, *248*(1323), 229–233. doi: 10.1098/rspb.1992.0066

Kościński, K. (2007). Facial attractiveness: General patterns of facial preferences. *Anthropological*

Review, *70*(1), 45–79. doi:10.2478/v10044-008-0001-9

Kościński, K. (2008). Facial attractiveness: Variation, adaptiveness and consequences of facial

preferences. *Anthropological Review*, *71*(1), 77–105. doi: 10.2478/v10044-008-0012-6

Kościński, K. (2009). Current status and future directions of research on facial attractiveness.

Anthropological Review, *72*(1), 45–65. doi: 10.2478/v10044-008-0015-3

Lander, K. (2008). Relating visual and vocal attractiveness for moving and static faces. *Animal*

Behaviour, *75*(3), 817–822. doi: 10.1016/j.anbehav.2007.07.001

Law Smith, M., Perrett, D., Jones, B., Cornwell, R., Moore, F., Feinberg, D., Hillier, S. (2006). Facial

appearance is a cue to oestrogen levels in women. *Proceedings of the Royal Society of London B:*

Biological Sciences, *273*(1583), 135-140. doi: 10.1098/rspb.2005.3296

Lee, A. J., Mitchem, D. G., Wright, M. J., Martin, N. G., Keller, M. C., & Zietsch, B. P. (2016). Facial

averageness and genetic quality: testing heritability, genetic correlation with attractiveness, and the

paternal age effect. *Evolution and Human Behavior*, *37*(1), 61–66.

doi:10.1016/j.evolhumbehav.2015.08.003

Li, N. P., Bailey, J. M., Kenrick, D. T., & Linsenmeier, J. A. W. (2002). The necessities and luxuries

of mate preferences: testing the tradeoffs. *Journal of Personality and Social Psychology*, *82*(6), 947–

955. doi: 10.1037/0022-3514.82.6.947

Lie, H. C., Rhodes, G., & Simmons, L. W. (2008). Genetic diversity revealed in human faces.

Evolution; International Journal of Organic Evolution, *62*(10), 2473–2486. doi:10.1111/j.1558-

5646.2008.00478.x

Little, A. C., Jones, B. C., & DeBruine, L. M. (2011). Facial attractiveness: evolutionary based

research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1571), 1638–

1659. doi: 10.1098/rstb.2010.0404

Liu, F., van der Lijn, F., Schurmann, C., Zhu, G., Chakravarty, M. M., Hysi, P. G., … Kayser, M.

(2012). A genome-wide association study identifies five loci influencing facial morphology in

Europeans. *PLoS Genetics*, *8*(9), e1002932. doi:10.1371/journal.pgen.1002932

Mitteroecker, P., Windhager, S., Müller, G. B., & Schaefer, K. (2015). The morphometrics of

"masculinity" in human faces. *PLoS ONE*, *10*(2). doi: 10.1371/journal.pone.0118374

Mydlová, M., Dupej, J., Koudelová, J., & Velemínská, J. (2015). Sexual dimorphism of facial

appearance in ageing human adults: A cross-sectional study. *Forensic Science International, 257*,

519.e1-519.e9. doi:10.1016/j.forsciint.2015.09.008

Oguchi, T., & Kikuchi, H. (1997). Voice and interpersonal attraction. *Japanese Psychological*

Research, *39*(1), 56–61. doi: 10.1111/1468-5884.00037

Partan, S. R., & Marler, P. (2005). Issues in the Classification of Multimodal Communication Signals.

The American Naturalist, *166*(2), 231–245. doi:10.1086/431246

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.

doi:10.1016/j.evolhumbehav.2004.04.003

Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., & Perrett, D. I.

(2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness.

Proceedings of the Royal Society of London B: Biological Sciences, *268*(1476), 1617-1623. doi:

10.1098/rspb.2001.1703

Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., … Akamatsu, S.

(1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, *394*(6696), 884–887. doi:

10.1038/29772

Puts, D. A. (2010). Beauty and the beast: mechanisms of sexual selection in humans. *Evolution and*

Human Behavior, *31*(3), 157–175. doi:10.1016/j.evolhumbehav.2010.02.005

Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, *57*,

199–226. doi:10.1146/annurev.psych.57.102904.190208

Rhodes, G., Zebrowitz, L. A., Clark, A., Kalick, S. M., Hightower, A., & McKay, R. (2001). Do facial

averageness and symmetry signal health? *Evolution and Human Behavior*, *22*(1), 31–46.

doi:10.1016/S1090-5138(00)00060-X

Saxton, T. K., Burriss, R. P., Murray, A. K., Rowland, H. M., & Roberts, C. S. (2009). Face, body and

speech cues independently predict judgments of attractiveness. *Journal of Evolutionary Psychology*,

7(1), 23–35. doi: 10.1556/JEP.7.2009.1.4

Saxton, T. K., Caryl, P. G., & Roberts, C. S. (2006). Vocal and Facial Attractiveness Judgments of

Children, Adolescents and Adults: the Ontogeny of Mate Choice. *Ethology*, *112*(12), 1179–1185. doi:

10.1111/j.1439-0310.2006.01278.x

Saxton, T. K., Mackey, L. L., McCarty, K., & Neave, N. (2016). A lover or a fighter? Opposing sexual

selection pressures on men's vocal pitch and facial hair. *Behavioral Ecology*, *27*(2), 512–519. doi:

10.1093/beheco/arv178

Schluter, D., & Price, T. (1993). Honesty, Perception and Population Divergence in Sexually Selected

Traits. *Proceedings: Biological Sciences*, *253*(1336), 117–122. doi: 10.1098/rspb.1993.0089

Scott, I. M. L., Clark, A. P., Boothroyd, L. G., & Penton-Voak, I. S. (2013). Do men's faces really

signal heritable immunocompetence? *Behavioral Ecology*, *24*(3), 579–589. doi:10.1093/beheco/ars092

Sheehan, M. J., Nachman, M. W., Dunbar, R. I. M., Apicella, C. L., Marlowe, F. W., Fowler, J. H., …

Tamura, K. (2014). Morphological and population genomic evidence that human faces have evolved

to signal individual identity. *Nature Communications*, *5*, 4800. doi: 10.1038/ncomms5800

Simmons, L. W., Rhodes, G., Peters, M., & Koehler, N. (2004). Are human preferences for facial

symmetry focused on signals of developmental instability? *Behavioral Ecology*, *15*(5), 864–871.

doi:10.1093/beheco/arh099

Soh, J., Chew, M. T., & Wong, H. B. (2007). An Asian community's perspective on facial profile

attractiveness. *Community Dentistry and Oral Epidemiology*, *35*(1), 18–24. doi: 10.1111/j.1600-

0528.2007.00304.x

Spyropoulos, M. N., & Halazonetis, D. J. (2001). Significance of the soft tissue profile on facial

esthetics. *American Journal of Orthodontics and Dentofacial Orthopedics*, *119*(5), 464–471. doi:

10.1067/mod.2001.113656

Swaddle, J. P., & Reierson, G. W. (2002). Testosterone increases perceived dominance but not

attractiveness in human males. *Proceedings. Biological Sciences*, *269*(1507), 2285–2289. doi:

10.1098/rspb.2002.2165

Tanner, J. M. (1989). *Fetus into Man: Physical Growth from Conception to Maturity* (2nd ed.). Ware:

Castlemead Publications.

Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty. *Human Nature*, *4*(3), 237–269.

doi:10.1007/BF02692201

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, *3*(12),

452–460. doi:10.1016/S1364-6613(99)01403-5

Thornhill, R., & Møller, A. P. (1997). Developmental stability, disease and medicine. *Biological*

Reviews, *72*(4), 497–548. doi: 10.1111/j.1469-185X.1997.tb00022.x

Třebický, V., Fialová, J., Kleisner, K., & Havlíček, J. (2016). Focal Length Affects Depicted Shape

and Perception of Facial Images. *PLOS ONE*, *11*(2), e0149313. doi:10.1371/journal.pone.0149313

Türkkahraman, H., & Gökalp, H. (2004). Facial profile preferences among various layers of Turkish

population. *The Angle Orthodontist*, *74*(5), 640–7. doi: 10.1043/0003-

3219(2004)074<0640:FPPAVL>2.0.(Valenzano et al., 2006)CO;2

Valentine, T., Darling, S., & Donnelly, M. (2004). Why are average faces attractive? The effect of

view and averageness on the attractiveness of female faces. *Psychonomic Bulletin & Review*, *11*(3),

482–487. doi: 10.3758/BF03196599

Valentová, J., Roberts, S. C., & Havlícek, J. (2013). Preferences for facial and vocal masculinity in

homosexual men: the role of relationship status, sexual restrictiveness, and self-perceived masculinity.

Perception, *42*(2), 187–197. doi: 10.1068/p6909

Valenzano, D. R., Mennucci, A., Tartarelli, G., & Cellerino, A. (2006). Shape analysis of female facial

attractiveness. *Vision Research*, *46*(8), 1282–1291. doi: 10.1016/j.visres.2005.10.024

Verdonck, A., Gaethofs, M., Carels, C., & de Zegher, F. (1999). Effect of low-dose testosterone

treatment on craniofacial growth in boys with delayed puberty. *The European Journal of*

Orthodontics, *21*(2), 137-143. doi:10.1093/ejo/21.2.137

Walker, D. A. (2003). JMASM9: Converting Kendall's Tau For Correlational Or Meta-Analytic

Analyses. *Journal of Modern Applied Statistical Methods*, *2*(2), 525–530. doi:

10.22237/jmasm/1067646360

Wang, M. F., Otsuka, T., Akimoto, S., & Sato, S. (2013). Vertical facial height and its correlation with

facial width and depth: Three dimensional cone beam computed tomography evaluation based on dry

skulls. *International Journal of Stomatology & Occlusion Medicine*, *6*, 120–129. doi:10.1007/s12548-

013-0089-4

Wedekind, C., & Folstad, I. (1994). Adaptive or Nonadaptive Immunosuppression by Sex Hormones?

The American Naturalist, *143*(5), 936–938. doi:10.1086/285641

Wells, T. J., Baguley, T., Sergeant, M., & Dunn, A. (2013). Perceptions of Human Attractiveness

Comprising Face and Voice Cues. *Archives of Sexual Behavior*, *42*(5), 805–811. doi: 10.1007/s10508-

012-0054-0

Wells, T. J., Dunn, A. K., Sergeant, M. J. T., & Davies, M. N. O. (2009). Multiple Signals in Human

Mate Selection: A Review and framework for investigating facial and vocal signals. *Journal of*

Evolutionary Psychology, *72*, 111–139. doi:10.1556/JEP.7.2009.2.2

Zahavi, A. (1975). Mate selection-a selection for a handicap. *Journal of Theoretical Biology*, *53*(1),

205–14. doi: 0.1016/0022-5193(75)90111-3

Zar, J. H. (1999). *Biostatistical analysis* (4th ed.). Upper Saddle River: Prentice Hall.

Zebrowitz, L. A., & Rhodes, G. (2004). Sensitivity to "Bad Genes" and the Anomalous Face

Overgeneralization Effect: Cue Validity, Cue Utilization, and Accuracy in Judging Intelligence and

Health. *Journal of Nonverbal Behavior*, *28*(3), 167–185. doi:10.1023/B:JONB.0000039648.30935.1b