Charles University

Faculty of Science

Department of Philosophy and History of Science

Theoretical and Evolutionary Biology

Mgr. Tomáš Kočnar

The Evolution and Functional Role of the Colour of Iris in Humans, Its Biological Role, and Cross-Cultural Perception

Evoluce a význam barvy duhovky u člověka, její biologická role a mezikulturní percepce

Doctoral thesis

Supervisor:

doc. Mgr. Karel Kleisner PhD.

Prague, 2021

Prohlášení

Prohlašuji, že jsem předkládanou práci vypracoval samostatně s využitím pouze uvedených a řádně citovaných pramenů a literatury. Dále prohlašuji, že práce ani její podstatná část nebyla využita k získání jiného nebo stejného titulu na této nebo jiné univerzitě.

V Praze dne 17. října 2021 Mgr. Tomáš Kočnar

..…………………………..

Acknowledgment

I am thankful to Karel Kleisner, a great teacher and friend, a buddy and supervisor, who has been the inspiration and support from the very beginning up to the present for my eye research. He has been a great companion on our field trips and fair and patient supervisor of my research papers.

I am thankful to my loving partner Anna Rosenová who supported me finalize this thesis so you can now read these lines. Her kindness, as well as the advice on English writing, final reading and great coffee made this happen.

My gratitude belongs to Anna Pilátová for thorough proofreading and valuable comments. I am also thankful to everybody who helped me on my study journey, namely Selahattin Adil Saribay, Tuncay Çelik, Robert Mbe Akoko, Vít Třebický, David Stella, and Petr Tureček. It was a pleasure to be a member of Department of Philosophy and History of Science and to found here and abroad many kind friends and colleagues.

Abstract

The human eye is a conspicuous and unique component of facial appearance. From other mammalian eyes it is set apart mainly by its unusual shape, visible white sclera, and a wide range of iris colours, which is something unique within a single species. Whether alone or in the context of the face as a whole, eye colour is an underexplored area within research into the perception of various personality traits. In this thesis, the author first reviews the physiological factors connected with eye colour and reported correlations between eye colour and different psychological and behavioural conditions. This is followed by an investigation of a possible relationship between eye colour and perceived dominance and attractiveness. The first and second study examines whether and to what extent eye colour is associated with facial morphology responsible for perceived dominance. The results are ambiguous. A cross-cultural comparison in the third study revealed that faces with blue eyes are judged as more attractive only in populations where individuals with darker eyes predominate. It is thus discussed whether this population-specific pattern is the consequence of a negative frequency-dependent selection that may have contributed to the present-day eye colour diversity. In short, the aim of this thesis was to investigate to what degree the eyes, and especially iris colour, are the subject of perception and what biological meanings people assign to them in different contexts.

Key words: *human eye; iris colour; perception; dominance; attractiveness; negative frequency-dependent selection*

Abstrakt

Lidské oko představuje výrazný a jedinečný prvek, který se podílí na vzhledu obličeje. Na rozdíl od očí jiných savců vyniká zejména svým neobvyklým tvarem, nápadnou bílou sklérou a širokou škálou barev oční duhovky, jakou nenalezneme u jiných živočichů. Barva očí samotná, i jako součást celkového vzhledu obličeje, je téma, které spíše zůstává stranou zájmu výzkumu percepce osobnostních faktorů. Tato práce nejprve shrnuje poznatky o souvislostech mezi faktory fyziologickými a barvou očí, a také se věnuje dosud zjištěným korelacím barvy očí s různými faktory psychologickými a behaviorálními. Práce dále představuje výzkum zabývající se potenciálním vztahem barvy očí a pociťované dominance a atraktivity. První a druhá studie zkoumají, zda a do jaké míry barva očí souvisí s morfologickými rysy obličeje, které zodpovídají za pociťovanou dominanci. Výsledky těchto studií nicméně poskytují nejednoznačné závěry. Třetí studie na základě mezikulturního srovnání ukázala, že obličeje nositelů modrých očí byly hodnoceny jako atraktivnější v populacích s majoritním zastoupením hnědookých jedinců. Je proto otázkou, zda tato zjištění, která se týkají jen určitých populací, jsou důsledkem negativního frekvenčně závislého výběru, který mohl ovlivnit současnou diverzitu barvy očí. Účelem této práce tedy bylo zjistit, do jaké míry jsou oči, zejména pak barva duhovky, předmětem percepce a jaké biologické významy jim lidé v různých kontextech přisuzují.

Klíčová slova: *lidské oko; barva duhovky; percepce; dominance; atraktivita; negativní frekvenčně závislý výběr*

Contents

The Evolution and Functional Role of the Colour of Iris in Humans, Its Biological Role, and Cross-Cultural Perception

> The field of pigmentation may not even be a suitable one for the student who wants a good quick dissertation project, or the faculty member who wants a publication in time for the next swindle sheet he sends to the dean. Perhaps it is a study only for the tenured. I guarantee you moments of madness when you try to decide how to classify medium brown hair and various other ambiguous phenotypes.
>
> Alice M. Brues

Introduction

The appearance of the human eye has been the subject of scientific research from many different perspectives. The aim of this introduction is neither to provide a complete list of these perspectives nor to describe the human eye in its full complexity, including the iris, a feature that is the focus of this dissertation. There is, however, one perspective which must not be omitted, a perspective that falls within the province of biosemiotics and evolutionary psychology: it is the human ability to perceive and be perceived.

The etymological meaning of the expression 'to perceive' – and even the term 'perspective' – may help us understand the importance of 'perception', 'human eye', and especially the 'iris', in the context of this thesis. The word 'perspective' comes from the Latin *perspectus* ('clearly perceived'), which is a past participle of *perspicere* ('inspect, look through, look closely at'). Surprisingly, the entry 'to perceive' offers a similar result: the word is derived from Latin *percipere* ('obtain, gather, seize entirely, take possession of'), which can also be used figuratively in the sense of 'to grasp with the mind, learn, comprehend' (literally 'to take entirely').[1] People inspect with their eyes, look closely at objects. Through eyes as organs of sight, humans can gather much information from and about the surrounding environment. And what about the appearance of the human eye? Could one to describe it as *perspectus*, that is, as something that can be 'clearly perceived'? Can the perceiver gather any information from the appearance of the human eye or even look through it?

In comparison with other primate species, human eyes have a unique appearance characterised chiefly by a horizontally prolonged shape, conspicuous white sclera, and a variety of iris colours. As such, they meet all conditions of functioning as semantic organs, that is, 'semiautonomous relational entities facilitated by exposed organismal surfaces and defined by the meaning they acquire due to a particular perceiver' (as defined in Kleisner, 2015). This

[1] https://www.etymonline.com/ . Accessed on 7 October 2021.

dissertation offers a short introduction to human eyes as a good example of a semantic organ and explores some of the ways people may perceive the appearance of eyes. In other words, it tries to answer the question to what degree the eyes or their particular characteristics, especially the iris colour, are also the subject of perception, and what biological meanings people assign to them in different contexts.[2]

Traits forming the appearance of the human eye

The following sections describe a number of eye features that contribute to the overall appearance of a human eye.

The sclera

The horizontally prolonged shape and contrasting white sclera of the human eye enhance the perception of gaze by conspecifics (Kobayashi & Kohshima, 2001). Tomasello et al. (2007) in their influential work introduced the cooperative eye hypothesis based on the suggestion that the apparent white sclera, which contrasts with a coloured iris and the surrounding skin, underpins cooperation and subsequently provides support to specific behaviours, such as language in humans. In other primate species, the sclera is less depigmented and gaze is thus less apparent ('gaze camouflage theory'; Kobayashi & Kohshima, 2001). Perea-García et al. (2019), on the other hand, pointed out that more relevant to the conspicuousness of gaze is the relative contrast between the sclera and the iris rather than scleral depigmentation. Consequently, they suggested that nonhuman great apes might also rely on gaze as a social cue. Moreover, Caspar et al. (2021) showed that differences in scleral pigmentation between great apes and humans are gradual and may have arisen via genetic drift and sexual selection rather than due to pressures on cooperation. Based on the observation that some humans do not have a completely depigmented sclera, Mayhew and Gómez (2015) stressed the importance of the horizontally prolonged shape of eyes, which sets apart human eyes from the eyes of other primates. According to Danel et al. (2020), the sclera surface is more horizontally exposed in Caucasian men and eye fissures are rounder (less rectangular) in women than in men, although the total surface area is in both sexes similar. The size of the exposed sclera moreover did not differ in the four races examined in the study of Danel et al. (2018). The same team of authors

[2] For a detailed introduction to the concept of semantic organ, see Kleisner (2008, 2015). For a specific case of semantic organs – a superficial similarity of eyes and eyespots and their both intra- and interspecific signification see the study of Kočnar and Kleisner (2009). For a recent example of interspecific importance of eye patterns as semantic organs, see Radford et al. (2020).

also found no link between the size of exposed sclera and trustworthiness, although trust is regarded as an important prerequisite for cooperation (Danel et al., 2018).

Further, it has been reported that changes in sclera colour function as cues to age, health, attractiveness (Gründl et al., 2012; Russell et al., 2014), but also emotional states, because eye redness is connected with perceived unhappiness and weaker health (Provine et al., 2011).

Size and shape

In the context of the face as a whole, eye size plays a role in the perception of different personality traits. It influences, for instance, the perception of attractiveness (Pettijohn & Tesser, 2005) and honesty (Atoum & Al-Simadi, 2019). Larger eyes, being one of the neonate features that contribute to the impression of babyfacedness, are positively associated with ratings of cuteness, youth, attractiveness, and babyishness of an infants' faces (Berry & McArthur, 1985; Zebrowitz & Montepare, 2008). In both sexes, larger eyes are connected with positive personality traits such as warmth, kindness, and honesty, but also social submissiveness, intellectual naiveté, and physical weakness (Berry & McArthur, 1985; McArthur & Apatow, 1984). Further, Gonçalves et al. (2014) observed that larger eyes lead to more positive perceptions of warmth and competence. It has been reported that preferences for larger eyes emerges in five-month-old infants (Geldart et al., 1999). The appearance of eyes that makes faces look adult is also responsible for perceived dominance (Keating, 1985).

Eye shape is another morphological feature responsible for the perception of attractiveness, age, and dominance. In connection with size, eye roundedness contributes to a younger appearance, whereas narrowing of the eyes can lead to the perception of higher dominance (Berry & McArthur, 1985). In other studies, however, youthful eyes were characterised by a narrow fissure, while rounding of the palpebral fissure was linked to a seemingly older form of the eye (e.g. Rohrich et al., 2004; Yaremchuk, 2004). Interestingly, almond-shaped eyes in females were rated as less attractive and older, although this study noted that the surrounding skin, as well as the other periorbital features, such as eyebrows, also contribute to the perception of attractiveness (Prantl et al., 2019).

Eyebrows play an important role also in the perception of other qualities, such as dominance (Keating, 1985), age (Russell et al., 2017), sex (Dupuis-Roy et al., 2019), emotions (Schmidt & Cohn, 2001), and even personality traits such as narcissism (Giacomin & Rule, 2019).

The iris

Human iris is a ring-shaped structure with a central aperture, the pupil. The iris forms a natural the centre in the whole context of the eye. Iris colour, relative iris luminance, characteristics of areas adjacent to the iris, such as the limbal ring, iridial characteristics, such as Fuchs crypts, contraction furrows, pigment dots, but also iris function (constriction and dilation) all contribute to the overall appearance of the eye.

The pupil

The sphincter and dilator muscles of iris constrict and dilate the pupil, respectively, in response to impulses from sympathetic and parasympathetic nerves. As a consequence, the observable size of pupil and iris changes.

Eyes with a larger pupil diameter signal youthfulness and are thus assessed as more attractive than eyes with smaller pupils (e.g. Gründl et al., 2012). Another interpretation was offered by Hess (1975), who also reported a preference for dilated pupils: positive emotions and sexual arousal influence pupil dilation, which is then perceived as a signal of sympathy and interest. Interestingly, faces with large pupils induce a heightened amygdala activation regardless of perceived attractiveness (Amemiya & Ohtomo, 2012).

Kret et al. (2015) showed that faces with dilated pupils are regarded as more trustworthy and people have the ability to mimic their partners' pupil size. Because this kind of dilation mimicry predicted trust among group members, it has been hypothesised that the relationship between pupil mimicry and trust evolved in social species (Kret et al., 2015; Kret & De Dreu, 2017).

Colours

Humans are only species in which one finds a wide range of eye colours. Although there are some notable exceptions among primates (Caspar et al., 2021; Perea-García et al., 2021), the variety of iris colours in humans is wider, comprising more than two distinct colours.

Histologically, the human iris consists of five cell layers: the anterior border layer, stroma, the sphincter muscle, dilator muscle, and the pigment iris epithelium. Melanocytes, which are located in the anterior border layer, the stroma, and the pigment iris epithelium produce a dark pigment called melanin. Melanin in conjunction with the density and distribution of melanosomes in the anterior layer and the stroma are the main determinants of eye colour (Sturm & Frudakis, 2004; Wilkerson et al., 1996). In the heavily pigmented posterior layer, pigment iris epithelium, the amount of melanin is constant across different eye colours and plays no role in perceivable eye colouration, except in individuals with albinism. The cells of pigment iris epithelium are of neuroectodermal origin, while melanocytes in the outer layers originate, just like dermal melanocytes, in the neural crest (Eagle, 1988; Sturm & Larsson, 2009). The number of melanocytes does not appear to substantially vary between different eye colours. These colour differences are mainly due to variable amounts and qualities of the melanosome particles in which the melanin pigment is packaged within the stromal cells (Eagle, 1988; Imesch et al., 1997). In a darker iris, high levels of melanin in the outer layers absorb some light and reflect back a brown colour, whereas the structure of light-coloured eyes scatters to the surface the shorter, blue wavelengths (Sturm & Larsson, 2009). Lighter-coloured irises thus appear as blue, green, or hazel not in consequence of their chemical composition but due to their stromal structure. That, however, is still only part of the answer: the range of human eye colours is determined by the quality, quantity, and ratio of melanin types (D. Duffy, 2015; Prota et al., 1998; Wakamatsu et al., 2008; Wielgus & Sarna, 2005).

Eye colour used to be considered a typical example of a simple Mendelian recessive-dominant gene trait and in fact, one can still encounter this idea in some textbooks for elementary and high schools. It has been well established, though, that eye colour is a polygenic trait determined by several genes (Sturm & Larsson, 2009; Sulem et al., 2007). Eye colour is highly heritable, with seven main factors explaining most of the genetic variance: OCA2, TYR, TYRP1, IRF4, SLC45A2, SLC24A5, and SLC24A4 (D. Duffy, 2015). As noted above, eye colours are controlled by the amount and ratio of melanin types. Both types, i.e., both eumelanin and pheomelanin, are produced in melanocytes derived from the neural crest. Yet while melanin, which is responsible for hair and skin pigmentation, is contained in melanosomes which are transferred into keratinocytes, stromal melanosomes remain in melanocytes. Blue and green eyes have a larger ratio of pheomelanin to eumelanin (14:1), whereas in brown eyes, the ratio is balanced (Pavan & Sturm, 2019). For detailed information about the functions of respective genes, as well as descriptions of biochemical pathways of melanin synthesis, see reviews by D. Duffy (2015) or Dorgaleleh et al. (2020).

Physiological factors connected with eye colour

There is some evidence to the effect that eye colour is linked to certain health conditions, diseases, or impairments. It is thus often considered a valuable medical prognostic factor. For instance, Sun et al. (2014) reviewed a number of studies and medical reports on eye-related diseases and concluded that increased risk of age-related cataract is consistently associated with darker eye colours (but see Hashemi et al., 2019, who reported association with light eye colour), and that the risk of uveal melanoma is higher in lighter eyes due to the synergic effect of light eyes and UV radiation exposure. On the other hand, the same review paper found no consistent evidence supporting the role of iris colour in the development of age-related macular degeneration nor any possible link between iris colour and myopia (Sun et al., 2014).

In a meta-analysis conducted by Nayman et al. (2017), lighter eyes were identified as a significant risk factor for uveal melanoma. Besides light eyes, light hair and skin that does not tan easily in conjunction with high levels of sun exposure are important risk factors for a melanoma (Cust et al., 2018; Hägg et al., 2019; Lock-Andersen et al., 1998). There are also records of increased risk of colorectal cancer observed among women with grey or green eyes (Yang et al., 2011; but cf. Vallès et al., 2018, who found a higher incidence of this type of cancer among individuals with brown hair and eyes).

Higher prevalence of diabetes was reported in light-eyed patients (Di Stasio et al., 2011; Ziegler et al., 1990; but see also Antonopoulos et al., 1993), while increased risk of hypertension was found in brown-eyed individuals (Friedman et al., 1990). There are also reports about associations between nephrological conditions and eye colour (Bodaghi et al., 2014; Fetter, 1958), while Ekmekci et al. (2014) remarked on a possible relationship between the geographical distribution of blue eyes and the prevalence of multiple sclerosis.

In a review dedicated to the association between eye colour and hearing loss, Mujica-Mota et al. (2015) provided evidence to the effect that brown-eyed individuals are better protected against noise-induced hearing loss. This review thus corroborated the assumption that eye colour is a possible indicator of melanin content in the inner ear (see also older studies of Da Costa et al., 2008; Hood et al., 1976). It has also been reported that light-eyed people suffer from hearing loss due to meningitis more frequently than dark-eyed people do (Cullington, 2001).

The following observations indicate that eye colour need not be only used as a medical prognostic factor but can also be put in a broader context. In Vercellini et al.'s study (2013), women with rectovaginal endometriosis were judged to be more attractive than those in the two control groups consisting of women with ovarian endometriosis and women without a history of endometriosis. Moreover, women with rectovaginal endometriosis had a leaner silhouette, larger breasts, earlier coitarche (Vercellini et al., 2013), and – as indirectly follows from Vercellini et al.'s follow-up study (2014) – they also had blue eyes. In this follow-up study, the association between blue eyes and rectovaginal endometriosis was explained by the fact that the genes associated with eye colour are located in a region with a pattern of linkage disequilibrium with genes involved in the invasiveness of endometriosis (Vercellini et al., 2014). An alternative explanation is that a higher risk of endometriosis may be associated with vitamin D deficiency, which is a consequence of reduced exposure to sunlight in the photosensitive phenotype. Blue eyes could be viewed as an indicator of this particular phenotype. Regardless of which explanation is more fitting, blue-eyed women from these Italian samples were both more prone to endometriosis and judged as more attractive (Vercellini et al., 2013, 2014).

In patients of Caucasian origin, the prevalence of varicocele, which is a venous weakness in scrotum, is higher in the brown-eyed than in blue-eyed men (Kumanov et al., 2014). The authors of that study speculated that light-eyed European ancestors might have had an evolutionary advantage due to hypothetically better sperm indices, presumably connected with a low rate of varicocele – and thus higher fertility – than dark-eyed men (Kumanov et al., 2014).

Psychological, behavioural and personality factors connected with eye colour

Inhibited behaviour and its correlates

A whole range of experiments investigated possible correlations between eye colour, reaction times, and various behavioural characteristics. It has been reported that brown-eyed individuals exhibit faster reaction times than blue-eyed individuals do (e.g. Hale et al., 1980; Rowe & Evans, 1994; Tedford et al., 1978; but not in Crowe & O'Connor, 2001) and score higher on sociability (Gary & Glover, 1975; but see Robinson, 1981), extraversion and neuroticism (Gentry et al., 1985), but also easier emotional arousal (Markle, 1975). See also a collection of reports compiled by Worthy (1999) for further speculative but interesting conclusions on this topic.

Based on a longitudinal analysis, Rosenberg and Kagan (1987) found out that, unlike their brown-eyed fellows, blue-eyed children tend to show inhibited behaviour towards unfamiliar stimuli. Along similar lines, Coplan et al. (1998) observed social wariness in blue-eyed male infants. Adult male individuals who displayed shyness in social interactions had also more often blue eyes, ectomorph somatotype, and a lower olfactory threshold for butanol (Herbener et al., 1989). Among people with speech disfluency, blue-eyed individuals tend to suffer from a more severe stuttering (Christensen & Sacco, 1989). Happy and Collins (1972) reported that autism and introversion were significantly more frequent in light-eyed than in dark-eyed individuals. Although the differences in withdrawal (an equivalent term for inhibition) between blue-eyed and brown-eyed individuals disappear in later childhood (Rubin & Both, 1989), some brain properties relating to temperament are preserved from infancy into early adulthood: individuals who had been assessed as inhibited show a greater functional MRI signal response within the amygdala to novel versus familiar faces (Schwartz et al., 2010).

Subjects with darker eyes experienced higher levels of dental pain (Sutton, 1959; but see also Hyde et al., 2018, who reported no association between dental injection pain and eye colour) and according to Teng and Belfer (2014), women with light-coloured eyes experience less pain while giving birth.

Furthermore, there is a considerable amount of evidence supporting the hypothesis that eye colour predicts a tendency for alcohol abuse. Light-eyed individuals drink substantially more alcohol than dark-eyed individuals do (Bassett & Dabbs, 2001; Bègue & Boudesseul, 2017; Sulovari et al., 2015). According to Bassett and Dabbs (2001), the greater amount of alcohol consumed by blue-eyed individuals may compensate for their otherwise inhibited behaviour. Alternatively, the same authors speculate that in brown-eyed individuals, greater sensitivity to alcohol does not lead to physical dependence, while blue-eyed persons, being less sensitive to alcohol, are more likely to develop an addiction. Bègue and Boudesseul (2017) noted that behavioural inhibition is a primary motivation system associated with anxiety, which is in turn related to alcohol disorders (Leonard & Blane, 1999). Sulovari et al. (2015) in their population-based study found evidence of an association between alcohol dependence and blue eye colour and described a statistically significant number of genetic interactions between eye colour genes and alcohol dependence-associated genes in subjects of European ancestry. Interestingly, a clinical study of Bremner (2019) found that cocaine – which he used to diagnose Horner syndrome – has a twice greater mydriatic effect (pupil dilation) on persons with blue and green eyes than on brown-eyed individuals. This finding could be explained by cocaine's strong affinity to melanin, which binds more cocaine and reduces its bioavailability (Bremner, 2019). One could thus speculate whether there are in fact any differences related to eye colour among cocaine users, too.

At this point, we should mention at least one hypothesis aimed at explaining the relationship between eye colours and behavioural patterns. It works on the assumption that the amount of melanin in the iris and in the central nervous system has a common embryologic origin: in brown-eyed individuals, more melanised axon sheaths facilitate faster conduction of nerve impulses, which then influence individual's behaviour (Hale et al., 1980). For elaboration of this explanation see, for example, Rosenberg and Kagan (1987).

Nevertheless, the notion that eye colour is an indicator of genetic predisposition toward certain behaviours both in humans and in animals has been challenged in the study of Elias et al. (2008): when examining the *Drosophila melanogaster*, these authors found no significant correlations between phenotypic eye colouration and behaviour. Still, their findings pointed to significant behavioural differences between cell-defect groups associated with eye colour. The particular cell defects that cause eye colour could thus indicate certain behaviour rather than eye colour itself (Elias et al., 2008).

Eye colour and other iris characteristics as possible biomarkers for personality traits

Trixler and Tényi (2017) studied relationships between iris characteristics and specific psychiatric disorders. They confirmed previous findings which indicated that Wölfflin nodules, which are small bundles of collagen, and pigment dots are more common in lighter-coloured irises (e.g. Larsson et al., 2007; Larsson & Pedersen, 2004). The results were also in accordance with the hypothesis that these iris structures – which are considered markers of neurodevelopment – are more prevalent in schizophrenic patients than in the control group (Trixler & Tényi, 2017). Further, a higher rate of concentric furrows was identified in dark-eyed subjects (Trixler & Tényi, 2017). Dark eyes with more layers of melanocytes are thicker and more prone to folding, which causes concentric furrows (Davidson, 2001). According to Larsson et al. (2007), people with many concentric furrows have a lower ability to control impulses than people with few such furrows. The development of concentric furrows has both a negative correlation with perseverance and a positive correlation with novelty seeking (Lim et al., 2014). As summed up in Trixler and Tényi's study (2017), novelty seeking individuals tend to be excitable, exploratory, but also more easily bored and frustrated by failure. Surprisingly, this study found no difference in Fuchs crypts, another iris characteristic that has a strongest heritable component and has been linked with personality in an earlier study by Larsson et al. (2007).

We can take these findings as a relevant contribution uncovering a possible relationship between personality and eye colour. The relationship could be clearer, if we submerge under the superficial layer of the human iris which is of the same ectodermic origin as the skin and central nervous system. As mentioned in Trixler and Tényi (2017), a specific part of the human brain, the anterior cingulate cortex, is responsible for emotion regulation, motoric functions, visuospatial and memory processing. Mutations in Pax6 gene region have been found in individuals showing disinhibition, impulsive behaviour, impaired social understanding or impaired verbal inhibition (Heyman et al., 1999). Pax6 is also a candidate gene for development of tissue differences in the iris examined in the study Larsson et al. (2007). Taking into account that the presence of concentric furrows, Wölfflin nodules or pigment dots are linked with a specific eye colour, we can cautiously speculate about the eye structures and the colour of iris as possible biomarkers for psychiatric disorders as well as personality traits.

Eye colour, light sensitivity, and its consequences

It is well documented that so-called ‘ocular straylight’, meaning intraocular light scattering, depends on eye pigmentation. It is greater in blue-eyed than in brown-eyed people (IJspeert et al., 1990) and blue eyes permit an increased light transmittance through the iris and the surrounding eye wall (van den Berg et al., 1991). In the human eye, retinal ganglion cells constitute a nonvisual pathway from the eye to the suprachiasmatic nucleus of the hypothalamus (Moore et al., 1995). Melanopsin, a protein contained in retinal ganglion cells, promotes one particular nonvisual function of the human eye, namely circadian adjustment to light (Provencio, 2011; Roecklein et al., 2009). This pathway thus does not convey information about visual images but rather the perception of the amount of short wavelength light. Depending on the amount of light, hypothalamus adjusts the release of two hormones: cortisol and melatonin. It is believed that the level of stimulation of suprachiasmatic nucleus via this pathway is related to the symptoms of seasonal affective disorder (SAD) (Workman et al., 2018).

In a study of Workman et al. (2018), individuals with brown eyes self-reported higher levels of mood variability depending on the seasons than blue-eyed individuals did. Interestingly, another result derived from this sample by the same authors did not support the latitude hypothesis of the seasonal affective disorder (SAD), which is based on the assumption that populations in higher latitudes suffer more from the SAD due to greater daylight deprivation during the winter months (e.g. Rosen et al., 1990). Still, the significant difference between the light-eyed and dark-eyed groups in Workman et al.’s sample (2018) indicates that blue-eyed individuals are more resilient to SAD than brown-eyed people are. This finding is in line with previous research made by Goel et al. (2002), who observed that darker-eyed patients with SAD are significantly more depressed and fatigued than blue-eyed patients. Moreover, Terman and Terman (1999) reported that blue-eyed persons show a greater summertime increase in retinal sensitivity than darker-eyed persons do and that a similar trend is observed in their response to morning light. In another study, dark-eyed people showed delayed chronotype and sleep phase than people with lighter eye colour did (White & Terman, 2003). In a recent study, lighter eyes were associated with greater response to light therapy treatment for fatigue (Connolly et al., 2021). Comparing Caucasian and Asian samples, Higuchi et al. (2007) found out that the percentage of suppression of nocturnal melatonin secretion by light was larger in light-eyed Caucasians than that in dark-eyed Asians. These results thus suggest that the variation in melatonin suppression is related to eye pigmentation and possibly also to ethnicity. In the Czech population, however, research so far found only minimal effects of eye colour on mental and physical health (Flegr & Sýkorová, 2019).

The perception of eye colour

Whether on its own or within the context of the whole face, eye colour, as one of facial characteristics, is an often neglected subject in studies investigating the perception of various personality traits. This is surprising for at least two reasons. Firstly, when looking at the face of another person, people pay attention to the eyes more often than to other facial regions (Birmingham et al., 2008; Henderson et al., 2005; Langton et al., 2000; Pelphrey et al., 2002). Secondly, humans have a well-developed ability to 'process, recognise and extract information from other's faces' (Little et al., 2011). Human face, even neutral in its expression, may provide information not only about age, health, but also about attractiveness and other personality traits and social characteristics of its bearer (e.g. Rhodes & Zebrowitz, 2002).

In the following section, we discuss relationships between eye colour and the perception of several personality traits, such as facial attractiveness, dominance, and trustworthiness. The papers attached to this introduction examine a possible association between eye colour and dominance (Kleisner et al., 2010[3]; Kočnar et al., 2012[4]), eye colour and attractiveness (Kleisner et al., 2010; Kočnar et al., 2019[5]), and eye colour as one of the attributes related to facial attractiveness in a cross-cultural comparison (Kočnar et al., 2019).

Eye colour and perceived dominance

In literature on facial perception, masculine facial features in men, such as large jaws and prominent brows, are reliably associated with perceived dominance (e.g. Cunningham et al., 1990; Mueller & Mazur, 1997). Men with masculine faces report lower incidence of disease (Thornhill & Gangestad, 2006), which is also why it has been suggested that features associated

[3] STUDY 1
[4] STUDY 2
[5] STUDY 3

with dominance function as honest signals of male genetic quality (Havlíček et al., 2005). In men, therefore, masculine faces thus should be attractive for the opposite sex.

In the first study, we found a significant correlation between eye colour and perceived dominance in a sample of Czech faces (Kleisner et al., 2010). Brown-eyed male faces were rated as more dominant than faces with blue eyes. When controlled for the effect of eye colour, other facial characteristics seemed responsible for perceived dominance: broader chin, laterally prolonged mouth, larger nose, and eyes that are closer together with thicker eyebrows. In women, we found no association between eye colour and rated dominance.

By contrast to dominant-looking male faces, round faces with round and large eyes, smallish nose, and high eyebrows are linked to submissiveness (e.g. Berry & McArthur, 1985; Cunningham et al., 1990). Male faces with blue eyes, judged as more submissive in a study of Kleisner et al. (2010), tended to have similar facial features: a smaller chin, smaller nose, and greater distance between the eyes. Interestingly, blue eyes may contribute to a child-like appearance: after all, new-born children usually have blue eyes and their colour stabilises and develops only later on (Bito et al., 1997). Based on this fact, Kleisner et al. (2010) formulated a hypothesis of social feedback, which draws on the observation of association between blue eyes and submissive-looking face in adult men as well as previous studies on behavioural inhibition (Rosenberg & Kagan, 1987) and social wariness of blue-eyed children (Coplan et al., 1998), that is, features that can be reinforced by others in social interaction. To test another possible explanation, the genetic linkage hypothesis, we tested the results on another sample of raters from a different population. This was undertaken in the second study (Kočnar et al., 2012).

Controlling for sample and location, our second study nevertheless found no association between eye colour and perceived dominance (Kočnar et al., 2012). Interestingly, visualisation of shape regression on eye colour in the sample used in this study yielded similar results as this analysis on the sample from the first study: averaged brown-eyed male face tended to have relatively broader chin, bigger nose, and thicker eyebrows, while averaged blue-eyed male face was rounder, with a smaller nose, and, though only apparently, greater distance between the eyes.[6]

[6] For a comparison between the averaged faces, see the attached STUDY 1 and STUDY 2.

Eye colour and other perceived characteristics

Several studies showed that behavioural intentions, including judgments about trustworthiness, are intuitively and consistently inferred from facial appearance (Oosterhof & Todorov, 2008; Willis & Todorov, 2006). Given that such cues from faces with a neutral expression might signal whether a person should be approached or avoided, these judgements could be crucial for one's survival but also play an important role in different social interactions (Rule et al., 2011; Todorov, 2008; van 't Wout & Sanfey, 2008). Kleisner et al. (2013) investigated the possible role of eye colour and facial shape features in judgments of trustworthiness. Based on a sample of Czech faces, they found that brown-eyed male faces were perceived significantly more trustworthy than blue-eyed ones and that correlations between facial shape and eye colour are significant. Similarly to findings on dominance in a study of Kleisner et al. (2010), the authors concluded that it is the facial morphology linked to brown eyes, not the eye colour as such, that is responsible for the perception of trustworthiness (Kleisner et al., 2013). In a study of Boeck and Ivan (2013), the same sample of stimuli were judged by Swedish raters: their results revealed no significant correlations between eye colour and perceived trustworthiness.

Using facial stimuli of persons wearing differently coloured contact lenses, Beattie and Shovelton (2002) conducted a study to ascertain whether eye colour can influence the perception of attractiveness, sociability, and intelligence. Despite Gary and Glover's (1976) prediction that dark-eyed people are more sociable, Beattie and Shovelton (2002) found that eye colour had no significant effect on judgments of sociability by female or male raters. Further, both men and women rated stimuli with blue eyes as more attractive and intelligent, which led them to suggest that the perception of blue-eyed persons as more intelligent is due to a positive 'halo' effect of attractiveness (Beattie & Shovelton, 2002). With respect to facial shape features (since eye colour was not a concern of their study), Kleisner et al. (2014) observed that faces which are perceived as highly intelligent are rather prolonged with a wider space between the eyes, whereas the perception of lower intelligence is associated with broader, more rounded faces with eyes closer to each other. Future studies thus should disentangle whether the suggested link between blue eyes and perceived intelligence is due to iris colour, facial shape, or interactions between these features. One would also expect that the reported effect of increased perceived intelligence linked to blue eyes is not universal and is limited to populations with variable iris colour.

Eye colour and perceived attractiveness

The role of facial attractiveness on perception is a rather comprehensively investigated subject. In general, physical appearance is important to humans as well as to a range of nonhuman species (Andersson, 1994; Møller & Thornhill, 1998). In humans, certain facial features tend to be perceived as attractive and accordingly influence the perceiver's attitudes in favour of their bearers (Langlois et al., 2000; Rhodes, 2006). Facial attractiveness may affect one's mate choice or decision about social partners (Eagly et al., 1991; Little et al., 2011). Furthermore, facial attractiveness is valued in a similar way across cultures and there is a broad intra- and intercultural consensus on what constitutes facial attractiveness (Langlois et al., 2000). According to existing research, the main factors involved in assessments of facial attractiveness are sexual shape dimorphism, facial averageness, and symmetry (Little et al., 2011; Rhodes, 2006; Thornhill & Gangestad, 1999).

The third study attached below aims to cross-culturally examine the effect of the abovementioned attractiveness-related factors as well as eye colour, a trait independent of shape proportion, on the perception of facial attractiveness (Kočnar et al., 2019). This study is, to the best of our knowledge, the first to investigate the influence of eye colour on rated attractiveness across different populations. Other features varying in colour, such as human skin, associated to perceived attractiveness are discussed elsewhere (e.g. Fink et al., 2011; Kleisner et al., 2017; Lefevre & Perrett, 2015).[7]

Human skin colouration tends to be viewed as primarily an adaptation to environment: its role is to regulate the penetration of ultraviolet radiation and, in the case of depigmented skin, to enable the production of vitamin D under low and highly seasonal UVB conditions (Jablonski & Chaplin, 2000, 2017). As documented by non-simultaneous changes in the diversification of skin, eye, and hair colours, hair colour and eye colour probably have not been under equally strong pressure of natural selection (Jablonski & Chaplin, 2017; Lazaridis et al., 2014). As a highly heritable trait, eye colour is frequently used in genome-wide population studies and for predictions in forensic genetics. The findings of such studies not only contribute to our knowledge of distribution of eye colours, but also reveal the evolutionary history of positive selection on eye colour during the period of 10,000–4,000 BP and even later (Allentoft et al., 2015; Frost, 2014; Wilde et al., 2014).

[7] A study on a related topic describing the influence of variations in facial skin colour on perceived attractiveness is attached below as an appendix, although eye colour was not included among the assessed features (Kleisner et al., 2017).

It has also been hypothesised, however, that recent variations in skin, hair, and eye colour are due not (only) to natural selection but also sexual selection (Frost, 2006, 2014; Jablonski & Chaplin, 2017; van den Berghe & Frost, 1986). In his theory of negative-frequency dependent selection on eye colour, Frost (2006) proposed a model where the rare colour advantage of light-eyed women on the mate market played a central role in the development of eye colour diversity in Europe (Frost, 2006, 2014; Walsh et al., 2012). According to Frost, such situation can arise only under special environmental conditions, a singularity among the many environments which modern humans entered while spreading out of Africa during the Palaeolithic (Frost, 2006). Such conditions resulted in an imbalanced sex ratio favouring women, which accelerated and shaped sexual selection (Frost 2006, 2014). But it is yet to be seen whether the point at which the founder mutation for eye colour occurred matched with the period of appropriate environmental conditions described in Frost's theory (Eiberg et al., 2008; Wilde et al., 2014). If it did, the much rarer blue-eyed women may have been preferred over brown-eyed women who were much more numerous. Consequently, sexual selection may have created a colour polymorphism where the new colour spread through the population until it lost its novelty value (Frost, 2014).

Interestingly, a genetic association study conducted by Martinez-Cadenas et al. (2013) revealed a strong association between gender and eye colour prediction: women tend to have darker eyes than males. In other words, some factors related to gender may contribute to human eye colour variation (Martinez-Cadenas et al., 2013, 2014; see also Liu et al., 2014; Pietroni et al., 2014). Questioning a large sample of Czech and Slovak population, Frost et al. (2017) reported that eye colour is equally dark among male and female respondents but eye colours are more diverse in women than in men. In a sample for the introductory statistics course, it was found that reported eye colour and gender are associated even though eye colour and gender are usually considered to be independent traits (Froelich & Stephenson, 2013). According to Froelich and Stephenson (2013), research based on self-reports of features that can vary in colour might be influenced by a sex-linked trait colour blindness, which has been described in 8–10% of males and less than 1% of females (Neitz & Neitz, 2000).

A number of authors described a 'novelty effect' in humans in the form of men preferring women with rarer hair colours (Swami et al., 2008; Thelen, 1983; but see Janif et al., 2015). This effect corresponds to some stereotypical beliefs about certain particular traits and it is possible that under specific circumstances, these beliefs could be more pronounced. For example, in a population where most people have dark hair and eyes, blond women earn around

9% more than individuals with dark hair (Filiz, 2021). Similarly, waitresses who wore blond wigs received more tips from male customers (Guéguen, 2012). Conversely, nurses of Turkish descent working in Germany felt that their visible traits, including dark eye colour, were a potential reason for the discrimination they experienced (Ulusoy & Schablon, 2020). In US racial minority groups, Latina participants reported significantly more dissatisfaction with their eyes and nose than white or black women did (Warren, 2014). Forti and Young (2016) demonstrated a negative frequency-dependent selection in commercial models from the UK and Brazil: most male and female models had less frequent eye colour than the majority population where they were models.

Interestingly, it seems that humans had the means to modify their appearance through the use of cosmetics for app. 100,000 years (Watts, 2010). In this context, eye colour might have acted as an honest, unforgeable signal of genetic uniqueness until the invention of coloured contact lenses.

Based on single population samples, some scholars reported different preferences for eye colour. For example, Feinman and Gill (1978) found out that men prefer blue eyes in women and women prefer dark eyes in men, whereas Beattie and Shovelton (2002) reported that both men and women rated stimuli with blue eyes as the most attractive. Gründl et al. (2012) compared the alleged preference for blue eyes with actual face ratings from which one could infer association between the eye colour and attractiveness (but the association was not a stated purpose of the rating). In this rating, the alleged preference for blue eyes was not borne out. This discrepancy led authors to describe beliefs about blue eyes as the 'blue-eyed stereotype'. Their results also showed that rather than the eye colour, it is a larger pupil diameter and bright sclera that positively correlate with attractiveness and youthfulness (Gründl et al., 2012). Furthermore, faces with lighter eyes were rated as more attractive if the irises feature a distinct limbal ring, a dark annulus where the iris meets the sclera (Peshek et al., 2011). The authors of that study suggest that this is because the limbal ring fades with age or poor health. Brown and Sacco (2017) provided further evidence on the importance of limbal rings as a health cue, while Ilicic et al. (2016) reported that the presence of limbal ring also increased trustworthiness judgments.[8]

[8] Interestingly, it has been hypothesised that various recently reported iris-related morphological structures in primates' eyes (including those of the ring shape) might have a communicative or protective function (Perea-García et al., 2021).

According to Bovet et al. (2012), eye colour does not appear to have any association with a person's fitness. Alongside hair colour, it is to be viewed as a 'neutral feature' that does not reflect mate quality. On the other hand, there is a relatively large body of literature that investigated eye and hair colour as reliable predictors in assortative mating. It seems that individuals prefer partners with the same eye or hair colour as their parents (Bressan & Damian, 2018; DeBruine et al., 2017; Little et al., 2003; Saxton, 2016; Štěrbová et al., 2019a, 2019b; Wilson & Barrett, 1987; but cf. Newman et al., 2018) or they themselves have (Jacobi & Cash, 1994; Laeng et al., 2007). According to Laeng et al. (2007) and Bressan (2021), blue-eyed men preferred blue-eyed women because recessive features may help them recognise their own – in this case most likely blue-eyed – offspring (but cf. Bovet et al., 2012; Prokop et al., 2010; Rantala & Marcinkowska, 2011, who did not observe a similar pattern). According to Štěrbová et al. (2019b), preferences for eye colour are determined by the imprinting-like effect rather than by homogamy, that is, the colour of parents' eyes is a better predictor of partner's eye colour than own eye colour is. Moreover, the same study also reported that the consistency of these preferences is higher in a long-term than in the short-term context.

Based on Frost's theory (Frost, 2006), Gardiner and Jackson (2010) investigated actual preferences for blue eyes in an Australian sample. Their study indicated that light-eyed individuals of Northern European descent have significantly higher levels of disagreeableness, which is a marker for competitiveness, than their brown-eyed counterparts. The authors argued that their findings support and extend Frost's hypothesis by reasoning that 'competitive females have advantages in terms of both competing with other females and in securing male interest and cooperation'.

As mentioned earlier, two studies examined a possible association between eye colour and perceived dominance (Kleisner et al., 2010; Kočnar et al., 2012), and one study focused on the relationship between eye colour and perceived trustworthiness (Kleisner et al., 2013). Based on a sample from the Czech population, Kleisner et al. (2010) also looked at a possible association between eye colour and attractiveness but found no significant correlations. Nevertheless, in a cross-cultural study, Kočnar et al. (2019) observed a pattern explicable by a negative frequency-dependent selection: blue eyes were judged as more attractive only in those populations (e.g. Turkish, Portuguese, and Brazilian) where individuals with darker eyes predominate.

Cross-cultural differences in the perception of eye colour and further possible consequences of these findings are discussed in the third study included in this thesis, at this point we introduce only a few additional comments.

Most importantly, it is possible that the rare colour advantage or negative frequency-dependent selection is not the only hypothesis that could shed more light on eye colour diversity in humans, although our results are generally in line with it. There are other findings, such as one regarding the correlation of eye colour with the seasonal affective disorder, which lend support to a more environmental view on this question. The pressure of sexual selection on bearers of lighter irises (or other traits) might contribute to the diversity of eye colours or play a role only in highly specific contexts.

Regarding the diversity of eye colour in other species, we should note that only humans and domestic animals show intraspecific eye colour diversity, while in wild animals, eye colours vary only interspecifically (Negro et al., 2017). Because the process of domestication is connected not only with a reduction in pigmentation, but also with non-aggressive and prosocial behaviour (e.g. Wilkins et al., 2014), we can view humans as also affected by domestication, or, to be more precise, by self-domestication[9] (e.g. Bruner & Gleeson, 2019; Leach, 2003). The light colours of human iris may have thus emerged as a phenotypic spandrel, a by-product of other selective pressures, possibly including human self-domestication.

As mentioned above, and as shown in the third study, preferences for eye colour and other facial characteristics are context-dependent. For more information about the role of context and perceivers' individual experience on the perception of facial attractiveness, see Little et al. (2011). From a cross-cultural view, there is another important factor that influences the processing of information about faces. There are two systems of processing, namely featural and configural, and people from different cultures use them differently (S. Duffy & Kitayama, 2010). Miyamoto et al. (2006) showed that the Japanese were more accurate than Americans in detecting configural changes (e.g. different distance between the eyes) than they were in detecting figural changes (for instance eye colour). This also suggests that in some cultures, face is perceived more holistically than in others. Interestingly, the mouth region is more informative in Caucasian facial expressions, whereas the eyes are more informative in East Asian facial expressions (Jack & Schyns, 2015; Koda & Ruttkay, 2017). Note also the East Asian emoticons such as (^.^) for happy and (>.<) for angry (Jack & Schyns, 2015).

[9] In fact, it is rather difficult to determine where to start and where to finish with argumentation that operates with the concept of self-domestication of humans. It is an idea that has its own rich and often problematic history, especially due to a misuse of this concept in eugenics. Moreover, the concept of human self-domestication was challenged by Shilton et al. (2020) who argued that human social evolution is more similar to that of other social mammals than to that of domesticated animals. This hypothesis implies that human social behaviour is the product of self-control rather than of self-domestication.

In further research on eye colour perception, we should carefully consider the context and possible further circumstances that may be involved. We have shown that one might succumb to the temptation of seeing the issue as solved whenever a suitable hypothesis fits the results regarding the association between eye colour and various other perceived characteristics. Bearing in mind that particular facial features, including eye colour, acquire different significance in different cultures, we can conclude that this extraordinary human trait, namely eye colour and its variations, is likely to be attractive (or not) to a perceiver not because it is directly related to 'genetic' fitness but because it is meaningful within a contextual framework ruled by interactions of organisms with their environment and among the organisms themselves. This capacity of meaning attribution would finally determine whether such subtle quality, which the eye colour undoubtedly is, may help biological lineages continue and flourish in the future.[10]

[10] For the biosemiotic metaphor of 'survival of the meaningful', its genesis and implications, see Maran and Kleisner (2010).

References

Allentoft, M. E., Sikora, M., Sjögren, K.-G., Rasmussen, S., Rasmussen, M., Stenderup, J., Damgaard, P. B., Schroeder, H., Ahlström, T., Vinner, L., Malaspinas, A.-S., Margaryan, A., Higham, T., Chivall, D., Lynnerup, N., Harvig, L., Baron, J., Casa, P. Della, Dąbrowski, P., … Willerslev, E. (2015). Population genomics of Bronze Age Eurasia. *Nature*, *522*(7555), 167–172. https://doi.org/10.1038/nature14507

Amemiya, S., & Ohtomo, K. (2012). Effect of the observed pupil size on the amygdala of the beholders. *Social Cognitive and Affective Neuroscience*, *7*(3), 332–341. https://doi.org/10.1093/scan/nsr013

Andersson, M. B. (1994). Sexual Selection. In *Princeton University Press.* https://doi.org/10.1016/j.cub.2010.11.053

Antonopoulos, A., Kosteletos, G., Stamatiadis, D., & Katsilambros, N. (1993). Eye color and IDDM. *Diabetes Care*, *16*(8), 1216 LP – 1216. https://doi.org/10.2337/diacare.16.8.1216a

Atoum, A. O., & Al-Simadi, P. A. (2019). The effect of presentation modality on judgments of honesty and attractiveness. *Social Behavior and Personality*, *28*(3), 269–278.

Bassett, J. F., & Dabbs, J. M. (2001). Eye color predicts alcohol use in two archival samples. *Personality and Individual Differences*, *31*(4), 535–539. https://doi.org/10.1016/S0191-8869(00)00157-4

Beattie, G., & Shovelton, H. (2002). Blue-eyed boys? A winning smile? An experimental investigation of some core facial stimuli that may affect interpersonal perception. *Semiotica*, *139*, 1–21. https://doi.org/10.1515/semi.2002.019

Bègue, L., & Boudesseul, J. (2017). Phenotypic association of alcohol consumption with eye color: a breathanalyzer assessment. *Journal of Substance Use*, *22*(2), 129–130. https://doi.org/10.3109/14659891.2016.1144807

Berry, D., & McArthur, L. Z. (1985). Some components and consequences of a babyface. *Journal of Personality and Social Psychology*, *48*, 312–323.

Birmingham, E., Bischof, W. F., & Kingstone, A. (2008). Gaze selection in complex social scenes. *Visual Cognition*, *16*(2–3), 341–355. https://doi.org/10.1080/13506280701434532

Bito, L. Z., Matheny, A., Cruickshanks, K. J., Nondahl, D. M., & Carino, O. B. (1997). Eye color changes past early childhood. The Louisville Twin Study. *Archives of Ophthalmology (Chicago, Ill. : 1960)*, *115*(5), 659–663. https://doi.org/10.1001/archopht.1997.01100150661017

Bodaghi, B., Massamba, N., & Izzedine, H. (2014). The eye: a window on kidney diseases. *Clinical Kidney Journal*, *7*(4), 337–338. https://doi.org/10.1093/ckj/sfu073

Boeck, M., & Ivan, C. E. (2013). Do Swedes perceive blue-eyed faces as more trustworthy than brown-eyed faces? *Unpublished Study. Department of Psychology, Lund University*.

Bovet, J., Barthes, J., Durand, V., Raymond, M., & Alvergne, A. (2012). Men's Preference for Women's Facial Features: Testing Homogamy and the Paternity Uncertainty Hypothesis. *PLoS ONE*, *7*(11). https://doi.org/10.1371/journal.pone.0049791

Bremner, F. (2019). Apraclonidine Is Better Than Cocaine for Detection of Horner Syndrome . In *Frontiers in Neurology* (Vol. 10, p. 55). https://www.frontiersin.org/article/10.3389/fneur.2019.00055

Bressan, P. (2021). Blue Eyes Help Men Reduce the Cost of Cuckoldry. *Archives of Sexual Behavior*.

https://doi.org/10.1007/s10508-021-02120-7

Bressan, P., & Damian, V. (2018). Fathers' eye colour sways daughters' choice of both long- and short-term partners. *Scientific Reports*, *8*(1), 1–9. https://doi.org/10.1038/s41598-018-23784-7

Brown, M., & Sacco, D. F. (2017). Put a (Limbal) Ring on It: Women Perceive Men's Limbal Rings as a Health Cue in Short-Term Mating Domains. *Personality and Social Psychology Bulletin*, *44*(1), 80–91. https://doi.org/10.1177/0146167217733072

Bruner, E., & Gleeson, B. T. (2019). Body Cognition and Self-Domestication in Human Evolution . In *Frontiers in Psychology* (Vol. 10, p. 1111). https://www.frontiersin.org/article/10.3389/fpsyg.2019.01111

Caspar, K. R., Biggemann, M., Geissmann, T., & Begall, S. (2021). Ocular pigmentation in humans, great apes, and gibbons is not suggestive of communicative functions. *Scientific Reports*, *11*(1), 12994. https://doi.org/10.1038/s41598-021-92348-z

Christensen, J. M., & Sacco, P. R. (1989). Association of hair and eye color with handedness and stuttering. *Journal of Fluency Disorders*, *14*(1), 37–45. https://doi.org/10.1016/0094-730X(89)90022-3

Connolly, L. J., Rajaratnam, S. M. W., Spitz, G., Lockley, S. W., & Ponsford, J. L. (2021). Factors Associated With Response to Pilot Home-Based Light Therapy for Fatigue Following Traumatic Brain Injury and Stroke. In *Frontiers in neurology* (Vol. 12, p. 651392). https://doi.org/10.3389/fneur.2021.651392

Coplan, R. J., Coleman, B., & Rubin, K. H. (1998). Shyness and little boy blue: Iris pigmentation, gender, and social wariness in preschoolers. *Developmental Psychobiology*, *32*(1), 37–44. https://doi.org/10.1002/(SICI)1098-2302(199801)32:1<37::AID-DEV4>3.0.CO;2-U

Crowe, M., & O'Connor, D. (2001). Eye Colour and Reaction Time to Visual Stimuli in Rugby League Players. *Perceptual and Motor Skills*, *93*(2), 455–460. https://doi.org/10.2466/pms.2001.93.2.455

Cullington, H. E. (2001). Light eye colour linked to deafness after meningitis. *British Medical Journal*, *322*(7282), 587. http://eprints.soton.ac.uk/10562/%5Cnhttp://www.bmj.com/content/322/7286/587.1.full

Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology*, *59*(1), 61–72. https://doi.org/10.1037/0022-3514.59.1.61

Cust, A. E., Drummond, M., Kanetsky, P. A., Goldstein, A. M., Barrett, J. H., MacGregor, S., Law, M. H., Iles, M. M., Bui, M., Hopper, J. L., Brossard, M., Demenais, F., Taylor, J. C., Hoggart, C., Brown, K. M., Landi, M. T., Newton-Bishop, J. A., Mann, G. J., & Bishop, D. T. (2018). Assessing the Incremental Contribution of Common Genomic Variants to Melanoma Risk Prediction in Two Population-Based Studies. *The Journal of Investigative Dermatology*, *138*(12), 2617–2624. https://doi.org/10.1016/j.jid.2018.05.023

Da Costa, E. A., Castro, J. C., & Macedo, M. E. G. (2008). Iris pigmentation and susceptibility to noise-induced hearing loss. *International Journal of Audiology*, *47*(3), 115–118. https://doi.org/10.1080/14992020701704776

Danel, D. P., Wacewicz, S., Kleisner, K., Lewandowski, Z., Kret, M. E., Żywiczyński, P., & Perea-Garcia, J. O. (2020). Sex differences in ocular morphology in Caucasian people: a dubious role of sexual selection in the evolution of sexual dimorphism of the human eye. *Behavioral Ecology and Sociobiology*, *74*(10), 115. https://doi.org/10.1007/s00265-020-02894-1

Danel, D. P., Wacewicz, S., Lewandowski, Z., Żywiczyński, P., & Perea-Garcia, J. O. (2018). Humans do not perceive conspecifics with a greater exposed sclera as more trustworthy: a preliminary cross-ethnic study of the function of the overexposed human sclera. *Acta Ethologica*, *21*(3), 203–208. https://doi.org/10.1007/s10211-018-0296-5

Davidson, R. J. (2001). Toward a biology of personality and emotion. In *Unity of knowledge: The convergence of natural and human science.* (pp. 191–207). New York Academy of Sciences.

DeBruine, L. M., Jones, B. C., & Little, A. C. (2017). Positive sexual imprinting for human eye color. *BioRxiv*, 135244. https://doi.org/10.1101/135244

Di Stasio, E., Maggi, D., Berardesca, E., Marulli, G. C., Bizzarri, C., Lauria, A., Portuesi, R., Cavallo, M. G., Costantino, F., Buzzetti, R., Astorri, E., Pitocco, D., Songini, M., Pozzilli, P., & Group, T. I. (2011). Blue eyes as a risk factor for type 1 diabetes. *Diabetes/Metabolism Research and Reviews*, *27*(6), 609–613. https://doi.org/https://doi.org/10.1002/dmrr.1214

Dorgaleleh, S., Naghipoor, K., Barahouie, A., Dastaviz, F., & Oladnabi, M. (2020). Molecular and biochemical mechanisms of human iris color: A comprehensive review. *Journal of Cellular Physiology*, *235*(12), 8972–8982. https://doi.org/https://doi.org/10.1002/jcp.29824

Duffy, D. (2015). Genetics of Eye Colour. In *eLS* (pp. 1–9). https://doi.org/https://doi.org/10.1002/9780470015902.a0024646

Duffy, S., & Kitayama, S. (2010). Cultural modes of seeing through cultural modes of being: Cultural influences on visual attention. In *Social psychology of visual perception.* (pp. 51–75). Psychology Press.

Dupuis-Roy, N., Faghel-Soubeyrand, S., & Gosselin, F. (2019). Time course of the use of chromatic and achromatic facial information for sex categorization. *Vision Research*, *157*, 36–43. https://doi.org/10.1016/J.VISRES.2018.08.004

Eagle, R. C. (1988). Iris pigmentation and pigmented lesions: an ultrastructural study. *Transactions of the American Ophthalmological Society*, *86*, 581–687. https://pubmed.ncbi.nlm.nih.gov/2979031

Eagly, A. H., Ashmore, R. D., Makhijani, M. G., & Longo, L. C. (1991). What is beautiful is good, but . . .: A meta-analytic review of research on the physical attractiveness stereotype. *Psychological Bulletin*, *110*(1), 109–128. https://doi.org/10.1037/0033-2909.110.1.109

Eiberg, H., Troelsen, J., Nielsen, M., Mikkelsen, A., Mengel-From, J., Kjaer, K. W., & Hansen, L. (2008). Blue eye color in humans may be caused by a perfectly associated founder mutation in a regulatory element located within the HERC2 gene inhibiting OCA2 expression. *Human Genetics*, *123*(2), 177–187. https://doi.org/10.1007/s00439-007-0460-x

Ekmekci, H., Yılmaz, B., Cubuklu, M., & Ozturk, S. (2014). *The Effects of Eye Color on Visual Evoked Potentials in Normal Population (ROC Curve and Confusion Matrix Analysis). Is A potential diagnostic tool for patients with multiple sclerosis?*

Elias, V. L., Nicolas, C. L., & Abramson, C. I. (2008). Eye Color as an Indicator of Behavior: Revisiting Worthy and Scott. *Psychological Reports*, *102*(3), 759–778. https://doi.org/10.2466/pr0.102.3.759-778

Feinman, S., & Gill, W. (1978). Sex differences in physical attractiveness preferences. In *The Journal of Social Psychology* (Vol. 105, pp. 43–52). http://www.tandfonline.com/doi/abs/10.1080/00224545.1978.9924089

Fetter, V. (1958). The Colour of Eyes nad Hair in Adults from Bohemia and Moravia. *Časopis Lékařů*

Českých, *97*(26), 819–823.

Filiz, E. S. (2021). Does it Payoff to be Blond in a Non-Blond Neighborhood? Eye Color, Hair Color, Ethnic Composition and Starting Wages. *Eastern Economic Journal*. https://doi.org/10.1057/s41302-021-00194-8

Fink, B., Matts, P. J., D'Emiliano, D., Bunse, L., Weege, B., & Röder, S. (2011). Colour homogeneity and visual perception of age, health and attractiveness of male facial skin. *Journal of the European Academy of Dermatology and Venereology*, *26*(12), no-no. https://doi.org/10.1111/j.1468-3083.2011.04316.x

Flegr, J., & Sýkorová, K. (2019). Skin fairness is a better predictor for impaired physical and mental health than hair redness. *Scientific Reports*, *9*(1), 18138. https://doi.org/10.1038/s41598-019-54662-5

Forti, I. R. N., & Young, R. J. (2016). Human Commercial Models' Eye Colour Shows Negative Frequency-Dependent Selection. *PloS One*, *11*(12), e0168458. https://doi.org/10.1371/journal.pone.0168458

Friedman, G. D., Selby, J. V., Quesenberry, C. P., Newman, B., & King, M. C. (1990). Eye color and hypertension. *Medical Hypotheses*, *33*(3), 201–206. https://doi.org/10.1016/0306-9877(90)90177-G

Froelich, A. G., & Stephenson, W. R. (2013). Does Eye Color Depend on Gender? It Might Depend on Who or How You Ask. *Journal of Statistics Education*, *21*(2), null-null. https://doi.org/10.1080/10691898.2013.11889680

Frost, P. (2006). European hair and eye color. A case of frequency-dependent sexual selection? *Evolution and Human Behavior*, *27*(2), 85–103. https://doi.org/10.1016/j.evolhumbehav.2005.07.002

Frost, P. (2014). The Puzzle of European Hair, Eye, and Skin Color. *Advances in Anthropology*, *04*(02), 78–88. https://doi.org/10.4236/aa.2014.42011

Frost, P., Kleisner, K., & Flegr, J. (2017). Health status by gender, hair color, and eye color: Red-haired women are the most divergent. *PLOS ONE*, *12*(12), e0190238. https://doi.org/10.1371/journal.pone.0190238

Gardiner, E., & Jackson, C. J. (2010). Eye color predicts disagreeableness in North Europeans: Support in favor of frost (2006). *Current Psychology*, *29*(1), 1–9. https://doi.org/10.1007/s12144-009-9070-1

Gary, A. L., & Glover, J. (1975). Eye color and sex: their relationship to modeled learning. *Psychotherapy*, *12*(4), 425–428. https://doi.org/10.1037/h0086473

Gary, A. L., & Glover, J. A. (1976). *Eye Color, Sex, and Children's Behavior*. Nelson-Hall Publishers.

Geldart, S., Maurer, D., & Carney, K. (1999). Effects of Eye Size on Adults' Aesthetic Ratings of Faces and 5-Month-Olds' Looking Times. *Perception*, *28*(3), 361–374. https://doi.org/10.1068/p2885

Gentry, T. A., Polzine, K. M., & Wakefield, J. A. (1985). Human genetic markers associated with variation in intellectual abilities and personality. *Personality and Individual Differences*, *6*(1), 111–113. https://doi.org/10.1016/0191-8869(85)90035-2

Giacomin, M., & Rule, N. O. (2019). Eyebrows cue grandiose narcissism. *Journal of Personality*, *87*(2), 373–385. https://doi.org/https://doi.org/10.1111/jopy.12396

Goel, N., Terman, M., & Su Terman, J. (2002). Depressive symptomatology differentiates subgroups of patients with seasonal affective disorder. *Depression and Anxiety*, *15*(1), 34–41. https://doi.org/10.1002/da.1083

Gonçalves, G., Gomes, A., Ferrão, M., Parreira, T., Santos, J., Giger, J.-C., & Martins, A. (2014). Once Upon a Face: the Effect of Eye Size, Observer and Stimulus Gender on Impression Formation. *Current Psychology*. https://doi.org/10.1007/s12144-014-9244-3

Gründl, M., Knoll, S., Eisenmann-Klein, M., & Prantl, L. (2012). The blue-eyes stereotype: Do eye color, pupil diameter, and scleral color affect attractiveness? *Aesthetic Plastic Surgery*, *36*(2), 234–240. https://doi.org/10.1007/s00266-011-9793-x

Guéguen, N. (2012). Hair color and wages: Waitresses with blond hair have more fun. *The Journal of Socio-Economics*, *41*(4), 370–372. https://doi.org/10.1016/J.SOCEC.2012.04.012

Hägg, D., Berglind, I. A., Kieler, H., Linder, M., & Odsbu, I. (2019). Eye color and risk of ocular melanoma in patients with glaucoma - a Swedish register study combining data from the Swedish police Authority’s register on passport applications and National Health Registers. *Pharmacoepidemiology and Drug Safety*, *28*(S2). https://doi.org/https://doi.org/10.1002/pds.4864

Hale, B. D., Landers, D. M., Snyder Bauer, R., & Goggin, N. L. (1980). Iris pigmentation and fractionated reaction and reflex time. *Biological Psychology*, *10*(1), 57–67. https://doi.org/10.1016/0301-0511(80)90007-1

Happy, R., & Collins, J. K. (1972). MELANIN IN THE ASCENDING RETICULAR ACTIVATING SYSTEM AND ITS POSSIBLE RELATIONSHIP TO AUTISM. *Medical Journal of Australia*, *2*(27), 1484–1486. https://doi.org/https://doi.org/10.5694/j.1326-5377.1972.tb92995.x

Hashemi, H., Pakzad, R., Yekta, A., Shokrollahzadeh, F., Ostadimoghaddam, H., Mahboubipour, H., & Khabazkhoob, M. (2019). Distribution of iris color and its association with ocular diseases in a rural population of Iran. *Journal of Current Ophthalmology*, *31*(3), 312–318. https://doi.org/10.1016/j.joco.2018.05.001

Havlíček, J., Roberts, S. C., & Flegr, J. (2005). Women’s preference for dominant male odour: Effects of menstrual cycle and relationship status. *Biology Letters*, *1*(3), 256–259. https://doi.org/10.1098/rsbl.2005.0332

Henderson, J. M., Williams, C. C., & Falk, R. J. (2005). Eye movements are functional during face learning. *Memory & Cognition*, *33*(1), 98–106. https://doi.org/10.3758/BF03195300

Herbener, E. S., Kagan, J., & Cohen, M. (1989). Shyness and olfactory threshold. *Personality and Individual Differences*, *10*(11), 1159–1163. https://doi.org/10.1016/0191-8869(89)90079-2

Hess, E. H. (1975). The role of pupil size in communication. In *Scientific American* (Vol. 233, Issue 5, pp. 110–112, 116–119). https://doi.org/10.1038/scientificamerican1175-110

Heyman, I., Frampton, I., van Heyningen, V., Hanson, I., Teague, P., Taylor, A., & Simonoff, E. (1999). Psychiatric disorder and cognitive function in a family with an inherited, novel mutation of the developmental control gene PAX6. *Psychiatric Genetics*, *9*(2). https://journals.lww.com/psychgenetics/Fulltext/1999/06000/Psychiatric_disorder_and_cognitive_function_in_a.6.aspx

Higuchi, S., Motohashi, Y., Ishibashi, K., & Maeda, T. (2007). Influence of eye colors of Caucasians and Asians on suppression of melatonin secretion by light. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *292*(6), R2352–R2356. https://doi.org/10.1152/ajpregu.00355.2006

Hood, J. D., Poole, J. P., & Freedman, L. (1976). Eye color and susceptibility to TTS. *The Journal of the Acoustical Society of America*, *59*(3), 706–707. https://doi.org/10.1121/1.380923

Hyde, J., Fowler, S., Drum, M., Reader, A., Nusstein, J., & Beck, M. (2018). Is Eye Color Related to Dental Injection Pain? A Prospective, Randomized, Single-blind Study. *Journal of Endodontics*, *44*(5), 734–737. https://doi.org/10.1016/j.joen.2018.01.009

IJspeert, J. K., de Waard, P. W. T., van den Berg, T. J. T. P., & de Jong, P. T. V. M. (1990). The intraocular straylight function in 129 healthy volunteers; Dependence on angle, age and pigmentation. *Vision Research*, *30*(5), 699–707. https://doi.org/10.1016/0042-6989(90)90096-4

Ilicic, J., Baxter, S. M., & Kulczynski, A. (2016). White eyes are the window to the pure soul: Metaphorical association and overgeneralization effects for spokespeople with limbal rings. *International Journal of Research in Marketing*, *33*(4), 840–855. https://doi.org/10.1016/j.ijresmar.2016.02.001

Imesch, P. D., Wallow, I. H., & Albert, D. M. (1997). The color of the human eye: a review of morphologic correlates and of some conditions that affect iridial pigmentation. *Survey of Ophthalmology*, *41 Suppl 2*(February), S117–S123. https://doi.org/10.1016/S0039-6257(97)80018-5

Jablonski, N. G., & Chaplin, G. (2000). The evolution of human skin coloration. *Journal of Human Evolution*, *39*(1), 57–106. https://doi.org/10.1006/jhev.2000.0403

Jablonski, N. G., & Chaplin, G. (2017). The colours of humanity: The evolution of pigmentation in the human lineage. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1724). https://doi.org/10.1098/rstb.2016.0349

Jack, R. E., & Schyns, P. G. (2015). The Human Face as a Dynamic Tool for Social Communication. *Current Biology : CB*, *25*(14), R621-34. https://doi.org/10.1016/j.cub.2015.05.052

Jacobi, L., & Cash, T. F. (1994). In Pursuit of the Perfect Appearance: Discrepancies Among Self-Ideal Percepts of Multiple Physical Attributes 1. *Journal of Applied Social Psychology*, *24*(5), 379–396. https://doi.org/https://doi.org/10.1111/j.1559-1816.1994.tb00588.x

Janif, Z. J., Brooks, R. C., & Dixson, B. J. (2015). Are Preferences for Women's Hair Color Frequency-Dependent? *Adaptive Human Behavior and Physiology*, *1*(1), 54–71. https://doi.org/10.1007/s40750-014-0008-y

Keating, C. F. (1985). Gender and the Physiognomy of Dominance and Attractiveness. *Social Psychology Quarterly*, *48*(1), 61. https://doi.org/10.2307/3033782

Kleisner, K. (2008). Homosemiosis, mimicry and superficial similarity: Notes on the conceptualization of independent emergence of similarity in biology. *Theory in Biosciences*, *127*(1), 15–21. https://doi.org/10.1007/s12064-007-0019-3

Kleisner, K. (2015). Semantic Organs: The Concept and Its Theoretical Ramifications. *Biosemiotics*, *8*. https://doi.org/10.1007/s12304-015-9246-z

Kleisner, K., Chvátalová, V., & Flegr, J. (2014). Perceived intelligence is associated with measured intelligence in men but not women. *PLoS ONE*, *9*(3). https://doi.org/10.1371/journal.pone.0081237

Kleisner, K., Kočnar, T., Rubešová, A., & Flegr, J. (2010). Eye color predicts but does not directly influence perceived dominance in men. *Personality and Individual Differences*, *49*(1), 59–64. https://doi.org/10.1016/j.paid.2010.03.011

Kleisner, K., Kočnar, T., Tureček, P., Stella, D., Akoko, R. M., Třebický, V., & Havlíček, J. (2017). African and European perception of African female attractiveness. *Evolution and Human Behavior*, *38*(6), 744–755. https://doi.org/10.1016/j.evolhumbehav.2017.07.002

Kleisner, K., Priplatova, L., Frost, P., & Flegr, J. (2013). Trustworthy-Looking Face Meets Brown Eyes. *PLoS ONE*, *8*(1), 1–7. https://doi.org/10.1371/journal.pone.0053285

Kobayashi, H., & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the primate eye. *Journal of Human Evolution*, *40*(5), 419–435. https://doi.org/10.1006/jhev.2001.0468

Kočnar, T., Adil Saribay, S., & Kleisner, K. (2019). Perceived attractiveness of Czech faces across 10 cultures: Associations with sexual shape dimorphism, averageness, fluctuating asymmetry, and eye color. *PLoS ONE*, *14*(11), 1–27. https://doi.org/10.1371/journal.pone.0225549

Kočnar, T., Drbalová, K. R., & Kleisner, K. (2012). Do dominant-looking males have brown eyes? A further investigation of the role of iris colour for dominance perception. *Anthropologie*, *50*(1), 25–32. https://doi.org/10.2307/26272384

Kočnar, T., & Kleisner, K. (2009). Oko za oko: Struktura a význam v evoluci ornamentury organismálních povrchů [An eye for an eye: Structure and significance in the evolution of ornamentation in organismal surfaces]. In K. Stibral & O. Dadejík (Eds.), *Krása, Krajina, příroda* (Issue July, pp. 254–264). Dokořán.

Koda, T., & Ruttkay, Z. (2017). Eloquence of eyes and mouth of virtual agents: cultural study of facial expression perception. *AI & SOCIETY*, *32*(1), 17–24. https://doi.org/10.1007/s00146-014-0571-6

Kret, M. E., & De Dreu, C. K. W. (2017). Pupil-mimicry conditions trust in partners: moderation by oxytocin and group membership. *Proceedings. Biological Sciences*, *284*(1850), 20162554. https://doi.org/10.1098/rspb.2016.2554

Kret, M. E., Fischer, A., & De Dreu, C. (2015). Pupil Mimicry Correlates With Trust in In-Group Partners With Dilating Pupils. *Psychological Science*, *26*. https://doi.org/10.1177/0956797615588306

Kumanov, P., Robeva, R., & Tomova, A. (2014). Does an association between the idiopathic left-sided varicocele and eye colour exist? *Advances in Urology*, *2014*. https://doi.org/10.1155/2014/524570

Laeng, B., Mathisen, R., & Johnsen, J. A. (2007). Why do blue-eyed men prefer women with the same eye color? *Behavioral Ecology and Sociobiology*, *61*(3), 371–384. https://doi.org/10.1007/s00265-006-0266-1

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, *126*(3), 390–423. https://doi.org/10.1037/0033-2909.126.3.390

Langton, S., Watt, R., & Bruce, I. (2000). Do the eyes have it? Cues to the direction of sTowards expressive gaze manner in embodied virtual agentsocial attention. *Trends in Cognitive Sciences*, *4*(2), 50–59. http://www.ncbi.nlm.nih.gov/pubmed/10652522

Larsson, M., & Pedersen, N. L. (2004). Genetic correlations among texture characteristics in the human iris. *Molecular Vision*, *10*(October), 821–831. http://www.ncbi.nlm.nih.gov/pubmed/15534585

Larsson, M., Pedersen, N. L., & Stattin, H. (2007). Associations between iris characteristics and personality in adulthood. *Biological Psychology*, *75*(2), 165–175. https://doi.org/10.1016/j.biopsycho.2007.01.007

Lazaridis, I., Patterson, N., Mittnik, A., Renaud, G., Mallick, S., Kirsanow, K., Sudmant, P. H., Schraiber, J. G., Castellano, S., Lipson, M., Berger, B., Economou, C., Bollongino, R., Fu, Q., Bos, K. I., Nordenfelt, S., Li, H., De Filippo, C., Prüfer, K., … Krause, J. (2014). Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature*, *513*(7518), 409–413. https://doi.org/10.1038/nature13673

Leach, H. (2003). Human Domestication Reconsidered. *Curant*, *44*, 349. https://doi.org/10.1086/368119

Lefevre, C. E., & Perrett, D. I. (2015). Fruit over sunbed: Carotenoid skin colouration is found more attractive than melanin colouration. *Quarterly Journal of Experimental Psychology*, *68*(2), 284–293. https://doi.org/10.1080/17470218.2014.944194

Leonard, K. E., & Blane, H. T. (1999). *Psychological Theories of Drinking and Alcoholism*. The Guilford Press.

Lim, Y.-W., Park, Y.-B., & Park, Y.-J. (2014). Experimental study of reliable iris parameters and their relationships with temperament, character, and heart rate variability. *European Journal of Integrative Medicine*, *6*(5), 524–531. https://doi.org/https://doi.org/10.1016/j.eujim.2014.06.002

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. https://doi.org/10.1098/rstb.2010.0404

Little, A. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2003). Investigating an imprinting-like phenomenon in humans partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behavior*, *24*(1), 43–51. https://doi.org/10.1016/S1090-5138(02)00119-8

Liu, F., Walsh, S., & Kayser, M. (2014). Of sex and IrisPlex eye colour prediction: a reply to Martinez-Cadenas et al. In *Forensic science international. Genetics* (Vol. 9, pp. e5-6). https://doi.org/10.1016/j.fsigen.2013.06.006

Lock-Andersen, J., Wulf, H. C., & Knudstorp, N. D. (1998). Interdependence of eye and hair colour, skin type and skin pigmentation in a Caucasian population. *Acta Dermato-Venereologica*, *78*(3), 214–219. https://doi.org/10.1080/000155598441567

Maran, T., & Kleisner, K. (2010). Towards an Evolutionary Biosemiotics: Semiotic Selection and Semiotic Co-option. *Biosemiotics*, *3*(2), 189–200. https://doi.org/10.1007/s12304-010-9087-8

Markle, A. (1975). Color and form perception on the Rorschach as a function of eye color. *Percept Mot Skills*, *41*(3), 831–834. https://doi.org/10.2466/pms.1975.41.3.831

Martinez-Cadenas, C., Peña-Chilet, M., Ibarrola-Villava, M., & Ribas, G. (2013). Gender is a major factor explaining discrepancies in eye colour prediction based on HERC2/OCA2 genotype and the IrisPlex model. *Forensic Science International. Genetics*, *7*. https://doi.org/10.1016/j.fsigen.2013.03.007

Martinez-Cadenas, C., Peña-Chilet, M., Llorca-Cardeñosa, M. J., Cervera, R., Ibarrola-Villava, M., & Ribas, G. (2014). Gender and eye colour prediction discrepancies: A reply to criticisms. *Forensic Science International: Genetics*, *9*, e7–e9. https://doi.org/10.1016/j.fsigen.2013.10.002

Mayhew, J. A., & Gómez, J.-C. (2015). Gorillas with white sclera: A naturally occurring variation in a morphological trait linked to social cognitive functions. *American Journal of Primatology*, *77*(8), 869–877. https://doi.org/10.1002/ajp.22411

McArthur, L. Z., & Apatow, K. (1984). Impressions of Baby-Faced Adults. *Social Cognition*, *2*(4), 315–

342. https://doi.org/10.1521/soco.1984.2.4.315

Miyamoto, Y., Nisbett, R. E., & Masuda, T. (2006). Culture and the Physical Environment. *Psychological Science*, *17*(2), 113–119. https://doi.org/10.1111/j.1467-9280.2006.01673.x

Møller, A. P., & Thornhill, R. (1998). Bilateral Symmetry and Sexual Selection: A Meta-Analysis. *The American Naturalist*. https://doi.org/10.1086/286110

Moore, R. Y., Speh, J. C., & Card, J. P. (1995). The retinohypothalamic tract originates from a distinct subset of retinal ganglion cells. *The Journal of Comparative Neurology*, *352*(3), 351–366. https://doi.org/10.1002/cne.903520304

Mueller, U., & Mazur, A. (1997). Facial dominance in Homo sapiens as honest signalling of male quality. *Behavioral Ecology*, *8*(5), 569–579. https://doi.org/10.1093/beheco/8.5.569

Mujica-Mota, M. A., Schermbrucker, J., & Daniel, S. J. (2015). Eye color as a risk factor for acquired sensorineural hearing loss: A review. *Hearing Research*, *320*, 1–10. https://doi.org/10.1016/j.heares.2014.12.002

Nayman, T., Bostan, C., Logan, P., & Burnier, M. N. (2017). Uveal Melanoma Risk Factors: A Systematic Review of Meta-Analyses. *Current Eye Research*, *42*(8), 1085–1093. https://doi.org/10.1080/02713683.2017.1297997

Negro, J. J., Carmen Blázquez, M., & Galván, I. (2017). Intraspecific eye color variability in birds and mammals: a recent evolutionary event exclusive to humans and domestic animals. *Frontiers in Zoology*, *14*(1), 53. https://doi.org/10.1186/s12983-017-0243-8

Neitz, M., & Neitz, J. (2000). Molecular Genetics of Color Vision and Color Vision Defects. *Archives of Ophthalmology*, *118*, 691–700. https://doi.org/10.1001/archopht.118.5.691

Newman, A., Pollet, T., Mccarty, K., Neave, N., & Saxton, T. (2018). *Isn't it eyeronic? Little evidence for consistent eye colour choices across relationships*. https://doi.org/10.31234/osf.io/dv93s

Oosterhof, N. N., & Todorov, A. (2008). The functional basis of face evaluation. *Proceedings of the National Academy of Sciences*, *105*(32), 11087–11092. https://doi.org/10.1073/pnas.0805664105

Pavan, W. J., & Sturm, R. A. (2019). The Genetics of Human Skin and Hair Pigmentation. *Annual Review of Genomics and Human Genetics*, *20*(1), 41–72. https://doi.org/10.1146/annurev-genom-083118-015230

Pelphrey, K. A., Sasson, N. J., Reznick, J. S., Paul, G., Goldman, B. D., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders*, *32*(4), 249–261. https://doi.org/10.1023/a:1016374617369

Perea-García, J. O., Danel, D. P., & Monteiro, A. (2021). Diversity in Primate External Eye Morphology: Previously Undescribed Traits and Their Potential Adaptive Value. In *Symmetry* (Vol. 13, Issue 7). https://doi.org/10.3390/sym13071270

Perea-García, J. O., Kret, M. E., Monteiro, A., & Hobaiter, C. (2019). Scleral pigmentation leads to conspicuous, not cryptic, eye morphology in chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(39), 19248–19250. https://doi.org/10.1073/pnas.1911410116

Peshek, D., Semmaknejad, N., Hoffman, D., & Foley, P. (2011). Preliminary evidence that the limbal ring influences facial attractiveness. *Evolutionary Psychology*, *9*(2), 137–146. https://doi.org/10.1177/147470491100900201

Pettijohn, T. F., & Tesser, A. (2005). Threat and Social Choice: When Eye Size Matters. In *The Journal of Social Psychology* (Vol. 145, Issue 5, pp. 547–570). Heldref Publications. https://doi.org/10.3200/SOCP.145.5.547-570

Pietroni, C., Andersen, J. D., Johansen, P., Andersen, M. M., Harder, S., Paulsen, R., Børsting, C., & Morling, N. (2014). The effect of gender on eye colour variation in European populations and an evaluation of the IrisPlex prediction model. *Forensic Science International: Genetics*, *11*(1), 1–6. https://doi.org/10.1016/J.FSIGEN.2014.02.002

Prantl, L., Heidekrueger, P. I., Broer, P. N., Knoll, S., Thiha, A., & Gründl, M. (2019). Female eye attractiveness – Where beauty meets science. *Journal of Cranio-Maxillofacial Surgery*, *47*(1), 73–79. https://doi.org/10.1016/J.JCMS.2018.05.034

Prokop, P., Obertová, Z., & Fedor, P. (2010). Paternity cues and mating opportunities: What makes fathers good? *Acta Ethologica*, *13*(2), 101–107. https://doi.org/10.1007/s10211-010-0079-0

Prota, G., Hu, D. N., Vincensi, M. R., McCormick, S. A., & Napolitano, A. (1998). Characterization of melanins in human irides and cultured uveal melanocytes from eyes of different colors. *Experimental Eye Research*, *67*(3), 293–299. https://doi.org/10.1006/exer.1998.0518

Provencio, I. (2011). The Hidden Organ in Our Eyes. *Scientific American - SCI AMER*, *304*, 54–59. https://doi.org/10.1038/scientificamerican0511-54

Provine, R. R., Cabrera, M. O., Brocato, N. W., & Krosnowski, K. A. (2011). When the Whites of the Eyes are Red: A Uniquely Human Cue. *Ethology*, *117*(5), 395–399. https://doi.org/10.1111/j.1439-0310.2011.01888.x

Radford, C., McNutt, J. W., Rogers, T., Maslen, B., & Jordan, N. (2020). Artificial eyespots on cattle reduce predation by large carnivores. *Communications Biology*, *3*(1), 430. https://doi.org/10.1038/s42003-020-01156-0

Rantala, M. J., & Marcinkowska, U. M. (2011). The role of sexual imprinting and the Westermarck effect in mate choice in humans. *Behavioral Ecology and Sociobiology*, *65*(5), 859–873. https://doi.org/10.1007/s00265-011-1145-y

Rhodes, G. (2006). The Evolutionary Psychology of Facial Beauty. *Annual Review of Psychology*, *57*(1), 199–226. https://doi.org/10.1146/annurev.psych.57.102904.190208

Rhodes, G., & Zebrowitz, L. (2002). *Facial attractiveness: Evolutionary, cognitive, and social perspectives*.

Robinson, T. N. (1981). Eye-Color, Sex and Personality: A Case of Negative Findings for Worthy's Sociability Hypothesis. *Perceptual and Motor Skills*, *52*(3), 855–863. https://doi.org/10.2466/pms.1981.52.3.835

Roecklein, K. A., Rohan, K. J., Duncan, W. C., Rollag, M. D., Rosenthal, N. E., Lipsky, R. H., & Provencio, I. (2009). A missense variant (P10L) of the melanopsin (OPN4) gene in seasonal affective disorder. *Journal of Affective Disorders*, *114*(1–3), 279–285. https://doi.org/10.1016/j.jad.2008.08.005

Rohrich, R. J., Coberly, D. M., Fagien, S., & Stuzin, J. M. (2004). Current Concepts in Aesthetic Upper Blepharoplasty. *Plastic and Reconstructive Surgery*, *113*(3). https://journals.lww.com/plasreconsurg/Fulltext/2004/03000/Current_Concepts_in_Aesthetic_Upper_Blepharoplasty.35.aspx

Rosen, L. N., Targum, S. D., Terman, M., Bryant, M. J., Hoffman, H., Kasper, S. F., Hamovit, J. R., Docherty, J. P., Welch, B., & Rosenthal, N. E. (1990). Prevalence of seasonal affective disorder at four latitudes. *Psychiatry Research*, *31*(2), 131–144. https://doi.org/10.1016/0165-1781(90)90116-m

Rosenberg, A., & Kagan, J. (1987). Iris Pigmentation and Behavioral-Inhibition. *Developmental Psychobiology*, *20*(4), 377–392.

Rowe, P. J., & Evans, P. (1994). Ball color, eye color, and a reactive motor skill. *Perceptual and Motor Skills*, *79*(1 Pt 2), 671–674. https://doi.org/10.2466/pms.1994.79.1.671

Rubin, K. H., & Both, L. E. (1989). Iris pigmentation and sociability in childhood: a re-examination. *Developmental Psychobiology*, *22 7*, 717–725.

Rule, N. O., Ishii, K., & Ambady, N. (2011). Cross-cultural impressions of leaders' faces: Consensus and predictive validity. *International Journal of Intercultural Relations*, *35*(6), 833–841. https://doi.org/10.1016/j.ijintrel.2011.06.001

Russell, R., Kramer, S. S., & Jones, A. L. (2017). Facial Contrast Declines with Age but Remains Sexually Dimorphic Throughout Adulthood. *Adaptive Human Behavior and Physiology*, *3*(4), 293–303. https://doi.org/10.1007/s40750-017-0068-x

Russell, R., Sweda, J., Porcheron, A., & Mauger, E. (2014). Sclera Color Changes With Age and Is a Cue for Perceiving Age, Health, and Beauty. *Psychology and Aging*, *29*, 626–635. https://doi.org/10.1037/a0036142

Saxton, T. K. (2016). Experiences during specific developmental stages influence face preferences. *Evolution and Human Behavior*, *37*(1), 21–28. https://doi.org/10.1016/j.evolhumbehav.2015.06.001

Schmidt, K. L., & Cohn, J. F. (2001). Human facial expressions as adaptations: Evolutionary questions in facial expression research. *American Journal of Physical Anthropology*, *116*(S33), 3–24. https://doi.org/10.1002/ajpa.20001

Schwartz, C. E., Wright, C. I., Shin, L. M., Kagan, J., & Rauch, S. L. (2010). *Inhibited and Uninhibited Infants " Grown Up ": Adult Amygdalar Response to Novelty*. *1952*(2003), 10–12. https://doi.org/10.1126/science.1083703

Shilton, D., Breski, M., Dor, D., & Jablonka, E. (2020). Human Social Evolution: Self-Domestication or Self-Control? . In *Frontiers in Psychology* (Vol. 11, p. 134). https://www.frontiersin.org/article/10.3389/fpsyg.2020.00134

Štěrbová, Z., Tureček, P., & Kleisner, K. (2019a). She always steps in the same river: Similarity among long-term partners in their demographic, physical, and personality characteristics. In *Frontiers in Psychology* (Vol. 10). Frontiers Media S.A. https://doi.org/10.3389/fpsyg.2019.00052

Štěrbová, Z., Tureček, P., & Kleisner, K. (2019b). Consistency of mate choice in eye and hair colour: Testing possible mechanisms. *Evolution and Human Behavior*, *40*(1), 74–81. https://doi.org/10.1016/J.EVOLHUMBEHAV.2018.08.003

Sturm, R. A., & Frudakis, T. N. (2004). Eye colour: Portals into pigmentation genes and ancestry. *Trends in Genetics*, *20*(8), 327–332. https://doi.org/10.1016/j.tig.2004.06.010

Sturm, R. A., & Larsson, M. (2009). Genetics of human iris colour and patterns. *Pigment Cell and Melanoma Research*, *22*(5), 544–562. https://doi.org/10.1111/j.1755-148X.2009.00606.x

Sulem, P., Gudbjartsson, D. F., Stacey, S. N., Helgason, A., Rafnar, T., Magnusson, K. P., Manolescu, A., Karason, A., Palsson, A., Thorleifsson, G., Jakobsdottir, M., Steinberg, S., Pálsson, S., Jonasson, F., Sigurgeirsson, B., Thorisdottir, K., Ragnarsson, R., Benediktsdottir, K. R., Aben, K. K., … Stefansson, K. (2007). Genetic determinants of hair, eye and skin pigmentation in Europeans.

Nature Genetics, *39*(12), 1443–1452. https://doi.org/10.1038/ng.2007.13

Sulovari, A., Kranzler, H. R., Farrer, L. A., Gelernter, J., & Li, D. (2015). Eye color: A potential indicator of alcohol dependence risk in European Americans. *American Journal of Medical Genetics, Part B: Neuropsychiatric Genetics*, *168*(5), 347–353. https://doi.org/10.1002/ajmg.b.32316

Sun, H.-P., Lin, Y., & Pan, C.-W. (2014). Iris color and associated pathological ocular complications: a review of epidemiologic studies. *International Journal of Ophthalmology*, *7*(5), 872–878. https://doi.org/10.3980/j.issn.2222-3959.2014.05.25

Sutton, P. R. (1959). Association between colour of the iris of the eye and reaction to dental pain. *Nature*, *184*, 122. https://doi.org/10.1038/184122a0

Swami, V., Rozmus-Wrzesinska, M., Voracek, M., Haubner, T., Danel, D., Pawłowski, B., Stanistreet, D., Chaplin, F., Chaudhri, J., Sheth, P., Shostak, A., Zhang, E. X., & Furnham, A. (2008). The influence of skin tone, body weight, and hair colour on perceptions of women's attractiveness and health: A cross-cultural investigation. *Journal of Evolutionary Psychology*, *6*(4), 321–341. https://doi.org/10.1556/JEP.6.2008.4.4

Tedford, W. H., Hill, W. R., & Hensley, L. (1978). Human Eye Color and Reaction Time. *Perceptual and Motor Skills*, *47*(2), 503–506. https://doi.org/10.2466/pms.1978.47.2.503

Teng, C., & Belfer, I. (2014). Correlation between eye color and pain phenotypes in healthy women. *Journal of Pain*, *15*(4), S25. https://doi.org/10.1016/j.jpain.2014.01.103

Terman, J. S., & Terman, M. (1999). Photopic and scotopic light detection in patients with seasonal affective disorder and control subjects. *Biological Psychiatry*, *46*(12), 1642–1648. https://doi.org/10.1016/s0006-3223(99)00221-8

Thelen, T. H. (1983). Minority type human mate preference. *Biodemography and Social Biology*, *30*(2), 162–180. https://doi.org/10.1080/19485565.1983.9988531

Thornhill, R., & Gangestad, S. W. (1999). *Facial attractiveness*. *3*(12), 452–460.

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior*, *27*, 131–144.

Todorov, A. (2008). Evaluating faces on trustworthiness: An extension of systems for recognition of emotions signaling approach/avoidance behaviors. *Annals of the New York Academy of Sciences*, *1124*, 208–224. https://doi.org/10.1196/annals.1440.012

Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: the cooperative eye hypothesis. *Journal of Human Evolution*, *52*(3), 314–320. https://doi.org/10.1016/j.jhevol.2006.10.001

Trixler, D., & Tényi, T. (2017). Iris structure and minor physical anomalies in schizophrenia. *Psychiatry Research*, *256*, 412–416. https://doi.org/10.1016/j.psychres.2017.07.004

Ulusoy, N., & Schablon, A. (2020). Discrimination in In-Patient Geriatric Care: A Qualitative Study on the Experiences of Employees with a Turkish Migration Background. In *International Journal of Environmental Research and Public Health* (Vol. 17, Issue 7). https://doi.org/10.3390/ijerph17072205

Vallès, X., Alonso, M. H., López-Caleya, J. F., Díez-Obrero, V., Dierssen-Sotos, T., Lope, V., Molina-Barceló, A., Chirlaque, M. D., Jiménez-Moleón, J. J., Fernández Tardón, G., Castilla, J., Amiano, P., Capelo, R., Castaño-Vinyals, G., Guinó, E., Molina de la Torre, A. J., Moreno-Iribas, C., Pérez Gómez, B., Aragonés, N., … Moreno, V. (2018). Colorectal cancer, sun exposure and dietary vitamin D and calcium intake in the MCC-Spain study. *Environment International*, *121*(Pt 1), 428–434. https://doi.org/10.1016/j.envint.2018.09.030

van 't Wout, M., & Sanfey, A. G. (2008). Friend or foe: the effect of implicit trustworthiness judgments in social decision-making. *Cognition*, *108*(3), 796–803. https://doi.org/10.1016/j.cognition.2008.07.002

van den Berg, T. J. T. P., Ijspeert, J. K., & de Waard, P. W. T. (1991). Dependence of intraocular straylight on pigmentation and light transmission through the ocular wall. *Vision Research*, *31*(7–8), 1361–1367. https://doi.org/10.1016/0042-6989(91)90057-C

van den Berghe, P. L., & Frost, P. (1986). Skin color preference, sexual dimorphism and sexual selection: A case of gene culture co-evolution? *Ethnic and Racial Studies*, *9*(1), 87–113. https://doi.org/10.1080/01419870.1986.9993516

Vercellini, P., Buggio, L., Somigliana, E., Barbara, G., Viganò, P., & Fedele, L. (2013). Attractiveness of women with rectovaginal endometriosis: a case-control study. *Fertility and Sterility*, *99*(1), 212–218. https://doi.org/10.1016/j.fertnstert.2012.08.039

Vercellini, P., Buggio, L., Somigliana, E., Dridi, D., Marchese, M. A., & Viganò, P. (2014). 'Behind blue eyes'†: The association between eye colour and deep in filtrating endometriosis. *Human Reproduction*, *29*(10), 2171–2175. https://doi.org/10.1093/humrep/deu169

Wakamatsu, K., Hu, D. N., McCormick, S. A., & Ito, S. (2008). Characterization of melanin in human iridal and choroidal melanocytes from eyes with various colored irides. *Pigment Cell and Melanoma Research*, *21*(1), 97–105. https://doi.org/10.1111/j.1755-148X.2007.00415.x

Walsh, S., Wollstein, A., Liu, F., Chakravarthy, U., Rahu, M., Seland, J. H., Soubrane, G., Tomazzoli, L., Topouzis, F., Vingerling, J. R., Vioque, J., Fletcher, A. E., Ballantyne, K. N., & Kayser, M. (2012). DNA-based eye colour prediction across Europe with the IrisPlex system. *Forensic Science International: Genetics*, *6*(3), 330–340. https://doi.org/10.1016/j.fsigen.2011.07.009

Warren, C. S. (2014). Body area dissatisfaction in white, black and Latina female college students in the USA: An examination of racially salient appearance areas and ethnic identity. *Ethnic and Racial Studies*, *37*(3), 537–556. https://doi.org/10.1080/01419870.2012.716520

Watts, I. (2010). The pigments from Pinnacle Point Cave 13B, Western Cape, South Africa. *Journal of Human Evolution*, *59*(3–4), 392–411. https://doi.org/10.1016/J.JHEVOL.2010.07.006

White, T., & Terman, M. (2003). Effect of Iris Pigmentation and Latitude on Chronotype and Sleep Timing. *Chronobiology International*, *20*, 1193–1195.

Wielgus, A. R., & Sarna, T. (2005). Melanin in human irides of different color and age of donors. *Pigment Cell Research*, *18*(6), 454–464. https://doi.org/10.1111/j.1600-0749.2005.00268.x

Wilde, S., Timpson, A., Kirsanow, K., Kaiser, E., Kayser, M., Unterländer, M., Hollfelder, N., Potekhina, I. D., Schier, W., Thomas, M. G., & Burger, J. (2014). Direct evidence for positive selection of skin, hair, and eye pigmentation in Europeans during the last 5,000 y. *Proceedings of the National Academy of Sciences*, *111*(13), 4832–4837. https://doi.org/10.1073/pnas.1316513111

Wilkerson, C. L., Syed, N. A., Fisher, M. R., Robinson, N. L., Wallow, I. H., & Albert, D. M. (1996). Melanocytes and iris color. Light microscopic findings. *Archives of Ophthalmology (Chicago, Ill. : 1960)*, *114*(4), 437–442. https://doi.org/10.1001/archopht.1996.01100130433014

Wilkins, A. S., Wrangham, R. W., & Fitch, W. T. (2014). The "Domestication Syndrome" in Mammals: A Unified Explanation Based on Neural Crest Cell Behavior and Genetics. *Genetics*, *197*(3), 795 LP – 808. https://doi.org/10.1534/genetics.114.165423

Willis, J., & Todorov, A. (2006). First Impressions: Making Up Your Mind After a 100-Ms Exposure to a

Face. *Psychological Science*, *17*(7), 592–598. https://doi.org/10.1111/j.1467-9280.2006.01750.x

Wilson, G. D., & Barrett, P. T. (1987). Parental characteristics and partner choice: Some evidence for oedipal imprinting. *Journal of Biosocial Science*, *19*(2), 157–161. https://doi.org/10.1017/S0021932000016758

Workman, L., Akcay, N., Reeves, M., & Taylor, S. (2018). *Blue Eyes Keep Away the Winter Blues: Is Blue Eye Pigmentation an Evolved Feature to Provide Resilience to Seasonal Affective Disorder?* 180002.

Worthy, M. (1999). *Eye Color: A Key to Human and Animal Behavior*. iUniverse.

Yang, L., Veierød, M. B., Löf, M., Sandin, S., Adami, H.-O., & Weiderpass, E. (2011). Prospective Study of UV Exposure and Cancer Incidence Among Swedish Women. *Cancer Epidemiology Biomarkers &Amp; Prevention*, *20*(7), 1358 LP – 1367. https://doi.org/10.1158/1055-9965.EPI-11-0071

Yaremchuk, M. J. (2004). Improving periorbital appearance in the “morphologically prone.” *Plastic and Reconstructive Surgery*, *114*(4), 980–987.

Zebrowitz, L. A., & Montepare, J. M. (2008). Social Psychological Face Perception: Why Appearance Matters. *Social and Personality Psychology Compass*, *2*(3), 1497–1517. https://doi.org/https://doi.org/10.1111/j.1751-9004.2008.00109.x

Ziegler, A. G., Baumgartl, H. J., Ede, G., Held, M., Vogt, H. J., Kolb, H. J., & Standl, E. (1990). Low-pigment skin type and predisposition for development of type I diabetes. *Diabetes Care*, *13*(5), 529–531. https://doi.org/10.2337/diacare.13.5.529

Published Studies

STUDY 1

Kleisner, K., **Kočnar, T.**, Rubešová, A., & Flegr, J. (2010). Eye color predicts but does not directly influence perceived dominance in men. Personality and Individual Differences, 49(1), 59–64.

Author's contribution:

TK contributed to the study design, collected and analysed the data, and contributed to the manuscript writing and subsequent revisions

Personality and Individual Differences 49 (2010) 59–64

Contents lists available at ScienceDirect

Personality and Individual Differences

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

Eye color predicts but does not directly influence perceived dominance in men

Karel Kleisner [a,*], Tomáš Kočnar [a], Anna Rubešová [b], Jaroslav Flegr [a]

[a] Department of Philosophy and History of Science, Charles University, Viničná 7, 128 44 Prague, Czech Republic
[b] Department of Anthropology, Faculty of Humanities, Charles University, Husníkova, Prague 2075, Czech Republic

ARTICLE INFO

Article history:
Received 10 December 2009
Received in revised form 6 March 2010
Accepted 12 March 2010
Available online 28 March 2010

Keywords:
Iris color
Face perception
Human evolution
Geometric morphometrics
Social feedback hypothesis

ABSTRACT

This study focuses on the relationship between eye color, gender, and psychological characteristics perceived from the human face. Photographs of 40 male and 40 female students were rated for perceived dominance and attractiveness. Attractiveness showed no relation with eye color. In contrast, eye color had a significant effect on perceived dominance in males: brown-eyed men were rated as more dominant than men with blue eyes. To control for the effect of eye color, we studied perceived dominance on the same photographs of models after changing the iris color. The eye color had no effect on perceived dominance. This suggests that some other facial features associated with eye color affect the perception of dominance in males. Geometric morphometrics have been applied to reveal features responsible for the differences in facial morphospace of blue-eyed and brown-eyed males.

1. Introduction

Eyes need not necessarily be regarded only as physiological devices of sight, as organs that receive information from outside the organism. Eyes certainly represent structures that offer information about both present and future behavior, as well as the inner attitude of the bearer. Colloquially, eyes are regarded as windows to the soul (Zebrowitz, 1997). Compared to the eyes of our closest relatives, human eyes are somewhat unusual in both color and shape. Specifically, our eyes have very apparent white sclera, the iris may potentially gain different colors spanning from dark brown to light blue, the overall shape is horizontally prolonged, etc. (Kobayashi & Kohshima, 1997, 2001; Tomasello, Hare, Lehmann, & Call, 2007). Eyes are therefore semantic organs to which different biological meanings may be attributed in different contexts (Kleisner, 2008a, 2008b).

There is some evidence of a relationship between iris color and a variety of other factors. Previous investigations have shown that blue-eyed Caucasian children are more behaviorally inhibited than brown-eyed children (Rosenberg & Kagan, 1987, 1989). Blue iris color also covaries with infant high-reactivity, timidness and shyness (Kagan & Snidman, 2004). Moreover, Coplan, Coleman, and Rubin (1998) suggested that eye color is a marker of social wariness in young children. Interestingly, Bassett and Dabbs (2001) reported a relation between eye color and alcohol consumption. The authors showed that individuals with light eyes consume significantly more alcohol than dark-eyed individuals. Dark-eyed individuals may be more sensitive to some drugs including alcohol, which may prevent them from hard drinking; conversely, light eyed subjects are more prone to anxiety, so they may compensate for their behavioral inhibition by consuming higher quantities of alcohol (Bassett & Dabbs, 2001). According to Christensen and Sacco, stuttering individuals with blond hair and blue eyes show more severe disfluency of speech than other stutterers (Christensen & Sacco, 1989). Eye color is also suspected for its role as a possible medicinal prognostic factor (Cumming, Mitchell, & Lim, 2000; Regan, Judge, Gragoudas, & Egan, 1999).

In many species, including humans (Havlicek, Roberts, & Flegr, 2005; Reynolds, 1996), dominance associated traits have been suggested as honest signals of male genetic quality ("good genes"). The main problem with using eye color as a useful indicator of dominance or submissiveness is that eye color is usually determined by a few genes with a large effect (Duffy et al., 2007; Kayser et al., 2008; Liu et al., 2009) while dominance is probably determined by many genes with additive and non-additive effects, and also by non-genetic factors. The color of an iris cannot change in response to the dominance of a subject. Therefore, to be a truthful indicator of dominance, iris color should either influence the dominance of a subject (for example due to a pleiotropic effect of the gene which directs eye color), or influence the perception of the observer – e.g. females seeking the "good genes" of dominant partners, should cue off of other physical traits which could change during the life of an individual in response to his/her dominance, and which for some reason usually covaries with brown or blue eye color.

* Corresponding author. Tel.: +420 6 08327772; fax: +420 2 24919704.
E-mail address: kleisner@seznam.cz (K. Kleisner).

0191-8869/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.paid.2010.03.011

Here, we searched for an association between iris color (blue or brown) and perceived dominance and attractiveness using photos of male and female university students. We also studied whether it is iris color or rather the presence of other morphological traits associated with blue or brown colored irises that play a role in the rater's judgment. Finally, we used a geometric morphometric approach to detect facial morphological traits associated with eye color that may be responsible for differences in raters' judgments.

2. Methods

2.1. Photographs

We took photographs of 80 students (40 males: mean age = 20.8, range: 19–26; 40 females: mean age = 21.2, range: 19–26) from the Faculty of Science, Charles University in Prague, Czech Republic, using digital camera Nikon D40X. All photos were taken using electronic flash and reflection screen; the subjects were seated in front of a white background. Models were instructed to adopt neutral, non-smiling expressions and to avoid any facial cosmetics and other face decorations. All photographs were cropped so that the eyes of all participants were horizontally at the same height and a standard length of neck was visible. Two of the authors (TK: brown-eyed and KK: blue-eyed) independently judged the photos, selecting individuals with either blue or brown eyes. We avoided the intermediate hues of irises usually designated as green. Eye color that does not correspond to blue or brown occurs only infrequently in the Czech population.

2.2. Rating of photographs

Sixty-two raters (31 females and 31 males), mainly students of faculties other than the Faculty of Science, aged 23.8 years on average (females: mean age = 23.4, range: 19–30; males: mean age = 24.2, range: 19–34), were individually invited to judge the photographs. Every person rated the whole set of 80 photos for dominance (or attractiveness) on a 10 point scale where one corresponds to very submissive (unattractive) and 10 to very dominant (attractive). We used ImageRater 1.1 software for the presentation and judgments of all photographs. Both traits, dominance and attractiveness, were judged by 31 raters: *attractiveness* was rated by 15 males and 16 females aged 24.2 years on average (males – 24.5; females – 23.9); *dominance*: 16 males and 15 females, average age: 23.4 (males – 23.9; females – 22.9). We also controlled for the rater's eye color by including the same number of raters with blue and brown eyes.

Raters saw images on a liquid crystal display computer screen with 1280 × 1024 pixel resolution, and indicated the chosen value by mouse clicks on the discontinuous 10 points scale. No time limits for choice indication were imposed; however, the time taken to rate a particular picture on the scale was usually 1–3 s. The order of the photographs was randomized for each rating session. In cases where a rater knew or was acquainted with a person pictured, she/he was instructed not to rate that picture. The ratings of all photographs evaluated by one rater were converted to Z-scores to eliminate the influence of individual differences between raters, and perceived dominance and attractiveness calculated for each photo as its average Z-score.

2.3. Rating of photographs with changed eye color

In order to find out whether there is any specific effect of eye color on perceived dominance (see Section 3) we used the Adobe Photoshop CS 3 software to change the eye color of all 40 photographs of males. The iris color of originally blue-eyed men was changed to brown and vice versa. This operation was performed in such a way that only the hue of the iris was changed, while the individually specific structural pattern of the iris remained intact.

The changed photographs were judged for perceived dominance by an additional group of 40 raters (20 males, 20 females) aged 22.5 years on average (males – 22.9; females – 22.0). None of the raters that have judged the original set of photographs were again invited to judge the photos with manipulated iris color. The raters were asked whether they noticed "something unusual" in the photographs presented. No mention was made of the manipulation of eye color. In order to be absolutely sure that iris color manipulation did not affect one group more than the other, we presented the photographs to an independent group of raters (11 females, 12 males) aged 17.4 years on average (males – 17.2; females – 17.6) and let them judge every picture on a 10 point scale where one corresponds to very natural and 10 to very unnatural. The photos were rated under the same conditions and using the same methods as described above for the original set of photographs.

2.4. Statistics

The relation between perceived dominance and attractiveness and eye color was tested by *General Linear Models* (GLM) using a mean Z-score of the trait as the dependent variable and the iris color and sex of the rater as factors: because dominance can be expected to correlate with the age of a subject, we included age of the photographed persons into the GLM as a covariate. Effect size was expressed by partial η^2. Ratings of each of these categories were analyzed separately for male and female sets of photographs. The differences of mean Z-score of the ratings of each photograph before and after eye color manipulation were calculated and tested separately for blue-eyed and brown-eyed male subjects by one sample t-test (H_0: dominance in original faces – dominance in manipulated faces = 0). The association between changed eye color and perceived naturalness of the manipulated photographs was tested by GLM with a mean Z-score of the trait as the dependent variable and the iris color as factor (the age of the photographed persons were added as covariate).

2.5. Geometric morphometrics

Photographs of 40 males (20 blue-eyed and 20 brown-eyed) were analyzed by geometric morphometric methods (GMM) to investigate the shape differences in faces of blue-eyed and brown-eyed males. The GMM represents a set of analytical methods for the multivariate statistical analysis of Cartesian coordinate data of landmark positions: its theoretical background is well understood and it has been widely used in different biological applications (see e.g. Bookstein, 1991; Dryden & Mardia, 1998; Mitteroecker & Gunz, 2009; Schaefer & Bookstein, 2009; Slice, 2005; Zelditch, Swiderski, Sheets, & Fink, 2004). The main advantage of GMM is that it takes into account information about the spatial relationships among the measured variables that is preserved during analysis and statistical results; this information can thus be later visualized in the form of thin-spline deformation grids.

The 72 landmarks (including 36 semilandmarks) were digitized in tpsDig2 software, ver. 2.14 (Rohlf, 2009a). Landmarks are represented as points that are anatomically (or at least geometrically) homologous while sliding semilandmarks serves to denote curves and outlines. Landmark and semilandmark locations on human faces were adjusted according to definitions in Schaefer et al. (2006) and Fink et al. (2005); see Fig. 1. All configurations of landmarks and semilandmarks were superimposed using the generalized Procrustes analysis (GPA), implemented in tpsRelw, ver.

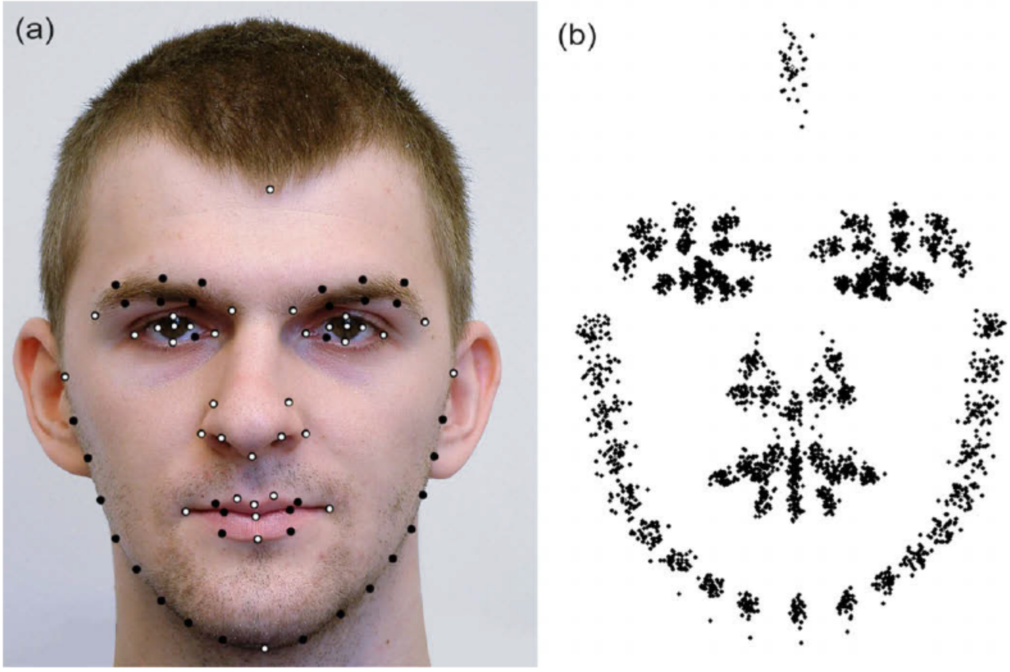

Fig. 1. (a) Configuration of 72 landmark locations on the face: landmarks that can be delimited as anatomically corresponding points – empty circles; semilandmarks that denote curves – filled circles and (b) the superposition of all 72 landmarks for 40 specimens (all males) after the Procrustes fit showing the shape variability in the sample. These data are used for all subsequent statistical procedures within GMM.

1.46. This procedure standardized the size of the objects and optimized their rotation and translation so that the distances between corresponding landmarks were minimized. To summarize: variation among the landmark data configurations of all specimens shape the principal component analysis (PCA) – i.e., the relative warp analysis for parameter $\alpha = 0$ – was carried out in tpsRelw, ver. 1.46. (Rohlf, 2008). Then, we used the scores for the object of the first 15 axes describing 93% of total variation to test for the group shape differences by means of the two-group permutation test on Mahalanobis distance with 10,000 permutations (computed in PAST; Hammer, Harper, & Ryan, 2001).

To determine the shape variation associated with eye color, we regressed GPA shape coordinates onto eye color using multivariate regression in which shape coordinates is the dependent variable and eye color the independent variable (conducted in tpsRegr, ver. 1.36; Rohlf, 2009b). Shape regressions were displayed by thin-plate splines as deformation from the overall mean configuration (the consensus) of landmarks. Composite pictures were made using tpsSuper, ver. 1.14 (Rohlf, 2004): 3× magnified estimated shape configurations were used as fixed templates to which the pictures of 20 brown-eyed and 20 blue-eyed males were unwarped.

3. Results

Iris color had a significant effect on perceived dominance in males ($p = 0.031$; $\eta^2 = 0.108$); brown-eyed males were rated as more dominant than blue-eyed, Fig. 2. However, no effect was observed for perceived dominance in females ($p = 0.942$; $\eta^2 = 0.001$). After the age of the rated subjects was added into the GLM as a covariate, the effect of eye color on the perceived dominance of males decreased; however, the effect was still present ($p = 0.050$; $\eta^2 = 0.100$). The effect of age of the rated person was not significant ($p = 0.128$; one-tailed test).

In order to find out whether it is eye color that specifically influences perceived dominance in males, and not other eye color-associated facial features, we changed the iris color of brown-eyed subjects to blue and vice versa. Changing the eye color had no effect on perceived naturalness of the manipulated photographs ($p = 0.345$; $\eta^2 = 0.023$; after adding age as covariate: $p = 0.356$; $\eta^2 = 0.023$). With this manipulation, males with eye color changed to blue (originally brown-eyed) were rated as more dominant than males with brown colored irises (originally blue-eyed). Nevertheless, this relation was not statistically significant ($p = 0.127$; $\eta^2 = 0.060$).

Clearer results were obtained by one sample t-test (that is in principle a paired test and therefore has higher statistical power). Mean differences of perceived dominance of subjects before and after eye color manipulation (−0.027 for blue-eyed subjects, 0.027 for brown-eyed subjects) were not different from zero (blue-eyed: $t = 0.222$, df = 19, $p = 0.826$; brown-eyed: $t = 0.171$, df = 19, $p = 0.866$), which suggests that the color of iris itself had no effect on perceived dominance.

The two-group permutation test for the GPA data rejected the null hypothesis of no association between facial shape and eye color. The effect of eye color on shape differences was clearly significant ($p = 0.0054$; Mahalanobis distance = 0.44; permutation $N = 10{,}000$). The shape regressions upon eye color visualized by thin-plate splines as predicted transformations in both directions from the consensus (mean) are shown in Fig. 3. The thin-plate spline deformations illustrate shape differences in the faces of blue-eyed and brown-eyed males. The grid deformations are especially visible on the differences in lateral compression (or dilations) in the chin, mouth, and eye region.

Our data suggested no relation between eye color and attractiveness, neither for rated photographs of males ($p = 0.678$; $\eta^2 = 0.005$) nor females ($p = 0.848$; $\eta^2 = 0.001$).

4. Discussion

In this study we found no effect of eye color on perceived dominance in women. On the contrary, we found a statistically significant association between the eye color and perceived dominance in men: brown-eyed men were perceived as more dominant.

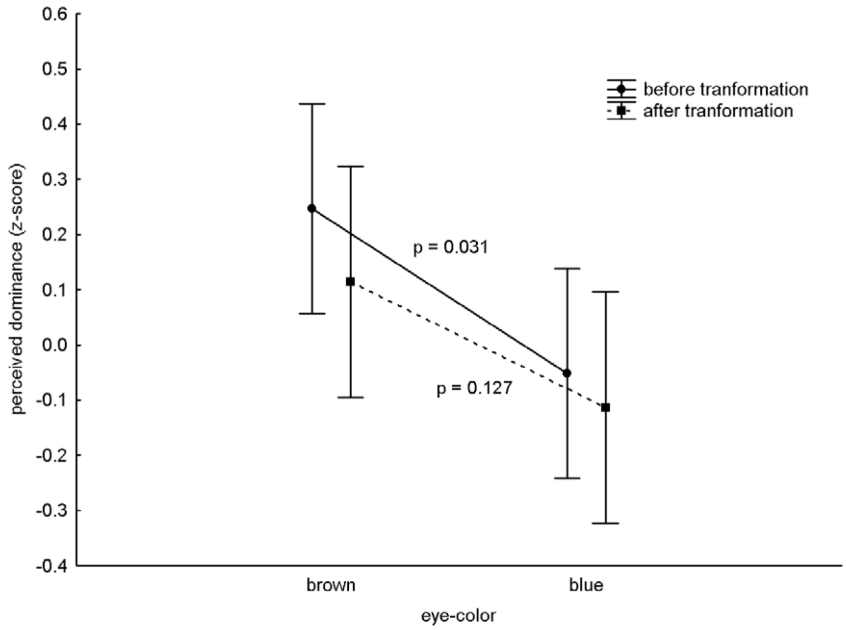

Fig. 2. Perceived dominance of males with iris color transformed from blue to brown and vice versa. Graph shows differences in perceived dominance of brown-eyed men (left) and blue-eyed men (right). The *y*-axis shows dominance expressed in *Z*-scores; whiskers denote standard deviations. (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

Furthermore, we show that iris color does *not* represent the trait that significantly influences perception of dominance in males. Hence, there must be some other facial characteristics responsible for the higher perceived dominance in brown-eyed males. It is evident, however, that the features standing for higher perceived dominance in males are correlated with presence of brown eyes; or alternatively, the features connected with higher perceived submissiveness in males with the blue eyes.

The question arises: why are brown-eyed males rated as more dominant than blue-eyed? Some facial features such as square jaws, thick eyebrows and broad cheekbones are linked with higher perceived dominance; facial submissiveness, on the other hand, is characterized by a round face with large eyes, smallish nose, and high eyebrows (Berry, 1990; Berry & Mcarthur, 1986; Cunningham, Barbee, & Pike, 1990; Mazur, Halpern, & Udry, 1994; Mueller & Mazur, 1997; Thornhill & Gangestad, 1994). The morphological differences between blue-eyed and brown-eyed males were visualized by deformation of thin-plate splines (Fig. 3). In contrast with blue-eyed males, brown-eyed males have statistically broader and rather massive chins, broader (laterally prolonged) mouths, larger noses, and eyes that are closer together with larger eyebrows. In contrast, blue-eyed males show smaller and sharper chins, mouths that are laterally narrower, noses smaller, and a greater span between the eyes. Especially the broader massive chin, bigger nose, and larger eyebrows of brown-eyed males may explain their higher perceived dominance.

However, it is not easy to explain how iris color, which is determined mostly by one or a few genes, can correlate with physiognomic dominance/submissiveness, which is determined by a combination of several independent morphological traits. Theoretically, the allele for brown eyes should "move" from "submissive physiognomy genotype" to "dominant physiognomy genotype" and back again from generation to generation due to genetic recombination and segregation.

In principle, there are three possible explanations for the higher perceived dominance of brown-eyed males, the pleiotropy hypothesis, genetic linkage hypothesis and social feedback hypothesis. The pleiotropy hypothesis presumes that the genes for iris color (such as HERC2 or OCA2) also influence other morphological traits associated with perceived dominance due to its pleiotropy effect. One can speculate, for instance, that the gene influences the production or metabolism of common precursors of adrenaline and melanin, e.g. DOPA or tyrosine.

The genetic linkage hypothesis presumes that the genes influencing iris color are in genetic linkage with genes influencing morphological traits associated with perceived dominance, for example the gene influencing the production of testosterone. If this is so, strong linkage disequilibrium between these loci should exist in the current Czech population. Repeating this study in other populations with polymorphism in eye color can test this hypothesis.

The social feedback hypothesis is based on the presumption that blue and brown-eyed subjects are treated differently within their social surroundings, e.g. by their parents and peers. Young children usually have blue eyes, while definitive iris color develops during the first years of life (Bito, Matheny, Cruickshanks, Nondahl, & Carino, 1997). It is possible that subjects with blue eyes are treated as a small child for a longer period than brown-eyed children. Such early social experience may have been literally "inscribed" into their faces, preserved until adulthood, and finally bring on the perception of higher submissiveness. Rosenberg and Kagan (1987, 1989) investigated the association between eye color and behavioral inhibition, revealing that children with blue eyes are more inhibited. Coplan et al. (1998) found a significant interaction between eye color and social wariness within preschoolers. Blue-eyed males were rated as more socially wary, i.e. being more temperamentally inhibited, displaying more reticent behavior and having more internalizing problems, than males with brown eyes, though there were no differences between blue- and brown-eyed females (Coplan et al., 1998). To test the third hypothesis, it would be necessary to perform a longitudinal study on preschool children to search whether the differences in perceived dominance (and social wariness) develops only after the transformation of iris color from blue to brown.

In this study, we did not observe any association between eye color and attractiveness, neither in men nor women, which seems to contradict the paternity-assurance hypothesis of the preference

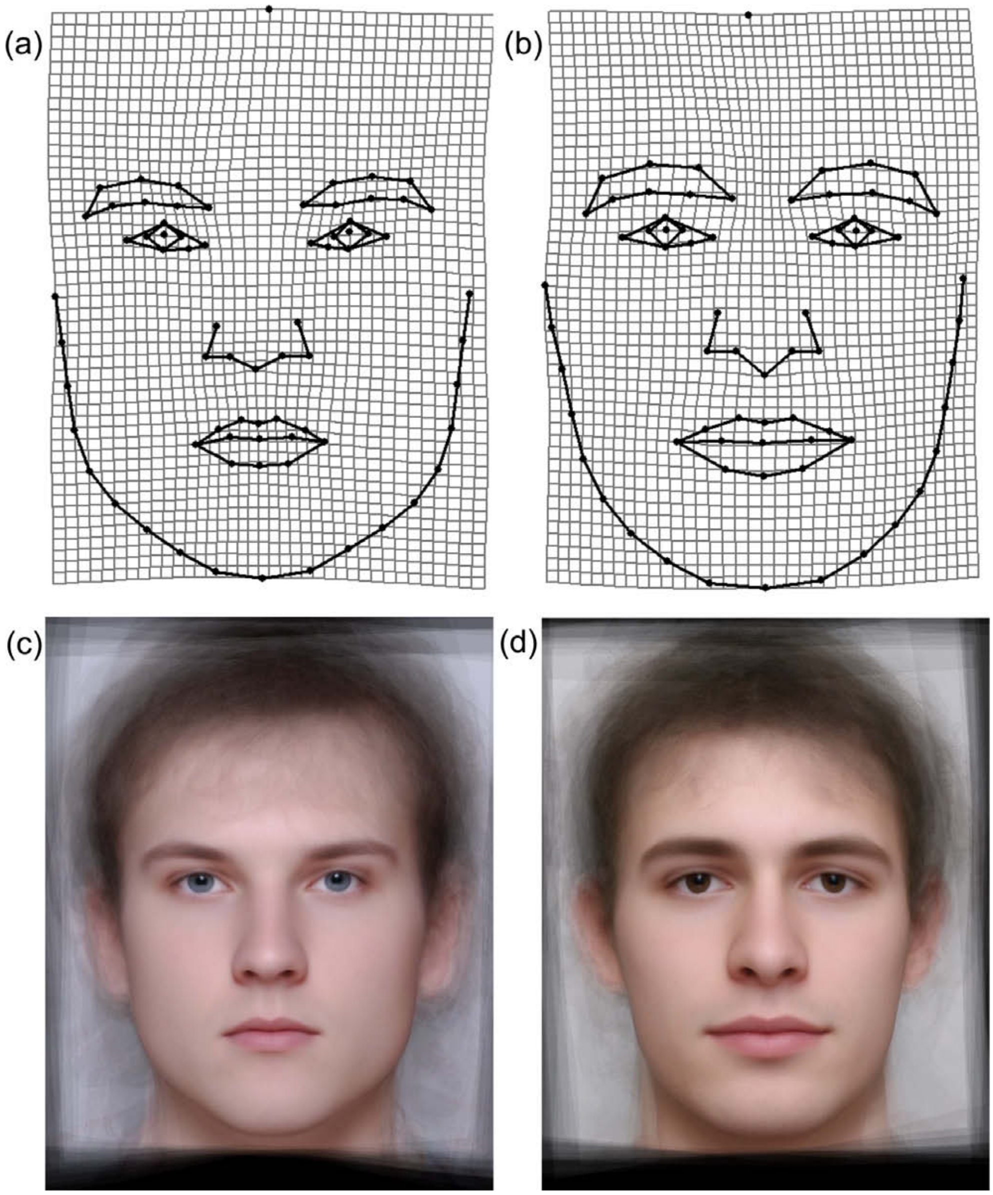

Fig. 3. (a and b): Visualizations of shape regression on eye color in males by thin-plate spline deformation grids illustrating differences in facial shape between blue-eyed (a) and brown-eyed (b) males; the links connecting the landmarks are drawn for better imaging of differences in the shape of face. (c and d): Composite images of 20 photographs of each group unwarped to fixed landmark configuration predicted by shape regression of blue-eyed (c) and brown-eyed (d) male faces. The predictions are magnified three times for better readability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of blue-eyed men for blue-eyed women (Laeng, Mathisen, & Johnsen, 2007). Attractiveness is usually associated with desirable personality traits (Langlois et al., 2000). The relationship of attractiveness and eye color may be obscured by the fact that brown eye color (or morphological traits of brown-eyed faces) is linked to perceived dominance, which is typically ascribed to masculine faces (Keating, 1985). It must be remembered, however, that male facial masculinity is a trait preferred in some circumstances or by some individuals, and at the same time disliked by others or in other circumstances. For example, female preferences differ in fertile and non-fertile phases of their menstrual cycle (Havlicek et al., 2005; Penton-Voak et al., 1999). Women in their fertile phase consider more dominant (masculine) men as more attractive and in non-fertile phases as less attractive. On the other hand, other authors have found that besides dominance, masculine features may indicate higher levels of rather undesirable traits, such as a lower willingness to invest in children, or higher aggressiveness and antisocial behavior (Mazur & Booth, 1998). Thus, it is possible that we were not able to identify the relationship between attractiveness and brown eye color (settled in dominant-looking, i.e. masculine faces) because this would demand inspection of some other characteristics of the raters (such as menstrual cycle phase, or partnership status), which were not included in our study.

The most important question is whether eye color honestly reflects a dominant character in a man and therefore can be used by a female, for instance, as the indicator of dominance in a potential sexual or social partner. It has been suggested and demonstrated that women follow mixed mating strategy: they prefer dominant males as extra-pair sexual partners while at the same time they are seeking males who are more willing to invest in their offspring as long-term or social partners (Havlicek et al., 2005; Reynolds, 1996). To answer this important question, it would be necessary to search for a correlation between psychological dominance and iris color in future studies.

Acknowledgements

We are grateful to Jiří Neustupa (Department of Botany, Charles University in Prague) for introducing us the GMM methods and providing valuable advice on data analysis. Special thanks belong to Katrin Schaefer (Department of Anthropology, University of Vienna) for advice considering the landmark locations on the human face, and for overall inspiration. We thank two anonymous referees for their worthy suggestions. The study was supported by Research Program CTS MSM 0021620845 and GAUK 2203/2007.

References

Bassett, J. F., & Dabbs, J. M. (2001). Eye color predicts alcohol use in two archival samples. *Personality and Individual Differences, 31*, 535–539.

Berry, D. S. (1990). Taking people at face value – Evidence for the kernel of truth hypothesis. *Social Cognition, 8*, 343–361.

Berry, D. S., & Mcarthur, L. Z. (1986). Perceiving character in faces – The impact of age-related craniofacial changes on social-perception. *Psychological Bulletin, 100*, 3–18.

Bito, L. Z., Matheny, A., Cruickshanks, K. J., Nondahl, D. M., & Carino, O. B. (1997). Eye color changes past early childhood – The Louisville Twin Study. *Archives of Ophthalmology, 115*, 659–663.

Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. New York: Cambridge University Press.

Christensen, J. M., & Sacco, P. R. (1989). Association of hair and eye color with handedness and stuttering. *Journal of Fluency Disorders, 14*, 37–45.

Coplan, R. J., Coleman, B., & Rubin, K. H. (1998). Shyness and little boy blue: Iris pigmentation, gender, and social wariness in preschoolers. *Developmental Psychobiology, 32*, 37–44.

Cumming, R. G., Mitchell, P., & Lim, R. (2000). Iris color and cataract: The blue mountains eye study. *American Journal of Ophthalmology, 130*, 237–238.

Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want – Facial metric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology, 59*, 61–72.

Dryden, I. L., & Mardia, K. V. (1998). *Statistical shape analysis*. New York: Wiley.

Duffy, D. L., Montgomery, G. W., Chen, W., Zhao, Z. Z., Le, L., James, M. R., et al. (2007). A three-single-nucleotide polymorphism haplotype in intron 1 of OCA2 explains most human eye-color variation. *American Journal of Human Genetics, 80*, 241–252.

Fink, B., Grammer, K., Mitteroecker, P., Gunz, P., Schaefer, K., Bookstein, F., et al. (2005). Second to fourth digit ratio and face shape. *Proceedings of the Royal Society B – Biological Sciences, 272*, 1995–2001.

Hammer, O., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica, 4*, 9.

Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: Effects of menstrual cycle and relationship status. *Biology Letters, 1*, 256–259.

Kagan, J., & Snidman, N. (2004). *The long shadow of temperament*. Cambridge, MA: Belknap Press.

Kayser, M., Liu, F., Cecile, A., Janssens, J. W., Rivadeneira, F., Lao, O., et al. (2008). Three genome-wide association studies and a linkage analysis identify HERC2 as a human iris color gene. *American Journal of Human Genetics, 82*, 411–423.

Keating, C. F. (1985). Gender and physiognomy of dominance and attractiveness. *Social Psychology Quarterly, 48*, 61–70.

Kleisner, K. (2008a). Homosemiosis, mimicry and superficial similarity: Notes on the conceptualization of independent emergence of similarity in biology. *Theory in Biosciences, 127*, 15–21.

Kleisner, K. (2008b). The semantic morphology of Adolf Portmann: A starting point for the biosemiotics of organic form? *Biosemiotics, 1*, 207–219.

Kobayashi, H., & Kohshima, S. (1997). Unique morphology of the human eye. *Nature, 387*, 767–768.

Kobayashi, H., & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the primate eye. *Journal of Human Evolution, 40*, 419–435.

Laeng, B., Mathisen, R., & Johnsen, J. A. (2007). Why do blue-eyed men prefer women with the same eye color? *Behavioral Ecology and Sociobiology, 61*, 371–384.

Langlois, J. H., Kalakanis, L. E., Rubenstein, A. J., Larson, A. D., Hallam, M. J., & Smoot, M. T. (2000). Maxims and myths of beauty: A meta-analytic and theoretical review. *Psychological Bulletin, 126*, 390–423.

Liu, F., van Duijn, K., Vingerling, J. R., Hofman, A., Uitterlinden, A. G., Janssens, A. J. W., et al. (2009). Eye color and the prediction of complex phenotypes from genotypes. *Current Biology, 19*, R192–R193.

Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences, 21*, 353–397.

Mazur, A., Halpern, C., & Udry, J. R. (1994). Dominant looking male teenagers copulate earlier. *Ethology and Sociobiology, 15*, 87–94.

Mitteroecker, P., & Gunz, P. (2009). Advances in geometric morphometrics. *Evolutionary Biology, 36*, 235–247.

Mueller, U., & Mazur, A. (1997). Facial dominance in Homo sapiens as honest signaling of male quality. *Behavioral Ecology, 8*, 569–579.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., et al. (1999). Menstrual cycle alters face preference. *Nature, 399*, 741–742.

Regan, S., Judge, H. E., Gragoudas, E. S., & Egan, K. M. (1999). Iris color as a prognostic factor in ocular melanoma. *Archives of Ophthalmology, 117*, 811–814.

Reynolds, J. D. (1996). Animal breeding systems. *Trends in Ecology and Evolution, 11*, 68–72.

Rohlf, J. F. (2004). *TpsSuper (version 1.14)*. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf, J. F. (2008). *TpsRelw (version 1.46)*. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf, J. F. (2009a). *TpsDig2 (version 2.14)*. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf, J. F. (2009b). *TpsRegr (version 1.36)*. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.

Rosenberg, A., & Kagan, J. (1987). Iris pigmentation and behavioral inhibition. *Developmental Psychobiology, 20*, 377–392.

Rosenberg, A., & Kagan, J. (1989). Physical and physiological correlates of behavioral inhibition. *Developmental Psychobiology, 22*, 753–770.

Schaefer, K., & Bookstein, F. L. (2009). Does geometric morphometrics serve the needs of plasticity research? *Journal of Biosciences, 34*, 589–599.

Slice, D. E. (Ed.). (2005). *Modern morphometrics in physical anthropology*. New York: Kluwer Academic/Plenum Press.

Schaefer, K., Grammer, K., Fink, B., Mitteroecker, P., Gunz, P., & Bookstein, F. L. (2006). Female appearance: Facial and bodily attractiveness as shape. *Psychology Science, 48*, 178–205.

Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual-behavior. *Psychological Science, 5*, 297–302.

Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution, 52*, 314–320.

Zebrowitz, L. A. (1997). *Reading faces: Windows to the soul?* Boulder, CO: Westview Press.

Zelditch, M. L., Swiderski, D. L., Sheets, D. H., & Fink, W. L. (2004). *Geometric morphometrics for biologists: A primer*. London: Elsevier.

STUDY 2

Kočnar, T., Drbalová, K. R., & Kleisner, K. (2012). Do dominant-looking males have brown eyes? A further investigation of the role of iris colour for dominance perception. Anthropologie, 50(1), 25–32.

Author's contribution:

TK developed the study concept, collected and analysed the data, and drafted manuscript

ANTHROPOLOGIE • XLIX/2 • pp. ???–??? • 2011

TOMÁŠ KOČNAR, KATEŘINA R. DRBALOVÁ, KAREL KLEISNER

DO DOMINANT-LOOKING MALES HAVE BROWN EYES? A FURTHER INVESTIGATION OF THE ROLE OF IRIS COLOUR FOR DOMINANCE PERCEPTION

ABSTRACT: The eyes represent a conspicuous facial element of unique appearance; they play an important role in signalling and communication within many animal species including humans. In this paper, we investigate the possible influence of eye colour on the perception of dominance. This research is based on our previous study (Kleisner et al., 2010: Pers. Individ. Dif. 49: 59–64*) showing that eye colour had a significant effect on perceived dominance. Facial photographs of university students were rated for perceived dominance. To control for a possible idiosyncratic effect of selected facial photographs, the two distinct samples were compiled. The first sample of photos consisted of 80 faces and the second of 120 faces; both were of students from the Faculty of Science, Charles University in Prague. The rating of photographs was performed by volunteers from three different regions: Prague, Ústí nad Labem (both Czech Republic), and Tartu (Estonia). Controlling for sample and location, we showed that there is no statistically significant relationship between eye colour and perceived dominance: Prague ($P = 0.822$), Ústí nad Labem ($P = 0.778$), and Tartu ($P = 0.565$). These negative results thus contradict the previous study, wherein males with brown eyes were perceived as more dominant than males with blue eyes. In this study we consider the possible local-specific differences and confounding random factors which might be responsible for the previous positive results on an association between eye colour and the perception of dominance.*

KEY WORDS: Eye colour – Perceived dominance – Facial appearance – Cross-cultural comparison

INTRODUCTION

A considerable number of studies have described facial appearance as a cue for attributing different psychological characteristics to the face bearer (Langlois *et al.* 2000, Zebrowitz 1997). To some extent, the personality judgments from facial appearance are based on psychological processes established during human evolution (e.g., Shevlin *et al.* 2003). However neutral in expression, mere facial appearance could give an

Received 15 October 2012; accepted 19 March 2013

impression of such characteristics as attractiveness, babyfaceness, racial, or sex prototypicality, dominance, sociability, or trustworthiness (Montepare, Dobish 2003, Todorov 2008, Zebrowitz 2011, Zebrowitz, Montepare 1992).

In the human face, the viewer's attention appears to be captured by the eyes (Langton *et al.* 2000). The eyes, then, are not solely light sensitive physiological organs that receive a wide range of information from the outside world. The unique appearance of human eyes may also serve as a source of information about the outer behaviour as well as the inner attitude of the bearer. Compared to the closest human relatives, human eyes have a horizontally prolonged shape (Kobayashi, Kohshima 1997, 2001), an exposed white sclera (Kaplan, Rogers 2002), and a conspicuously coloured iris characterized by a variety of hues spanning from light blue to dark brown (e.g., Sturm, Frudakis 2004). The white sclera enables others to follow gaze direction (Tomasello *et al.* 2007). However, the very appearance of eyes including their colour is a quite often a neglected component in facial perception research.

There is some evidence of a relationship between iris colour and various physiological or psychological factors. The close metabolic relation of melanins to catecholamines indicates the possibility of hypertension in dark-eyed persons (Friedman *et al.* 1990), whose iris pigment epithelium contains a relatively greater amount of melanin when compared with those of blue-eyed persons (Prota *et al*. 1998). Some authors suggest a relation of eye colour to specific aspects of psychological functioning. Basset and Dabbs (2001) reported an increased amount of alcohol consumption by individuals with blue eyes, which could result from their alleged behavioural inhibition and proneness to anxiety. Blue-eyed children were reported both as more behaviourally inhibited (Rosenberg, Kagan 1987, 1989), high-reactive (Kagan, Snidman 2004), and socially wary (Coplan *et al.* 1998).

Human eye colour is also one of the traits investigated as a responsible factor in assortative mating. Little *et al*. (2003) suggested that the single best predictor of both male and female partner eye colour is the opposite-sex parents' eye colour. In the study of Laeng *et al*. (2007), male blue-eyed participants rated blue-eyed women as more attractive than brown-eyed women. Contrary to these findings, our own study did not show any relation between perceived attractiveness and eye colour in either males or females (Kleisner *et al.* 2010).

Based on the study of Coplan *et al.* (1998), we also asked whether eye colour may influence the perception of other personality traits, such as dominance (Kleisner *et al.* 2010). Coplan *et al.* (1998) found a correlation between eye colour and social wariness within preschoolers: blue-eyed males were rated as more socially wary than males with brown eyes, more temperamentally inhibited and displaying more reticent behaviour. Along with Coplan's finding we asked whether there is association between eye colour and perceived dominance or submissiveness in adult individuals (Kleisner *et al.* 2010). We found that eye colour had a significant effect on perceived dominance in males: brown-eyed men were rated as more dominant than blue-eyed men (Kleisner *et al.* 2010). To control this non-obvious correlation, the actual iris colour of brown-eyed subjects was changed to blue and vice versa. With this manipulation, males with eye colour changed to blue were rated as more dominant than males with brown coloured irises. Therefore, the perception was not an effect of eye colour, but a likely effect of particular morphological facial features, which cause the differences in perceived dominance/–submissiveness between brown-eyed and blue-eyed subjects. A geometric morphometric approach was used to detect those morphological features associated with eye colour (Kleisner *et al.* 2010). The presence of brown eyes was correlated with broader chin, prolonged mouth, larger nose, closer position of eyes, and thick eyebrows, i.e., characteristics largely linked with higher perceived dominance (Berry 1990, Cunningham *et al.* 1990, Mazur *et al.* 1994, Mueller, Mazur 1997, Thornhill, Gangestad 1994).

This study follows the previous work on a possible association between eye colour and perceived dominance (Kleisner *et al.* 2010). Here, we used the same methodological approach, but the tests were provided in two different regions of the Czech Republic and in Estonia. Our main objective was to re-test our previous findings, and also to test whether the correlation between eye colour and perceived dominance validates across different populations.

MATERIAL AND METHODS

Photographs

Photographs of students from the Faculty of Science at Charles University in Prague were taken with a digital camera, Nikon D90, using a 50 mm lens, studio flash, and a reflection screen. The photographed subjects were seated in front of a white background, 1.5 m distant from the camera, and instructed to adopt a neutral facial

TABLE 1. Age structure of the raters.

		All raters			Males				Females			
Locality	SET	*N*	Mean	SD	*N*	Mean	SD	Range	*N*	Mean	SD	Range
Ústí nad Labem	80	92	22.6	4.1	40	23.4	4.0	18–34	52	22.1	4.1	19–40
Tartu	80	30	23.8	4.3	13	24.1	4.0	20–32	17	23.6	4.5	19–38
Prague	120	84	20.8	1.9	24	22.0	2.6	19–29	60	20.3	1.2	19–24

expression. All of the participants were informed in advance to avoid any facial decorations. The photographs were all standardized regarding the eye position and the clothing of the photographed subjects was digitally cropped so that a standard, minimal length of neck was visible. The hair of the photographed subjects was left uncovered. From our collection of digital photos we selected 100 females and 100 males, both with unambiguous hues of blue and brown irises. Individuals with intermediate and green eye colour were excluded from the sample. To control for a possible idiosyncratic effect of selected facial photographs, we compiled two distinct sets, which consist of 80 (40 males: mean age = 20.8 years, range: 19–26 years; 40 females: mean age = 21.2 years, range: 19–26 years) and 120 photographs (60 males: mean age = 21.2 years, range: 19–34 years; 60 females: mean age = 20.6 years, range: 18–24 years), respectively. The age of participants did not significantly vary between the individual sets (Mann-Whitney *U* test; males: $P = 0.828$; females: $P = 0.145$). In each set, there were an equal number of blue-eyed and brown-eyed subjects of both sexes.

Ratings of photographs

The set of 80 photographs (SET 80) was judged mainly by the university students in Ústí nad Labem, Czech Republic and in Tartu, Estonia. We also repeated previous research in Prague (Kleisner *et al.* 2010), where we had originally used the same SET 80. Now, another sample of local students rated a larger sample of 120 photographs (SET 120). *Table 1* gives a detailed overview of the structure of all raters participating in the research.

Each person rated the complete set of photos for dominance on a 10 point scale where the lowest number stands for very submissive and the highest for very dominant. We used ImageRater 1.1 software, adapted for the presentation of photos for judgment. Raters saw images on a standard LCD 14" displays with 1280×1024 pixel resolution and clicked the selected value. There was no time limit to rate a particular photo. The order of the displayed pictures was randomised for each rating session. In the case that a rater might know a photographed subject, the software enabled us to skip the rating of that particular picture. After the rating of all the photographs, we asked each participant for his or her own eye-colour.

Statistics

The ratings of all photographs evaluated by each single rater were converted to *z*-scores to eliminate possible influence of individual differences in the raters use of the scale. Perceived dominance was calculated for each photo as its mean *z*-score. Dominance ratings of male and female raters in all locations were highly correlated (*Table 2*) so the ratings of both sexes were merged for all subsequent statistical analysis. The relation between perceived dominance and eye colour was tested by univariate General Linear Models (GLM), using SPSS 17 software. We built a linear model wherein a mean *z*-score of perceived dominance was a dependent variable, and the eye colour of the rated subjects was set as a fixed factor. Following the approach originally used in Kleisner *et al.* (2010), the analysis was performed separately for male and female sets of photographs. Effect size was expressed by partial η^2.

TABLE 2. Correlation between the number of male and female raters.

Locality	SET	Males	Females	*r*
Ústí nad Labem	80	40	52	0.875**
Tartu	80	13	17	0.666**
Prague	120	24	60	0.858**

** $P \leq 0.01$.

RESULTS

The relatively balanced ratio of blue-eyed and brown-eyed raters in Czech samples was controlled: 39 blue-eyed, 42 brown-eyed, and 11 green-eyed in Ústí nad Labem, and 38 blue-eyed, 32 brown-eyed, and 14 green-

TABLE 3. A possible association between perceived dominance and eye colour investigated in Prague, Ústí nad Labem (Czech Republic), and Tartu (Estonia).

	Males			Females		
	F	*P*	η^2	*F*	*P*	η^2
Ústí nad Labem (SET 80)	0.081	0.778	0.002	0.320	0.575	0.008
Tartu (SET 80)	0.337	0.565	0.009	2.687	0.109	0.066
Prague (SET 120)	0.051	0.822	0.001	0.068	0.795	0.001
Prague (SET 80)[a]	5.035	0.031	0.117	0.005	0.942	0.000

[a] Kleisner *et al.* (2010).

eyed in Prague, respectively. However, in Tartu we collected data from 13 blue-eyed, 5 brown-eyed, and 10 green-eyed participants. A frequency distribution of eye colours between our three samples was thus significantly different (Pearson's chi-squared test: $\chi^2 = 11.356$, $P = 0.022$, contingency coefficient $C = 0.229$).

The participants in Ústí nad Labem, in north Bohemia, judged a perceived dominance of 40 male faces (SET 80). Eye colour had no significant effect on dominance attribution ($F_{1,38} = 0.081$, $P = 0.778$, $\eta^2 = 0.002$). When we used the same SET 80 in Tartu (Estonia), we again found no significant effect of eye colour relating to dominance attribution ($F_{1,38} = 0.337$, $P = 0.565$, $\eta^2 = 0.009$).

Trying to replicate our previous significant results from Charles University in Prague, we repeated the same test using the larger set of photos (SET 120). We did not find any statistically significant effect of eye colour on perceived dominance in males ($F_{1,58} = 0.051$, $P = 0.822$, $\eta^2 = 0.001$).

We also did not observe any significant effect for perceived dominance in females (Ústí: $F_{1,38} = 0.320$, $P = 0.575$, $\eta^2 = 0.008$; Tartu: $F_{1,38} = 2.687$, $P = 0.109$, $\eta^2 = 0.066$; Prague: $F_{1,58} = 0.068$, $P = 0.795$, $\eta^2 = 0.001$). See *Table 3* for summary of results, including those published in Kleisner *et al.* (2010).

DISCUSSION

In the present study we found no statistical support for the hypothesis that eye colour affects perceived dominance in males. Our recent findings thus do not support the previous suggestion that brown-eyed men are perceived as more dominant than men with blue eyes (Kleisner *et al.* 2010). Previous research also revealed that brown-eyed and blue-eyed male faces show significant morphological differences in their particular facial features (Kleisner *et al.* 2010). We obtained a similar result after the comparison of the facial photographs from SET 120. On average, a brown-eyed male face shows a relatively massive chin and lips, bigger nose, broader bizygomatic width, and thick eyebrows whereas blue-eyed males had rounder faces, smaller noses and lips, and a seemingly greater span between the eyes (*Figure 1*, for a discussion of the methodology of geometrics morphometrics and the results of shape regressions, see Kleisner *et al.* 2010, 2013). Facial features – such as squared jaws, thick eyebrows, or broader bizygomatic width – are linked with higher perceived dominance and masculinity (Mueller, Mazur 1997, Thornhill, Gangestad 1994). On the contrary, a round face with large eyes, smallish nose, and thinner eyebrows (i.e., babyfaceness) is perceived as more submissive (Berry 1990, Berry, McArthur 1986).

Why didn't repeated tests show significant differences in perceived dominance between blue-eyed and brown-eyed males, despite the differences in the shape of their faces? First, we consider why the sensitivity of association between the perception of dominance and eye colour is not generally valid. The other option is that such a relationship is specific to raters in Prague where the previous research was done. To control the effect of the local community of raters, we invited raters from another Czech city (Ústí nad Labem) and from different country (Estonia) to judge the same photographs (SET 80). The individuals from different geographical regions are exposed to different environmental and cultural influences that presumably affect their perception. Moreover, different European populations reveal significant differences in frequencies of the expression of phenotypic traits such eye and hair colour. For example, the Baltic region, which includes Estonia, has a higher percentage of blue-eyed than brown-eyed inhabitants (Beals, Hoijer 1965, Frost 2006). In contrast to the positive results from a sample in Prague as reported Kleisner *et al.* (2010), neither Estonian ratings nor data from Ústí nad Labem have shown any association between eye colour and perceived

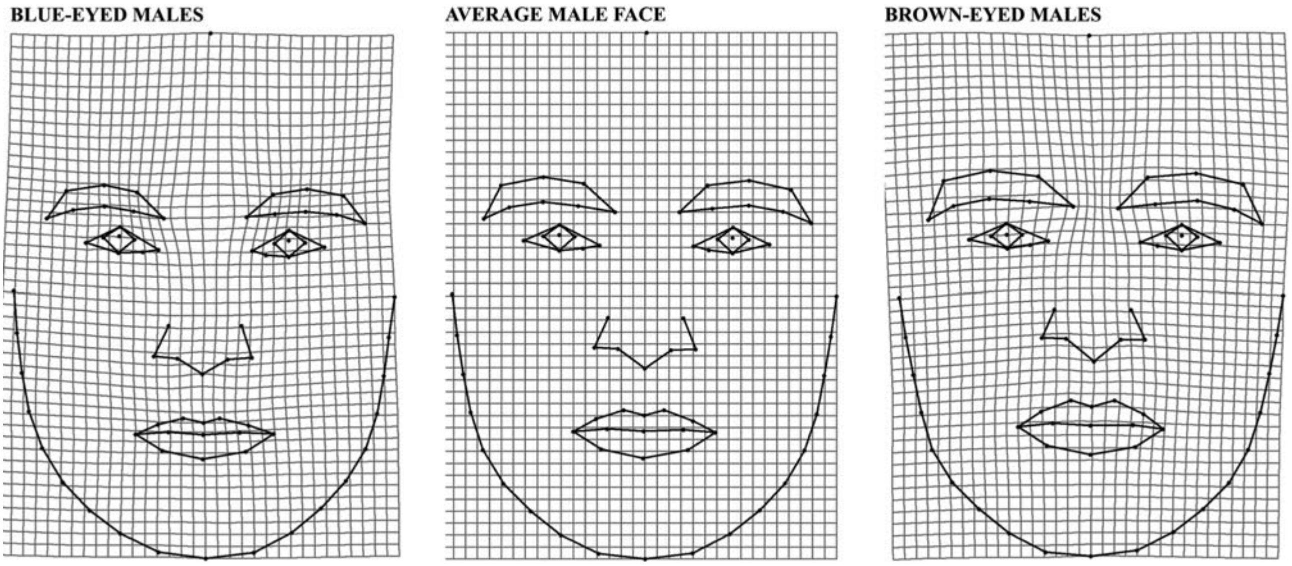

FIGURE 1. Shape changes associated with eye colour in males (SET 120). Photos of 30 brown-eyed and 30 blue-eyed men were analysed by geometric morphometrics (for a discussion of the methodology of geometrics morphometrics, see Kleisner *et al.* 2010, 2013). The effect of eye colour on shape differences was significant ($P = 0.012$; permutation $N = 10{,}000$). Visualisation of shape regression on eye colour in males by thin-plate spline deformation grids illustrates differences between blue-eyed (left) and brown-eyed (right) males compared to average male face (middle). The generated facial images were magnified 3×.

dominance. As we did not report any effect in Prague using the new SET 120, it is unlikely that there were any differences between the local raters. Most likely, the positive results of the original Prague set were due to unknown effects that led authors to unjustifiably reject the null hypothesis of no relationship between eye colour and perceived dominance (Type I Error). To test this assumption we performed another rating study in Prague using a larger set of photos (SET 120) that were non-identical with those of SET 80. In contrast to the previous study (Kleisner *et al.* 2010), we found no association between eye colour and perceived dominance. These results do not provide any support for the hypothesis of a higher sensitivity of Prague raters to association between eye colour and perceived dominance.

It may also have been that the target samples were not large enough to detect the effect we searched for. This means that we could possibly reject the null hypothesis of no association between perceived dominance and eye colour, even though the null hypothesis was false (Type II error). Nevertheless, we do not think that this was the case in our study. The number of 80 and 120 targets should be sufficient for testing our hypothesis as comparable sample sizes occurs in the majority of face perception studies (DeBruine 2002, Campbell *et al.* 1996, Rhodes *et al.* 2003). Moreover, the test was repeated both with a higher number of stimuli and different photos using three independent populations of raters. In addition to the above, post-hoc calculation of the observed power of a test from GLM analysis is considered a pure re-stating of the statistical significance of the test rather than rigorous solution to a problem of minimum sample size (Thomas, Krebs 1997). The *P*-value and observed effect size itself should provide sufficient evidence of the power of a statistical test (Thomas 1997).

CONCLUSION

To sum up, based on the new negative results of three independent tests, we suggest that the significant correlation of the perceived dominance with eye colour reported by Kleisner *et al.* (2010) might be due to chance. More specifically, we suggest that a combination of a random idiosyncrasy of a particular sample of facial photos used in the original research, together with further confounding factors led to an erroneous rejection of the hypothesis of no association between perceived dominance and eye colour (Type I error). The take-home message of this study is that the re-test of already published "facts" of association between perception of psychological factors and physical appearance might be more than relevant. However, there is a pitfall. Independently repeated experiments are not a common practice in contemporary biological and anthropological science due to increasing requirements for higher number of published results. Simply put, the reliability of scientific discovery is not always congruent with pressure for a steep production of novel scientific facts – especially nowadays.

ACKNOWLEDGEMENTS

We are grateful to all students who participated in this research. We thank Ondřej Bradáč for collecting data in Tartu, Estonia. We thank two anonymous reviewers for many worthy suggestions. This research was supported by Czech Grant Agency project P407/11/1464.

REFERENCES

BASSETT J. F., DABBS J. M., 2001: Eye colour predicts alcohol use in two archival samples. *Pers. Individ. Dif.* 31, 4: 535–539.

BEALS R. L., HOIJER H., 1965: *An introduction to anthropology*. Macmillan, New York.

BERRY D. S., 1990: Taking people at face value – Evidence for the kernel of truth hypothesis. *Soc. cognition* 8, 4: 343–361.

BERRY D. S., MCARTHUR L. Z., 1986: Perceiving character in faces – The impact of age-related craniofacial changes on social-perception. *Psychol. Bull*. 100, 1: 3–18.

CAMPBELL R., WALLACE S., BENSON P. J., 1996: Real men don't look down: Direction of gaze affects sex decisions of faces. *Vis. Cogn*. 3, 4: 393–412.

COPLAN R. J., COLEMAN B., RUBIN K. H., 1998: Shyness and little boy blue: Iris pigmentation, gender, and social wariness in preschoolers. *Dev. Psychobiol*. 32, 1: 37–44.

CUNNINGHAM M. R., BARBEE A. P., PIKE C. J. 1990: What do women want – Facial metric assessment of multiple motives in the perception of male facial physical attractiveness. *J. Pers. Soc. Psychol.* 59, 1: 61–72.

DEBRUINE L. M., 2002: Facial resemblance enhances trust. *P. Roy. Soc. Lond. B Bio*. 269, 1498: 1307–1312.

FRIEDMAN G. D., SELBY J. V., QUESENBERRY C. P., NEWMAN B., KING M. C., 1990: Eye colour and hypertension. *Med. Hypotheses* 33, 3: 201–206.

FROST P., 2006: European hair and eye colour: A case of frequency-dependent sexual selection? *Evol. Hum. Behav*. 27, 2: 85–103.

KAGAN J., SNIDMAN N., 2004: *The long shadow of temperament.* Cambridge, MA, Belknap Press.

KAPLAN G., ROGERS L. J., 2002: Patterns of gazing in orangutans. *Int. J. Primatol*. 23, 3: 501–526.

KLEISNER K., KOCNAR T., RUBESOVA A., FLEGR J., 2010: Eye colour predicts but does not directly influence perceived dominance in men. *Pers. Individ. Dif.* 49, 1: 59–64.

KLEISNER K., PRIPLATOVA L., FROST P., FLEGR J., 2013: Trustworthy-looking face meets brown eyes. *PLoS One* 8, 1: e53285. doi:10.1371/journal.pone.0053285.

KOBAYASHI H., KOHSHIMA S., 1997: Unique morphology of the human eye. *Nature* 387, 6635: 767–768.

KOBAYASHI H., KOHSHIMA S., 2001: Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. *J. Hum. Evol*. 40, 5: 419–435.

LAENG B., MATHISEN R., JOHSEN J. A., 2007: Why do blue-eyed men prefer women with the same eye colour? *Behav. Ecol. Sociobiol*. 61, 3: 371–384.

LANGLOIS I. H., KALAKANIS L. E., RUBENSTEIN A. J., LARSON A. D., HALLAM M. J., SMOOTH M. T., 2000: Maxims and myths of beauty: A meta-analytic and theoretical review. *Psychol. Bull*. 126, 3: 390–423.

LANGTON S. R. H., WATT R. J., BRUCE V., 2000: Do the eye have it? Cues to the direction of social attention. *Trends Cogn. Sci*. 4, 2: 50–59.

LITTLE A. C., PENTON-VOAK I. S., BURT D. M., PERRETT D. I., 2003: Investigating an imprinting-like phenomenon in humans: Partners and opposite-sex parents have similar hair and eye colour. *Evol. Hum. Behav*. 24, 1: 43–51.

MAZUR A., HALPERN C., UDRY J. R., 1994: Dominant looking male teenagers copulate earlier. *Ethol. Sociobiol*. 15, 2: 87–94.

MONTEPARE J. M., DOBISH H., 2003: The contribution of emotion perceptions and their overgeneralizations of trait impressions. *J. Nonverbal. Behav*. 27, 4: 237–254.

MUELLER U., MAZUR A., 1997: Facial dominance in Homo sapiens as honest signaling of male quality. *Behav. Ecol*. 8, 5: 569–579.

PROTA G., HU D., VINCENSI M. R., MCCORMICK S. A., NAPOLITANO A., 1998: Characterization of melanins in human irides and cultured uveal melanocytes from eyes of different colors. *Exp. Eye. Res*. 67, 3: 293–299.

RHODES G., JEFFERY L., WATSON T. L., CLIFFORD C. W. G., NAKAYAMA K., 2003: Fitting the mind to the world: Face adaptation and attractiveness aftereffects. *Psychol. Sci*. 14, 6: 558–566.

ROSENBERG A. A., KAGAN J., 1987: Iris pigmentation and behavioral inhibition. *Dev. Psychobiol.* 20, 4: 377–392.

ROSENBERG A. A., KAGAN J., 1989: Physical and physiological correlates of behavioral inhibition. *Dev. Psychobiol.* 22, 8: 753–770.

SHEVLIN M., WALKER S., DAVIES M. N. O., BANYARD P., LEWIS C. A., 2003: Can you judge a book by its cover? Evidence of self-stranger agreement on personality at zero acquaintance. *Pers. Individ. Dif*. 35, 6: 1373–1383.

STURM R. A., FRUDAKIS T. N., 2004: Eye colour: portals into pigmentation genes and ancestry. *Trends Genet*. 20, 8: 327–332.

THOMAS L., 1997: Retrospective power analysis. *Conserv. Biol*. 11, 1: 276–280.

THOMAS L., KREBS C., 1997: A review of statistical power analysis software. *Bull. Ecol. Soc. Am*. 78, 2: 128–139.

THORNHILL R., GANGESTAD S. W., 1994: Human Fluctuating Asymmetry and Sexual-Behavior. *Psychol. Sci*. 5, 5: 297–302.

TODOROV A., 2008: Evaluating faces on trustworthiness – An extension of systems for recognition of emotions signaling approach/avoidance behaviors. In: A. Kingstone, M. Miller

(Eds.): *The Year in Cognitive Neuroscience 2008*. Pp. 208–224. Ann. N. Y. Acad. Sci. 1124.

TOMASELLO M., HARE B., LEHMAN H., CALL J., 2007: Reliance on head versus eyes in the gaze following of great apes and human infants: the cooperative eye hypothesis. *J. Hum. Evol*. 52, 3: 314–320.

ZEBROWITZ L. A., 1997: *Reading the faces. Window to the soul?* Westview Press, Oxford.

ZEBROWITZ L. A., 2011: Ecological and social approaches to face perception. In: A. J. Calder, G. Rhodes, M. H. Johnson, J. V. Haxby (Eds.): *The Oxford handbook of face perception*. Pp. 31–50. Oxford University Press, New York.

ZEBROWITZ L. A., MONTEPARE J. M., 1992: Impressions of babyfaced individuals across the life span. *Dev. Psychol*. 28, 6: 1143–1152.

Tomáš Kočnar
Karel Kleisner
Department of Philosophy and History
of Science
Faculty of Science
Charles University in Prague
Viničná 7
128 44 Prague
Czech Republic
E-mail: tomas.kocnar@gmail.com
E-mail: kleisner@seznam.cz

Kateřina Radana Drbalová
Department of Biology
Faculty of Science
The University J. E. Purkyně
in Ústí nad Labem
Za Válcovnou 1000/8
400 96 Ústí nad Labem, Předlice
Czech Republic
E-mail: katerina.drbalova@ujep.cz

STUDY 3

Kočnar, T., Adil Saribay, S., & Kleisner, K. (2019). Perceived attractiveness of Czech faces across 10 cultures: Associations with sexual shape dimorphism, averageness, fluctuating asymmetry, and eye color. PLoS ONE, 14(11), 1–27.

Author's contribution:

TK contributed to the study design, collected and analysed the data, and drafted manuscript

RESEARCH ARTICLE

Perceived attractiveness of Czech faces across 10 cultures: Associations with sexual shape dimorphism, averageness, fluctuating asymmetry, and eye color

Tomáš Kočnar[1]*, S. Adil Saribay[2], Karel Kleisner[1]

1 Department of Philosophy and History of Science, Charles University in Prague, Prague, Czech Republic, **2** Department of Psychology, Boğaziçi University, Istanbul, Turkey

* tomas.kocnar@gmail.com

Citation: Kočnar T, Saribay SA, Kleisner K (2019) Perceived attractiveness of Czech faces across 10 cultures: Associations with sexual shape dimorphism, averageness, fluctuating asymmetry, and eye color. PLoS ONE 14(11): e0225549. https://doi.org/10.1371/journal.pone.0225549

Editor: Piotr Sorokowski, University of Wroclaw, POLAND

Received: June 25, 2019

Accepted: November 6, 2019

Published: November 21, 2019

Data Availability Statement: All relevant data are within the manuscript and its Supporting Information files.

Funding: The research was supported by the Czech Science Foundation project reg. no 18-10298S. The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Abstract

Research on the perception of faces typically assumes that there are some universal values of attractiveness which are shared across individuals and cultures. The perception of attractiveness may, however, vary across cultures due to local differences in both facial morphology and standards of beauty. To examine cross-cultural consensus in the ratings of attractiveness, we presented a set of 120 non-manipulated photographs of Czech faces to ten samples of raters from both European (Czech Republic, Estonia, Sweden, Romania, Turkey, Portugal) and non-European countries (Brazil, India, Cameroon, Namibia). We examined the relative contribution of three facial markers (sexual shape dimorphism, averageness, fluctuating asymmetry) to the perception of attractiveness as well as the possible influence of eye color, which is a locally specific trait. In general, we found that both male and female faces which were closer to the average and more feminine in shape were regarded as more attractive, while fluctuating asymmetry had no effect. Despite a high cross-cultural consensus on attractiveness standards, significant differences in the perception of attractiveness seem to be related to the level of socio-economic development (as measured by the Human Development Index, HDI). Attractiveness ratings by raters from low-HDI countries (India, Cameroon, Namibia) converged less with ratings from Czech Republic than ratings from high-HDI countries (European countries and Brazil). With respect to eye color, some local patterns emerged which we discuss as a consequence of negative frequency-dependent selection.

Introduction

In social interactions, human attention is rapidly and strongly oriented toward the rich and complex content of human faces. Mere exposure to a face, even one neutral in its expression, can provide information regarding the health condition, age, sex prototypicality, ethnicity, personality, dominance, prestige, trustworthiness, or attractiveness of its bearer [1–5].

Moreover, facial attractiveness conveys information regarding reproductive potential of prospective mating partners [3, 6, 7].

The evolutionary perspective of facial perception assumes that universally shared values of attractiveness exist across individuals and cultures [8, 9]. Because certain individual features such as coloration and symmetry convey valuable genetic information, they are perceived as attractive even in many non-human species [10, 11]. These concepts of attractiveness generally contrast with the maxim 'beauty is in the eye of the beholder' [7]. Nonetheless, people do not entirely agree in their assessments of facial attractiveness [12–14]. Agreement in the perception of attractiveness is greater within a single culture than between cultures [15, 16] and some studies have shown that the perception of attractiveness varies across cultures depending on the socio-cultural environment [13, 16–18].

Attractiveness assessments have an impact on an individual's reproductive success as well as other aspects of social interactions [9, 19, 20]. Facial attractiveness may serve as an indicator of actual health or overall phenotypic condition. The most commonly studied traits involved in judgements of facial attractiveness are sexual shape dimorphism, facial averageness, and symmetry [3, 7, 21]. Below, we briefly review evidence pertaining to these target traits as well as examine the influence of eye color on the perception of facial attractiveness.

Sexual shape dimorphism (SShD)

Sex-typical facial features are influenced by sex hormones and might thus affect the perception of masculinity, femininity, and also attractiveness. Whereas higher femininity in female faces, interpreted as a signal of fertility [22], is reported as responsible for higher ratings of attractiveness [15, 23–25], women's preference for masculinity in male faces exhibits a more complex pattern [6, 26]. Masculine facial traits are interpreted as a signal of phenotypic and genetic quality [7], but see [27]. Facial masculinity may further reflect the dominance and social status, which enhance individual's mate value [4, 28]. For long-term partnership, however, dominance and other personal characteristics connected with masculinity such as aggressiveness are seen as negative or undesirable [29]. In a specific context, more feminine male faces, on the other hand, are preferred as an honest signal of paternal investment [25]. Male facial masculinity is thus preferred only in some contexts or by some individuals, and reasons underlying such contextual and individual differences are not entirely clear.

Facial averageness

The 'average is attractive' hypothesis was introduced by Langlois and Roggman [30], who found that composite faces are more attractive than majority of the individual faces from which the composites were assembled. Even when controlling for a possible confounding effect of smoothness of skin and facial symmetry of composite faces, averageness still retains its influence on attractiveness [31, 32]. Faces closer to the population mean may be favored by stabilizing selection [30]. Indeed, both averageness [33] and attractiveness [34] positively correlate with heterozygosity in major histocompatibility complex genes responsible for immunocompetence. Moreover, averageness is positively related to health [35] and developmental stability [36]. From this point of view, more average faces reflect the health and greater genetic diversity of face bearers who in turn may be preferred in the mate market as attractive, healthy, and parasite-free individuals [3, 37]. Lee et al. [38] reported a genetic component of facial averageness and a significant phenotypic correlation between facial averageness and attractiveness. Facial averageness was not, however, genetically correlated with attractiveness, which contradicts the assumption that averageness reflects genetic quality [38]. Further challenging the 'average is attractive' hypothesis, other studies have shown that while average faces of both sexes are perceived as attractive, they are not viewed as the most attractive, that is, it seems that under certain conditions, the perception of attractiveness is independent of averageness [39, 40]. Previous studies have presented an alternative hypothesis, namely that average face is not attractive, and demonstrated that facial attractiveness can be enhanced by atypical characteristics that include a degree of juvenility and/or sex-typicality [41–44]. Nevertheless, it has also been demonstrated that averageness has a greater effect on the perception of attractiveness than juvenilization does [45].

Fluctuating asymmetry

Traits which are symmetrical at a population level can be described by their degree of fluctuating asymmetry (FA). It is believed that FA reflects developmental instability of an individual, and therefore also genetic and phenotypic conditions that could influence further reproduction [7]. In human faces, exposure to stress during ontogeny is expressed in higher levels of FA [46, 47]. High levels of FA have been linked to various somatic and mental disorders [11], low intelligence [48], and lower health assessment [49]. Studies which used both photographs of real faces and manipulated faces have shown a positive correlation between symmetry and rated attractiveness, e.g., [50]. Some other studies, however, found no such a correlation [51, 52]. Another study [53] found that FA was not an important factor in long-term mating preferences and some scholars believe that the evolutionary importance of FA in determining human attractiveness has been overstated [54]. The hypothesis, that FA honestly signals an individual's genetic quality, is also criticized based on the argument that many studies supporting this hypothesis used inappropriate statistical methodologies often resulting in overestimated effect sizes [55]. It should also be noted that experiments with manipulated faces may well have yielded varied outcomes largely due to the nature of artificial manipulation [3]. Further research with faces that naturally vary in terms of FA may therefore shed more light on whether and to what extent FA plays a role in attractiveness judgments.

Eye color

Independently of shape proportions, the coloration of human face is a trait that offers an entirely different type of variability. Whereas the influence of skin texture and color on attractiveness judgments is discussed elsewhere, e.g., [21, 56–58], in our study we focus on eye color, a feature variable mainly in European populations. Unlike the factors presented above, eye color does not seem to have any association with an individual's fitness [59]. Notwithstanding changes in the brightness of coloration caused by ageing and health condition, eye (as well as hair) color have been considered 'neutral features', unlikely to reflect mate quality [59]. According to Edwards et al. [60], iris coloration might be the result of pleiotropic effect associated with selection on pigmentation genes primarily engaged in determining skin or hair color, but not iris coloration. It has been hypothesized that not only natural selection but also sexual selection contributed to recent variations of skin, hair, and eye color [61–63]. A negative frequency-dependent selection in mate choice [64, 65] is a prerequisite for a model introduced by Frost [61, 62] which offers an explanation of the geographical distribution of various eye and hair colors. Frost [61, 62] assumes that 'rare-color advantage' of individuals with blue eyes and fair hair could have arisen only in special environmental conditions, a singularity among the many environments which modern humans entered while spreading out from Africa during the Paleolithic.

In comparison with studies on human hair color [65–70], relatively little attention has been paid to eye color's role in sexual selection. Along with hair color, eye color is a reliable predictor in assortative mating: with respect to these traits individuals prefer partners who resemble their opposite-sex parents [71–73]. Bovet et al. [59] found preferences for self-resembling mates in eye and hair color. In a Norwegian study, Laeng, Mathisen, and Johnsen [74] presented results which support the paternity assurance hypothesis [75]. In his study, blue-eyed men preferred blue-eyed women because such partners provided males greater assurance of recognizing their own offspring. Nevertheless, further evidence did not support this finding, because recessive features were not preferred by male raters in Finland [76], France [59] or among married couples in Slovakia [77]. Kleisner, Kočnar, Rubešová, and Flegr [78] found no relation between perceived attractiveness and eye color in a Czech sample, but revealed a relationship between eye color and facial morphology responsible for the perception of dominance [78] and trustworthiness [79]. Unlike hair color preferences [80, 81], cross-cultural evidence for eye color preferences is lacking.

Cross-cultural perspective

Cultural context that potentially influence the perception of facial attractiveness can be described in terms of environmental harshness, pathogen load, income inequality, visual experience, and cultural standards. Much of cross-cultural research assumes that mate preferences are shaped towards sex-typical facial characteristics, i.e. femininity in women and masculinity in men, and that this preference is especially strong in areas with limited resources and high pathogen prevalence (for a review, see [17]). Moore et al. [82] described a relationship between Human Developmental Index and women's preference for cues to testosterone in male faces, while other researchers reported that pathogen stress predicts regional differences in mate preferences [83–87]. These studies generally show that masculine features in male faces are preferred in regions with a high pathogen stress, harsh environment, or low levels of socio-economic development. In these environments, women appear to value masculinity as a cue for protective qualities and/or immunocompetence, which is of potential benefit to the offspring [88], but cf. [89]. Interestingly, male preference for feminine female faces is less pronounced in countries with harsher environment than in countries with better health conditions, and it has been hypothesized that this the result of strategies aimed at resource-holding potential rather than fecundity [86]. A study of Scott et al. [18], on the other hand, showed that both feminine female faces and masculine male faces were less favored in low-HDI than in high-HDI countries. They suggested that the novel environment of industrialized, high-HDI countries may modify attractiveness preferences due to the specific visual diet of their inhabitants. Nonetheless, a recent study by Dixson, Little, Dixson, and Brooks [90] found no support for the hypothesis that pronounced sex-typical facial traits are preferred either in areas with higher urbanization or in environments with a higher pathogen load.

Preference for facial symmetry was reported in harsher and more pathogenic environments [90]. Based on Hadza and European samples, Little, Apicella, and Marlowe [91] suggested that preferences for symmetry can be derived from different ecological conditions, whereby harsher environments lead to a higher preference of symmetry. Using samples of the same populations, Apicella, Little, and Marlowe [92] have also shown that preferences for facial averageness, though reported cross-culturally, are reinforced by visual experience with one's own population.

The present study

In summary, a considerable number of studies on face perception brought to light various evidence to the effect that sexual dimorphism, facial averageness, and symmetry influence human mating preferences and most likely have an adaptive value [3, 7, 9]. However, it has also been shown that attractiveness perception is modified by various internal factors, by perceivers' visual experience, and by the mating context [3, 93]. While emphasizing the environmental context and visual experience, in the present study we engage in a cross-cultural investigation of the relative importance of four facial characteristics–sexual dimorphism, averageness, fluctuating asymmetry, and eye color–for the perception of attractiveness. A set of Czech faces was rated for attractiveness by participants from the Czech Republic, and five other European and four non-European countries.

Based on previous studies, we hypothesize that for both sexes, raters from all populations would rate faces which are closer to the average and have a lower degree of fluctuating asymmetry as more attractive. Further, we hypothesize that possible differences in ratings between the populations should reflect differences in the socio-economic conditions (assessed as HDI) of the target countries. In other words, we expect that the closer the socio-economic environment of raters' population is to the environment of population of rated faces, i.e. Czech Republic, the greater should be the ratings' agreement with Czech raters. Based on existing literature, we also expect that symmetrical faces of both sexes and masculine male faces should be rated as more attractive rather in low-HDI than in high-HDI countries. In accordance with Marcinkowska et al. [86] and Scott et al. [18], we suppose that female facial femininity will be more appreciated in industrialized, high-HDI countries. We also assume that preferences for facial averageness will not be substantially affected by socio-economic development. And finally, according to the hypothesis of negative frequency-dependent selection, the ratio of eye color present in a particular population of raters should influence preferences in favor of a characteristic which represents a minority type in that population. We therefore hypothesize that blue-eyed individuals should be perceived as more attractive in populations with a relatively low frequency of blue eyes, and vice-versa, that brown-eyed individuals' eyes should be preferred in populations with a relatively low frequency of this phenotype.

Materials and methods

The research was approved by The Institutional Review Board of Charles University, Faculty of Science. Written informed consent was obtained from all participants involved in our study. The data were analyzed anonymously.

Acquisition of facial photographs

We used a sample of 120 facial photographs (en face portraits): 60 women (mean age ±SD = 20.6± 1.2, range: 18–24) and 60 men (mean age±SD = 21.2±2.5, range: 19–34), equally divided between those who have blue and brown color of irises. Individuals with intermediate eye color and those with green eyes were not included due to their ambiguous eye color and relative rareness of these eye colors in the Czech population.

All photographed participants were students of the Faculty of Science, Charles University in Prague, Czech Republic. Participants were asked in advance to refrain from any facial cosmetics and other face decorations. Photographs were taken using a digital camera Nikon D90 with a 50mm lens (full frame equivalent of 75 mm), studio flash, and a reflection screen. The subjects were seated in front of a white background, 1.5m from the camera, and instructed to adopt a neutral facial expression [94]. All photographs were standardized with respect to eye position and clothing of the photographed subjects was digitally cropped so that only a standard, minimal length of neck was visible.

The rating of photographs

The set of photographs was rated for attractiveness by volunteers, predominantly university students, in the Czech Republic, Estonia, Sweden, Romania, Turkey, Portugal, Brazil, India, Cameroon, and Namibia. In most cases, data were collected during the year 2014. The Czech participants were recruited from the Charles University in Prague, the Estonian ones from the University of Tartu and Tallinn University, Swedish ones from the Lund University, Romanian ones from the University of Bucharest and West University of Timişoara, Turkish from the Adıyaman University, Portuguese from the Catholic University of Portugal in Braga, Brazilian from the University of São Paulo, Cameroonian from the University of Buea, the Indian sample was drawn from the population of the Sivasagar district in Assam state, and the Namibian sample from suburban sites of the Tseiblaagte and Karasburg communities of the Karas region. For a detailed overview of the demographic characteristics of invited raters, see Fig 1.

Each person rated 60 photographs of faces of the opposite sex on a 7-point, verbally anchored scale, where the lowest number was labelled "very unattractive" and the highest number "very attractive" in the rater's native language. The sequence of photographs was randomized for each rating session. In countries where daily use of the internet is common, we recruited raters by email invitation and the study was administered online using Qualtrics. Indian, Cameroonian, and Namibian participants were invited personally to a local laboratory and the study was administered offline using the original ImageRater software developed for offline data acquisition. All participants were instructed to rate the photographs in a full screen mode. No time limit was imposed. The rating of all photographs assessed by each rater was converted to Z-scores to eliminate the influence of individual differences in scale use between raters, and perceived attractiveness was calculated for each photograph as its average Z-score across raters of the same sex from the same country.

Geometric morphometrics

We defined 72 landmarks on each portrait photograph so as to capture the variation in facial shape. To make the description of facial morphology sensitive to curves and locations between true landmarks, we specified 36 sliding landmarks (semilandmarks) from the total of 72 landmarks on each photograph (for definitions of landmark and semilandmark locations on the human face, see [95]). The whole set of faces were landmarked twice to capture information about measurement error for purposes of fluctuating asymmetry quantification. All configurations of landmarks and semilandmarks were superimposed by Generalized Procrustes Analysis (GPA) using the gpagen function included in the geomorph package in R [96]. Positions of semilandmarks were optimized along the tangent directions of facial curves based on minimizing Procrustes distances. Facial averageness was computed as the Procrustes distance between the consensus and each configuration in the set. As a result, the shorter the distance of a face from consensus, the more average the face, whereby lower values indicate higher levels of averageness.

		Men				Women			
			Age				Age		
Country	HDI	n	Mean±SD	Range	Cronbach's α	n	Mean±SD	Range	Cronbach's α
Czech Republic	0.87	32	21.72±2.76	19–31	0.93	80	20.36±1.70	19–27	0.96
Estonia	0.86	25	32.44±8.84	20–62	0.91	61	25.61±6.79	16–49	0.96
Sweden	0.91	43	30.33±11.25	20–69	0.97	43	28.14±11.44	19–65	0.94
Romania	0.79	34	30.68±7.19	18–45	0.93	41	27.62±9.68	18–51	0.91
Turkey	0.76	33	28.36±7.11	18–51	0.91	23	26.43±7.38	16–42	0.68
Portugal	0.83	17	26.82±8.13	19–52	0.90	68	23.91±6.69	17–45	0.94
Brazil	0.76	20	26.25±5.16	20–39	0.92	28	25.11±4.74	18–41	0.86
India	0.61	31	27.32±5.03	20–41	0.98	27	24.33±4.50	17–34	0.94
Cameroon	0.51	51	23.71±5.42	18–44	0.95	51	25.04±8.30	17–54	0.93
Namibia	0.63	29	22.34±4.36	18–36	0.87	25	21.28±3.93	18–30	0.79

Fig 1. A List of raters according to their country of origin, age distribution, and inter-rater agreement (Cronbach's α). HDI = Human Development Index.

https://doi.org/10.1371/journal.pone.0225549.g001

To numerically express the degree of individual expression of facial traits responsible for sexual shape dimorphism, we first pooled the shape coordinates for male and female facial configurations and ran a GPA analysis on these joined male and female coordinates. Then we calculated the position of each individual facial shape along the axis of male–female mean shapes by projecting individual faces onto a vector connecting the male and female consensus [97].

We calculated scores of fluctuating asymmetry using Procrustes ANOVA within MorphoJ, version 1.06d. Facial coordinates of the original and mirrored landmark coordinates (reflected along vertical axis and relabeled) were used as the dependent variable [98, 99]. Independent variables include the main effect of "individuals" (variation among individuals corrected for any effect of asymmetry), the main effect of sides that corresponds to the average difference between the left and right side of the face (directional symmetry), and interaction term of these main effects. Fluctuating asymmetry is quantified as an interaction between the main effects of "individuals" and "sides". Measurement error was assessed from variations between replicate measurements [100]. Higher FA scores indicate higher facial fluctuating asymmetry.

Human development index

To approximate cultural differences between the populations of raters, we used the Human Development Index as an appropriate characteristic of each of these populations [18, 82]. HDI scores were extracted from United Nations Development Programme webpage [101], whereby HDI is used to categorize countries by their standard of living as a composite score from 0 to 1 (1 = highest standard of living) calculated from measures of longevity, education, and income.

Eye color distribution

To compare possible eye color preferences between the populations involved in our study, we first had to establish the relative representation of eye colors in each target population. Since literature on eye color distribution either does not cover the populations we used in our study [102] or is outdated (see the maps based on old and ambiguous data in [103], or [61]), we asked the participants to self-report their own eye color. The data were compiled from a broader set of questionnaires that was based on a larger number of participants than those who participated in the current research. To approximate the eye color distribution in each population, participants were asked to select the category which best corresponds to their own eye color: black-brown, green, grey-blue, or other (see the structure of data in Table 1). Estimated variation is in line with both existing older sources [61, 104] and the European Eye Study [105], which indicates a gradual increase in the frequency of blue-eyed individuals and decrease in those with brown eyes from southern to northern Europe [102].

Statistics

To assess inter-rater reliability, we computed Cronbach's alpha for each population. Pearson product-moment correlation coefficient was used to explore relationships between all variables. Using Multiple Linear Regression implemented in SPSS 21, we ran 10 separate analyses per sex of the rated faces, one for each population, whereby the mean Z-score of rated attractiveness was used as the dependent variable and measured averageness, SShD, FA, age, and eye color of targets as the predictors. Ratings from the Czech Republic were used as a standard for attractiveness of Czech faces. Pearson's correlations between attractiveness ratings from the Czech Republic (i.e., the country of origin of individuals whose photographs were rated) and ratings obtained in the other target countries were used for a subsequent Kendall correlation with HDI.

Table 1. Proportional eye color distribution among raters (%).

Country	n	Black–Brown	Green	Grey–Blue	Other[a]
Czech Republic	377	38.5	22.0	39.5	—
Men	277	33.0	21.0	46.0	—
Women	100	40.4	22.4	37.2	—
Estonia	282	14.5	21.3	56.0	8.2
Men	186	19.8	10.4	60.4	9.4
Women	96	11.8	26.9	53.8	7.5
Sweden	134	19.4	12.7	50.0	17.9
Men	73	16.4	13.1	50.8	19.7
Women	61	21.9	12.3	49.3	16.4
Romania	185	58.9	21.1	20.0	—
Men	108	57.1	22.1	20.8	—
Women	77	60.2	20.4	19.4	—
Turkey	127	85.0	11.0	3.9	—
Men	57	87.1	11.4	1.4	—
Women	70	82.5	10.5	7.0	—
Portugal	85	84.7	10.6	4.7	—
Men	68	64.7	29.4	5.9	—
Women	17	89.7	5.9	4.4	—
Brazil	48	75.0	16.7	8.3	—
Men	28	70.0	25.0	5.0	—
Women	20	78.6	10.7	10.7	—
India	79	97.5	1.3	1.3	—
Men	37	97.6	0	2.4	—
Women	42	97.3	2.7	0	—
Cameroon	201	100	0	0	—
Men	100	100	0	0	—
Women	101	100	0	0	—
Namibia	54	100	0	0	—
Men	29	100	0	0	—
Women	25	100	0	0	—

Absolute numbers of raters were obtained also from other questionnaires.

[a] The category "other" was included only in questionnaires for Estonian and Swedish raters.

https://doi.org/10.1371/journal.pone.0225549.t001

Additionally, we ran complementary analysis on the level of individual ratings with linear mixed-effect models using the "lmer" function within the "lmerTest" R package [106]. Attractiveness ratings were specified as a response variable and age, averageness, FA, SShD, eye color, and HDI as the independent variables. Rater and participant (face) identities were used as random intercepts. The separate models were built for men and women.

Results

Cronbach's alpha was high for most groups of raters (αs > 0.90). Lower values were recorded for male raters from Namibia (α = 0.87), female raters from Turkey (α = 0.68), and for Brazilian (α = 0.86) and Namibian raters (α = 0.79). For more details, see Fig 1. Descriptive values of all variables as well as Pearson's correlations between rated attractiveness and physical measurements are listed in Fig 2. Correlation values between countries were obtained from correlations between the average attractiveness score given to individual photographs in one target country and the same score from another target country. Attractiveness ratings both for male and female photographs were relatively constant across all populations. See an overview of all correlations in Fig 2.

Factors related to perception of attractiveness

To examine the contribution of facial characteristics to attractiveness ratings, we built a linear model with perceived attractiveness as the dependent variable and physical measurements as multiple predictors (see Table 2). Faces closer to the average, both male and female, tended to be regarded as more attractive in a majority of the sampled populations; a significant finding in 6 out of 10 cultures. A similar pattern based on sexual shape dimorphism indicated a relationship between attractiveness and facial femininity: more feminine female faces were rated as more attractive by respective opposite-sex raters. This was a significant finding in all cultures except India. In majority of high-HDI countries, namely in Estonia, Sweden, Romania, Turkey, and Portugal, female raters preferred also more feminine faces in men. In some cultures, attractiveness ratings were also influenced by targets' age, whereby younger female faces were perceived as more attractive. This was a significant finding in the Czech Republic, Estonia, Portugal, and Brazil. In Cameroon, Namibia, and India, neither facial averageness nor age significantly influenced the attractiveness ratings of female photographs. Indian raters of both sexes seem exceptional in the sense that their attractiveness ratings did not reveal any significant importance of averageness, age, or even SShD. Further, we found no effect of fluctuating asymmetry on attractiveness ratings in any of the rater populations.

The eye color of targets had a limited impact on attractiveness ratings. Blue-eyed men were perceived as more attractive than brown-eyed men by female Portuguese raters ($r = -0.36$, $n = 60$, $p < 0.01$, 95% CI [-0.60, 0.08]). Blue-eyed women were significantly preferred as more attractive by male Turkish raters ($r = -0.35$, $n = 60$, $p < 0.01$, 95% CI [-0.54, -0.10]).

Cross-cultural agreement in the perception of attractiveness

To explain the pattern of correlations among different countries, we examined the relationship between HDI and facial attractiveness. We computed Kendall correlations between the HDI

M (n = 60)	CZE	EST	SWE	ROU	TUR	PRT	BRA	IND	CMR	NAM	Averag.	FA	SShD	Age	EC
Mean±SD	2.72±0.47	2.72±0.61	2.31±0.52	1.96±0.47	1.83±0.35	1.83±0.37	3.48±0.78	3.14±0.65	3.40±0.63	3.47±0.68	0.06±0.01	0.02±0.00	-0.02±0.02	21.17±2.52	—
CZE	—	0.94**	0.87**	0.79**	0.69**	0.82**	0.83**	0.28*	0.54**	0.47**	-0.25	0.12	0.25*	-0.07	-0.12
EST	[0.89, 0.96]	—	0.90**	0.80**	0.71**	0.84**	0.85**	0.26*	0.49**	0.46**	-0.27*	0.13	0.29*	-0.04	-0.19
SWE	[0.80, 0.91]	[0.84, 0.94]	—	0.81**	0.67**	0.79**	0.81**	0.23	0.52**	0.54**	-0.27*	0.18	0.27*	-0.12	0
ROU	[0.61, 0.90]	[0.65, 0.89]	[0.68, 0.90]	—	0.74**	0.76**	0.80**	0.34**	0.58**	0.48**	-0.14	0.12	0.32*	0.01	-0.07
TUR	[0.50, 0.82]	[0.55, 0.82]	[0.50, 0.81]	[0.57, 0.86]	—	0.77**	0.75**	0.48**	0.70**	0.58**	-0.21	0.05	0.33*	-0.02	-0.1
PRT	[0.69, 0.90]	[0.72, 0.92]	[0.64, 0.90]	[0.59, 0.87]	[0.61, 0.88]	—	0.82**	0.27*	0.46**	0.42**	-0.2	0.05	0.38**	-0.02	-0.36**
BRA	[0.73, 0.89]	[0.76, 0.90]	[0.69, 0.88]	[0.67, 0.89]	[0.62, 0.54]	[0.71, 0.90]	—	0.41**	0.58**	0.59**	-0.30*	0.1	0.25*	0	-0.24
IND	[0.08, 0.50]	[0.05, 0.46]	[0.04, 0.42]	[0.15, 0.54]	[0.27, 0.66]	[0.06, 0.49]	[0.20, 0.59]	—	0.61**	0.38**	-0.17	0.12	0.07	0	-0.04
CMR	[0.33, 0.72]	[0.27, 0.67]	[0.30, 0.69]	[0.38, 0.73]	[0.54, 0.82]	[0.21, 0.66]	[0.36, 0.76]	[0.44, 0.74]	—	0.71**	-0.24	-0.08	0.16	-0.09	0.04
NAM	[0.25, 0.67]	[0.25, 0.67]	[0.33, 0.72]	[0.33, 0.63]	[0.42, 0.74]	[0.22, 0.64]	[0.42, 0.75]	[0.18, 0.57]	[0.56, 0.82]	—	-0.28*	-0.09	0.19	-0.17	0.1
Averag.	[-0.45, 0.02]	[-0.47, -0.05]	[-0.49, -0,03]	[-0.38, 0.12]	[-0.44, 0.02]	[-0.41, 0.02]	[-0.54, -0.08]	[-0.40, 0.08]	[-0.48, 0.03]	[-0.52, -0.04]	—	-0.03	0.06	0.05	-0.12
FA	[-0.11, 0.34]	[-0.12, 0.36]	[-0.01, 0.37]	[-0.12, 0.34]	[-0.20, 0.31]	[-0.17, 0.28]	[-0.16, 0.32]	[-0.13, 0.36]	[-0.30, 0.15]	[-0.28, 0.08]	[-0.24, 0.21]	—	0.04	0.02	0.01
SShD	[0.04, 0.47]	[0.08, 0.48]	[0.06, 0.47]	[0.13, 0.51]	[0.13, 0.50]	[0.21, 0.52]	[0.02, 0.46]	[-0.19, 0.31]	[-0.10, 0.40]	[-0.04, 0.41]	[-0.33, 0.45]	[-0.23, 0.29]	—	0.03	-0.27*
Age	[-0.33, 0.28]	[-0.32, 0.31]	[-0.30, 0.13]	[-0.22, 0.31]	[-0.21, 0.25]	[-0.22, 0.25]	[-0.25, 0.33]	[-0.22, 0.27]	[-0.33, 0.21]	[-0.35, 0.06]	[-0.15, 0.24]	[-0.21, 0.27]	[-0.16, 0.23]	—	-0.30*
EC	[-0.37, 0.14]	[-0.45, 0.08]	[-0.26, 0.26]	[-0.32, 0.19]	[-0.34, 0.17]	[-0.60, 0.08]	[-0.48, 0.02]	[-0.28, 0.22]	[-0.22, 0.30]	[-0.18, 0.35]	[-0.38, 0.16]	[-0.26, 0.26]	[-0.47, -0.02]	[-0.49, -0.09]	—
W (n = 60)	CZE	EST	SWE	ROU	TUR	PRT	BRA	IND	CMR	NAM	Averag.	FA	SShD	Age	EC
Mean±SD	2.81±0.67	3.10±0.65	2.62±0.69	2.67±0.69	2.51±0.67	2.46±0.69	4.09±1.17	3.33±0.97	3.27±0.66	4.09±0.68	0.05±0.01	0.02±0.00	0.02±0.01	20.60±1.16	—
CZE	—	0.91**	0.90**	0.65**	0.87**	0.93**	0.91**	0.64**	0.68**	0.70**	-0.25	0.09	0.39**	-0.29*'	-0.07
EST	[0.85, 0.95]	—	0.90**	0.67**	0.82**	0.87**	0.88**	0.60**	0.65**	0.71**	-0.2	-0.01	0.37**	-0.26*	-0.01
SWE	[0.85, 0.94]	[0.84, 0.95]	—	0.69**	0.86**	0.89**	0.93**	0.57**	0.62**	0.64**	-0.30*	0.02	0.37**	-0.25*	-0.17
ROU	[0.46, 0.80]	[0.48, 0.80]	[0.52, 0.84]	—	0.60**	0.71**	0.67**	0.36**	0.51**	0.58**	-0.25	-0.1	0.44**	-0.11	-0.05
TUR	[0.81, 0.92]	[0.72, 0.89]	[0.77, 0.93]	[0.42, 0.77]	—	0.91**	0.91**	0.59**	0.59**	0.61**	-0.2	-0.01	0.45**	-0.2	-0.35**
PRT	[0.88, 0.96]	[0.79, 0.92]	[0.83, 0.93]	[0.57, 0.83]	[0.85, 0.95]	—	0.92**	0.61**	0.66**	0.72**	-0.25	0.08	0.45**	-0.27*	-0.24
BRA	[0.86, 0.94]	[0.81, 0.93]	[0.89, 0.96]	[0.49, 0.82]	[0.85, 0.95]	[0.86, 0.96]	—	0.64**	0.62**	0.62**	-0.26*	0.02	0.37**	-0.30*	-0.19
IND	[0.47, 0.77]	[0.41, 0.76]	[0.37, 0.74]	[0.13, 0.62]	[0.42, 0.75]	[0.43, 0.76]	[0.46, 0.80]	—	0.59**	0.49**	-0.09	0.02	0.19	-0.15	0.05
CMR	[0.52, 0.80]	[0.49, 0.77]	[0.47, 0.75]	[0.34, 0.67]	[0.42, 0.73]	[0.50, 0.79]	[0.45, 0.76]	[0.43, 0.74]	—	0.80**	-0.09	-0.05	0.28*	-0.24	0.16
NAM	[0.56, 0.82]	[0.59, 0.80]	[0.51, 0.75]	[0.40, 0.72]	[0.46, 0.74]	[0.60, 0.82]	[0.47, 0.75]	[0.33, 0.65]	[0.66, 0.90]	—	-0.06	-0.14	0.39**	-0.2	0.04
Averag.	[-0.49, 0.01]	[-0.45, 0.09]	[-0.52, -0.05]	[-0.47, 0.00]	[-0.42, 0.05]	[-0.48, 0.00]	[-0.49, 0.01]	[-0.34, 0.17]	[-0.41, 0.19]	[-0.34, 0.20]	—	0.06	0.08	0.1	0.21
FA	[-0.14, 0.32]	[-0.24, 0.23]	[-0.20, 0.24]	[-0.33, 0.14]	[-0.25, 0.24]	[-0.17, 0.29]	[-0.21, 0.23]	[-0.23, 0.27]	[-0.27, 0.17]	[-0.36, 0.11]	[-0.19, 0.31]	—	-0.11	-0.16	0.13
SShD	[0.16, 0.58]	[0.19, 0.56]	[0.16, 0.56]	[0.25, 0.62]	[0.24, 0.64]	[0.23, 0.65]	[0.13, 0.58]	[-0.06, 0.45]	[0.02, 0.51]	[0.14, 0.57]	[-0.24, 0.38]	[-0.37, 0.17]	—	-0.03	-0.08
Age	[-0.46, 0.09]	[-0.43, -0.05]	[-0.42, -0.08]	[-0.33, 0.11]	[-0.38, 0.00]	[-0.44, -0.07]	[-0.46, -0.11]	[-0.39, 0.11]	[-0.50, 0.07]	[-0.42, 0.06]	[-0.20, 0.38]	[-0.39, 0.13]	[-0.25, 0.24]	—	-0.14
EC	[-0.32, 0.21]	[-0.25, 0.30]	[-0.41, 0.11]	[-0.28, 0.20]	[-0.54, -0.10]	[-0.45, 0.03]	[-0.42, 0.10]	[-0.21, 0.33]	[-0.10, 0.40]	[-0.23, 0.28]	[-0.05, 0.43]	[-0.14, 0.37]	[-0.31, 0.17]	[-0.41, 0.10]	—

Fig 2. Pearson's correlations between perceived attractiveness judged by opposite-sex raters and physical traits. Confidence intervals are displayed in lower part (CI level = 95%). M = male photos; W = female photos; CZE = Czech Republic; EST = Estonia; SWE = Sweden; ROU = Romania; TUR = Turkey; PRT = Portugal; BRA = Brazil; IND = India; CMR = Cameroon; NAM = Namibia; Averag. = Averageness; FA = Fluctuating Asymmetry; SShD = Sexual Shape Dimorphism; EC = Eye color; Significance levels: * $p < 0.05$; ** $p < 0.01$.

https://doi.org/10.1371/journal.pone.0225549.g002

Table 2. Relationship between rated attractiveness and variables measured by multiple regression.

	Men					Women				
Predictors per country	**Full model**	**B**	**SE**	**t-value**	**p-value**	**Full model**	**B**	**SE**	**t-value**	**p-value**
Czech Republic	F = 2.071					F = 4.658				
	p = 0.083					p = **0.001**				
	R^2 = 0.161					R^2 = 0.301				
Averageness		-11.351	5.307	-2.139	**0.037**		-15.911	7.195	-2.211	**0.031**
SShD		8.070	4.419	1.826	0.073		19.220	5.436	3.536	**0.001**
FA		11.443	13.136	0.871	0.388		14.042	14.649	0.959	0.342
Age		-0.021	0.027	-0.760	0.450		-0.119	0.060	-1.989	0.052
Eye Color		-0.122	0.143	-0.855	0.396		-0.035	0.140	-0.247	0.806
Estonia	F = 2.808					F = 4.415				
	p = **0.025**					p = **0.002**				
	R^2 = 0.206					R^2 = 0.290				
Averageness		-12.978	5.340	-2.430	**0.018**		-14.969	7.882	-1.899	0.063
SShD		8.999	4.447	2.024	**0.048**		19.783	5.955	3.322	**0.002**
FA		12.421	12.220	0.940	0.352		4.961	16.047	0.309	0.758
Age		-0.020	0.027	-0.718	0.476		-0.159	0.066	-2.423	**0.019**
Eye Color		-0.199	0.144	-1.377	0.174		0.089	0.154	0.580	0.564
Sweden	F = 2.534					F = 4.729				
	p = **0.039**					p = **0.001**				
	R^2 = 0.190					R^2 = 0.305				
Averageness		-11.906	5.420	-2.197	**0.032**		-18.923	7.917	-2.390	**0.020**
SShD		10.037	4.513	2.224	**0.030**		19.909	5.981	3.329	**0.002**
FA		17.767	13.416	1.324	0.191		7.842	16.118	0.487	0.629
Age		-0.024	0.028	-0.874	0.386		-0.126	0.066	-1.905	0.062
Eye Color		0.015	0.146	0.100	0.921		-0.158	0.154	-1.025	0.310
Romania	F = 1.752					F = 4.314				
	p = 0.139					p = **0.002**				
	R^2 = 0.140					R^2 = 0.282				
Averageness		-5.933	4.840	-1.226	0.226		-5.201	2.182	-2.383	**0.021**
SShD		9.977	4.031	2.475	**0.016**		6.517	1.649	3.953	**<0.001**
FA		9.962	11.982	0.831	0.409		-1.699	4.443	-0.382	0.704
Age		0.000	0.025	0.015	0.988		-0.010	0.018	-0.553	0.582
Eye Color		-0.002	0.131	-0.017	0.987		0.014	0.043	0.317	0.752
Turkey	F = 2.090					F = 6.724				
	p = 0.081					p < **0.001**				
	R^2 = 0.162					R^2 = 0.384				
Averageness		-6.521	3.591	-1.816	0.075		-8.511	6.355	-1.339	0.186
SShD		7.621	2.991	2.548	**0.014**		19.271	4.801	4.014	**<0.001**
FA		2.032	8.891	0.229	0.820		6.353	12.938	0.491	0.625
Age		-0.005	0.018	-0.280	0.781		-0.102	0.053	-1.936	0.058
Eye Color		-0.031	0.097	-0.321	0.749		-0.362	0.124	-2.919	**0.005**
Portugal	F = 4.349					F = 6.782				
	p = **0.002**					p < **0.001**				
	R^2 = 0.287					R^2 = 0.386				
Averageness		-9.462	4.398	-2.151	**0.036**		-15.252	7.393	-2.063	**0.044**
SShD		9.168	3.663	2.503	**0.015**		23.481	5.585	4.204	**<0.001**
FA		3.566	10.887	0.327	0.745		17.974	15.052	1.194	0.238
Age		-0.022	0.023	-0.998	0.323		-0.135	0.062	-2.195	**0.033**

(*Continued*)

Table 2. (Continued)

	Men					Women				
Predictors per country	Full model	B	SE	t-value	p-value	Full model	B	SE	t-value	p-value
Eye Color		-0.321	0.119	-2.700	**0.009**		-0.268	0.144	-1.856	0.069
Brazil	F = 3.064					F = 4.857				
	p = **0.017**					p = **0.001**				
	R^2 = 0.221					R^2 = 0.310				
Averageness		-11.969	4.292	-2.789	**0.007**		-16.109	8.122	-1.983	0.052
SShD		5.873	3.574	1.643	0.106		19.832	6.136	3.232	**0.002**
FA		6.707	10.624	0.631	0.531		7.275	16.537	0.440	0.662
Age		-0.011	0.022	-0.509	0.613		-0.161	0.068	-2.382	**0.021**
Eye Color		-0.218	0.116	-1.882	0.065		-0.209	0.158	-1.319	0.193
India	F = 0.590					F = 0.808				
	p = 0.708					p = 0.549				
	R^2 = 0.052					R^2 = 0.070				
Averageness		-9.620	7.179	-1.340	0.186		-8.820	11.291	-0.781	0.438
SShD		2.806	5.979	0.469	0.641		12.769	8.531	1.497	0.140
FA		15.626	17.772	0.879	0.383		3.525	22.989	0.153	0.879
Age		-0.002	0.037	-0.048	0.962		-0.086	0.094	-0.910	0.367
Eye Color		-0.061	0.194	-0.313	0.756		0.111	0.220	0.503	0.617
Cameroon	F = 1.269					F = 2.309				
	p = 0.291					p = 0.057				
	R^2 = 0.105					R^2 = 0.176				
Averageness		-8.475	4.483	-1.890	0.064		-7.589	7.352	-1.032	0.307
SShD		5.420	3.734	1.452	0.152		12.908	5.554	2.324	**0.024**
FA		-7.986	11.098	-0.720	0.475		-8.310	14.962	-0.555	0.581
Age		-0.011	0.023	-0.500	0.619		-0.095	0.061	-1.553	0.126
Eye Color		0.035	0.121	0.289	0.773		0.215	0.143	1.497	0.140
Namibia	F = 2.212					F = 2.833				
	p = 0.066					p = **0.024**				
	R^2 = 0.170					R^2 = 0.208				
Averageness		-9.700	4.287	-2.263	**0.028**		-3.949	6.167	-0.640	0.525
SShD		6.800	3.578	1.905	0.062		14.288	4.659	3.067	**0.003**
FA		-8.935	10.613	-0.842	0.404		-13.360	12.557	-1.064	0.292
Age		-0.023	0.022	-1.029	0.308		-0.077	0.051	-1.492	0.142
Eye Color		0.082	0.116	0.713	0.479		0.069	0.120	0.575	0.568

Results which reached the level of significance ($p<0.05$) are in boldface. Correlation of perceived attractiveness with SShD of women perceived by Czech, Estonian, Swedish, Romanian, Turkish, Portuguese, Brazilian, and Namibian male raters, and correlation with eye color of women perceived by Turkish male raters remained statistically significant ($p<0.05$) after Bonferroni correction. SShD = Sexual Shape Dimorphism; FA = Fluctuating Asymmetry.

https://doi.org/10.1371/journal.pone.0225549.t002

and values of bivariate correlations between the Czech ratings and ratings of each target country. Fig 3 shows a significant relationship for male faces ($\tau = 0.67$, n = 9, p = 0.01, 95% CI [0.25, 1]), but not female ones ($\tau = 0.44$, n = 9, p = 0.10, 95% CI [-0.10, 0.86]). Graphs for both sexes, however, indicate that participants in low-HDI countries disagree with Czech raters more, whereas European and Brazilian participants, i.e. raters from countries with HDI scores closer to the Czech Republic (HDI = 0.87), do converge with the Czech ratings. Only Romanian male raters are an exception: their ratings were in a relatively low agreement with Czech raters (r = 0.68, n = 60, p < 0.01, 95% CI [0.46, 0.80]).

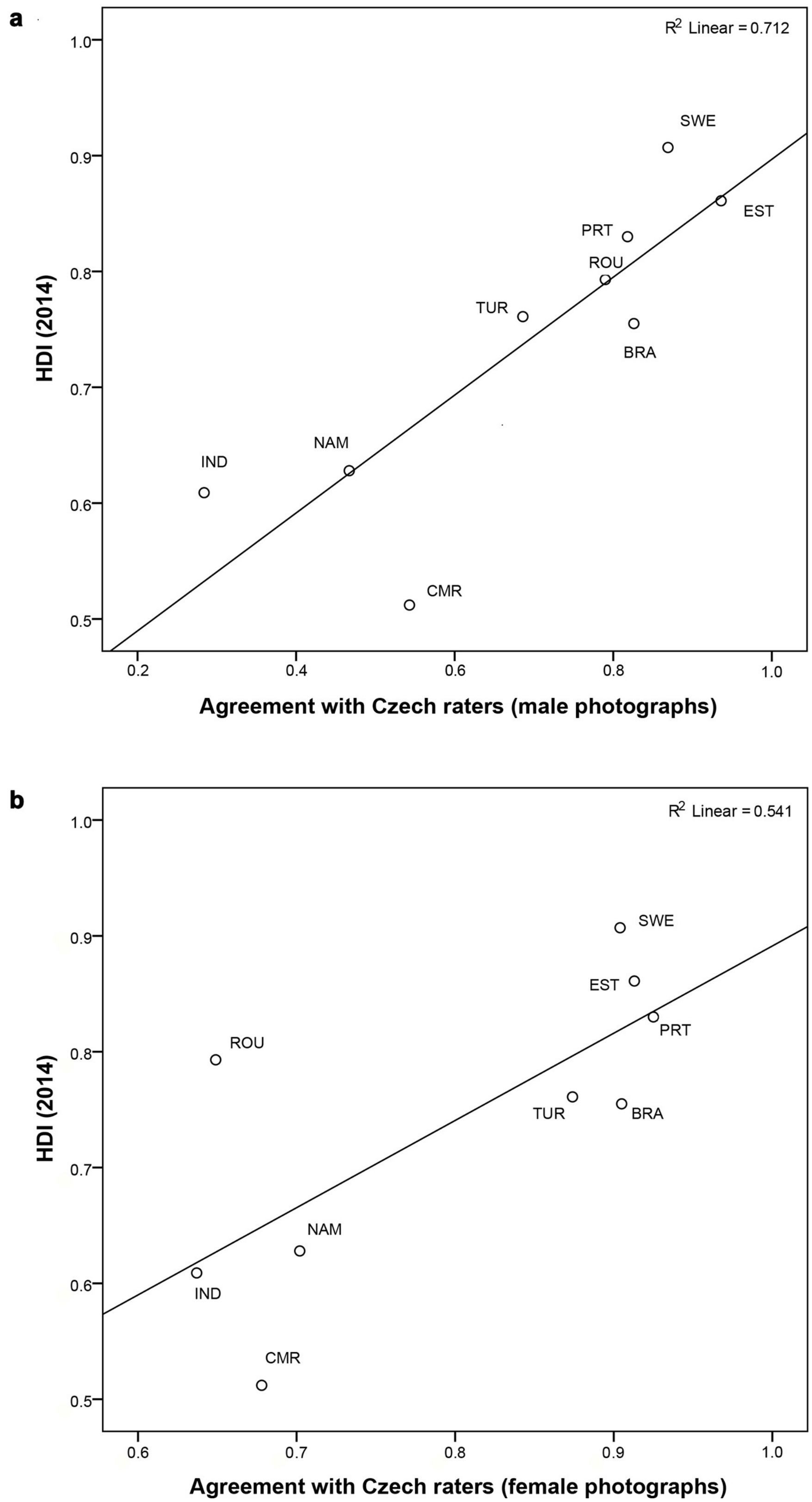

Fig 3. Relationship between the Human Development Index (HDI) and Agreement with Czech Raters. Using Kendall correlation, we identified a significant relationship for (a) male ($\tau = 0.67$, $n = 9$, $p = 0.01$, 95% CI [0.25, 1]) but

not (b) female faces (τ = 0.44, n = 9, p = 0.10, 95% CI [-0.10, 0.86]). On x-axis, agreement with Czech raters is expressed by values of bivariate correlations between Czech ratings and ratings of each target country.

https://doi.org/10.1371/journal.pone.0225549.g003

Linear mixed-effect modelling corroborated the general pattern of results from regression analyses based on averages of attractiveness ratings. Detailed results for mixed-effect models are summarized in Table 3.

Discussion

In our study, we offer further support for the hypothesis that although certain features of the human face are perceived as attractive across cultures, this perception is variable. Our findings indicate that this variability is related to environmental and socio-cultural factors. We found significant correlations between two facial shape traits–sexual shape dimorphism and averageness–and perceived attractiveness. With respect to the third examined trait, fluctuating asymmetry, we found no relation to rated attractiveness in any of the target populations. We also found that eye color seems to be a culture-specific cue to the perception of attractiveness. Findings for each of these facial traits are discussed below.

Sexual shape dimorphism

More feminine female faces were perceived as more attractive in all populations except for India. In men, facial attractiveness was also influenced by sex-typicality in favor of feminized rather than masculinized faces. Note, however, that this was a significant effect only in Sweden, Estonia, Romania, Turkey, and Portugal. This indicates that the perception of an attractive face is influenced more by sex-typical traits than by averageness. Using a sample of non-manipulated faces, we have demonstrated a cross-cultural validity of findings of Perrett et al. [25] who reported agreement in preference for feminized female faces in both Japanese and European perceivers. Unlike in Perrett et al. [25], our results do not run counter the averageness hypothesis but rather show that female attractiveness is driven by both sex-typicality and averageness. Nevertheless, feminized rather than average faces in women were preferred in a larger group of countries (see results for Turkey, Brazil, and Namibia).

None of the cultures we studied exhibited a preference for masculinized male faces. Quite the contrary, feminized male faces were preferred by women in most European populations. Equivocal role of sexual dimorphism in male facial attractiveness has been interpreted as a consequence of female tradeoff strategies [25, 83, 107]. Preferences for feminized facial shapes in men may be motivated by prospective partner's characteristics such paternal skills, cooperativeness, and trustworthiness [25]. These characteristics may compensate for preference for those masculine facial traits which are believed to be cues to dominance [108], or aggressiveness and competitiveness [109], in short, for traits associated with ease of access to resources and ability to protect mate and offspring [110]. It has been also shown that women who control their own resources may prefer men who are 'helpers in the nest' over masculine men who promise the benefit of good genes [111]. One limitation of our study is that we did not ask our raters about their relationship status, because this factor might further modulate the effects of environmental conditions on women's preferences for facial masculinity as reported in Lyons, Marcinkowska, Moisey, and Harrison [112]. (See also further discussion on preferences for SShD from a cross-cultural perspective below.)

Alternatively, absence of preference for masculinity in male faces could be examined from the perspective of conflicting preferences for relatively feminine shape but relatively masculine skin color. This model was theoretically proposed by Said and Todorov [40] and

Table 3. Summary of the results of linear mixed-effects modeling.

Men	Random effects	Variance	SD		
	Rater's identity	0.563	0.751		
	Face's identity	0.177	0.420		
	Fixed effects	**Estimate**	**SE**	**t-value**	**p-value**
	Intercept	3.898	0.658	5.923	<0.001***
	Averageness	-11.096	4.443	-2.498	0.016*
	SShD	8.384	3.700	2.266	0.028*
	FA	8.072	10.997	0.734	0.466
	Age	-0.017	0.023	-0.744	0.460
	Eye Color	-0.110	0.120	-0.919	0.362
	Estonia	-0.057	0.130	-0.443	0.658
	Sweden	-0.470	0.144	-3.260	0.001**
	Romania	-0.821	0.145	-5.653	<0.001***
	Turkey	-0.947	0.180	-5.249	<0.001***
	Portugal	-0.954	0.126	-7.584	<0.001***
	Brazil	-0.129	0.167	-0.773	0.440
	India	0.362	0.170	2.130	0.034*
	Cameroon	0.618	0.137	4.522	<0.001***
	Namibia	0.689	0.175	3.942	<0.001***
Women	**Random effects**	**Variance**	**SD**		
	Rater's identity	0.788	0.888		
	Face's identity	0.308	0.555		
	Fixed effects	**Estimate**	**SE**	**t-value**	**p-value**
	Intercept	5.748	1.444	3.981	<0.001***
	Averageness	-14.928	7.739	-1.929	0.059
	SShD	20.135	5.847	3.444	0.001**
	FA	3.949	15.756	0.251	0.803
	Age	-0.121	0.064	-1.885	0.065
	Eye Color	-0.039	0.151	-0.260	0.796
	Estonia	0.292	0.240	1.217	0.225
	Sweden	-0.189	0.210	-0.902	0.368
	Romania	-0.144	0.221	-0.649	0.517
	Turkey	-0.299	0.223	-1.340	0.181
	Portugal	-0.350	0.270	-1.298	0.195
	Brazil	0.250	0.256	0.976	0.330
	India	0.519	0.226	2.291	0.023*
	Cameroon	0.465	0.203	2.294	0.022*
	Namibia	1.279	0.230	5.554	<0.001***

SShD = Sexual Shape Dimorphism; FA = Fluctuating Asymmetry

Significance levels

*p <0.05

**p<0.01

***p<0.001

https://doi.org/10.1371/journal.pone.0225549.t003

experimentally tested using composite faces by Carrito et al. [113], who found a preference for feminine-shaped European male faces and a preference for masculinization in the color component relative to the shape component of male faces. We did not examine the perception of skin coloration in our study and due to low variation of skin color in Czech, and indeed most

European populations [58], it is not certain that in our sample of non-manipulated photographs these two aspects could be differentiated.

Facial averageness

Facial averageness was generally perceived as attractive: the correlation was significant in about one half of the target populations, predominantly the European ones. Considering that only Czech faces were rated, these results may indicate that non-European raters are not sensitive to a prototypical European face since their visual experience is guided by prototypic standards which are based on their own population. This seems to partly contradict the results of studies by Rhodes et al. [32, 35] who found that faces manipulated to appear closer to the average are rated as more attractive irrespective of ethnicity of either the targets or the raters. In the latter study, Asian perceivers did not prefer own-ethnicity averaged composites over other-ethnicity or mixed ethnicity composites [35]. Rhodes, Jeffery, Watson, Clifford, and Nakayama [114] suggest that a process of perceptual adaptation can rapidly adjust raters' preferences to fit the rated faces and thus re-set an average prototypical face. It is, however, questionable to what degree these mechanisms are involved when raters are confronted with an unusual population of faces [88]. Our results from non-European raters may indicate that raters cannot recalibrate their prototype of averageness when exposed to other-ethnicity photographs for just a short time during evaluation.

Fluctuating asymmetry

In our results, the degree of FA in faces of either sex did not seem to be linked to the perception of attractiveness. This contrasts with several previous studies [32, 50, 115–117]. Nevertheless, it should be noted that research on the relation between facial symmetry and perceived attractiveness has been yielding inconsistent results, as documented in a considerable number of reports of negative results [51, 52, 118, 119], or in meta-analyses by Rhodes and Simmons [55], Van Dongen [54, 120], and Van Dongen and Gangestad [121]. Rhodes and Simmons [55] reported moderate effect of facial FA on attractiveness but found little evidence for a hypothesis that FA signals mate quality. In a recent study, facial averageness yielded a large effect whereas FA yielded a small effect on attractiveness [122]. In a study of Mogilski and Welling [123], potential mate's facial sexual dimorphism was prioritized over facial symmetry. In our study, we used a similar sample of non-manipulated photographs (120 compared to 200 subjects, in both studies the subjects were students from European universities) and used same method of FA computation as Van Dongen [119] who found no association between FA and facial attractiveness. Our results are also in line with Kleisner et al. [58] who found no relation between FA and rated attractiveness in two samples of African faces rated across three populations. Moreover, Graham and Özener [124] in their thorough review on fluctuating asymmetry in humans questioned the importance of FA as an honest indicator of fitness and suggested that research should rather focus on examining the relation of FA to directional asymmetry which correlates with the individual's low developmental stability.

Eye color

With respect to the influence of eye color on the perception of attractiveness, we observed a pattern explicable by a negative frequency-dependent selection. Specifically, we found preference for blue eyes in Turkey and Portugal where the trait is not common. In contrast, however, we found no similar preference for the less common brown eyes in Estonia or Sweden. Our data also show a notable difference in preference for blue eyes between the sexes. While in Portugal and in Brazil, blue-eyed men–but not women–were preferred as more attractive, in

Turkey, blue-eyed women–but not men–were rated as more attractive. This could be interpreted from the perspective of the social status of women in a given society. Given that the Turkish society is characterized by a relatively high degree of gender inequality [125–127], one could speculate that the position of Turkish women in courting is rather passive, which is in turn reflected in a more conservative rating of facial attractiveness. In other words, it is possible that unlike their Portuguese counterparts, Turkish women do not pay attention to special and 'redundant' traits such as eye color. Or, from the perspective of Turkish men, the traditional structure of Turkish society allows only men to take initiative in courtship and this may in turn influence their preferences. Karandashev et al. [128] reported that eyes play a role in romantic courtship among Georgian, Portuguese, French, but not Russian respondents, yet only Georgian men, not women, focused their attention more on eyes than any other facial feature. Taking into account that Georgia is a geographical neighbor to Turkey, it is possible that these cultures, however distinct in religious beliefs, share a similar view on the importance of eyes in the perceived attractiveness of women. This preference may have been strengthened by a Muslim tradition of female face covering in the Middle East which leaves only the eyes and their surrounding visible and available for non-verbal facial communication [128].

Further, the attractiveness preferences of Turkish population might be significantly shaped by relatively long period of cultural and political interconnectedness with East-Central European region. Beside the well-documented genetic impact of Ottoman occupation on ethnic groups of East-Central Europe [129], the admixture with Slavic genes has taken part in the very center of the empire–a royal harem [130]. In recent times, Russian immigration to Turkey may enrich the mate market [131,132] with rare, and thus desirable phenotypes, including blue eyes. Preferences for atypical appearance of women are also reflected in popular folk songs of the region such as *Sarı Gelin*, i.e. blond-haired bride [133].

Another factor related to perception of eyes in Turkey is the concept of evil eye (*nazar*), a still-present superstition with different additional cultural layers ascribed to otherwise ancient meanings [134]. A widespread amulet in Middle-East, an evil eye bead, has the shape and color of a blue eye. Blue eye color might be assigned a special meaning because in a predominantly brown-eyed society, blue eyes are uncommon, strange, and therefore perceived as potentially dangerous. Alternatively, blue eye color may be valued because the highest deity in old Turkic religions resides in the blue sky. The recent meaning of the blue eye amulet, popular in all segments of society, may be based either on its original protective role, whereby it is viewed as an expression of good luck and greetings, or just on an aesthetic function [134]. It is therefore possible that both Turkish men and women unconsciously attach different importance to the same facial feature.

Alternatively, preferences for eye colors may be driven by repeated exposure. The more one is exposed to a particular trait (e.g., eye color), the greater should be the positive evaluation of that trait [72, 80, 135]. On a population level, we did not find that the prevailing eye color is more preferred than a rare one in any of the target countries. On the other hand, one cannot draw conclusions based solely on the ratio of eye colors in populations. To remove these limitations, we should have also asked the raters about their parents' and partner's eye colors. That would at least approximately determine the environment in which the participants have been brought up and currently live.

Cross-cultural agreement and differences

Despite a generally high agreement in attractiveness ratings between cultures, which has been reported in other studies [43, 136], we have also observed a prominent pattern in correlations which might reflect differences in the HDI of participating populations, see [18, 82]. Most notable is the gap between two clusters, one consisting of European countries plus Brazil, the other of other non-European populations. The disparity between European and non-European populations is parallel to a greater agreement on facial attractiveness perception within than between populations [25, 109, 137, 138]. As pointed out by Sorokowski et al. [138], criteria of attractiveness may vary between cultures due to the ecological conditions of a given population, but all populations substantially agree on unattractiveness, which is according to this study a better proxy of health and biological quality. If there is a common basis for agreement on what is not attractive, or, to express it less crudely, if the perception of attractiveness is part of our evolutionary heritage [139], can we at least partly identify the source of culture-specific tastes?

Our data indicate that we may see fundamental differences in the perception of attractiveness due to (1) the degree of divergence in ecological conditions approximated by the level of socio-economic development, and due to (2) familiarity with the population to which the preferences are attached. It is well known that socio-economic development influences the perception of attractiveness of human bodily morphology [140–143]. In a review dedicated to the perception of body size, Swami [143] argued that despite a large degree of uniformity in body size ideals due to Westernization [140], the socio-economic status of perceivers does lead to significant differences in preferences.

Whereas the body or its particular features such as muscularity, fat level, waist-to-hip ratio, or height can be directly related to fitness-dependent qualities and it has been reported that their perception is influenced by environmental conditions and moderated by Westernization, the perception of faces is influenced by yet another important component, namely familiarity with facial diversity within a population. It has been shown that familiarity with facial proportions results in a more accurate estimation of body weight in a population of one's own ethnicity than other ethnicity [144] and may be the cause of differences in preferences between rural and urban populations [145]. Perceived attractiveness of Czech faces in populations like India, Cameroon, or Namibia could thus be influenced by a relative lack of familiarity with European faces. Different experiences may result in different norms of attractiveness and this could not only overshadow sensitivity to specific, unfamiliar traits such as eye color, but also influence the perception of biologically-based traits of attractiveness such as averageness and sexual dimorphism. On the example of chin morphology, Thayer and Dobson [146] documented that geographic differences in chin shape are consistent with population-specific mating preferences that favor a familiar appearance. Additionally, the perception of an 'unfamiliar' population may be influenced by cross-race effect, that is, by a more accurate recognition of own-culture than other-culture faces [147].

Although we found correlations between perceived facial attractiveness and the level of socio-economic development, one ought to consider with caution the degree to which one can rely on HDI to explain cross-cultural differences. Our findings are in line with Marcinkowska et al. [86], who used the National Health Index as a proxy for regional differences in men's attractiveness preferences and found that facial femininity was less favored in countries with worse health conditions. Similarly, Scott et al. [18] found that men's preferences for feminine female faces are less pronounced in low-HDI countries. On the other hand, we cannot simply infer that masculinity in men is preferred in high-HDI countries [18]. Quite the opposite, preferences for feminine male faces in relatively wealthy regions rather than in harsher environments correspond with earlier findings that masculinity is more valued in less developed regions [82–85, 148]. Nevertheless, an even more complex pattern emerges from the findings of Batres and Perrett [149] who had shown that raters without internet access perceive feminine male faces as more attractive, or Dixson et al. [90] who reported no preference for masculine male faces and feminine female faces neither in regions with high pathogen load nor in areas of urban development. It is therefore evident that rather than relying solely on differences between countries as approximated by HDI, pathogen stress, national income inequality, or other indices, a detailed cross-cultural investigation requires awareness of the sub-structure and cultural specifics of the target regions [150]. Nevertheless, our contribution supports a conclusion that both facial femininity in women and averageness in general do play a decisive role especially in countries with a higher HDI. In this sense, we can agree with the argument proposed by Scott et al. [18] who claimed that the novel environment of Westernized, urban, high-HDI society creates space for new opportunities where a broader scale of attractiveness attributes is taken in consideration. Finally, we should keep in mind that we used a European photoset, which implies that participants from low-HDI countries such as Cameroon, Namibia, and India have naturally less direct contact with facial stimuli of European origin compared to cultures in closer physical proximity to the Czech Republic.

Limitations and future directions

A cross-cultural comparison would have provided more insights into local cultural specifics had we asked a broader set of questions related to the raters themselves. Factors which influenced the raters' assessment of attractiveness could be influenced by their marital status, family background, personality traits, sociosexuality, social class, and other additional considerations. For example, due to absence of relevant information about Indian raters it is difficult to figure out why, in case of this particular culture, we found no association between perceived attractiveness and the traits followed by this study. It is then only an uncorroborated assumption to claim that the decisions of Indian men might be moderated by, for instance, social class or traditional familial rules. Their perception of female attractiveness could be influenced by a mixture of various factors involved in mate preferences, such as religiosity ('religious' as a preferred trait in women is reported by Basu and Ray [151]). It is also possible that the perception of male attractiveness is influenced by the sexually restricted behavior of Indian women [152]. Further, the participants' attitudes to traditional marriage practices could also significantly uncover the differences in preferences of collectivistic societies such as India or Turkey [153, 154]. Moreover, information about the eye color of family members and partners of our raters would have helped to answer questions related to assortative mating [72]. Similarly, in order to disentangle the variance in women's preference for male facial masculinity on a cross-cultural level, one should first of all investigate the various differences that could reflect a trade-off between costs and benefits, where preferences for a more masculine or more feminine male mate are dependent on the phase of the menstrual cycle [155], partnership status [156], relationship type [157], self-rated attractiveness [158], or the male counterpart's hormone levels [159].

While a set of non-manipulated photographs has the advantage of reflecting a natural variation in appearance, it also carries a disadvantage because variation in facial features may conceal possible attractiveness-influencing factors that would be more apparent in manipulated images. Moreover, we did not sort our set by hair colors. Different combinations of hair and eye color on the one hand and hair style on the other may have also partly influenced the ratings. Further, some limitations may be due to the fact that we have intentionally reduced eye colors to only two distinct categories of brown and blue. Nevertheless, one fifth of Czech population reports having green eyes. In one study, green-eyed women also reported better health condition than participants with other eye colors [160]. Both due to its rareness and a putative link associating eye color with health, this particular eye color might be considered as most appealing in women. In India, for example, green eyes might be perceived as exceptionally attractive: note, for instance, the Bollywood female star Aishwarya Rai [161]. Alongside other rare traits, green eye color might further play a role in some Asian cultures where local standards of beauty are gradually conforming to international standards of beauty [162].

To assure a reliable cross-cultural comparison that would reflect the differences in HDI, one should consider increasing the number of cultures involved or include subsamples from non-European countries which vary in their degree of Westernization. It is worth noting, for instance, that our Turkish sample was drawn from Adıyaman, a city located in southeastern Turkey, an area that more traditional than most other Turkish regions. Recruiting a sample from northwestern Turkey, which has historically been more open to European influence and is socially more liberal, could produce different results. In sum, in interpreting our results, it should be kept in mind that our samples are not nationally representative.

Conclusions

Based on the rating of European faces in ten populations, both European and non-European, we found support for the hypothesis that averageness and sexual dimorphism in human face play a significant role for attractiveness assessment, whereas the influence of fluctuating asymmetry is negligible. In line with negative frequency-dependent selection, the blue-eyed phenotype influenced ratings only in those cultures where it is present but not common. And last but not least, we found that factors which influence the perception of facial attractiveness in different populations are affected by the relevant socio-cultural background, here reflected in the HDI index: more convergent socio-cultural background of raters' population and the population whose faces are rated leads to more similar ratings in these two populations. Explanations of our findings are tentative, and we offer directions for further examination, especially with respect to involving other cultures of both perceivers and, particularly, the rated subjects.

Supporting information

S1 Table. Results of procrustes analysis and attractiveness ratings for each photo.
(XLSX)

Acknowledgments

We would like to thank all participants and our colleagues who kindly helped us to collect ratings in Estonia (Ondřej Bradáč, Riin Magnus), Sweden (Martina Boeck, Åse Innes-Ker, Cristina Elena Ivan), Romania (Silviu Apostol, Sorin Paliga, Carmen Strungaru, Dan Ungureanu), Turkey (Tuncay Çelik), Portugal (Romão Araújo, João Carlos Major), Brazil (Vít Třebický, Jaroslava Varella Valentova, Marco Antonio Corrêa Varella), India (Veronika Pichová), Cameroon (Robert Mbe Akoko, Vít Třebický, Jana Vokurková), and Namibia (Jan Havlíček, Rosina Jash), Petr Tureček for help with mixed-effect model analysis, Anna Pilátová for valuable comments and proofreading of the manuscript, and Alex Jones and two anonymous reviewers for constructive feedback on the paper.

Author Contributions

Conceptualization: S. Adil Saribay, Karel Kleisner.

Data curation: Tomáš Kočnar.

Formal analysis: Tomáš Kočnar, Karel Kleisner.

Funding acquisition: Karel Kleisner.

Investigation: Tomáš Kočnar, Karel Kleisner.

Methodology: Karel Kleisner.

Writing – original draft: Tomáš Kočnar, S. Adil Saribay, Karel Kleisner.

References

1. Henderson AJ, Holzleitner IJ, Talamas SN, Perrett DI. Perception of health from facial cues. Philos Trans R Soc Lond B Biol Sci [Internet]. The Royal Society; 2016 May 5 [cited 2018 Jul 22];371(1693). Available from: http://www.ncbi.nlm.nih.gov/pubmed/27069057
2. Keating CF. Charismatic faces: Social status cues put face appeal in context. Facial attrativeness: Evolutionary, cognitive, and social perspectives. Westport, CT, US: Ablex Publishing; 2002. p. 153–92.
3. Little AC, Jones BC, Debruine LM. Facial attractiveness: Evolutionary based research. Philos Trans R Soc B Biol Sci [Internet]. 2011 Jun 12 [cited 2017 Feb 2]; 366(1571):1638–59. Available from: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3130383&tool=pmcentrez&rendertype=abstract
4. Mueller U, Mazur A. Facial dominance in Homo sapiens as honest signalling of male quality. Behav Ecol. 1997; 8(5):569–79.
5. Todorov A. Evaluating faces on trustworthiness: An extension of systems for recognition of emotions signaling approach/avoidance behaviors. Ann N Y Acad Sci. 2008; 1124:208–24. https://doi.org/10.1196/annals.1440.012 PMID: 18400932
6. Rhodes G. The Evolutionary Psychology of Facial Beauty. Annu Rev Psychol [Internet]. 2006; 57 (1):199–226. Available from: http://www.annualreviews.org/doi/10.1146/annurev.psych.57.102904.190208
7. Thornhill R, Gangestad SW. Facial attractiveness. 1999; 3(12):452–60.
8. Cunningham MR, Roberts AR, Barbee AP, Druen PB, Wu C-H. "Their ideas of beauty are, on the whole, the same as ours": Consistency and variability in the cross-cultural perception of female physical attractiveness. J Pers Soc Psychol [Internet]. 1995 [cited 2018 Jul 25]; 68(2):261–79. Available from: http://doi.apa.org/getdoi.cfm?doi=10.1037/0022-3514.68.2.261
9. Langlois JH, Kalakanis L, Rubenstein AJ, Larson A, Hallam M, Smoot M. Maxims or myths of beauty? A meta-analytic and theoretical review. Psychol Bull [Internet]. 2000; 126(3):390–423. Available from: http://doi.apa.org/getdoi.cfm?doi=10.1037/0033-2909.126.3.390 PMID: 10825783
10. Andersson MB. Sexual Selection. Princeton University Press. 1994.
11. Møller AP, Thornhill R. Bilateral Symmetry and Sexual Selection: A Meta-Analysis. Am Nat. 1998;
12. Bronstad PM, Russell R. Beauty is in the "we" of the beholder: Greater agreement on facial attractiveness among close relations. Perception. 2007; 36(11):1674–81. https://doi.org/10.1068/p5793 PMID: 18265847
13. Germine L, Russell R, Bronstad PM, Blokland GAM, Smoller JW, Kwok H, et al. Individual Aesthetic Preferences for Faces Are Shaped Mostly by Environments, Not Genes. Curr Biol. 2015; 25 (20):2684–9. https://doi.org/10.1016/j.cub.2015.08.048 PMID: 26441352
14. Hönekopp J. Once more: Is beauty in the eye of the beholder? Relative contributions of private and shared taste to judgments of facial attractiveness. J Exp Psychol Hum Percept Perform. 2006; 32 (2):199–209. https://doi.org/10.1037/0096-1523.32.2.199 PMID: 16634665
15. Jones D, Hill K. Criteria of facial attractiveness in five populations. Hum Nat. 1993; 4(3):271–96. https://doi.org/10.1007/BF02692202 PMID: 24214367
16. Penton-Voak IS, Jacobson A, Trivers R. Populational differences in attractiveness judgements of male and female faces: Comparing British and Jamaican samples. Evol Hum Behav. 2004; 25(6):355–70.
17. Pisanski K, Feinberg DR. Cross-Cultural Variation in Mate Preferences for Averageness, Symmetry, Body Size, and Masculinity. Cross-Cultural Res [Internet]. 2013; 47(2):162–97. Available from: https://doi.org/10.1177/1069397112471806
18. Scott IM, Clark AP, Josephson SC, Boyette AH, Cuthill IC, Fried RL, et al. Human preferences for sexually dimorphic faces may be evolutionarily novel. Proc Natl Acad Sci [Internet]. 2014; 111(40):14388–93. Available from: http://www.pnas.org/lookup/doi/10.1073/pnas.1409643111 PMID: 25246593
19. Jokela M. Physical attractiveness and reproductive success in humans: Evidence from the late 20 century United States. Evol Hum Behav. 2009; 30(5):342–350. https://doi.org/10.1016/j.evolhumbehav.2009.03.006 PMID: 21151758
20. Prokop P, Fedor P. Physical attractiveness influences reproductive success of modern men. Journal of Ethology. 2011; 29(3):453–458.

21. Foo YZ, Simmons LW, Rhodes G. Predictors of facial attractiveness and health in humans. Sci Rep [Internet]. Nature Publishing Group; 2017; 7(June 2016):1–12. Available from: https://doi.org/10.1038/s41598-016-0028-x

22. Johnston VS. Female facial beauty: The fertility hypothesis. Pragmat Cogn [Internet]. 2000 May 22 [cited 2018 Jul 24]; 8(1):107–22. Available from: https://benjamins.com/catalog/pc.8.1.06joh

23. Grammer K, Thornhill R. Human (Homo sapiens) facial attractiveness and sexual selection: The role of symmetry and averageness. J Comp Psychol [Internet]. 1994 [cited 2018 Jul 24]; 108(3):233–42. Available from: http://doi.apa.org/getdoi.cfm?doi=10.1037/0735-7036.108.3.233 PMID: 7924253

24. Little AC, Jones BC, Feinberg DR, Perrett DI. Men's strategic preferences for femininity in female faces. Br J Psychol [Internet]. Wiley/Blackwell (10.1111); 2014 Aug [cited 2018 Jul 24]; 105(3):364–81. Available from: https://doi.org/10.1111/bjop.12043 PMID: 25040006

25. Perrett DI, Lee KJ, Penton-Voak I, Rowland D, Yoshikawa S, Burt DM, et al. Effects of sexual dimorphism on facial attractiveness. Nature. 1998; 394(6696):884–7. https://doi.org/10.1038/29772 PMID: 9732869

26. Rennels JL, Bronstad PM, Langlois JH. Are attractive men's faces masculine or feminine? The importance of type of facial stimuli. J Exp Psychol Hum Percept Perform [Internet]. 2008 [cited 2018 Jul 24]; 34(4):884–93. Available from: http://doi.apa.org/getdoi.cfm?doi=10.1037/0096-1523.34.4.884 PMID: 18665733

27. Zaidi A, White J, Mattern B, Liebowitz C, Puts D, Claes P et al. Facial masculinity does not appear to be a condition-dependent male ornament and does not reflect MHC heterozygosity in humans. Proceedings of the National Academy of Sciences. 2019; 116(5):1633–1638.

28. Keating CF. Gender and the Physiognomy of Dominance and Attractiveness. Soc Psychol Q [Internet]. 1985; 48(1):61. Available from: http://www.jstor.org/stable/3033782?origin=crossref

29. Swaddle JP, Reierson GW. Testosterone increases perceived dominance but not attractiveness in human males. Proc R Soc B Biol Sci. 2002; 269(1507):2285–9.

30. Langlois J, Roggman L. Attractive Faces Are Only Average. Psychological Science. 1990; 1(2):115–121.

31. Rhodes G, Tremewan T. Understanding face recognition: Caricauture effects, inversion, and the homogeneity problem. Vis cogn [Internet]. Taylor & Francis Group; 1994 Apr 24 [cited 2018 Jul 24]; 1 (2–3):275–311. Available from: https://www.tandfonline.com/doi/full/10.1080/13506289408402303

32. Rhodes G, Sumich A, Byatt G. Are Average Facial Configurations Attractive Only Because of Their Symmetry? Psychol Sci [Internet]. 1999 Jan 6 [cited 2018 Jul 24]; 10(1):52–8. Available from: http://journals.sagepub.com/doi/10.1111/1467-9280.00106

33. Lie HC, Rhodes G, Simmons LW. GENETIC DIVERSITY REVEALED IN HUMAN FACES. Evolution (N Y) [Internet]. 2008 Oct [cited 2018 Jul 24]; 62(10):2473–86. Available from: http://www.ncbi.nlm.nih.gov/pubmed/18691260

34. Roberts SC, Little AC, Gosling LM, Jones BC, Perrett DI, Carter V, et al. MHC-assortative facial preferences in humans. Biol Lett. 2005; 1(4):400–3. https://doi.org/10.1098/rsbl.2005.0343 PMID: 17148217

35. Rhodes G, Yoshikawa S, Clark A, Kieran L, McKay R, Akamatsu S. Attractiveness of facial averageness and symmetry in non-western cultures: In search of biologically based standards of beauty. Perception. 2001; 30(5):611–25. https://doi.org/10.1068/p3123 PMID: 11430245

36. Scheib JE, Gangestad SW, Thornhill R. Facial attractiveness, symmetry and cues of good genes. Proceedings Biol Sci [Internet]. The Royal Society; 1999 Sep 22 [cited 2018 Jul 24]; 266(1431):1913–7. Available from: http://www.ncbi.nlm.nih.gov/pubmed/10535106

37. Thornhill R, Gangestad SW. Human facial beauty. Hum Nat [Internet]. 1993 Sep [cited 2018 Jul 24]; 4 (3):237–69. Available from: http://www.ncbi.nlm.nih.gov/pubmed/24214366 https://doi.org/10.1007/BF02692201 PMID: 24214366

38. Lee AJ, Mitchem DG, Wright MJ, Martin NG, Keller MC, Zietsch BP. Facial averageness and genetic quality: Testing heritability, genetic correlation with attractiveness, and the paternal age effect. Evol Hum Behav [Internet]. Elsevier Inc.; 2016; 37(1):61–6. Available from: http://dx.doi.org/10.1016/j.evolhumbehav.2015.08.003 PMID: 26858521

39. DeBruine LM, Jones BC, Unger L, Little AC, Feinberg DR. Dissociating Averageness and Attractiveness: Attractive Faces Are Not Always Average. J Exp Psychol Hum Percept Perform. 2007; 33 (6):1420–30.

40. Said CP, Todorov A. A statistical model of facial attractiveness. Psychol Sci. 2011; 22(9):1183–90. https://doi.org/10.1177/0956797611419169 PMID: 21852448

41. Alley TR, Cunningham MR. Article Commentary: Averaged Faces Are Attractive, but Very Attractive Faces Are Not Average. Psychol Sci [Internet]. SAGE PublicationsSage CA: Los Angeles, CA; 1991

Mar 25 [cited 2018 Jul 23]; 2(2):123–5. Available from: http://journals.sagepub.com/doi/10.1111/j.1467-9280.1991.tb00113.x

42. Baudouin JY, Tiberghien G. Symmetry, averageness, and feature size in the facial attractiveness of women. Acta Psychol (Amst). 2004; 117(3):295–312.

43. Jones D. Sexual Selection, Physical Attractiveness, and Facial Neoteny. 1995; 36(December).

44. Perrett DI, May KA, Yoshikawa S. Facial shape and judgements of female attractiveness. Nature [Internet]. Nature Publishing Group; 1994 Mar 17 [cited 2018 Jul 23]; 368(6468):239–42. Available from: http://www.nature.com/doifinder/10.1038/368239a0 PMID: 8145822

45. Wehr P, MacDonald K, Lindner R, Yeung G. Stabilizing and directional selection on facial paedomorphosis. Hum Nat [Internet]. Springer-Verlag; 2001 Dec [cited 2018 Jul 23]; 12(4):383–402. Available from: http://link.springer.com/10.1007/s12110-001-1004-z PMID: 26192413

46. Özener B, Fink B. Facial symmetry in young girls and boys from a slum and a control area of Ankara, Turkey. Evol Hum Behav [Internet]. Elsevier; 2010 Nov 1 [cited 2018 Jul 24]; 31(6):436–41. Available from: http://linkinghub.elsevier.com/retrieve/pii/S109051381000070X

47. Thornhill R, Gangestad SW. Human Fluctuating Asymmetry and Sexual Behavior. Psychol Sci [Internet]. SAGE PublicationsSage CA: Los Angeles, CA; 1994 Sep 6 [cited 2018 Jul 24]; 5(5):297–302. Available from: http://journals.sagepub.com/doi/10.1111/j.1467-9280.1994.tb00629.x

48. Banks GC, Batchelor JH, Mcdaniel MA. Intelligence Smarter people are (a bit) more symmetrical: A meta-analysis of the relationship between intelligence and fl uctuating asymmetry. Intelligence [Internet]. Elsevier Inc.; 2010; 38(4):393–401. Available from: http://dx.doi.org/10.1016/j.intell.2010.04.003

49. Jones BC, Little AC, Tiddeman BP, Burt DM, Perrett DI. Facial symmetry and judgements of apparent health Support for a "'good genes"' explanation of the attractiveness–symmetry relationship. 2001; 22:417–29.

50. Muñoz-Reyes JA, Iglesias-Julios M, Pita M, Turiegano E. Facial Features: What Women Perceive as Attractive and What Men Consider Attractive. PLoS One [Internet]. 2015 Jan [cited 2017 Feb 11]; 10(7):e0132979. Available from: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4498779&tool=pmcentrez&rendertype=abstract https://doi.org/10.1371/journal.pone.0132979 PMID: 26161954

51. Farrera A, Villanueva M, Quinto-Sánchez M, González-José R. The relationship between facial shape asymmetry and attractiveness in Mexican students. Am J Hum Biol. 2015; 27(3):387–96. https://doi.org/10.1002/ajhb.22657 PMID: 25400276

52. Penton-Voak IS, Jones BC, Little AC, Baker S, Tiddeman B, Burt DM, et al. Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. Proc R Soc B Biol Sci. 2001; 268(1476):1617–23.

53. Soler C, Kekäläinen J, Núñez M, Sancho M, Núñez J, Yaber I, et al. Male Facial Anthropometry and Attractiveness. Perception [Internet]. 2012 Oct [cited 2017 Feb 11]; 41(10):1234–45. Available from: http://journals.sagepub.com/doi/10.1068/p7214 PMID: 23469703

54. Van Dongen S. Associations between asymmetry and human attractiveness: Possible direct effects of asymmetry and signatures of publication bias. Ann Hum Biol [Internet]. 2011 May [cited 2017 Feb 11]; 38(3):317–23. Available from: http://www.ncbi.nlm.nih.gov/pubmed/21271817 https://doi.org/10.3109/03014460.2010.544676 PMID: 21271817

55. Rhodes G, & Simmons LW. Symmetry, attractiveness and sexual selection. In: Dunbar RIM, Barrett L, eds. The Oxford handbook of evolutionary psychology. Oxford: University Press; 2007. p. 333–364.

56. Fink B, Matts PJ, D'Emiliano D, Bunse L, Weege B, Röder S. Colour homogeneity and visual perception of age, health and attractiveness of male facial skin. J Eur Acad Dermatology Venereol [Internet]. Wiley/Blackwell (10.1111); 2011 Nov [cited 2018 Jul 24]; 26(12):no-no. Available from: http://doi.wiley.com/10.1111/j.1468-3083.2011.04316.x

57. Lefevre CE, Perrett DI. Fruit over sunbed: Carotenoid skin colouration is found more attractive than melanin colouration. Q J Exp Psychol [Internet]. 2015 Feb [cited 2018 Jul 24]; 68(2):284–93. Available from: http://www.ncbi.nlm.nih.gov/pubmed/25014019

58. Kleisner K, Kočnar T, Tureček P, Stella D, Akoko RM, Třebický V, et al. African and European perception of African female attractiveness. Evol Hum Behav. 2017; 38(6):744–55.

59. Bovet J, Barthes J, Durand V, Raymond M, Alvergne A. Men's Preference for Women's Facial Features: Testing Homogamy and the Paternity Uncertainty Hypothesis. PLoS One. 2012; 7(11).

60. Edwards M, Cha D, Krithika S, Johnson M, Cook G, Parra EJ. Iris pigmentation as a quantitative trait: Variation in populations of European, East Asian and South Asian ancestry and association with candidate gene polymorphisms. Pigment Cell Melanoma Res. 2016; 29(2):141–62. https://doi.org/10.1111/pcmr.12435 PMID: 26547379

61. Frost P. European hair and eye color. A case of frequency-dependent sexual selection? Evol Hum Behav. 2006; 27(2):85–103.
62. Frost P. The Puzzle of European Hair, Eye, and Skin Color. Adv Anthropol [Internet]. 2014; 04(02):78–88. Available from: http://www.scirp.org/journal/doi.aspx?DOI = 10.4236/aa.2014.42011
63. Jablonski NG, Chaplin G. The colours of humanity: The evolution of pigmentation in the human lineage. Philos Trans R Soc B Biol Sci. 2017; 372(1724).
64. Janif ZJ, Brooks RC, Dixson BJ. Negative frequency-dependent preferences and variation in male facial hair. Biol Lett. 2014; 10(4).
65. Thelen TH. Minority type human mate preference. Biodemography Soc Biol [Internet]. 1983; 30 (2):162–80. Available from: http://www.tandfonline.com/doi/abs/10.1080/19485565.1983.9988531
66. Fink B, Hufschmidt C, Hirn T, Will S, McKelvey G, Lankhof J. Age, health and attractiveness perception of virtual (rendered) human hair. Front Psychol. 2016; 7(DEC):1–12.
67. Janif ZJ, Brooks RC, Dixson BJ. Are Preferences for Women's Hair Color Frequency-Dependent? Adapt Hum Behav Physiol. 2015; 1(1):54–71.
68. Lawson ED. Hair Color, Personality, and the Observer. Psychol Rep [Internet]. SAGE Publications-Sage CA: Los Angeles, CA; 1971 Feb 1 [cited 2018 Jul 24]; 28(1):311–22. Available from: http://journals.sagepub.com/doi/10.2466/pr0.1971.28.1.311 PMID: 5549452
69. Sorokowski P. Attractiveness of Blonde Women in Evolutionary Perspective: Studies with Two Polish Samples. Percept Mot Skills [Internet]. SAGE PublicationsSage CA: Los Angeles, CA; 2008 Jun 1 [cited 2018 Jul 24]; 106(3):737–44. Available from: http://journals.sagepub.com/doi/10.2466/pms.106.3.737-744 PMID: 18712194
70. Swami V, Barrett S. British men's hair color preferences: An assessment of courtship solicitation and stimulus ratings. Scand J Psychol. 2011; 52(6):595–600. https://doi.org/10.1111/j.1467-9450.2011.00911.x PMID: 21883260
71. Bressan P, Damian V. Fathers' eye colour sways daughters' choice of both long- and short-term partners. Sci Rep [Internet]. Springer US; 2018; 8(1):1–9. Available from: http://dx.doi.org/10.1038/s41598-018-23784-7
72. Little AC, Penton-Voak IS, Burt DM, Perrett DI. Investigating an imprinting-like phenomenon in humans partners and opposite-sex parents have similar hair and eye colour. Evol Hum Behav. 2003; 24(1):43–51.
73. Wilson GD, Barrett PT. Parental characteristics and partner choice: Some evidence for oedipal imprinting. J Biosoc Sci. 1987; 19(2):157–61. https://doi.org/10.1017/s0021932000016758 PMID: 3584173
74. Laeng B, Mathisen R, Johnsen JA. Why do blue-eyed men prefer women with the same eye color? Behav Ecol Sociobiol. 2007; 61(3):371–84.
75. Salter F. Carrier females and sender males: An evolutionary hypothesis linking female attractiveness, family resemblance, and paternity confidence. Ethol Sociobiol. 1996; 17(4):211–20.
76. Rantala MJ, Marcinkowska UM. The role of sexual imprinting and the Westermarck effect in mate choice in humans. Behav Ecol Sociobiol. 2011; 65(5):859–73.
77. Prokop P, Obertová Z, Fedor P. Paternity cues and mating opportunities: what makes fathers good?. acta ethologica. 2010; 13(2):101–107.
78. Kleisner K, Kočnar T, Rubešová A, Flegr J. Eye color predicts but does not directly influence perceived dominance in men. Pers Individ Dif. 2010; 49(1):59–64.
79. Kleisner K, Priplatova L, Frost P, Flegr J. Trustworthy-Looking Face Meets Brown Eyes. PLoS One. 2013; 8(1):1–7.
80. Hinsz VB, Stoesser CJ, Matz DC. The Intermingling of Social and Evolutionary Psychology Influences on Hair Color Preferences. Curr Psychol. 2013; 32(2):136–49.
81. Swami V, Rozmus-Wrzesinska M, Voracek M, Haubner T, Danel D, Pawłowski B, et al. The influence of skin tone, body weight, and hair colour on perceptions of women's attractiveness and health: A cross-cultural investigation. J Evol Psychol [Internet]. 2008; 6(4):321–41. Available from: http://www.akademiai.com/doi/abs/10.1556/JEP.6.2008.4.4
82. Moore FR, Coetzee V, Contreras-Garduño J, Debruine LM, Kleisner K, Krams I, et al. Cross-cultural variation in women's preferences for cues to sex- and stress-hormones in the male face. Biol Lett [Internet]. The Royal Society; 2013 Jun 23 [cited 2018 Jul 24]; 9(3):20130050. Available from: http://www.ncbi.nlm.nih.gov/pubmed/23536442 PMID: 23536442
83. DeBruine LM, Jones BC, Crawford JR, Welling LLM, Little AC. The health of a nation predicts their mate preferences: Cross-cultural variation in women's preferences for masculinized male faces. Proc R Soc B Biol Sci. 2010; 277(1692):2405–10.

84. DeBruine LM, Jones BC, Little AC, Crawford JR, Welling LLM. Further evidence for regional variation in women's masculinity preferences. Proc R Soc B Biol Sci [Internet]. The Royal Society; 2011 Mar 22 [cited 2018 Jul 24]; 278(1707):813–4. Available from: http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2010.2200

85. DeBruine LM, Little AC, Jones BC. Extending parasite-stress theory to variation in human mate preferences. Behav Brain Sci [Internet]. 2012 Apr [cited 2018 Jul 24]; 35(02):86–7. Available from: http://www.ncbi.nlm.nih.gov/pubmed/22289354

86. Marcinkowska UM, Kozlov MV, Cai H, Contreras-Garduño J, Barnaby J, Oana GA, et al. Cross-cultural variation in men's preference for sexual dimorphism in women's faces Cross-cultural variation in men's preference for sexual dimorphism in women's faces. Biol Lett. 2014; 10:2013–6.

87. Marcinkowska U, Rantala M, Lee A, Kozlov M, Aavik T, Cai H et al. Women's preferences for men's facial masculinity are strongest under favorable ecological conditions. Scientific Reports. 2019; 9(1).

88. Rhodes G, Chan J, Zebrowitz LA, Simmons LW. Does sexual dimorphism in human faces signal health? Proc R Soc B Biol Sci [Internet]. 2003 Aug 7 [cited 2018 Aug 6]; 270(Suppl_1):S93–5. Available from: http://www.ncbi.nlm.nih.gov/pubmed/12952647

89. Scott IML, Clark AP, Boothroyd LG, Penton-Voak IS. Do men's faces really signal heritable immunocompetence? Behav Ecol. 2013; 24(3):579–89. https://doi.org/10.1093/beheco/ars092 PMID: 23555177

90. Dixson BJ, Little AC, Dixson HG, Brooks RC. Do prevailing environmental factors influence human preferences for facial morphology? Behav Ecol. 2017; 28(5):1217–27.

91. Little AC, Apicella CL, Marlowe FW. Preferences for symmetry in human faces in two cultures: Data from the UK and the Hadza, an isolated group of hunter-gatherers. Proc R Soc B Biol Sci. 2007; 274 (1629):3113–7.

92. Apicella CL, Little AC, Marlowe FW. Facial averageness and attractiveness in an isolated population of hunter-gatherers. Perception. 2007; 36(12):1813–20. https://doi.org/10.1068/p5601 PMID: 18283931

93. Little AC. Facial appearance and leader choice in different contexts: Evidence for task contingent selection based on implicit and learned face-behaviour/face-ability associations. Leadersh Q [Internet]. Elsevier Inc.; 2014; 25(5):865–74. Available from: http://dx.doi.org/10.1016/j.leaqua.2014.04.002

94. Třebický V, Fialová J, Kleisner K, Havlíček J. Focal length affects depicted shape and perception of facial images. PLoS One. 2016; 11(2):1–14.

95. Danel DP, Dziedzic-Danel A, Kleisner K. Does age difference really matter? Facial markers of biological quality and age difference between husband and wife. HOMO- J Comp Hum Biol [Internet]. Elsevier GmbH.; 2016; 67(4):337–47. Available from: http://dx.doi.org/10.1016/j.jchb.2016.05.002

96. Adams DC, Otárola-Castillo E. geomorph: an r package for the collection and analysis of geometric morphometric shape data. Methods Ecol Evol [Internet]. Wiley/Blackwell (10.1111); 2013 [cited 2018 Jul 24]; 4(4):393–9. Available from: https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.12035%4010.1111/%28ISSN%292041-210X.TOPMETHODS

97. Mitteroecker P, Windhager S, Müller GB, Schaefer K. The Morphometrics of "Masculinity" in Human Faces. Raia P, editor. PLoS One [Internet]. 2015 Feb 11 [cited 2018 Jul 24]; 10(2):e0118374. Available from: http://www.ncbi.nlm.nih.gov/pubmed/25671667 https://doi.org/10.1371/journal.pone.0118374 PMID: 25671667

98. Klingenberg C, McIntyre G. Geometric Morphometrics of Developmental Instability: Analyzing Patterns of Fluctuating Asymmetry with Procrustes Methods. Evolution. 1998; 52(5):1363. https://doi.org/10.1111/j.1558-5646.1998.tb02018.x PMID: 28565401

99. Mardia K, Bookstein F, Moreton I. 'Statistical assessment of bilateral symmetry of shapes'. Biometrika. 2005; 92(1):249–250.

100. Klingenberg C, Barluenga M, Meyer A. SHAPE ANALYSIS OF SYMMETRIC STRUCTURES: QUANTIFYING VARIATION AMONG INDIVIDUALS AND ASYMMETRY. Evolution. 2002; 56(10):1909–1920. https://doi.org/10.1111/j.0014-3820.2002.tb00117.x PMID: 12449478

101. United Nations Development Programme. Human development report 2015. New York; 2015.

102. Walsh S, Wollstein A, Liu F, Chakravarthy U, Rahu M, Seland JH, et al. DNA-based eye colour prediction across Europe with the IrisPlex system. Forensic Sci Int Genet [Internet]. Elsevier Ireland Ltd; 2012; 6(3):330–40. Available from: http://dx.doi.org/10.1016/j.fsigen.2011.07.009 PMID: 21813346

103. Balaresque P, King TE. Human Phenotypic Diversity: An Evolutionary Perspective. Curr Top Dev Biol. 2016; 119:349–90. https://doi.org/10.1016/bs.ctdb.2016.02.001 PMID: 27282030

104. Beals RL., Hoijer H. An introduction to anthropology. New York: Macmillan; 1965.

105. Augood C, Fletcher A, Bentham G, Chakravarthy U, de Jong PTVM, Rahu M, et al. Methods for a population-based study of the prevalence of and risk factors for age-related maculopathy and macular

degeneration in elderly European populations: the EUREYE study. Ophthalmic Epidemiol [Internet]. 2004 Apr [cited 2018 Jul 24]; 11(2):117–29. Available from: http://www.ncbi.nlm.nih.gov/pubmed/15255027 https://doi.org/10.1076/opep.11.2.117.28160 PMID: 15255027

106. Kuznetsova A, Brockhoff P, Christensen R. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software. 2017; 82(13).

107. Cunningham MR, Barbee AP, Pike CL. What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. J Pers Soc Psychol [Internet]. 1990 [cited 2018 Jul 25]; 59(1):61–72. Available from: http://doi.apa.org/getdoi.cfm?doi=10.1037/0022-3514.59.1.61 PMID: 2213490

108. Stirrat M, Perrett DI. Valid facial cues to cooperation and trust: Male facial width and trustworthiness. Psychol Sci. 2010; 21(3):349–54. https://doi.org/10.1177/0956797610362647 PMID: 20424067

109. Stephen ID, Scott IML, Coetzee V, Pound N, Perrett DI, Penton-Voak IS. Cross-cultural effects of color, but not morphological masculinity, on perceived attractiveness of men's faces. Evol Hum Behav. 2012; 33(4):260–7.

110. Puts DA. Beauty and the beast: mechanisms of sexual selection in humans. Evol Hum Behav [Internet]. 2010 May [cited 2018 Jul 25]; 31(3):157–75. Available from: http://linkinghub.elsevier.com/retrieve/pii/S1090513810000279

111. Lu HJ, Zhu XQ, Chang L. Good genes, good providers, and good fathers: Economic development involved in how women select a mate. Evol Behav Sci [Internet]. 2015 [cited 2018 Jul 25]; 9(4):215–28. Available from: http://doi.apa.org/getdoi.cfm?doi=10.1037/ebs0000048

112. Lyons M, Marcinkowska U, Moisey V, Harrison N. The effects of resource availability and relationship status on women's preference for facial masculinity in men: An eye-tracking study. Pers Individ Dif [Internet]. Elsevier Ltd; 2016; 95:25–8. Available from: http://dx.doi.org/10.1016/j.paid.2016.02.025

113. Carrito M de L, Santos IMB dos, Lefevre CE, Whitehead RD, Silva CF da, Perrett DI. The role of sexually dimorphic skin colour and shape in attractiveness of male faces. Evol Hum Behav [Internet]. Elsevier Inc.; 2016; 37(2):125–33. Available from: http://dx.doi.org/10.1016/j.evolhumbehav.2015.09.006

114. Rhodes G, Jeffery L, Watson TL, Clifford CWG, Nakayama K. Fitting the Mind to the World: Face Adaptation and Attractiveness Aftereffects. Psychol Sci. 2003; 14(6):558–66. https://doi.org/10.1046/j.0956-7976.2003.psci_1465.x PMID: 14629686

115. Abend P, Pflüger LS, Koppensteiner M, Coquerelle M, Grammer K. The sound of female shape: A redundant signal of vocal and facial attractiveness. Evol Hum Behav. 2015; 36(3):174–81.

116. Komori M, Kawamura S, Ishihara S. Averageness or symmetry: Which is more important for facial attractiveness? Acta Psychol (Amst) [Internet]. Elsevier B.V.; 2009; 131(2):136–42. Available from: http://dx.doi.org/10.1016/j.actpsy.2009.03.008

117. Perrett DI, Burt DM, Penton-Voak IS, Lee KJ, Rowland DA, Edwards R. Symmetry and Human Facial Attractiveness. Evol Hum Behav [Internet]. Elsevier; 1999 Sep 1 [cited 2018 Jul 25]; 20(5):295–307. Available from: http://linkinghub.elsevier.com/retrieve/pii/S1090513899000148

118. Pound N, Lawson DW, Toma AM, Richmond S, Zhurov AI, Penton-Voak IS. Facial fluctuating asymmetry is not associated with childhood ill-health in a large British cohort study. Proc R Soc B Biol Sci. 2014; 281(1792).

119. Van Dongen S. Associations among facial masculinity, physical strength, fluctuating asymmetry and attractiveness in young men and women. Ann Hum Biol. 2014; 41(3):205–13. https://doi.org/10.3109/03014460.2013.847120 PMID: 24555492

120. Van Dongen S. Fluctuating asymmetry and masculinity/femininity in humans: A meta-analysis. Arch Sex Behav. 2012; 41(6):1453–60. https://doi.org/10.1007/s10508-012-9917-7 PMID: 22437551

121. Van Dongen S, Gangestad SW. Human fluctuating asymmetry in relation to health and quality: a meta-analysis. Evol Hum Behav [Internet]. 2011 Nov [cited 2018 Jul 25]; 32(6):380–98. Available from: http://linkinghub.elsevier.com/retrieve/pii/S1090513811000249

122. Jones A, Jaeger B. Biological Bases of Beauty Revisited: The Effect of Symmetry, Averageness, and Sexual Dimorphism on Female Facial Attractiveness. Symmetry. 2019; 11(2):279.

123. Mogilski JK, Welling LLM. The Relative Importance of Sexual Dimorphism, Fluctuating Asymmetry, and Color Cues to Health during Evaluation of Potential Partners' Facial Photographs: A Conjoint Analysis Study. Hum Nat. Human Nature; 2017; 28(1):53–75. https://doi.org/10.1007/s12110-016-9277-4 PMID: 27752965

124. Graham J, Özener B. Fluctuating Asymmetry of Human Populations: A Review. Symmetry (Basel) [Internet]. 2016; 8(12):154. Available from: http://www.mdpi.com/2073-8994/8/12/154

125. Kavas S, Thornton A. Adjustment and hybridity in Turkish family change: Perspectives from developmental idealism. J Fam Hist. 2013; 38(2):223–41.

126. Sakallı-Uğurlu N. Quantitative Empirical Studies on Women's Issues in Islamic Cultures: Introduction to Special Issue. Sex Roles. 2016; 75(11–12):535–42.

127. Yüksel-Kaptanoğlu İ, Ergöçmen BA. Early Marriage: Trends in Turkey, 1978–2008. J Fam Issues. 2014; 35(12):1707–24.

128. Karandashev V, Zarubko E, Artemeva V, Neto F, Surmanidze L, Feybesse C. Sensory Values in Romantic Attraction in Four Europeans Countries: Gender and Cross-Cultural Comparison. Cross-Cultural Res. 2016; 50(5):478–504.

129. Bánfai Z, Melegh B, Sümegi K, Hadzsiev K, Miseta A, Kásler M et al. Revealing the Genetic Impact of the Ottoman Occupation on Ethnic Groups of East-Central Europe and on the Roma Population of the Area. Frontiers in Genetics. 2019; 10.

130. Iyigun M. Lessons from the Ottoman Harem on Culture, Religion, and Wars. Economic Development and Cultural Change. 2013; 61(4):693–730.

131. Deniz A., Özgür E.M. Rusya'dan Türkiye'ye ulus aşırı göç: Antalya'daki Rus göçmenler. Ege Coğrafya Dergisi 2010; 19(1): 13–30.

132. Deniz A, Özgür E. Antalya'daki Rus Gelinler: Göçten Evliliğe, Evlilikten Göçe. İstanbul Üniversitesi Sosyoloji Dergisi. 2014; 3(27): 175–151.

133. Davidjants B, Ross J. Conflicts in music in the South Caucasus: The case of Armenians and Azerbaijanis. Musicae Scientiae. 2016; 21(4):430–441.

134. Türkmenoğlu Berkan S, Manzakoğlu B. Evil Eye Belief in Turkish Culture: Myth of Evil Eye Bead. Turk Online J Des Art Commun. 2016; 6(2):193–204.

135. Perrett DI, Penton-Voak IS, Little AC, Tiddeman BP, Burt DM, Schmidt N, et al. Facial attractiveness judgements reflect learning of parental age characteristics. Proc R Soc B Biol Sci. 2002; 269 (1494):873–80.

136. Coetzee V, Greeff JM, Stephen ID, Perrett DI. Cross-cultural agreement in facial attractiveness preferences: The role of ethnicity and gender. PLoS One. 2014; 9(7).

137. Danel DP, Fedurek P, Coetzee V, Stephen ID, Nowak N, Stirrat M, et al. A Cross-Cultural Comparison of Population-Specific Face Shape Preferences (Homo sapiens). Ethology. 2012; 118(12):1173–81.

138. Sorokowski P, Kościński K, Sorokowska A. Is beauty in the eye of the beholder but ugliness culturally universal? Facial preferences of polish and yali (papua) people. Evol Psychol. 2013; 11(4):907–25.

139. Rhodes G, Yoshikawa S, Palermo R, Simmonst LW, Peters M, Lee K, et al. Perceived health contributes to the attractiveness of facial symmetry, averageness, and sexual dimorphism. Perception. 2007; 36(8):1244–52. https://doi.org/10.1068/p5712 PMID: 17972486

140. Gray PB, Frederick DA. Body image and body type preferences in st. kitts, caribbean: A cross-cultural comparison with U.S. samples regarding attitudes towards muscularity, body fat, and breast size. Evol Psychol. 2012; 10(3):631–55. PMID: 22995446

141. Mo JJY, Cheung KWK, Gledhill LJ, Pollet T V., Boothroyd LG, Tovée MJ. Perceptions of Female Body Size and Shape in China, Hong Kong, and the United Kingdom. Cross-Cultural Res [Internet]. 2014; 48(1):78–103. Available from: http://journals.sagepub.com/doi/10.1177/1069397113510272

142. Tovée M, Swami V, Furnham A, Mangalparsad R. Changing perceptions of attractiveness as observers are exposed to a different culture☆. Evol Hum Behav [Internet]. 2006 Nov [cited 2018 Jul 26]; 27 (6):443–56. Available from: http://linkinghub.elsevier.com/retrieve/pii/S1090513806000584

143. Swami V. Cultural Influences on Body Size Ideals. Eur Psychol [Internet]. Hogrefe Publishing; 2015 Jan 1 [cited 2018 Jul 26]; 20(1):44–51. Available from: http://econtent.hogrefe.com/doi/abs/10.1027/1016-9040/a000150

144. Schneider TM, Hecht H, Stevanov J, Carbon CC. Cross-ethnic assessment of body weight and height on the basis of faces. Pers Individ Dif. Elsevier Ltd; 2013; 55(4):356–60.

145. Batres C, Kannan M, Perrett DI. Familiarity with Own Population's Appearance Influences Facial Preferences. Hum Nat. Human Nature; 2017; 28(3):344–54. https://doi.org/10.1007/s12110-017-9289-8 PMID: 28516361

146. Thayer ZM, Dobson SD. Geographic Variation in Chin Shape Challenges the Universal Facial Attractiveness Hypothesis. PLoS One. 2013; 8(4):1–5.

147. Young SG, Hugenberg K, Bernstein MJ, Sacco DF. Perception and Motivation in Face Recognition: A Critical Review of Theories of the Cross-Race Effect. Personal Soc Psychol Rev. 2012; 16(2):116–42.

148. Brooks R, Scott IM, Maklakov AA, Kasumovic MM, Clark AP, Penton-Voak IS. National income inequality predicts women's preferences for masculinized faces better than health does. Proceedings Biol Sci [Internet]. The Royal Society; 2011 Mar 22 [cited 2018 Jul 26]; 278(1707):810–2; discussion 813–4. Available from: http://www.ncbi.nlm.nih.gov/pubmed/21147809

149. Batres C, Perrett DI. The influence of the digital divide on face preferences in El Salvador: People without internet access prefer more feminine men, more masculine women, and women with higher adiposity. PLoS One. 2014; 9(7).

150. Pollet T V., Tybur JM, Frankenhuis WE, Rickard IJ. What can cross-cultural correlations teach us about human nature? Hum Nat. 2014; 25(3):410–29. https://doi.org/10.1007/s12110-014-9206-3 PMID: 25092392

151. Basu J, Ray R. Friends and Lovers: A Study of Human Mate Selection in India. Psychol -An Int J Psychol Orient [Internet]. Psychologia Society; 2001 [cited 2018 Jul 26]; 44(4):281–91. Available from: http://joi.jlc.jst.go.jp/JST.JSTAGE/psysoc/2001.281?from=CrossRef

152. Muggleton NK, Fincher CL. Unrestricted sexuality promotes distinctive short- and long-term mate preferences in women. Pers Individ Dif. Elsevier Ltd; 2017; 111:169–73.

153. Bejanyan K, Marshall T, Ferenczi N. Romantic ideals, mate preferences, and anticipation of future difficulties in marital life: a comparative study of young adults in India and America. Frontiers in Psychology. 2014; 5.

154. Bugay A, Delevi R. "How can I say I love you to an American man and mean it?" Meaning of marriage among Turkish female students living in the U.S. Procedia—Social and Behavioral Sciences. 2010; 5:1464–1470.

155. Penton-Voak IS, Perrett DI, Castles DL, Kobayashi T, Burt DM, Murray LK, et al. Menstrual cycle alters face preference. Nature [Internet]. Nature Publishing Group; 1999 Jun 24 [cited 2018 Jul 26]; 399 (6738):741–2. Available from: http://www.nature.com/articles/21557 https://doi.org/10.1038/21557 PMID: 10391238

156. Little AC, Jones BC, Penton-Voak IS, Burt DM, Perrett DI. Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. Proc R Soc B Biol Sci. 2002; 269(1496):1095–100.

157. Little AC, Cohen DL, Jones BC, Belsky J. Human preferences for facial masculinity change with relationship type and environmental harshness. Behav Ecol Sociobiol. 2007; 61(6):967–73.

158. Little AC, Mannion H. Viewing attractive or unattractive same-sex individuals changes self-rated attractiveness and face preferences in women. Anim Behav [Internet]. Academic Press; 2006 Nov 1 [cited 2018 Jul 26]; 72(5):981–7. Available from: https://www.sciencedirect.com/science/article/pii/S0003347206002697?via%3Dihub

159. Boothroyd LG, Jones BC, Burt DM, DeBruine LM, Perrett DI. Facial correlates of sociosexuality. Evol Hum Behav [Internet]. 2008 May [cited 2018 Jul 23]; 29(3):211–8. Available from: http://linkinghub.elsevier.com/retrieve/pii/S1090513808000032

160. Frost P, Kleisner K, Flegr J. Health status by gender, hair color, and eye color: Red-haired women are the most divergent. PLOS ONE. 2017; 12(12):e0190238. https://doi.org/10.1371/journal.pone.0190238 PMID: 29284020

161. Mitra S. 'Miss World' meets 'dutiful daughter-in-law': modernity, marriage, motherhood and the Bollywood female star. Celebrity Studies. 2018; 10(2):228–246.

162. Gelles, Rebecca. Fair and Lovely: Standards of Beauty, Globalization, and the Modern Indian Woman. Independent Study Project (ISP) Collection 2011; 1145.

Appendix

Kleisner, K., Kočnar, T., Tureček, P., Stella, D., Akoko, R. M., Třebický, V., & Havlíček, J. (2017). African and European perception of African female attractiveness. Evolution and Human Behavior, 38(6), 744–755. https://doi.org/10.1016/j.evolhumbehav.2017.07.002

Evolution and Human Behavior 38 (2017) 744–755

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

African and European perception of African female attractiveness

Karel Kleisner [a,*], Tomáš Kočnar [a], Petr Tureček [a], David Stella [a], Robert Mbe Akoko [c], Vít Třebický [a,d], Jan Havlíček [b,d]

[a] Department of Philosophy and History of Sciences, Faculty of Sciences, Charles University in Prague, Czech Republic
[b] Department of Zoology, Faculty of Sciences, Charles University in Prague, Czech Republic
[c] Department of Sociology and Anthropology, Faculty of Social and Management Sciences, University of Buea, Republic of Cameroon
[d] National Institute of Mental Health, Klecany, Czech Republic

ARTICLE INFO

Article history:
Initial receipt 29 September 2016
Final revision received 21 July 2017

Keywords:
Cross-culture
Face
Averageness
Sexual dimorphism
Skin color, fluctuating asymmetry

ABSTRACT

Majority of research on attractiveness is restricted to faces of European origin. The perception of attractiveness may, however, vary across communities due to variations in both facial morphology and local standards of beauty. We investigated the relative contribution of four facial markers of attractiveness based on 101 female facial portraits (standardized, non-manipulated) from Cameroon and Namibia, which were assessed by local male raters and by raters from a distant European population, the Czech Republic. Images from Cameroon include only women of Bantu origin, while Namibians are represented by women of both Bantu (Owambo/Herero) and Nama origin. While controlling for age and BMI, we explored the relationship between female attractiveness and a set of facial traits: fluctuating asymmetry, averageness, shape sexual dimorphism, and skin color (rated and measured in CIELab color space).

In the Cameroonian sample, local male raters favored lighter-skinned female faces with morphology closer to average. The attractiveness of Nama women as rated by Nama men positively correlated with lighter complexion, but this did not extend to rating by Cameroonian men. The attractiveness of Namibian Owambo/Herero women was positively associated with facial femininity and lighter complexion when judged by both Cameroonian and Nama male raters. In all samples, the attractiveness as rated by Czech men was predicted by age and BMI, but not by skin color. We found no significant association between attractiveness and fluctuating asymmetry in any of the tested samples. When controlling for age, the effect of skin color on attractiveness turned to be non-significant in the Owambo/Herrero and Nama sample, but remained significant in the Cameroonian sample. Variations in skin color thus represent an important factor of African female attractiveness within the African context, but they do not seem to affect judgements made by European raters. Sensitivity to some facial markers of female attractiveness thus seems to be restricted to regional populations and/or constrained by shared ethnicity.

1. Introduction

Evidence from many previous studies demonstrates a substantial agreement in preferences regarding facial attractiveness both within and between various human populations (Burke, Nolan, Hayward, Russell, & Sulikowski, 2013; Coetzee, Greeff, Stephen, & Perrett, 2014; Little, Hockings, Apicella, & Sousa, 2012; Rhodes, 2006; Stephen et al., 2012). A crucial question is to what extent are facial preferences universal and whether sensitivity to particular attractiveness cues is adaptive across populations (Pisanski & Feinberg, 2013). A meta-analysis by Langlois et al. (2000) showed a relatively high overall cross-ethnic agreement in the perception of facial attractiveness ($r = 0.88$). This meta-analysis was, however, based mainly on raters who had been exposed to Western standards of beauty and might, as a result, underestimate cross-cultural variations in facial attractiveness judgements. Nevertheless, a relatively high agreement in attractiveness judgements regarding European-looking individuals from the USA (rho = 0.64) was found in raters from Lagos (Nigeria). The agreement was paradoxically lower in attractiveness ratings of Afro-Americans (rho = 0.44) (Martin, 1964). Similar levels of agreement ($r = 0.60$) were found in a cross-cultural comparison of attractiveness ratings of individuals from the USA when they were assessed by people from rural Senegal and the UK (Silva, Lummaa, Muller, Raymond, & Alvergne, 2012). Zebrowitz et al. (2012), on the other hand, found only a moderate agreement between ratings of faces of one's own and the other ethnic group in Tsimané Indians (Bolivia) and people from the USA. Jones and Hill (1993) also found that assessments of facial attractiveness made by the Aché (Paraguay) and Hiwi (Venezuela) Indians corresponded only very weakly with ratings made by Americans,

* Corresponding author at: Department of Philosophy and History of Science, Faculty of Science, Charles University, Viničná 7, 128 44 Prague, Czech Republic.
E-mail address: karel.kleisner@natur.cuni.cz (K. Kleisner).

http://dx.doi.org/10.1016/j.evolhumbehav.2017.07.002
1090-5138/

Russians, and Brazilians (mean $r = 0.13$). Further, Sorokowski, Kościński, and Sorokowska (2013a) observed significant cross-cultural differences in attractiveness ratings between Poles and Yali people (West Papua) when Polish faces were assessed by both Poles and Yalis. These findings show that despite a significant cross-cultural agreement in the perception of attractiveness, there is also substantial amount of variation unique to individual cultures.

Yet although the attractiveness of human faces has been widely studied, evidence is markedly sparse outside the Western world, and while several studies compare attractiveness assessments between African and European/Asian individuals (Coetzee et al., 2014; Jones, 1995; Jones & Hill, 1993; Little, Apicella, & Marlowe, 2007; Martin, 1964; Stephen et al., 2012; Zebrowitz, Montepare, & Lee, 1993), to our best knowledge, there is currently no study comparing the perception of attractiveness among different African populations. Previous research had identified several facial characteristics which are systematically associated with the perception of facial attractiveness, such as averageness, symmetry, sexual dimorphism, as well as skin tone, which in African populations is a highly variable visual trait.

According to the "average is attractive" hypothesis, faces closer to the population mean with low levels of distinctiveness are regarded as more attractive (Alley & Cunningham, 1991; Langlois & Roggman, 1990). It was hypothesized that facial averageness indicates heterozygosity and a greater genetic diversity (Little, Jones, & DeBruine, 2011; Rhodes, 2006; Thornhill & Gangestad, 1999). Faces closer to the average are thus believed to reflect higher biological quality, such as increased immunocompetence and disease resistance (Gangestad & Buss, 1993; Lie, Rhodes, & Simmons, 2008; Little et al., 2011; Thornhill & Gangestad, 1993). The alternative hypothesis, i.e., "attractive faces are not average", may be the result of directional selection towards increasingly juvenile facial features which display a certain level of paedomorphosis or sex-typicality, such as babyfacedness in woman (Alley & Cunningham, 1991). Yet while both factors contribute to facial attractiveness, averageness has been shown to have a larger effect on attractiveness than juvenilization (Wehr, MacDonald, Lindner, & Yeung, 2001).

Faces computer-manipulated to higher averageness have been shown to be positively related to perceived health in both men and women (Rhodes et al., 2001). The association between averageness and attractiveness seems to be more general and hold not only of human faces, but also for instance fishes and even inanimate objects (Halberstadt & Rhodes, 2000; Halberstadt & Rhodes, 2003). When, however, familiarity of the objects is partialized out, association between attractiveness and averageness persists only in animate objects (birds, human faces). This may indicate the existence of an evolved preference for markers of biological quality in objects we encountered in the course of our evolutionary history (Halberstadt & Rhodes, 2003). It has also been proposed that average faces are not attractive because of a preference for a population mean, but due to a symmetry resulting from the mathematical averaging during the preparation of composite images (Alley & Cunningham, 1991; Pittenger, 1991). On the other, it ought to be noted that averageness accounts for a significant part of attractiveness even when the effect of symmetry is controlled for (Rhodes, Sumich, & Byatt, 1999), and although attractive faces tend to be average, the most attractive faces are not the most average ones (Baudouin & Tiberghien, 2004; Perrett, May, & Yoshikawa, 1994).

It has been suggested that high levels of fluctuating asymmetry (FA) indicate developmental instability, that is, an individual's in/ability to cope with stress factors during ontogeny (Özener & Fink, 2010; Thornhill & Gangestad, 1994; Thornhill & Møller, 1997). Low FA is associated with higher attractiveness in both sexes (Hume & Montgomerie, 2001), while high levels of FA have been related to various somatic and mental disorders (Thornhill & Møller, 1997), low intelligence (Banks, Batchelor, & McDaniel, 2010), and lower health assessment (Jones et al., 2001). Pound et al. (2014), however, found no association between low FA and health, while a recent meta-analysis revealed only a weak association between FA and developmental instability (Van Dongen & Gangestad, 2011).

Sexual shape dimorphism has been shown to be systematically associated with female attractiveness as well. Along with sex typicality, more feminine female faces are perceived as more attractive both within and between cultures (Dixson, Little, Dixson, & Brooks, 2017; Jones & Hill, 1993; Perrett et al., 1998; Rhodes, 2006; Scott, Swami, Josephson, & Penton-Voak, 2008). The association between sexual dimorphism and facial attractiveness, on the other hand, seems to vary across cultures and it has recently been suggested that it is an evolutionarily novel feature which emerged in urban Western societies (Scott et al., 2014). Moreover, the link between the degree of sexual dimorphism and attractiveness may be more complex due to various methodological issues in femininity/masculinity measurements (Mitteroecker, Windhager, Müller, & Schaefer, 2015).

Attractiveness research conducted predominantly in European populations led to a certain underestimation of the variation in skin color as an important marker of attractiveness. Nevertheless, skin color seems to be a crucial component of facial attractiveness in populations with a high variation of this trait, for instance, among Indian (Badaruddoza, 2007), Japanese (Hulse, 1967; Wagatsuma, 1967), Chinese (Dixson, Dixson, Li, & Anderson, 2007a), island communities in Vanuatu (Dixson et al., 2017), people of New Zealand and U.S.A. (Dixson, Dixson, Bishop, & Parish, 2010), and various African populations (Coetzee et al., 2012; Coetzee et al., 2014; Dixson, Dixson, Morgan, & Anderson, 2007b). Preference for lighter skin in women – but not men – has appeared independently (convergently) in Asia and Europe (Lie et al., 2008). This preference appears to predate colonialism and the introduction of Western standards of beauty (Wagatsuma, 1967). Irrespective of ethnicity, women after puberty have on average a lighter complexion than their male counterparts. This dimorphism in skin pigmentation has been interpreted as a result of sexual selection to facilitate male attraction to females (Van den Berghe & Frost, 1986). Skin color has been shown to be a marker of attractiveness and perceived current health status for both Europeans and Africans when judging faces from one's own population (Coetzee et al., 2012; Stephen, Coetzee, Smith, & Perrett, 2009).

Existing research brings compelling evidence that facial averageness, symmetry, sexual dimorphism, as well as skin color influence human mating preferences and most likely have an adaptive value (Danel, Dziedzic-Danel, & Kleisner, 2016; Jones & Hill, 1993; Little et al., 2007; Little et al., 2011; Rhodes, 2006; Swami et al., 2008; Thornhill & Gangestad, 1999, but see also Foo, Simmons, & Rhodes, 2017; Silva et al., 2012). Even so, a comparison with facial attractiveness perception among various African populations seems to be lacking. In this study, we investigate four facial markers such as fluctuating asymmetry, averageness, shape sexual dimorphism, and skin color controlled for BMI and age for female facial attractiveness assessment in two African populations as perceived by raters from Namibia, Cameroon, and the Czech Republic. Based on previous studies, we expect that male raters from all cultures will prefer more average and more feminine female faces with low levels of fluctuating asymmetry. We also hypothesize that African raters will be more sensitive to variation in skin color while Czech raters will not utilize skin color as a cue to attractiveness judgment.

2. Material and methods

2.1. Acquisition of facial images

We collected facial portraits of 102 Cameroonian participants (51 women: Mean Age ± SD = 24.92 ± 8.4, range: 17–54; 52 men: Mean Age ± SD = 23.75 ± 5.49, range 17–44) and 98 Namibian participants (50 women: Mean Age ± SD = 23.28 ± 3.87, range 18–30; 48 men: Mean Age ± SD = 23.04 ± 3.59, range 18–30). The Namibian sample consisted of a subset of 18 Owambo/Herero women

(Mean Age ± SD = 25.47 ± 3.36, range: 18–30) and 32 Nama women (Mean Age ± SD = 22.11 ± 3.65, range: 18–30). Cameroonian and Owambo/Herero people are both of Bantu origin, while the Nama belong to the Khoikhoi ethnolinguistic group. Cameroonian data were collected in the regional capital town of Buea, which is located in the English-speaking Southwest Region. The town of Buea is the site of several universities and has recently attracted people from various parts of Cameroon. The selection of participants for our research took into consideration this ethnic diversity by ensuring that various groups living in Cameroon were represented in the sample. Images of the Namibian participants were acquired in the suburban township Tseiblaagte in the Karas region in southern Namibia.

Facial portraits were collected using a standardized procedure (Třebický, Fialová, Kleisner, & Havlíček, 2016). Participants were photographed in front of a white background in full color with a DSLR camera, using studio electronic flash and an oval collapsible reflector. The subjects were asked to adopt a neutral, non-smiling expression, and to remove any facial cosmetics, jewelry, or other decorations. The photographs were adjusted so as to place the eyes horizontally at the same height and leave a standard length of neck visible.

For the purposes of this study, only facial portraits of women were rated for attractiveness. Photographs of men were used only as a reference to compute the scores of shape sexual dimorphism (morphological femininity) of women's faces.

2.2. Ratings of facial images

Facial portraits were assessed for attractiveness by a panel of male raters from Namibia, Cameroon, and the Czech Republic. Facial images of Namibian women were rated by 20 Namibian men (all of them of Nama ethnicity; Mean Age ± SD = 22.19 ± 4.62, range 18–36, one of these raters rated all faces with the same number and was excluded from further analyses; 19 raters were used), 50 Cameroonian men (Mean Age ± SD = 23.74 ± 5.55, range 17–44), and 36 Czech men (Mean Age ± SD = 21.5 ± 2.35, range 18–27). Photos of the Cameroonian women were rated by 48 Cameroonian men (Mean Age ± SD = 22 ± 2.18, range 17–30) and 70 Czech men (Mean Age ± SD = 23.29 ± 7.11, range 16–56).

The raters assessed the whole set of either 51 Cameroonian or 50 Namibian female photographs for attractiveness on a seven-point scale, where 1 represented very unattractive and 7 very attractive. Each rater viewed facial images on a computer screen. There was no time limit on the rating process. Order of the photographs was randomized for each rating session. If a rater was acquainted with the person on the photo, he was told not to rate it.

2.3. Skin color measurement and assessment

Participants' facial skin color was measured on three different patches on human face (forehead, left and right cheek) in CIELab color space (Hunter, 1958). Perimeter of analyzed patch was set to 1200 px, i.e., XY lengths around 300 px. We computed lightness (L^*) grand mean of all three patches for each individual. Mean values of lightness (L^*) were recorded and used for further analysis. All measurements were taken from images standardized in color using Image J software (Schneider, Rasband, & Eliceiri, 2012).

Skin color was also assessed by six researchers from the Faculty of Sciences, Charles University, Prague, for lightness using five-point scale, where 1 means very light and 5 very dark skin color. Mean scores of assessed lightness strongly correlated with lightness measurement in the CIELab color space (see Table 1).

Samples showed very similar levels of variation of skin lightness (CV = 0.16 in Cameroonian, 0.18 in Nama, and 0.19 in Owambo/Herero sample). The mean deviation from sample means (4.62 in Cameroonian, 5.78 in Nama, 3.96 in Owambo/Herrero) did not differ significantly between the samples ($F_{2,\,98} = 1.63$, $p = 0.2$).

2.4. Geometric morphometrics

Methods of geometric morphometrics were applied to measure the shape variation of faces, their level of fluctuating asymmetry, and sexual shape dimorphisms. Frontal portraits were landmarked twice in order to determine any measurement error between replicates during the computation of fluctuating asymmetry. Landmarks are anatomically, or at least geometrically, corresponding homologous points in different individuals, while semilandmarks denote curves and outlines. We used landmark and semilandmark locations on human faces as defined in our previous work (Danel et al., 2016; Kleisner, Priplatova, Frost, & Flegr, 2013; Linke, Saribay, & Kleisner, 2016). All configurations of landmarks and semilandmarks were superimposed by generalized Procrustes analysis (GPA) using the "gpagen" function implemented in the geomorph package in R (Adams & Otárola-Castillo, 2013). This procedure converted all specimens to the origin, standardized the size of facial configurations, and optimized their rotation until the coordinates of corresponding points aligned as closely as possible. Semilandmarks were allowed to slide along tangents to a curve to minimize bending energy between each specimen and the Procrustes mean shape. Mean configuration (consensus) was computed separately for each set of photos. "Averageness" score was computed as Procrustes distances between the mean shape and each configuration in the set. In this way, a higher score indicates a lower facial averageness.

To measure the degree of sexual shape dimorphism (morphological femininity), we calculated a mean shape separately for male and female configurations. The position of an individual face along the axis connecting the male and female mean shape then defined its degree of geometric sexual dimorphism (Mitteroecker et al., 2015; Valenzano, Mennucci, Tartarelli, & Cellerino, 2006). This position, i.e., degree of geometric femininity (femaleness), can be mathematically represented by individual scores of ordination constrained by sex. This was done using the "rda" function provided by the Vegan package (Oksanen et al., 2016).

Fluctuating asymmetry was computed by Procrustes ANOVA analysis implemented in MorphoJ, version 1.06d. Shape coordinates of both the original and the mirrored configurations (i.e., configurations reflected along the axis of symmetry and relabeled) were used as an independent variable (Klingenberg & McIntyre, 1998; Mardia, Bookstein, & Moreton, 2000). In the ANOVA design, the main effect of "individuals" is a variation among individuals corrected for any effect of asymmetry, while the main effect of sides corresponds to the average difference between the left and right side of the face (directional symmetry). Fluctuating asymmetry was quantified as an interaction between the main effects of "individuals" and "sides". Measurement error was computed from variations between replicate measurements (Klingenberg, Barluenga, & Meyer, 2002). Scores of fluctuating asymmetry were saved and used for further analysis (higher scores indicated higher facial fluctuating asymmetry).

2.5. Statistics

Relationship between variables was investigated using Pearson's zero order correlation coefficient. For this purpose, average ratings were calculated for individual pictures. Ratings by individuals from different cultures were calculated separately. Inter-rater agreement was calculated using Cronbach's alpha. The coefficient of variation (CV) was used to compare variability of skin lightness (L^* measured in CIELab color space) between three samples. Mixed-effect models were run to investigate the influence of individuals' facial features on the perceived attractiveness. Random effects of individual raters and stimuli were included in the models. In each test, variables which were not set as a fixed effect and regressed on ratings were also treated as random effects. Mixed-effect models were conducted for each available combination of raters and stimuli set separately. Continuous variables were standardized prior to the analysis.

Table 1
Descriptive values of all variables, and Pearsons's correlations between Male-rated attractiveness and anthropometric traits.

Nama photos ($N = 32$)	NAM-Attr.	CMR-Attr.	CZE-Attr.	Age	BMI	Fluctuating assymetry	SSh dimorph.	Averageness	Rated lightness	CIELab L*
Mean ± SD	3.28 ± 0.71	2.88 ± 0.8	2.35 ± 0.58	22.11 ± 3.65	21.28 ± 4.84	0.022 ± 0.01	−1831 ± 66.2	0.056 ± 0.012	2.64 ± 0.96	38.70 ± 6.97
NAM-Attr.		0.77***	0.59***	−0.41*	−0.27	0.13	−0.07	0.02	−0.46**	0.44*
CMR-Attr.			0.78***	−0.54**	−0.16	0.24	−0.23	−0.12	−0.27	0.31***
CZE-Attr.				−0.55**	−0.31	0.12	−0.18	−0.20	0.05	−0.03
Age					0.43*	−0.17	0.09	0.26	0.41*	−0.42*
BMI						0.32	0.11	0.40*	0.31	−0.25
Fluctuating assymetry							−0.09	0.21	−0.03	−0.06
SSh dimorphism								0.18	−0.02	−0.02
Averageness									−0.06	−0.19
Rated lightness										−0.87***
Owambo/Herrero photos ($N = 18$)	**NAM-Attr.**	**CMR-Attr.**	**CZE-Attr.**	**Age**	**BMI**	**Fluctuating assymetry**	**SSh dimorph.**	**Averageness**	**Rated lightness**	**CIELab L***
Mean ± SD	2.75 ± 0.58	2.66 ± 0.66	2.36 ± 0.39	25.47 ± 3.36	23.07 ± 5.88	0.022 ± 0.01	−1810 ± 70.4	0.056 ± 0.13	4.1 ± 0.72	26.08 ± 4.97
NAM-Attr.		0.81***	0.40***	−0.62*	0.08	0.30	−0.48.	0.12	−0.71**	0.61**
CMR-Attr.			0.67**	−0.71**	−0.32	0.32	−0.63*	0.22	−0.64**	0.54*
CZE-Attr.				−0.49.	−0.66**	0.28	−0.26	0.08	−0.11	0.03
Age					0.41	−0.33	0.17	−0.20	0.57*	−0.61*
BMI						−0.30	−0.01	−0.17	−0.07	0.01
Fluctuating assymetry							−0.65**	0.43	−0.45***	0.35
SSh dimorphism								−0.44***	0.47***	−0.26
Averageness									−0.15	0.10
Rated lightness										−0.93***
Cameroonian photos ($N = 51$)	**NAM-Attr.**	**CMR-Attr.**	**CZE-Attr.**	**Age**	**BMI**	**Fluctuating assymetry**	**SSh dimorph.**	**Averageness**	**Rated lightness**	**CIELab L***
Mean ± SD	NA	3.81 ± 0.67	2.32 ± 0.71	24.92 ± 8.4	25.84 ± 5.15	0.018 ± 0.01	−3662 ± 86	0.055 ± 0.012	3.28 ± 0.89	38.0 ± 6.1
NAM-Attr.		NA	NA	NA	NA	NA	NA	NA	NA	NA
CMR-Attr.			0.55***	−0.34*	−0.27***	−0.07	0.01	−0.30*	−0.54**	0.45**
CZE-Attr.				−0.54***	−0.55***	−0.17	0.02	−0.18	0.03	0.02
Age					0.51***	0.24***	−0.12	0.17	0.00	−0.01
BMI						−0.04	−0.02	0.15	0.01	0.14
Fluctuating assymetry							−0.16	0.29*	0.04	−0.09
SSh dimorphism								−0.14	0.13	−0.12
Averageness									0.18	−0.12
Rated lightness										−0.74***

Attr. = average attractiveness rating, NAM = Namibia, CMR = Cameroon, CZE = Czech Republic, BMI = body mass index, SSh dimorph. = sexual shape dimorphism, CIELab L* - Skin lightness measured in CIELab color space, Correlation coefficients significantly different from 0 are indicated.
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Further, we used path analysis to investigate directed dependencies between perceived attractiveness (averaged ratings), skin color, and age of the photographed individuals. Skin color was set as a mediator between the age and perceived attractiveness. The direct effect between the age and perceived attractiveness was also included in the model. BMI is often correlated with both age and attractiveness, but also with skin color (Armstead, Hébert, Griffin, & Prince, 2014; Löffler, Aramaki, & Effendy, 2002). We therefore ran the same path analyses with BMI as an additional mediator which affects lightness and attractiveness and is age-dependent. Finally, we also ran similar analyses using structural equation modeling to test whether possible loss of information in path analysis which used averaged ratings did not bias the pattern of the results (Fig. 2). Attractiveness was modelled as a latent variable measured by independent ratings. Only those raters who evaluated all faces were included in the analysis and, as mentioned above, one Namibian rater was excluded. The same analyses were run with constrained factor loadings. This approach gave us the results of mixed-effect path analysis with participants' preferences and rating tendencies treated as a random effect. All variables were standardized prior to analyses. Path analyses and structural equations models were conducted using the “sem” function implemented in the “lavaan” package within R software for statistical computing (Rosseel, 2012). Output visualizations were generated using the “semPlot” package and subsequently edited by CorelDRAW 12 software.

3. Results

Cronbach's alpha showed a high inter-rater agreement for Nama raters judging the attractiveness of Nama ($\alpha = 0.83$) and Owambo/Herrero photographs ($\alpha = 0.82$), for Czech raters judging Nama ($\alpha = 0.94$), Owambo/Herrero ($\alpha = 0.86$) and Cameroonian photographs ($\alpha = 0.98$), as well as for Cameroonian ratings of Nama ($\alpha = 0.98$), Owambo/Herrero ($\alpha = 0.96$), and Cameroonian ($\alpha = 0.96$) female photographs. Correlations between African raters were generally higher (for Nama photos: $r = 0.77$ and for Owambo/Herrero photos: $r = 0.81$) than between African and Czech raters ($r = 0.40$–0.78).

Descriptive values of all variables as well as Pearson's zero order correlations between male-rated attractiveness and anthropometric measurements are summarized in Table 1. Average ratings from all three cultures were strongly correlated. Rated skin lightness strongly correlated with measured skin lightness in all three samples. Fluctuating asymmetry did not seem to have any significant effect on attractiveness ratings in either of the photosets. The more feminine Owambo/Herrero faces were judged to be significantly more attractive by Cameroonian raters and a similar trend was observed in the Namibian raters, while Czech ratings did not show a significant association. No significant association between femininity and attractiveness was observed in a set of Nama and Cameroonian faces. Faces closer to the average were rated as more attractive only when Cameroonians rated Cameroonian female

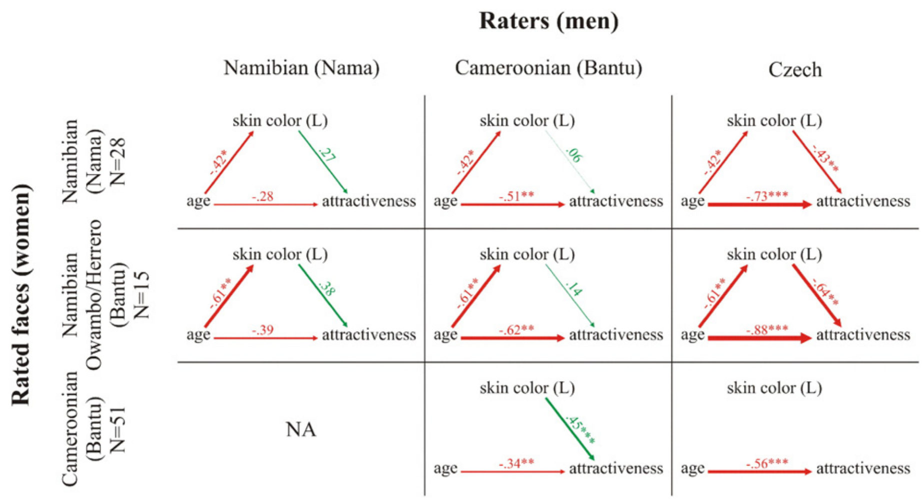

Fig. 1. Results of the path analyses between age, skin color, and perceived attractiveness. Labels on the edge indicate estimated correlation coefficients in a standardized model, positive correlation being green, negative red. Asterisks represent the level of significance ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$) of correlation coefficients being different from 0. For estimated $r < 0.05$, arrows are not shown at all.

photographs. Skin lightness was negatively correlated with age in the Nama and Owambo/Herrero photographs. Besides age, skin lightness seems to be the strongest correlate of attractiveness as judged by African raters. Czech ratings, on the other hand, show no correlation with skin color.

Mixed-effect models corroborated pattern of the results reported above and did not provide any additional information to simple correlational analysis (Table 1). This is most likely due to high inter-rater agreement (see above). Complete results of mixed-effect models are summarized in the appendix (Table 2).

We used a path analysis to trace interrelations between attractiveness, skin lightness, age, and BMI. First, we analyzed associations between age, skin lightness, and perceived attractiveness separately for each group of female photographs (Nama, Owambo/Herrero, and Cameroonians) as rated by Nama, Cameroonian, and Czechs male raters. The results are summarized in Fig. 1.

When judged by African raters (from Cameroon or Namibia), facial attractiveness always positively correlated with skin lightness (although in most cases non-significantly). Czech ratings, on the other hand, show either the opposite or no association with skin lightness. Age was significantly associated with both attractiveness and skin lightness in both Namibian sets. In Cameroonians, age also correlated with attractiveness, but showed no association with skin lightness.

After the inclusion of BMI into path analyses, the relationship between age, skin lightness, and perceived attractiveness still followed the same pattern. Fewer parameters were, however, significantly different from zero due to a greater number of equations in the model. All these path models were also executed using latent variable modeling and mixed-effect approach. These results were highly similar to results yielded by simple path analysis. Results of all the analyses with BMI and path analyses based on structural equation modeling are reported in the Appendix (Fig. 3-7).

4. Discussion

Our study provides further empirical support for a claim that despite substantial generalizability of attractiveness assessment across cultures, some facial characteristics are not universally linked to perceived attractiveness, and their role tends to vary due to exposure to different environmental and socio-cultural factors. The effects of three shape traits and skin color were examined in relation to facial attractiveness as rated by African and European men. Of the four traits we followed, skin color seemed especially important when African female attractiveness was assessed by African male raters. In their rating, lighter skin was associated with higher attractiveness. When controlling for age, association between attractiveness and skin lightness remained significant only for the Cameroonian sample. In the Nama and Owambo/Herrero photographs, the effect of skin color on attractiveness was strongly confounded by age. The other three facial markers of facial attractiveness – fluctuating asymmetry, shape sexual dimorphism, and averageness – had only a weak or no significant effect on perceived facial attractiveness.

A significant association between averageness and attractiveness was found only in faces of Cameroonian women rated by Cameroonian men. This may either indicate that Czech raters (Namibians did not rate Cameroonian faces) did not have enough visual experience with Cameroonians for creating a norm of a prototype, or preferred less prototypical faces at the expense of other facial characteristics, such as femininity. The latter explanation, however, does not seem to be supported by our results because Czech raters did not associate attractiveness with sexual dimorphism. Alternatively, averageness was not preferred because it does not reflect the biological quality of an individual: in fact, a recent study reports a negative relationship between averageness and semen quality (Foo et al., 2017).

Namibian and Cameroonian raters preferred more feminine faces, although the results were significant only for the Owambo/Herrero women. Reported signals for male raters' preference for feminine traits are thus either weak or null. Nevertheless, the attractiveness of traits associated with sexual dimorphism may depend on environmental conditions (Scott et al., 2008). This explanation finds support in some cross-cultural research on preferences for physical features of bodies (Tovée, Swami, Furnham, & Mangalparsad, 2006). As shown in male faces, women's preferences for cues to high testosterone significantly vary with pathogenic stress and societal development (Moore et al., 2013). In contrast, Scott et al. (2014) based on cross-cultural evidence suggest that preference for sexually dimorphic traits occurs mainly in developed urban populations and might thus be relatively novel. Furthermore, perception of sexually dimorphic traits unusual by Western standards can also play a role, as evidenced by the preference and actual choice of body height in Tanzanian Hadza people (Sear & Marlowe, 2009) and by body height preference in the Namibian Himba people (Sorokowski, Sorokowska, Danel, Mberira, & Pokrywka, 2012a; Sorokowski, Sorokowska, Fink, & Mberira, 2012b). Similarly, also among the Himba people, both men and women with a more masculine 2D:4D were more likely to be married, though not necessarily to each other (Sorokowski et al., 2012a, 2012b). In some traditional societies, we find not only the perception but also atypical expression of certain dimorphic traits:

for instance, Hadza men do not have more masculine digit ratios than women (Apicella, Tobolsky, Marlowe, & Miller, 2016). Nonetheless, reasons for the equivocal preference of facial femininity by Cameroonian and Namibian raters remain to be discovered. The findings of Scott et al. (2014) suggest that a possible explanation may be that these populations are transiting from rural to urban lifestyle, and preferences are therefore not clearly biased to either masculine or feminine traits.

In contrast to several previous studies (Abend, Pflüger, Koppensteiner, Coquerelle, & Grammer, 2015; Grammer & Thornhill, 1994; Komori, Kawamura, & Ishihara, 2009; Perrett et al., 1999; Rhodes et al., 2001), our results showed no significant association between FA and attractiveness in either of the studied cultures. In their cross-cultural comparison, Hill et al. (2016) overall found evidence for association between vocal attractiveness and FA, but –probably due to a low sample size – they were not able to demonstrate such an association for the Hadza individuals. Likewise, no association between FA and facial attractiveness has been found by Van Dongen (2014), who used the same method of FA computation as we did and worked with a sample size of 200 subjects. The null results might be also due to the fact that FA seems to be a weak proxy to developmental instability, especially when applied to modest sample sizes (Van Dongen & Gangestad, 2011). Evidence that fluctuating asymmetry is related to attractiveness or reflects mate quality thus seems equivocal (Farrera, Villanueva, Quinto-Sánchez, & González-José, 2015; Gangestad, Thornhill, & Yeo, 1994; Van Dongen, 2012). These results also do not contradict cross-cultural preference for total symmetry, which is documented not only in Western populations but also in a relatively isolated hunter-gatherer population (Little et al., 2007).

To understand the differences in association between attractiveness and skin color in women, two questions need to be answered. Why do Czech raters show limited or no sensitivity to skin color when rating African women? Why do African raters systematically prefer lighter women? First of all, Czech men show either no preference for lighter skinned individuals or tend to prefer the darker Owambo/Hererro and Nama women when their attractiveness is controlled for age. It could be explained by the fact that Czechs do not perceive any connection between skin color and youthfulness. This is probably due to a low variation of skin color in the Czech (and most of European) population, which also corresponds to a low level of exposure to variation in skin color and its social cueing.

The second question seems to be more complex. We need to consider the positive correlation between skin lightness and age of women in the Owambo/Herrero and Nama samples. Women with a lighter complexion were rated as more attractive because they are most likely perceived as younger, since skin color may be a reliable cue to age. Variation in skin color may thus serve as a cue of youthfulness, which may also reflect women's residual reproductive capacity (Van den Berghe & Frost, 1986). A significant correlation between age and skin color explains why a positive association between attractiveness and skin lightness is not significant for the Owambo/Herrero and Nama photographs when controlling for the age. The lack of association between age and skin color in the Cameroonian sample, on the other hand, explains why the effect of skin lightness on attractiveness remains significant within this sample. We do not, however, know why age is associated with Namibian photographs of women of Bantu and Nama origin, but not in Cameroonian (Bantu) women. Moreover, a darkening of skin color with increasing age has been reported also in African-American, European, and Asian populations (De Rigal et al., 2010). Age is further associated with imperfections in the homogeneity of skin color distribution which negatively influence the judgments of attractiveness, health, and youth (Fink, Grammer, & Matts, 2006; Matts, Fink, Grammer, & Burquest, 2007). The relationship between ageing and changes in skin color may vary across human populations and more data is needed to satisfactorily explain this issue.

Nevertheless, the significant positive relationship between skin lightness and perceived attractiveness of Cameroonian women may indicate that residual reproductive capacity need not be solely determined by age. It has been reported that women's skin darkens during the infertile phases of the menstrual cycle, during pregnancy, and when women use hormonal contraceptives (Muzaffar, Hussain, & Haroon, 1998; Steinberger, Rodriguez-Rigau, Smith, & Held, 1981; Van den Berghe & Frost, 1986). There is room for a study which would investigate the relationship between skin color and various predictors of residual reproductive capacity, such as the number of children, subsistence, health indicators, and the like. For instance, lighter skin may offer an advantage in the context of photosynthesis of vitamin D, a vitamin which helps the absorption of calcium (Chaplin & Jablonski, 2009; Jablonski & Chaplin, 2000; Jablonski & Chaplin, 2010). Moreover, vitamin D requirements are elevated during pregnancy and lactation (Boyle, 2014; Dror, 2013). On the other hand, skin depigmentation seems to be constrained by the disadvantage brought about by the photolysis of folic acid (folate), an essential precursor necessary for the correct functioning of many processes which are part of embryonic development (Cohn, 2002; Jablonski & Chaplin, 2000). It should be further investigated how these "physiological explanations" correspond to local perception of women's attractiveness.

Explanations of preference for lighter skin in women of non-European origin often refer to various notions of cultural dominance and/or consequences of contact with other cultures (Martin, 1964; Sorokowski, Sorokowska, & Kras, 2013b). Yet lighter skin in women has been associated with beauty in several mutually independent traditional societies ever since the pre-colonial era and African preferences seem to conform to this general pattern (Ardener, 1954; Van den Berghe & Frost, 1986; Wagatsuma, 1967). Despite some consensus in facial attractiveness attributions among cultures, the pervasive Europocentric view of female attractiveness cannot be simply expanded to other cultures without further ado. Western researchers should be better acquainted with indigenous African conceptions of female attractiveness, which are attuned to a more graded skin color perception as reflected in local languages, music, and other cultural sources (Tembo, 2010).

Insufficient statistical power due to a low sample size (especially in Owambo/Herrero sample) may be responsible for some negative results regarding the association between attractiveness and fluctuating asymmetry, facial femininity, and averageness. Skin color, on the other hand, had a decisive effect on African perception of women's attractiveness based on the same sample size. Moreover, sexual dimorphism has been reported to have a significant effect on attractiveness only in studies which manipulate only this particular factor while other variables remain fixed (Penton-Voak & Perrett, 2000; Perrett et al., 1998; Scott, Pound, Stephen, Clark, & Penton-Voak, 2010). Natural variation in non-manipulated stimuli may conceal a possible effect on attractiveness. Despite some limitations, our results do show a general pattern. While Nama men tend to use a variation in skin color as a marker of attractiveness irrespective of ethnicity, Cameroonian men seem to be more sensitive to skin color in Bantu women. Our study focused primarily on the perception of African faces by both African and European raters. A complementary design which would study the perception of European faces by both African and European raters was beyond the scope of the current study. Moreover, studies of this kind have been undertaken by other researchers in several African locations (Apicella, Little, & Marlowe, 2007; Jones & Hill, 1993; Little & Apicella, 2016; Sorokowski et al., 2012a, 2012b).

To sum up, it seems that both place of origin and shared ethnicity influence the relative contribution of some facial markers to perception of female attractiveness. The interplay between ethnicity, age, and attractiveness may therefore be more complex than previously thought. One conclusion, however, can be firmly stated: raters from populations with high variation in skin color tend to perceive individuals with lighter skin as more attractive, whereas raters without such experience do not, and this hold regardless of the actual causal chain which may underlie this phenomenon.

Data availability

Supplementary data to this article are available online at https://figshare.com/s/62f06061cf7ceaf01429.

Funding

This study was supported by the Czech Science Foundation project GA15-05048S.

Acknowledgements

We wish to thank Rosina Jash for help with data collection in Namibia and Jana Vokurková for assistance with research in Cameroon. We also thank two anonymous reviewers for their helpful suggestions.

Appendix A

Table 2
Results of mixed–effect models investigating the relationship between several variables and rating of attractiveness. Tests were conducted for each available combination of raters and stimuli set. Random effects of rater and face intercepts were included in the models. All variables were standardized prior to analyses. Due to the fact, that we conduct 6 tests on one dataset, the significance should be interpreted with caution.

Namibian (Nama $N = 28$) women rated by Namibian (Nama $N = 19$) men				
	Estimate	Std. Err.	t-Value	*p*-Value
Age	−0.30	0.13	−2.31	0.03^{*}
BMI	−0.20	0.13	−1.50	0.14
Fluct.	0.09	0.14	0.62	0.57
SSh dim.	−0.05	0.13	−0.38	0.70
Aver.	0.02	0.14	0.18	0.86
CIELab L*	0.29	0.13	2.23	0.03^{*}

Namibian (Nama $N = 28$) women rated by Cameroonian (Bantu $N = 50$) men				
	Estimate	Std. err.	t-Value	*p*-Value
Age	−0.40	0.13	−3.09	0.00^{**}
BMI	−0.11	0.15	−0.77	0.45
Fluct.	0.19	0.15	1.28	0.22
SSh dim.	−0.17	0.14	−1.21	0.23
Aver.	−0.00	0.15	−0.03	0.98
CIELab L*	0.16	0.15	1.12	0.29

Namibian (Nama $N = 28$) women rated by Czech ($N = 36$) men				
	Estimate	Std. Err.	t-Value	*p*-Value
Age	−0.31	0.09	−3.13	0.00^{**}
BMI	−0.17	0.10	−1.59	0.13
Fluct.	0.04	0.11	0.39	0.71
SSh dim.	−0.09	0.10	−0.89	0.38
Aver.	−0.08	0.11	−0.73	0.47
CIELab L*	−0.13	0.11	−1.25	0.24

Namibian Owambo/Herrero (Bantu $N = 15$) women rated by Namibian (Nama $N = 19$) men				
	Estimate	Std. err.	t-Value	*p*-Value
Age	−0.32	0.11	−2.96	0.01^{**}
BMI	0.22	0.10	2.23	0.11
Fluct.	0.21	0.12	1.72	0.11
SSh dim.	−0.32	0.12	−2.70	0.03^{*}
Aver.	0.00	0.13	0.07	0.95
CIELab L*	0.32	0.10	3.26	0.01^{**}

Namibian Owambo/Herrero (Bantu $N = 15$) women rated by Cameroonian (Bantu $N = 50$) men				
	Estimate	Std. err.	t-Value	*p*-Value
Age	−0.43	0.11	−3.82	0.00^{**}
BMI	0.03	0.10	0.28	0.81
Fluct.	0.09	0.12	0.80	0.49
SSh dim.	−0.28	0.11	−2.47	0.02^{*}
Aver.	−0.14	0.09	−1.52	0.22
CIELab L*	0.24	0.10	2.35	0.03^{*}

Namibian Owambo/Herrero (Bantu $N = 15$) women rated by Czech ($N = 36$) men				
	Estimate	Std. Err.	t-Value	*p*-Value
Age	−0.18	0.08	−2.10	0.05^{*}
BMI	−0.22	0.07	−3.19	0.01^{**}
Fluct.	0.08	0.09	0.84	0.57
SSh dim.	−0.06	0.10	−0.62	0.71
Aver.	−06	0.08	−0.71	0.58
CIELab L*	0.11	0.09	−1.29	0.29

Cameroonian (Bantu) women rated by Namibian men
NA

Cameroonian (Bantu $N = 51$) women rated by Cameroonian (Bantu $N = 48$) men				
	Estimate	Std. Err.	t-Value	*p*-Value
Age	−0.18	0.07	−2.60	0.01^{*}
BMI	−0.14	0.07^{***}	−1.87	0.07
Fluct.	−0.03	0.07	−0.47	0.64
SSh dim.	−0.00	0.07	−0.02	0.98
Aver.	−0.15	0.07	−2.22	0.03^{*}
CIELab L*	0.27	0.06	4.52	0.00^{***}

Cameroonian (Bantu $N = 51$) women rated by Czech ($N = 70$) men				
	Estimate	Std. Err.	t-Value	*p*-Value
Age	−0.28	0.06	−0.4.74	0.00^{***}
BMI	−0.27	0.06	−4.63	0.00^{***}
Fluct.	−0.07	0.07	−1.11	0.28
SSh dim.	0.01	0.07	0.22	0.85
Aver.	−7.15	5.99	−1.19	0.26
CIELab L*	0.04	0.07	0.51	0.64

BMI = body mass index, Fluct. = fluctuating asymmetry, SSh dim. = sexual shape dimorphism, Aver. = averageness (lower number means more average face), CIELab L* - Skin lightness measured in CIELab color space.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

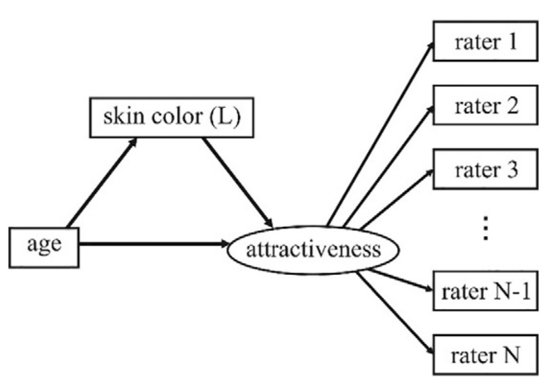

Fig. 2. Structural Equation model (SEM) used in the analysis of the relationship between 2 measured variables (age and skin color) and attractiveness measured by individual ratings on N raters. Each rater included in the analysis rated all faces in the set. In standard path analysis attractiveness was calculated as mean rating. In SEM approach attractiveness was modelled as a latent variable loaded with N factors – raters. In mixed-effect path analysis, the factor loadings were constrained.

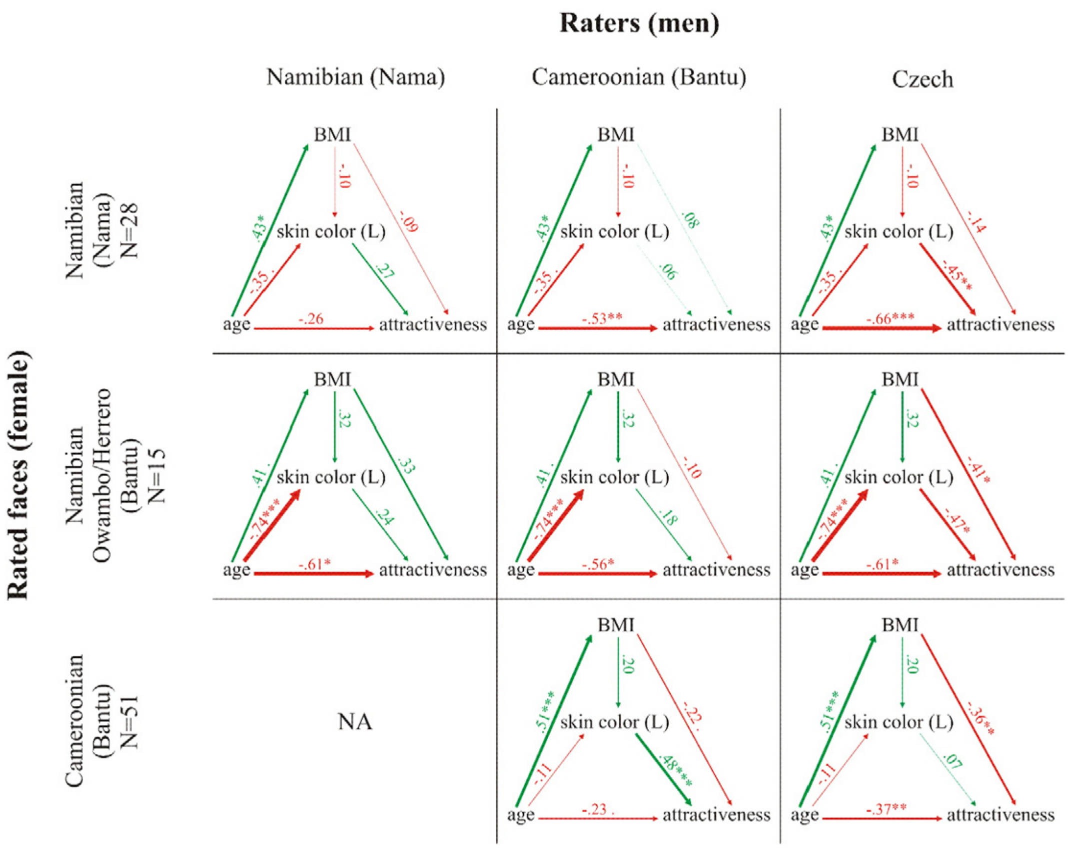

Fig. 3. The results of the path analyses between age, BMI, skin color and perceived attractiveness (averaged ratings). The edge labels indicate estimated correlation coefficients in standardized model, positive correlations are green, negative red. The asterisks represent the level of significance ($p < 0.10.$, $p < .05^*$, $p < .01^{**}$, $p < .001^{***}$) of the correlation coefficients being different from 0. For estimated r < 0.05 the arrows are not shown.

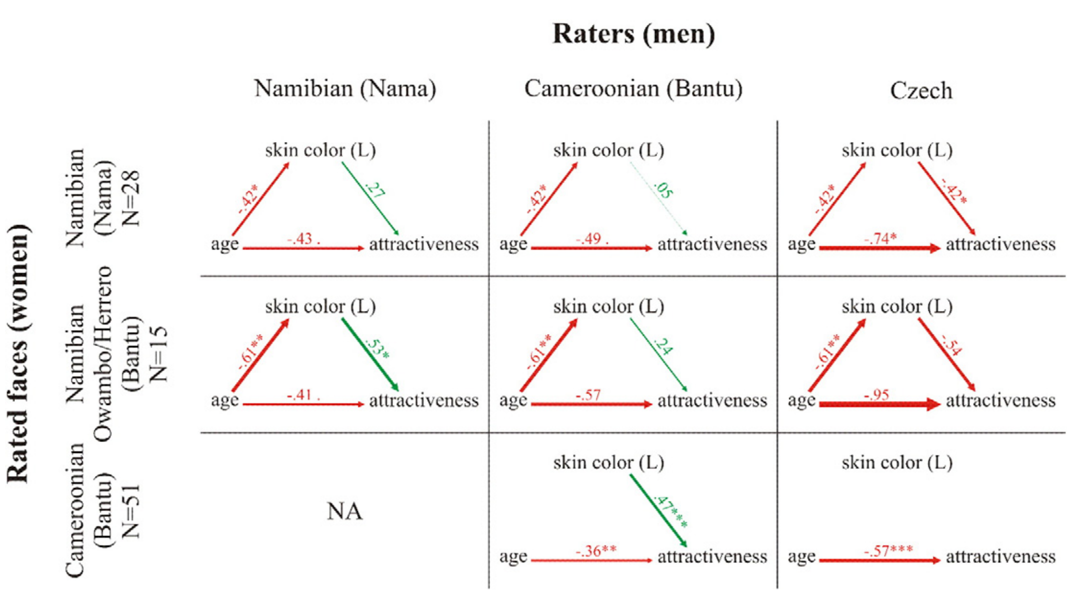

Fig. 4. The results of the latent variable model with measured age and skin color and attractiveness as latent variable measured by ratings of N raters (only relationships between age, L and latent attractiveness are shown). The edge labels indicate estimated regression coefficients in standardized model, positive associations being green, negative red. The asterisks represent the level of significance ($p < .10.$, $p < .05^*$, $p < .01^{**}$, $p < .001^{***}$). For estimated r < 0.05 the arrows are not shown.

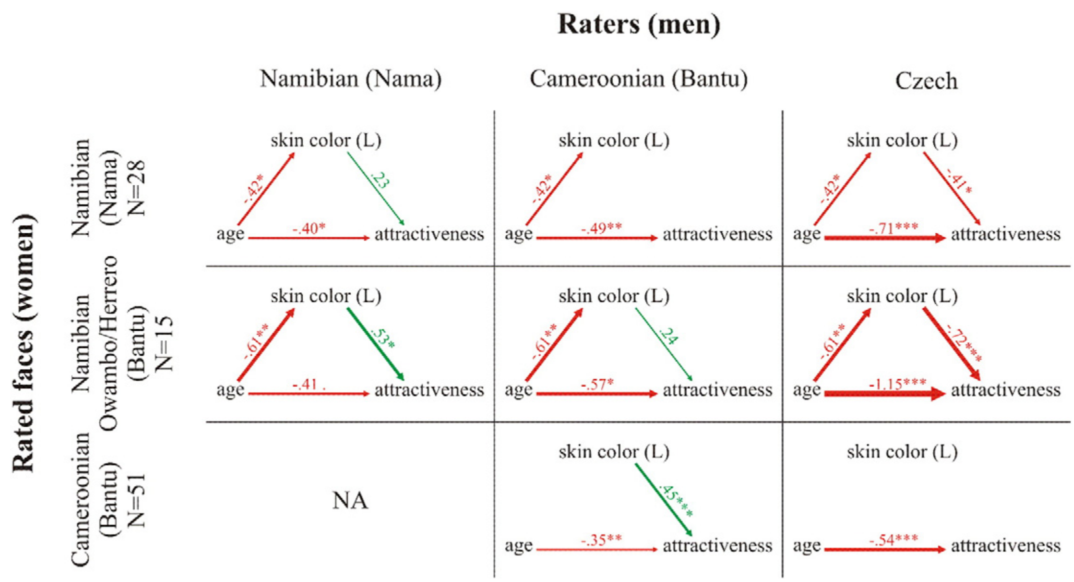

Fig. 5. The results of the mixed-effect path analysis with age and skin color regressing on attractiveness with possible influence of raters and stimuli treated as random effects. The edge labels indicate estimated regression coefficients in standardized model, positive associations are being green, negative red. The asterisks represent the level of significance ($p < 0.10.$, $p < .05^*$, $p < .01^{**}$, $p < .001^{***}$). For estimated r < 0.05 the arrows are not shown.

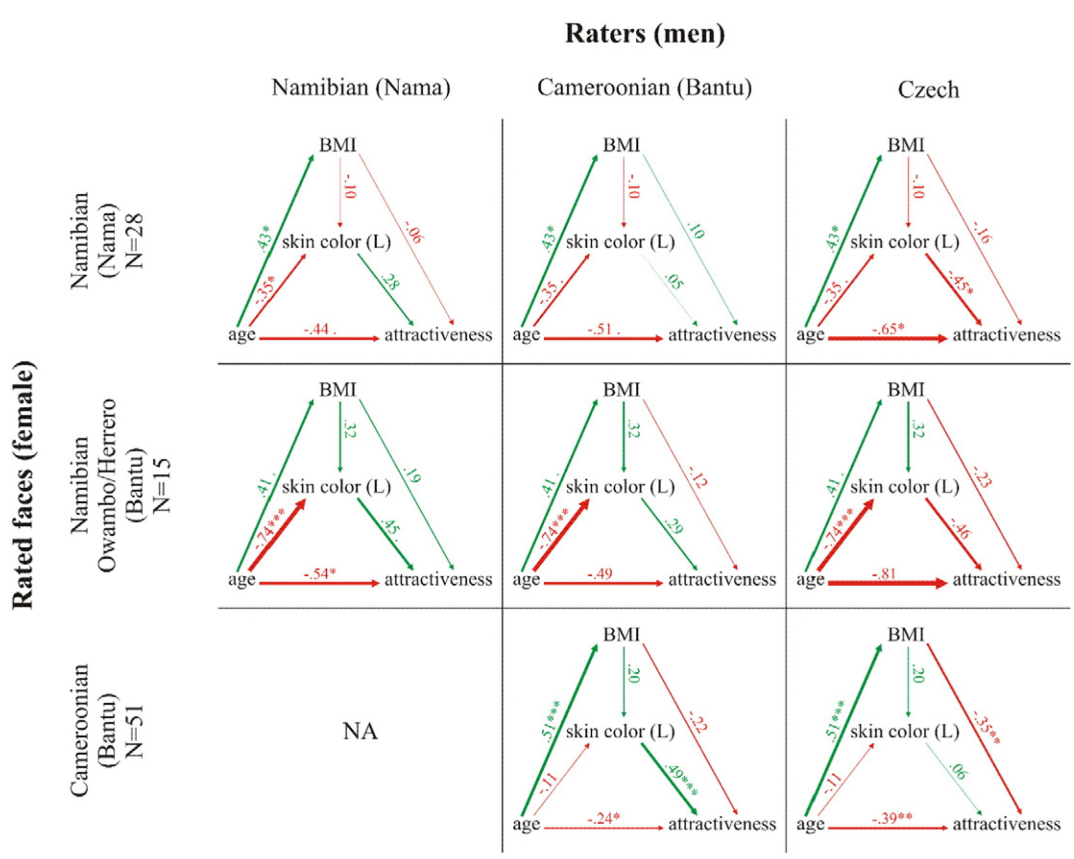

Fig. 6. The results of the latent variable model with measured age, BMI and skin color and attractiveness as latent variable (only relationships between age, L and latent attractiveness are shown). The edge labels indicate estimated regression coefficients in standardized model, positive associations being green, negative red. The asterisks represent the level of significance ($p < .10.$, $p < .05^*$, $p < .01^{**}$, $p < .001^{***}$). For estimated r < 0.05 the arrows are not shown.

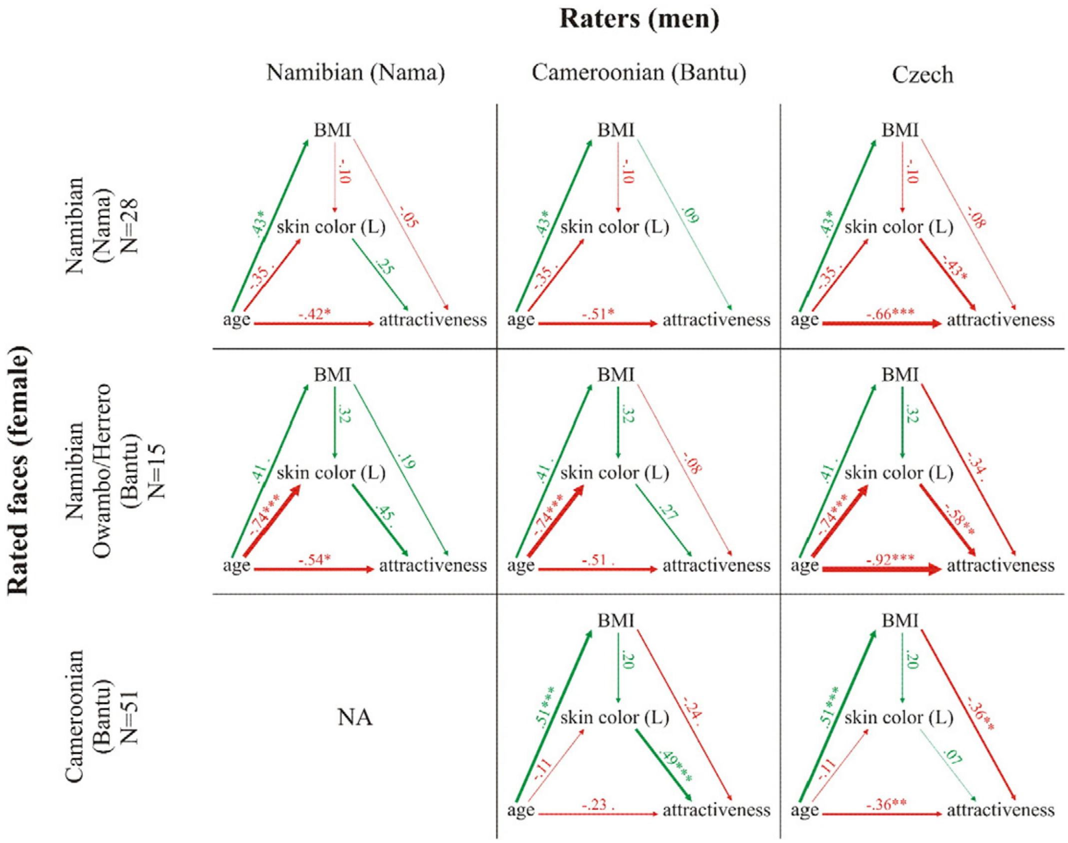

Fig. 7. The results of the mixed-effect path analysis with age, BMI, skin color and attractiveness with possible influence of raters and stimuli treated as random effects. The edge labels indicate estimated regression coefficients in standardized model, positive associations being green, negative red. The asterisks represent the level of significance ($p < 0.10.$, $p < .05^*$, $p < .01^{**}$, $p < .001^{***}$). For estimated r < 0.05 the arrows are not shown.

References

Abend, P., Pflüger, L. S., Koppensteiner, M., Coquerelle, M., & Grammer, K. (2015). The sound of female shape: A redundant signal of vocal and facial attractiveness. *Evolution and Human Behavior*, *36*, 174–181.

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*, 393–399.

Alley, T. R., & Cunningham, M. R. (1991). Averaged faces are attractive, but very attractive faces are not average. *Psychological Science*, *2*, 123–125.

Apicella, C. L., Little, A. C., & Marlowe, F. W. (2007). Facial averageness and attractiveness in an isolated population of hunter-gatherers. *Perception*, *36*, 1813–1820.

Apicella, C. L., Tobolsky, V. A., Marlowe, F. W., & Miller, K. W. (2016). Hadza hunter-gatherer men do not have more masculine digit ratios (2D: 4D). *American Journal of Physical Anthropology*, *159*, 223–232.

Ardener, E. W. (1954). Some Ibo attitudes to skin pigmentation. *Man*, *54*, 71–73.

Armstead, C. A., Hébert, J. R., Griffin, E. K., & Prince, G. M. (2014). A question of color, the influence of skin color and stress on resting blood pressure and body mass among African American women. *Journal of Black Psychology*, *40*, 424–450.

Badaruddoza (2007). A paradox of human mate preferences and natural selection. *Journal of Human Ecology*, *21*, 195–197.

Banks, G. C., Batchelor, J. H., & McDaniel, M. A. (2010). Smarter people are (a bit) more symmetrical: A meta-analysis of the relationship between intelligence and fluctuating asymmetry. *Intelligence*, *38*, 393–401.

Baudouin, J. -Y., & Tiberghien, G. (2004). Symmetry, averageness, and feature size in the facial attractiveness of women. *Acta Psychologica*, *117*, 313–332.

Boyle, V. (2014). Vitamin D and pregnancy. *Obstetrics, Gynaecology & Reproductive Medicine*, *24*, 315–316.

Burke, D., Nolan, C., Hayward, W. G., Russell, R., & Sulikowski, D. (2013). Is there an own-race preference in attractiveness? *Evolutionary Psychology*, *11*, 855–872.

Chaplin, G., & Jablonski, N. G. (2009). Vitamin D and the evolution of human depigmentation. *American Journal of Physical Anthropology*, *139*, 451–461.

Coetzee, V., Faerber, S. J., Greeff, J. M., Lefevre, C. E., Re, D. E., & Perrett, D. I. (2012). African perceptions of female attractiveness. *PloS One*, *7*, e48116.

Coetzee, V., Greeff, J. M., Stephen, I. D., & Perrett, D. I. (2014). Cross-cultural agreement in facial attractiveness preferences: The role of ethnicity and gender. *PloS One*, *9*, e99629.

Cohn, B. A. (2002). Sunlight, skin color, and folic acid. *Journal of the American Academy of Dermatology*, *46*, 317–318.

Danel, D., 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*, 337–347.

De Rigal, J., Des Mazis, I., Diridollou, S., Querleux, B., Yang, G., Leroy, F., & Barbosa, V. H. (2010). The effect of age on skin color and color heterogeneity in four ethnic groups. *Skin Research and Technology*, *16*, 168–178.

Dixson, B. J., Dixson, A. F., Li, B., & Anderson, M. J. (2007a). Studies of human physique and sexual attractiveness: Sexual preferences of men and women in China. *American Journal of Human Biology*, *19*, 88–95.

Dixson, B. J., Dixson, A. F., Morgan, B., & Anderson, M. J. (2007b). Human physique and sexual attractiveness: Sexual preferences of men and women in Bakossiland, Cameroon. *Archives of Sexual Behavior*, *36*, 369–375.

Dixson, B. J., Dixson, A. F., Bishop, P. J., & Parish, A. (2010). Human physique and sexual attractiveness in men and women: A New Zealand–US comparative study. *Archives of Sexual Behavior*, *39*, 798–806.

Dixson, B. J., Little, A. C., Dixson, H. G., & Brooks, R. C. (2017). *Do prevailing environmental factors influence human preferences for facial morphology?* Behavioral: Ecology http://dx.doi.org/10.1093/beheco/arx067.

Dror, D. (2013). Vitamin D in pregnancy. In R. Watson (Ed.), *Handbook of vitamin D in human health* (pp. 670–691). New York: Springer.

Farrera, A., Villanueva, M., Quinto-Sánchez, M., & González-José, R. (2015). The relationship between facial shape asymmetry and attractiveness in Mexican students. *American Journal of Human Biology*, *27*, 387–396.

Fink, B., Grammer, K., & Matts, P. J. (2006). Visible skin color distribution plays a role in the perception of age, attractiveness, and health in female faces. *Evolution and Human Behavior*, *27*, 433–442.

Foo, Y. Z., Simmons, L. W., & Rhodes, G. (2017). Predictors of facial attractiveness and health in humans. *Scientific Reports*, *7*, 39731.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology*, *14*, 89–96.

Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, *15*, 73–85.

Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, *108*, 233.

Halberstadt, J., & Rhodes, G. (2000). The attractiveness of nonface averages: Implications for an evolutionary explanation of the attractiveness of average faces. *Psychological Science*, *11*, 285–289.

Halberstadt, J., & Rhodes, G. (2003). It's not just average faces that are attractive: Computer-manipulated averageness makes birds, fish, and automobiles attractive. *Psychonomic Bulletin & Review*, *10*, 149–156.

Hill, A. K., Cárdenas, R. A., Wheatley, J. R., Welling, L. L. M., Burriss, R. P., Claes, P., ... Puts, D. A. (2016). Are there vocal cues to human developmental stability? Relationships between facial fluctuating asymmetry and voice attractiveness. *Evolution and Human Behavior*, *38*, 249–258.

Hulse, F. S. (1967). Selection for skin color among the Japanese. *American Journal of Physical Anthropology*, *27*, 143–155.

Hume, D. K., & Montgomerie, R. (2001). Facial attractiveness signals different aspects of "quality" in women and men. *Evolution and Human Behavior*, *22*, 93–112.

Hunter, R. S. (1958). Photoelectric color difference meter. *Josa*, *48*, 985–995.

Jablonski, N. G., & Chaplin, G. (2000). The evolution of human skin coloration. *Journal of Human Evolution*, *39*, 57–106.

Jablonski, N. G., & Chaplin, G. (2010). Human skin pigmentation as an adaptation to UV radiation. *Proceedings of the National Academy of Sciences*, *107*, 8962–8968.

Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Facial symmetry and judgements of apparent health: Support for a "good genes" explanation of the attractiveness–symmetry relationship. *Evolution and Human Behavior*, *22*, 417–429.

Jones, D. (1995). Sexual selection, physical attractiveness, and facial neoteny – cross-cultural evidence and implications. *Current Anthropology*, *36*, 723–748.

Jones, D., & Hill, K. (1993). Criteria of facial attractiveness in five populations. *Human Nature*, *4*, 271–296.

Kleisner, K., Priplatova, L., Frost, P., & Flegr, J. (2013). Trustworthy-looking face meets brown eyes. *PloS One*, *8*, e53285.

Klingenberg, C. P., Barluenga, M., & Meyer, A. (2002). Shape analysis of symmetric structures: Quantifying variation among individuals and asymmetry. *Evolution*, *56*, 1909–1920.

Klingenberg, C. P., & McIntyre, G. S. (1998). Geometric morphometrics of developmental instability: Analyzing patterns of fluctuating asymmetry with Procrustes methods. *Evolution*, 1363–1375.

Komori, M., Kawamura, S., & Ishihara, S. (2009). Averageness or symmetry: Which is more important for facial attractiveness? *Acta Psychologica*, *131*, 136–142.

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, *126*, 390–423.

Langlois, J. H., & Roggman, L. A. (1990). Attractive faces are only average. *Psychological Science*, *1*, 115–121.

Lie, H. C., Rhodes, G., & Simmons, L. W. (2008). Genetic diversity revealed in human faces. *Evolution*, *62*, 2473–2486.

Linke, L., Saribay, S. A., & Kleisner, K. (2016). Perceived trustworthiness is associated with position in a corporate hierarchy. *Personality and Individual Differences*, *99*, 22–27.

Little, A. C., & Apicella, C. L. (2016). Face adaptation in an isolated population of African hunter-gatherers: Exposure influences perception of other-ethnicity faces more than own-ethnicity faces. *Psychonomic Bulletin and Review*, *23*, 439–444.

Little, A. C., Apicella, C. L., & Marlowe, F. W. (2007). *Preferences for symmetry in human faces in two cultures: data from the UK and the Hadza, an isolated group of hunter-gatherersProceedings of the Royal Society of London B: Biological Sciences*, *274*, 3113–3117.

Little, A. C., Hockings, K. J., Apicella, C. L., & Sousa, C. (2012). Mixed-ethnicity face shape and attractiveness in humans. *Perception*, *41*, 1486–1496.

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*, 1638–1659.

Löffler, H., Aramaki, J., & Effendy, I. (2002). The influence of body mass index on skin susceptibility to sodium lauryl sulphate. *Skin Research and Technology*, *8*, 19–22.

Mardia, K. V., Bookstein, F. L., & Moreton, I. J. (2000). Statistical assessment of bilateral symmetry of shapes. *Biometrika*, *87*, 285–300.

Martin, J. G. (1964). Racial ethnocentrism and judgment of beauty. *The Journal of Social Psychology*, *63*, 59–63.

Matts, P. J., Fink, B., Grammer, K., & Burquest, M. (2007). Color homogeneity and visual perception of age, health, and attractiveness of female facial skin. *Journal of the American Academy of Dermatology*, *57*, 977–984.

Mitteroecker, P., Windhager, S., Müller, G. B., & Schaefer, K. (2015). The morphometrics of "masculinity" in human faces. *PloS One*, *10*, e0118374.

Moore, F. R., Coetzee, V., Contreras-Garduño, J., Debruine, L. M., Kleisner, K., Krams, I., ... Rantala, M. J. (2013). Cross-cultural variation in women's preferences for cues to sex-and stress-hormones in the male face. *Biology Letters*, *9*, 20130050.

Muzaffar, F., Hussain, I., & Haroon, T. (1998). Physiologic skin changes during pregnancy: A study of 140 cases. *International Journal of Dermatology*, *37*, 429–431.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., ... Wagner, H. (2016). *Vegan: Community ecology package. R package version 2, 0–2.*

Özener, B., & Fink, B. (2010). Facial symmetry in young girls and boys from a slum and a control area of Ankara, Turkey. *Evolution and Human Behavior*, *31*, 436–441.

Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior*, *21*, 39–48.

Perrett, D., Lee, K., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D., ... Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, *394*, 884–887.

Perrett, D., May, K., & Yoshikawa, S. (1994). Facial shape and judgements of female attractiveness. *Nature*, *368*, 239–242.

Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A., & Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, *20*, 295–307.

Pisanski, K., & Feinberg, D. R. (2013). Cross-cultural variation in mate preferences for averageness, symmetry, body size, and masculinity. *Cross-Cultural Research*, *47*, 162–197.

Pittenger, J. B. (1991). On the difficulty of averaging faces: Comments on Langlois and Roggman. *Psychological Science*, *2*, 351–353.

Pound, N., Lawson, D. W., Toma, A. M., Richmond, S., Zhurov, A. I., & Penton-Voak, I. S. (2014). Facial fluctuating asymmetry is not associated with childhood ill-health in a large British cohort study. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*, 20141639.

Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, *57*, 199–226.

Rhodes, G., Sumich, A., & Byatt, G. (1999). Are average facial configurations attractive only because of their symmetry? *Psychological Science*, *10*, 52–58.

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*, 31–46.

Rosseel, Y. (2012). *Lavaan: An R package for structural equation modeling and more. Version 0.5–12 (BETA).* Ghent, Belgium: Ghent University.

Scott, I., Swami, V., Josephson, S. C., & Penton-Voak, I. S. (2008). Context-dependent preferences for facial dimorphism in a rural Malaysian population. *Evolution and Human Behavior*, *29*, 289–296.

Scott, I. M., Clark, A. P., Josephson, S. C., Boyette, A. H., Cuthill, I. C., Fried, R. L., Gibson, M. A., Hewlett, B. S., Jamieson, M., Jankowiak, W., Honey, P. L., Huang, Z., Liebert, M. A., Purzycki, B. G., Shaver, J. H., Snodgrass, J. J., Sosis, R., Sugiyama, L. S., Swami, V., Yu, D. W., et al. (2014). *Human preferences for sexually dimorphic faces may be evolutionarily novelProceedings of the National Academy of Sciences*, *111*, 14388–14393.

Scott, I. M., Pound, N., Stephen, I. D., Clark, A. P., & Penton-Voak, I. S. (2010). Does masculinity matter? The contribution of masculine face shape to male attractiveness in humans. *PloS One*, *5*, e13585.

Sear, R., & Marlowe, F. W. (2009). How universal are human mate choices? Size does not matter when Hadza foragers are choosing a mate. *Biology Letters*, rsbl20090342.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675.

Silva, A. S., Lummaa, V., Muller, U., Raymond, M., & Alvergne, A. (2012). Facial attractiveness and fertility in populations with low levels of modern birth control. *Evolution and Human Behavior*, *33*, 491–498.

Sorokowski, P., Kościński, K., & Sorokowska, A. (2013a). Is beauty in the eye of the beholder but ugliness culturally universal? Facial preferences of Polish and Yali (Papua) people. *Evolutionary Psychology*, *11*, 907–925.

Sorokowski, P., Sorokowska, A., Fink, B., & Mberira, M. (2012b). Variable preferences for sexual dimorphism in stature (SDS) might not be universal: Data from a semi-nomad population (Himba) in Namibia. *Journal of Cross-Cultural Psychology*, *43*, 32–37.

Sorokowski, P., Sorokowska, A., Danel, D., Mberira, M. L., & Pokrywka, L. (2012a). The second to fourth digit ratio and age at first marriage in semi-nomadic people from Namibia. *Archives of Sexual Behavior*, *41*, 703–710.

Sorokowski, P., Sorokowska, A., & Kras, D. (2013b). Face color and sexual attractiveness preferences of Yali people of Papua. *Cross-Cultural Research*, *47*, 415–427.

Steinberger, E., Rodriguez-Rigau, L., Smith, K., & Held, B. (1981). The menstrual cycle and plasma testosterone levels in women with acne. *Journal of the American Academy of Dermatology*, *4*, 54–58.

Stephen, I. D., Coetzee, V., Smith, M. L., & Perrett, D. I. (2009). Skin blood perfusion and oxygenation colour affect perceived human health. *PloS One*, *4*, e5083.

Stephen, I. D., Scott, I. M., Coetzee, V., Pound, N., Perrett, D. I., & Penton-Voak, I. S. (2012). Cross-cultural effects of color, but not morphological masculinity, on perceived attractiveness of men's faces. *Evolution and Human Behavior*, *33*, 260–267.

Swami, V., Rozmus-Wrzesinska, M., Voracek, M., Haubner, T., Danel, D., Pawłowski, B., ... Sheth, P. (2008). The influence of skin tone, body weight, and hair colour on perceptions of women's attractiveness and health: A cross-cultural investigation. *Journal of Evolutionary Psychology*, *6*, 321–341.

Tembo, M. S. (2010). The rediscovery of the beautiful woman in African societies. http://people.bridgewater.edu/~mtembo/menu/articles/AfricanBeautyRevisedMarch162010.pdf.

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

Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual-behavior. *Psychological Science*, *5*, 297–302.

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, *3*, 452–460.

Thornhill, R., & Møller, A. P. (1997). Developmental stability, disease and medicine. *Biological Reviews of the Cambridge Philosophical Society*, *72*, 497–548.

Tovée, M. J., Swami, V., Furnham, A., & Mangalparsad, R. (2006). Changing perceptions of attractiveness as observers are exposed to a different culture. *Evolution and Human Behavior*, *27*, 443–456.

Třebický, V., Fialová, J., Kleisner, K., & Havlíček, J. (2016). Focal length affects depicted shape and perception of facial images. *PloS One*, *11*, e0149313.

Valenzano, D. R., Mennucci, A., Tartarelli, G., & Cellerino, A. (2006). Shape analysis of female facial attractiveness. *Vision Research*, *46*, 1282–1291.

Van den Berghe, P. L., & Frost, P. (1986). Skin color preference, sexual dimorphism and sexual selection: A case of gene culture co-evolution? *Ethnic and Racial Studies*, *9*, 87–113.

Van Dongen, S. (2012). Fluctuating asymmetry and masculinity/femininity in humans: A meta-analysis. *Archives of Sexual Behavior*, *41*, 1453–1460.

Van Dongen, S. (2014). Associations among facial masculinity, physical strength, fluctuating asymmetry and attractiveness in young men and women. *Annals of Human Biology*, *41*, 205–213.

Van Dongen, S., & Gangestad, S. W. (2011). Human fluctuating asymmetry in relation to health and quality: A meta-analysis. *Evolution and Human Behavior*, *32*, 380–398.

Wagatsuma, H. (1967). The social perception of skin color in Japan. *Daedalus*, *96*, 407–443.

Wehr, P., MacDonald, K., Lindner, R., & Yeung, G. (2001). Stabilizing and directional selection on facial paedomorphosis. *Human Nature*, *12*, 383–402.

Zebrowitz, L. A., Montepare, J. M., & Lee, H. K. (1993). They don't all look alike: Individual impressions of other racial groups. *Journal of Personality and Social Psychology*, *65*, 85.

Zebrowitz, L. A., Wang, R., Bronstad, P. M., Eisenberg, D., Undurraga, E., Reyes-García, V., & Godoy, R. (2012). First impressions from faces among U.S. and culturally isolated Tsimane' people in the Bolivian rainforest. *Journal of Cross-Cultural Psychology*, *43*, 119–134.