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VZTAH PERCEPCE MUŽSKÉHO OBLIČEJE A SCHOPNOSTI OBSTÁT VE FYZICKÉ KONFRONTACI

Disertační práce

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RELATIONSHIP BETWEEN MALE FACIAL MORPHOLOGY AND ASSESSMENTS OF FIGHTING ABILITY

Dissertation thesis

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Abstrakt

Sociální interakce mohou někdy vyústit v neporozumění a konflikt, který lze řešit mimo jiné i za použití fyzického násilí. Fyzická konfrontace s sebou nese i rizika zranění nebo jiných, biologickou zdatnost ovlivňujících, následků. Dá se tedy očekávat, že se pomocí přírodního výběru vyvinuly kognitivní a behaviorální procesy ke zhodnocení bojeschopnosti ostatních, které by jedinci pomáhaly se adekvátně a adaptivně rozhodnout tak, aby minimalizoval ztráty a maximalizoval své zisky z případné konfrontace.

Hodnocení ostatních často probíhá na základě fyzického vzhledu, například vzhledu obličeje. Lidé jsou na základě rysů tváře schopni poměrně přesně a rychle přisuzovat vlastnosti, jako je fyzická síla nebo sklony k agresivitě. Nicméně slabinou dosavadních výzkumů je, že nebyly založeny na skutečné schopnosti obstát ve fyzické konfrontaci. Z tohoto důvodu jsme v sérii empirických studií testovali hodnocení bojeschopnosti, přesnost tohoto hodnocení a zkoumali morfologii obličeje, která je s těmito hodnoceními a skutečnou schopností obstát v souboji spojena. Pro tyto účely jsme využili údaje od bojovníků smíšených bojových umění, včetně počtu jejich výher a proher.

Výsledky první studie ukazují, že lidé jsou skutečně schopni na základě rysů obličeje poměrně přesně ohodnotit schopnost daných jedinců obstát ve fyzické konfrontaci. Samotná schopnost obstát v konfrontaci a hodnocení této schopnosti je spojena s konkrétními rysy obličeje, jako je pozice a tvar očí, tvar rtů nebo tvar a velikost brady. Druhá studie ukázala, že lidé jsou těchto hodnocení schopni i v situaci, kdy vybírají, který ze dvou protivníků bude vítěz potenciálního souboje. Tento úspěšnější bojovník je pak hodnocen nejen jako lepší, ale také jako silnější, dominantnější a atraktivnější. Třetí studie se pak zaměřila na analýzu relativní šířky obličeje jako markeru bojeschopnosti. Naše výsledky ukazují, že relativní šířka obličeje koreluje s přisouzenou schopností obstát ve fyzické konfrontaci a skutečným úspěchem v ní.

Pro popis procesu rozhodování, zda do blížící se konfrontace vstoupit či nikoliv, navrhujeme víceúrovňový model hodnocení nebezpečnosti. Prvním stupněm toho rozhodovacího procesu je hodnocení celkové velikosti oponenta. Pokud jsou soupeři podobně velcí, přichází na řadu další stupeň hodnocení, ve kterém se mohou uplatnit hodnocení dalších vodítek a markerů nebezpečnosti, jako jsou například rysy obličeje.

Klíčová slova

Pohlavní výběr; obličej; sociální percepce; morfologie tváře; kompetice; nebezpečnost

Abstract

Social interactions may sometimes collide and result in conflicts which can be solved among others by means of physical violence. However, physical confrontations entail a risk of injuries and other fitness-affecting consequences. Thus, it seems likely that cognitive and behavioural processes to assess the fighting ability may have evolved by means of natural selection. This would facilitate adaptive decisions and responses to decrease costs and increase benefits from potential confrontations.

Behavioural characteristics are often assessed according to physical traits such as facial appearance. People are relatively accurate in attributions of certain characteristics from facial traits, like physical strength or propensity for aggression. However, previous research was not based on data about actual fighting ability. Therefore, we conducted a series of empirical studies testing perception of formidability, accuracy of the perception and attempted to identify facial morphological traits related to the assessments and actual fighting performance. To test these issues, we employed Mixed Martial Arts contestants and used their record of victories and defeats.

The results of our first study revealed that people are indeed able to relatively accurately assess the fighting ability of others. The fighting ability and its assessment is connected to certain facial morphological features, for instance the position and shape of eyes, mouth and chin. The second study showed that people are above chance successful when asked to choose the winner of a fight out of two potential opponents. The more formidable fighter is judged as stronger, more dominant and attractive. In the third study, we analysed relative facial width which is hypothesised to serve as a marker of formidability. Our results showed positive correlation between rated formidability, real fighting success and relative facial width.

We propose a model of multi-level assessments of formidability that describes processes behind fight-or-flight decision. When an individual encounter a potential antagonist, the first step in such decision-making process might depend predominantly on the overall size of the opponent. When the rivals are of roughly equal size, a next level of assessment primarily related to perception of facial features takes place.

Keywords

Sexual selection; face; perception; morphology; competition; formidability

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Part 1

Introduction

Activities that individuals pursue on a daily basis may sometimes collide and social interactions may result in conflict. Conflicts can be resolved through many ways and one of them is physical encounter or aggressive act against the opponents.

Getting involved in antagonistic interactions has presented a recurrent problem over evolutionary history, and the ability to accurately gauge one's fighting ability as well as potential competitors' is undoubtedly a fitness-affecting issue. Thus, it seems likely that natural selection has favoured the evolution of cognitive and behavioural mechanisms that are involved in assessment of fighting ability and that promote the most appropriate and adaptive response. Individuals that possess such abilities would have been better at assessing the likelihood of overcoming a physical conflict, which in turn would have facilitated their decisions to involve in or withdraw from potential conflicts. If these conflicts escalate, they would need to be resolved in one's favour by preventing the other from acting. One way of such prevention is to defeat one's opponent or make him surrender using physical aggression.

Being aggressive and fighting with conspecifics carry the inevitable risk of injury or even death due to damage of vulnerable body parts, bleeding from open wounds, or subsequent infections. Besides these risks, aggression entails additional and diverse types of costs ranging from physiological a/psychological stress and energy expenditure to damaged social relationships, to trade-offs with other fitness-related activities like feeding or mating.

Unlike some other animals, humans are not equipped with dangerous weapons such as sharp canines, claws, horns or poisonous glands. Before humans started using various objects as weapons, physical combat had depended on hits executed by hand, wrestling, choking, kicking, and perhaps scratching and biting. The risk of fatal injury that results from male-to-male fight is relatively low. Humans also exhibit diverse acts of competition apart from direct combat, like indirect aggression in the form of verbal derogation, social manipulation, and self-promotion (Arnocky & Carré, 2017; David M. Buss & Dedden, 1990).

Nevertheless, antagonistic interactions have surely had profound implications in our evolutionary past, and in some geographical areas they continue to have significant consequences in contemporary societies. Injuries and deaths caused by interpersonal violence constitute a worldwide health problem. Forensic evidence suggests that aggressive conflict among our ancestors has been a significant selection force (Manson et al., 1991; P. L. Walker, 1997). Across many contemporary foraging societies, the average proportion of male deaths resulting from violent confrontations is approximately 30%. In modern Western societies homicide is still a prevailing cause of death, for instance it accounts for almost 1% of male deaths in the US (Sell, Hone, & Pound, 2012).

Evolutionary-informed scholars therefore argue that physical encounters have probably generated powerful selection pressures that have contributed to the establishment of various neurocognitive and behavioural complexes, whose function is to perceive, assess, and specifically act in antagonist situations or even prior to actual encounters (Carré, Murphy, & Hariri, 2013; Puts, 2010; Sell, Cosmides, et al., 2009).

Historical records of physical violence

Paleontological and bioarchaeological findings of traumatic injuries (i.e., skull fractures) in human skeletal remains stand as a direct source of forensic evidence showing that throughout the history of our species, physical aggression and interpersonal violence - especially among men- have been rather common in our ancestral environment (Walker, 1997, 2001).

An analysis of ancestral forms of aggression shows that upper-body strength was the most crucial part of fighting ability. Upper-body strength is considered as critical for physical encounters, particularly for wrestling, punching, or choking, which were the most common types of combats in ancestral populations according to analyses of skeletal remains (Walker, 1997, 2001). According to a common folk misconception, there is little evidence showing that fighting with bare hands exists in human evolutionary history. However, evidence of facial skeletal trauma caused by fist fighting exists in the fossil record of Australopithecus (i.e., Roper, 1969) and early Homo (i.e., Wu, Schepartz, Liu, & Trinkaus, 2011). Facial skeletal trauma due to fist fighting has also been observed in many other samples of historic skeletal remains (for review see Walker, 1997). Historical records and ethnography literature contain many examples from different regions of the world including Chinese Xia dynasty, Greece or Sahel region of Africa, Tonga and, Eskimo populations, showing that acts of physical encounters -particularly among male antagonists- are not exceptional in many human cultures across the globe (Archer, 2009; Horns, Jung, & Carrier, 2015; Walker, 1997, 2001).

Ritualized combat performed by men in the form sports such as folk wrestling and martial arts are also common and they take many forms, such as Sumo in Japan, Muay Thai in Thailand, stick-fighting in the Suri of Ethiopia, or Glima wrestling from Viking era Scandinavia to Pankration in Ancient Greece. These ritualized forms of combat have a long-recorded history, including medieval sword fighting, fencing in the 16th century Germany, gladiatorial games in Ancient Rome, and palestraes of Ancient Greece.

Differences in use of aggression

Violent crimes have been reported in every human society, and wars and mass killings have occurred continuously throughout our history (Pinker, 2001). These phenomena of interpersonal violence share a common nature, even though they differ in magnitude of damage they caused, number of individuals involved, or reason of the violence. Acts of war and mass violence have surely played an important role in the development of human populations (i.e., Lopez, 2015) (at least in recent development from an evolutionary point of view), this current investigation will focus solely on interpersonal conflicts as they seem to be a substantially larger selective force during the evolution of our species (Puts, 2010).

Humans seem to have a high potential for violent aggression, and since practically all wars were fought by men and most murders and other violent crimes are committed by men (Archer, 2004), this potential seems to be much higher among men than women. The lower use of physical force by women compared to men is cross-culturally well-documented (Archer, 2009). Meta-analytic studies show that men from various cultures are more prone to use physical violence and are more frequently involved in such acts compared to women (Archer, 2004). Men are more than twice as likely as women to engage in physical fighting (Pickett et al., 2013), they are more likely to initiate physical attacks, and they are also more likely to produce physical injures, whereas women are more likely to be attacked and injured (Felson, 1996). Importantly, such aggressive acts aimed mostly other men (Archer, 2004). The sex differences in physical encounters are therefore thought to be a result of sex differences in some aspects of human physique and psychology (Puts, 2010).

These differences are shown to emerge at certain points during development. According to some studies, it is as early in postnatal life as 2 years of age (Tremblay et al., 1999) (though, other studies show that differences are not present until the age of 6, see Archer, 2004).. These differences reach maximum levels during adolescence and early adulthood, hence around the peak years of sexual activity between 18 and 30 years of age, and they decline thereafter (for review see Archer, 2004). This period was therefore labelled as "Young Male Syndrome" (Margo Wilson & Daly, 1985), the period in which young men are frequently the perpetrators and victims of interpersonal violence and show considerably high levels of risk-taking behaviour in general.

The early onset of sex differences in physical aggression is assumed to be an adaptation to competition among same-sex groups during childhood or a preparation for upcoming potential adult aggression (Archer, 2004). During the adolescence, male skeletal structure becomes more durable, and with the help of increased muscle tissue growth upper body becomes stronger, thus males' chances to successfully compete with others increase (Sell et al., 2012). The decline in physical aggression with age is speculated to be a result of declining physical strength, which makes physical confrontations less effective and more demanding (Walker, Richardson, & Green, 2000). Additionally, it might be the case that as proneness to get angry declines with age, male status may become more dependent on social power and achievement (i.e., employment, having a high income or an influential role in society) after adolescence and early adulthood years (Price, Dunn, Hopkins, & Kang, 2012).

Other forms of indirect or verbal aggression may also come into play as, the use of direct physical aggression may have prohibitive costs especially for people that are involved in specific cultural contexts (e.g., occupational settings). Nevertheless, it seems that choosing the most appropriate form of aggression is contextual, and in situations in which physical aggression has more benefits and fewer costs, men are willing to engage in this type of aggression more frequently compared to other types of aggression (Archer & Coyne, 2005). Relative costs and benefits of aggression should also be considered since they are differently distributed across society. Compared to their high-status counterparts, low-status men may have relatively little to lose and more to gain from aggressive behaviour (M. Wilson, Daly, & Pound, 2010). For high-status men, the costs of aggression (like a possible decline in social status), may outweigh the potential benefits. On the other hand, the benefits of aggression may outweigh its costs for low-status men.

For instance, success in an aggressive interaction may protect one's reputation or increase one's access to valued resources (e.g., social status and mating opportunities), therefore it may lead to an ultimate increase in one's reproductive fitness (M. Wilson et al., 2010).

Testosterone and aggression

The importance of physical aggression during late adolescence might increase because of competitive social interactions, since intra-sexual competition and reproductive activities are more salient during late adolescence (Gallup, O'Brien, White, & Wilson, 2010). Similarly, in many other vertebrate species, young adult males show heightened levels of physical aggression and violence toward other males, and homicide of members of same sex become more likely to occur (Archer, 2004) when reproductive competition is most intense. In many vertebrates, the rise in testosterone at this developmental phase is responsible for such behavioural trait (Sell, 2011).

During adolescence, significant changes in skeletal muscle volume and muscular strength onsets due to elevated levels of testosterone. Another effect of these elevated levels might be dispositions to act aggressively that were described above (e.g., Book, Starzyk, & Quinsey, 2001). Traditionally, it was argued that baseline levels of testosterone are linked to aggressive behaviour, however research findings concerning the role of base level testosterone in promoting human aggression have been mostly weak and somewhat inconsistent (for review see Archer, 2006). It has been speculated that not the baseline levels of testosterone but rather acute changes in it may serve to uplift competitive and aggressive behaviour (Archer, 2006). The claim that context-dependent increases in testosterone levels are associated with aggression is known as Challenge hypothesis (see Archer, 2006; Wingfield, Hegner, Dufty, & Ball, 1990). Consistent with this hypothesis, a growing body of evidence indicates that testosterone levels, elicited by laboratory manipulation (i.e., injecting a dose of testosterone) or real-life events (i.e., watching sports competition), but not baseline levels, positively predict increase in men's perception of their own facial dominance (Welling, Moreau, Bird, Hansen, & Carré, 2016), competitive motivation, and aggressive behaviour (Carré et al., 2016). However, such increase in aggressive behaviour seems to emerge only in men that score relatively high in trait dominance and/or low in trait self-control (Carré et al., 2016).

Theories of sex differences in aggression

Several theories across different scientific fields try to explain sex differences in proneness to physical aggression. One of them, The Social Role Theory (Eagly & Wood, 2016) claims that sex differences in social behaviour such as aggression arose from the historical division of labour as the homemaker and the worker outside the home (Eagly & Wood, 1999). Roles create certain expectancies about gendered characteristics, which leads to differentiated behaviours that are transmitted across generations through socialization process (Eagly, Wood, & Diekman, 2000). According to this theory, boys learn that aggressive response is an appropriate behaviour which fits the ascribed masculine role. Social expectations associated with the masculine role then maintain aggression as a part of one's proper behavioural inventory. Being tough is a significant component of social status in boyhood, and boys learn that being afraid to fight is unmanly, so they experience more encouragement and fewer limitations for aggression and competition compared to girls. Physical aggression may be particularly encouraged by the masculine role, especially among individuals that are associated with masculine roles that require physical strength (i.e., military personals or athletes). Social status is considered as another domain where men display aggressive tendencies (Eagly & Wood, 2016). Higher social status does not necessarily create a need to display more aggression toward others, particularly in a physical form, but the quest to maintain high-status positions may require resorting to more verbal and indirect forms of aggression.

Social role theory accentuates socialization, the learning processes through which aggressive behaviour is learned and maintained during individual's development (Eagly & Wood, 2016). This process enables cultural values to be transmitted by parents, peers, the educational system, television and other media, which reinforce greater direct aggression displayed by males than females (Archer, 2004). Based on this assumption, sex differences in aggression should be initially non-existent or very small, and they should progressively increase as a consequence of the cumulative effect of socialization processes. However, the early occurrence of sex differences in physical aggression contradicts these explanations (Archer, 2004).

Even though the impact of socialization on one's behavioural patterns is undeniable, it provides proximate level explanation. Sexual selection theory, on the other hand, provides evolutionary (i.e., ultimate level) explanation for the described sex differences in physical aggressiveness (Archer, 2009; Puts, 2010). The benefits of both intra- and inter-sexual aggression are more prevalent for men than women, and they are all related to fitness increasing effort. Men's aggression peaks at the age of greatest mating competition and cross-cultural evidence indicates that one's fighting ability is a significant determinant of resource access in virtually all cultures (Archer, 2009). Men have high propensity to compete for resources with others, especially with non-group members by using violent aggression (Georgiev, Klimczuk, Traficonte, & Maestripieri, 2013). This characteristic of our nature probably has evolved because our ancestors could fight with their rivals with relatively low costs (insignificant risk of lethal injury, or social stigmatization) but with significant benefits (i.e., access to resources and fertile women). Although, literature provides robust evidence showing that men confront others in a direct fashion to gain social status (von Rueden, Gurven, & Kaplan, 2011), others argue that direct competition is less frequent in current Western societies, compared to our ancestors (Puts, 2010). Selection could reduce the rate of potentially dangerous use of direct and physical aggression in favour of indirect competition mechanisms that would be sufficient for acquisition of corresponding social position and acceptance among potential partners.

Sexual selection theory proposes the origins of greater male physical aggressiveness and competitiveness in unequal parental investment which leads to greater male than female reproductive competition (Trivers, 1972) among most mammalian species. Sex differences are then the output of a greater male willingness to show anger when reproductive competition is highest and when the benefits obtained through violent behaviour outweighs potential costs.

Evolutionary perspective on conflict resolution

In antagonistic encounters with other individuals of the same species, the benefits to be gained (like status, resources, or territory) must be weighed against the costs (i.e., risk of injury or even death) and the key decision between fight or flight should be made

Indeed, there is evidence showing that animals like domestic pigs (Rushen, 1987) or gelada baboons (Bergman, Ho, & Beehner, 2009) make such decisions based on the assessment of relative fighting abilities of their opponents. This assessment is a crucial determinant of the outcome of conflicts (Arnott & Elwood, 2009), and specific traits in some species can be related to fighting success (i.e., Gosling, Atkinson, Dunn, & Collins, 1996). Across diverse species, intra-sexual contests frequently involve displays and mutual assessments of formidability, and these contests are frequently resolved when one of the antagonists surrenders before either of them gets injured during the contest (Smith & Parker, 1976). Any individual that can assess the chance to win a conflict in advance and that can make more sensible decisions about whether to initiate, escalate, or retreat from a potential fight is likely to obtain selective advantage.

Fighting ability could be described as an ability to efficiently use physical violence, among other means, against a conspecific antagonist. The greater the fighting ability of the individual, the more costs it can inflict. The willingness to use ones' fighting ability against competitors is commonly mediated by anger. Ancestral individuals are deemed to used anger to convince others to treat them better, and the more power they had to harm others, the more convincing they would have been (Price et al., 2012). Anger is thought to be responsible for a substantial portion of human aggressive acts, but not for all of them (Sell, 2011). It rather seems that aggressive behaviour is an option to be used under limited circumstances and often only after other less dangerous tactics fail (Sell, 2011).

The recalibrational theory of anger (Sell, 2011) is a computational evolutionary model which proposes that the function of anger is to recalibrate individuals who place insufficient weight on the welfare of the angry individual when making fight-or-flight decisions. According to this theory, I) individuals differ in terms of their anger thresholds and selective usage of negotiation tactics, II) they need to estimate others' traits relevant to the ability to inflict any costs (e.g. fighting ability) and provide any benefits (e.g. mate value or resource gathering potential), III) and use these estimates to calibrate their welfare trade-off ratios (Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008) so that more weight is placed on the welfare of individuals who have the abilities and willingness to inflict higher costs or obtain benefits from others (Sell, 2011). Natural selection is expected to have designed individuals to calibrate their welfare trade-off ratios to maximize their own welfare. Such strategy confers important selective advantage over fighting without prior assessment. Outputs of these assessments and results of any previous conflict provide information about relative bargaining power or Resource Holding Power (i.e., the ability to impose costs and deny benefits) (Parker, 1974) of each individual and establishes a dominance hierarchy (Sell, Eisner, & Ribeaud, 2016). Individuals with higher resource holding power easily win conflicts, attain preferential access to mates, and benefit themselves at the expense of others in other ways (Sell et al., 2017).

Individuals with more bargaining power should expect and demand higher welfare trade-off ratios from others (i.e., Sell, Tooby, & Cosmides, 2009), and anger-based bargaining will be connected to bargaining power in a fashion that more powerful individuals could afford to deploy anger in wider range of circumstances, insist on better treatment from others, and deploy aggressive tactics more frequently (Sell, Tooby, et al., 2009). This relationship between an individual's fighting ability (the most important component of bargaining power in many species) and the respect it receives from others was consistently shown by behavioural science studies (see Sell et al., 2016).

According to the recalibration theory of anger (Sell, 2011), benefits of minimizing the costs of engaging in violent conflict are thought to have shaped adaptations for the assessment of others' capacity to cause physical harm.

In following chapters, studies suggesting that human body morphology, especially the male face, contains information about males' threat potential, as well as studies investigating humans' utilizations of cues such as facial appearance to assess other's formidability will be discussed (i.e., Little, Třebický, Havlíček, Roberts, & Kleisner, 2015; Sell, Cosmides, et al., 2009; Třebický et al., 2015; Třebický, Havlíček, Roberts, Little, & Kleisner, 2013).

Sexual selection and adaptation for intra-sexual competition

Due to the significant role of reproduction in evolutionary theorizing, the vast majority of investigations in current behavioural sciences emphasise that intersexual selection (i.e., processes underlying mate choice) is responsible for male phenotype, therefore they often focus solely on the influence of men's physical attractiveness on one's reproductive success (for review see Třebický, Kleisner, & Havlíček, 2012).

It is well known that mate choice in humans partly relies on morphological traits of the opposite sex (Barber, 1995; Hatfiels, Aronson, Abrahams, & Rottman, 1966) and some of them are assumed to be a result of inter-sexual selection (Dixson, Dixson, Li, & Anderson, 2007). Current line of reasoning considers attractive traits as markers of one's genetic qualities (e.g. developmental stability, heterozygosity, immunocompetence) that could be transmitted to a potential offspring, and/or as cues for the potential to provide direct benefits (e.g. paternal care, protection against attackers, or supply of calories) (Třebický et al., 2012). However, in recent years we can see a re-evaluation of sexual selection in humans with an increased attention being paid to intra-sexual competition, a selection pressure whose influence appears to have been underestimated in human males (Hill et al., 2013; Morgan & Carrier, 2013; Puts, 2010; Puts, Bailey, & Reno, 2015). Even though several sexually dimorphic traits are indeed perceived as attractive (e.g., a certain level of muscular development or stature), a higher degree of development of these traits increases perception of dominance more substantially than it increases ratings of attractiveness (Hill et al., 2013; Třebický et al., 2012). Recent studies showed that a variety of masculine traits appears to be designed for intra-sexual competition rather than for attraction of potential mates (Hill et al., 2013). Since men are on average stronger, more physically aggressive, and engage in physical contests more frequently than women in societies that have been studied so far (Archer, 2004), these patterns suggest a relatively high level of male (compared to female) intra-sexual competition in human evolutionary history. This may account for some typical features of the human male physique, especially for the upper body shape and a greater amount of muscle mass compared to the female body (Lassek & Gaulin, 2009).

Despite the existence of an enormous body of literature on physical attractiveness published during the past decades, the interplay between mate-choice and contest competition remains open for further investigation (Puts, 2010). An alternative explanation for sexual dimorphism in humans proposes that it is a product of a sexual division of labour, rather than intra- and/or inter- sexual selection. Ecological selection may have contributed to men's greater size, strength, and weapon use as they had higher success rates during hunting compared to women (Kaplan, Hill, Lancaster, & Hurtado, 2000). Nonetheless, occurrence of behaviours like frequent same-sex aggression (Archer, 2004) cannot be easily explained solely by adaptations for hunting and gathering. Hence, as Hill et al. (2016) point out, it is more likely that the sexual division of labour can be seen as a consequence rather than the initial cause of sexual dimorphisms. Even so, importance of hunting as an additional selection pressure on these male traits should not be overlooked. Another alternative explanation for our morphology in the sense of intra- and/or inter- sexual selection is phylogenetic inertia, an idea of inheritance of traits that were developed in our ancestors, rather than experiencing a selection by our own species. Paleoanthropological and comparative research indicates that we did inherit traits such as greater male size and aggression (compared to females) from an ancient hominin ancestor (Hill et al., 2016).

Based on current evidence, preferences for the physique with signs of high levels of physical fitness and genetic quality could be adaptive cues for women, since men with such physiques might be successful in intimidating potential rivals in the intra-sexual competition (Barber, 1995) and might provide indirect (i.e., genetic material for an offspring with a greater potential for biological fitness) or direct (i.e., parental care, protection, and calorie supply for the offspring) benefits (Třebický et al., 2012). In sum, previous studies suggest that neither intra- nor inter- sexual selection has been the single most important selection pressure in the course of human evolution. They have rather interactive role in shaping the human male phenotype. Male physique thus not only increases attractiveness for the opposite sex, but also plays a key role in competition for access to resources or potential mates.

Sexual dimorphism in body morphology

The expression or development of sexually dimorphic traits serve as cues to what is assumed that only high-quality individuals may afford to develop. In order to develop a trait, energy must be acquired from the environment. Life-history theory (Roff, 1992) assumes that the budget of energy available is limited and an individual must allocate a substantial proportion of energy to activities that increase the chances to survive and reproduce. The development of masculine traits is strongly related to testosterone levels (Bhasin, 2003). Testosterone adjusts the use of energy and can allocate it for the development of behaviours like mate-seeking or intra-sexual competition (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007). Such traits might also include the amount of muscle mass and physical strength.

The largest differences in body constitution between men and women arise during puberty and early reproductive age, and these differences are stimulated by levels of sex hormones regulating lipid tissue distribution and muscle mass hypertrophy (Vague, 1956). Steroid hormones form either android- (high testosterone level, typical with lipid tissue allocated in abdominal area) or gynoid- (high oestrogen levels, typical with lipid tissue allocated to hips and buttocks area) scheme of fat distribution and body shape. Even though humans seem to have reduced levels of sexual dimorphism compared to great apes (McHenry, 1994), muscle mass and resulting muscular strength are very sexually dimorphic traits (Lassek & Gaulin, 2009). If we take a simple look at overall comparisons of body weight as expressed by body-mass indices (controlling for height), the sexes appear quite similar. But women's fat mass largely compensates for men's greater muscle mass. Men have twice as much muscle mass as women. Relatively more of this muscle mass is located in the upper body, with men having about 75% more arm muscle mass than women, while dimorphism in the lower-body muscularity is almost the same as the upper body (Lassek & Gaulin, 2009). As a result, the average man has approximately 90% greater upper body strength compared to the average woman (Lassek & Gaulin, 2009).

Another rather physiological sexual dimorphism exists in pain thresholds. Physical pain signals actual or potential damage to one's body and can motivate withdrawal from a damaging situation. Compared to women, men can endure higher levels of physical pressure for longer periods of time before experiencing pain and they are able to tolerate more pain (Fillingim, King, Ribeiro-Dasilva, Rahim-Williams, & Riley, 2009). Moreover, men experience analgesia in situations of male-male competition regardless of exercise, whereas women experience analgesia only after exercise (Sternberg, Boka, Kas, Alboyadjia, & Gracely, 2001).

These very different developmental investment strategies suggest divergent evolutionary histories for men and women. Although many physiological human traits are thought to have evolved in hunter-gatherer populations (Marlowe, 2005), there is no agreement regarding which behaviours were specifically affected by natural selection, and which environmental pressures (e.g., foraging for survival, occurrence of aggression, physical competition) played a more important role in the development of these traits.

Morphological adaptations for physical competition

Physical competition often favours evolution of anatomical armaments. Compared to our closest relatives, humans possess relatively small canines for effective biting of others (Wood, Li, & Willoughby, 1991). One hypothesis for reduction in canines and the use of biting in competition is that canines as weapons were surpassed by our freed forelimbs and handheld weapons following the emergence of bipedal locomotion (Carrier, 2011; Hill et al., 2016).

Bipedal adaptation for contest competition

In many species, bipedal stance on hindlimbs is commonly observed when they fight. Male great apes routinely display bipedal stance and physically compete by striking and grappling with their forelimbs. This posture may provide a performance advantage by allowing the forelimbs to strike with a wider range of motion, reaching higher speeds while maintaining position and balance, and allow one to utilize dexterities like running, jumping, and rapid change of direction (Carrier & Cunningham, 2017) which provide a competition advantage. Unlike most primates, great apes evolved feet in which the heel supports bodyweight during terrestrial locomotor and non-locomotor behaviours. This ability appears to be basal for mammals. So-called plantigrade foot posture has been retained, lost, and re-evolved in several mammalian lineages including the great apes (for review see Carrier & Cunningham, 2017). This posture brought the ability to apply free moments to the ground which could be seen as a significant feature. Humans perform brawling, striking, and grappling with heels in touch with the ground. Advantage of this posture is that plantigrade foot enhances fighting performance by increasing the ability to apply free moments to the ground – so that balance is not lost while striking and grappling with an opponent (Carrier & Cunningham, 2017).

Importance of lower limbs during physical confrontations

Injuries sustained during physical assaults most often result from punching (holding the biggest share), and kicking (Shepherd, Shapland, Pearce, & Scully, 1990). Lower limbs are rather muscular and strong parts of our musculoskeletal system (Lassek & Gaulin, 2009), so using them as an anatomical weapon seems like a straightforward option.

In chimpanzees and bonobos, using lower limbs for kicking, stamping, or jumping on the victim's back is well documented, while fighting techniques of gorillas and orangutans remain poorly understood, (for review see Carrier, 2007). Many traditional and modern martial arts such as Wushu, Pankration, Karate, Kick-box, and Mixed Martial Arts focus on kicking techniques, but kicking one's opponents during street fights or brawls is surprisingly not much documented in the available scientific literature. Anecdotal evidence may cover "techniques" such as stamping on or soccer-like kicking of one's opponent while he is on the ground virtually defenceless, though kicking the opponent while facing each other in stance seems scarcely utilized. And interestingly, no traditional weapon that would be primarily propelled by lower-body has ever been found, in comparison with the variety of handheld weapons (Sell et al., 2012).

Bipedalism seems like an important feature that improves strength and stability, hence enhances fighting performance. It allows lowering the centre of mass during hindlimb stance (Carrier, 2007, 2011), and by increasing the leverage through which muscle forces can be applied to the ground (Carrier & Cunningham, 2017), it allows greater power with which roundhouse and over-the-head blows and punches could be delivered to an opponent (Carrier, 2007). Performing effective kicks is a demanding act regarding dexterity and certain need for certain level of training it requires. When not performed competently, this technique entails a high risk of leg injuries (see also Macan, Bundalo-Vrbanac, & Romic, 2006), and also a risk of losing the balance for the kicking fighter. These possibilities render this technique rather ineffective and dangerous to apply in folk brawls.

Hand morphology in service of violence

Although descriptions of how humans fight with their arms are rare in the scientific literature (P. L. Walker, 2001), striking with fists appears to be universally employed in martial arts in many cultures across the globe and it is the dominant striking technique (see Horns et al., 2015) used in modern combatant arts (Scoggin et al., 2010) and in "street fights" as well (i.e. Morgan & Carrier, 2013).

Hand morphology which is similar to modern humans was present in basal hominins (Horns et al., 2015) and their proportions are considered as crucial for the manipulative skills and human-specific behaviours such as tool making, tool using, preparing food, building shelters, producing various arts, and nurturing. Therefore, these manual skills seem to be significant for humans and they certainly played a crucial role in the evolution of the human hand. The precise and gentle handling seems to require a relatively fragile and vulnerable hand morphology, which is a weak feature of our musculoskeletal system when physical confrontations are considered. Yet, the mobility and strength of the thumb make possible two very different hand grips that characterize us – holding objects and clenching our hand into fist – making our hand also our prominent anatomical weapon (Morgan & Carrier, 2013). The proportions of our hands may have been influenced by selection for fighting performance due to the frequent presence, importance, and universality of male–male physical competition among humans and all species of extant great apes (Carrier, 2007; Hill et al., 2013; Puts, 2010).

However, this hypothesis is rather controversial (King, 2013) at first. It seems contradictory that the capable part of human hand that uses and manufactures faint tools is also an important anatomical weapon. Nevertheless, proportions of the hand may improve manual dexterity while at the same time making it possible for the hand to be used as a club against opponents. The protective buttressing hypothesis states that bones of the human hand are proportioned in a way so that they provide a supportive buttress which protects the hand from injuries and also that the human fist functions effectively to strengthen and stabilize the hand during striking, which allows competing males to strike with higher force while significantly reducing the risk of hand injury (Horns et al., 2015; Morgan & Carrier, 2013).

To test this hypothesis Horns and colleagues (2015) purchased male cadavers' arms cut in mid-humerus and used them to measure in vitro strain during various buttressed and unbuttressed strikes. Results suggest that the fully clenched fist really provides significant protection to the metacarpal bones (Horns et al., 2015) so that humans can safely strike with more force with a fully buttressed fist compared to an unbuttressed fist or an open-hand slap. Although striking with a fist appears not to result in more forceful strikes compared to slapping, clenched fist increases the peak stress imposed on the target through a smaller area of impact, therefore it results in up to 3 times greater impact force compared to palm strikes (Morgan & Carrier, 2013).

Nevertheless, the relatively high frequency of hand bone fractures that occur during fighting (Jeanmonod et al., 2011) has been used to argue that the hand is too fragile to have evolved as a weapon (King, 2013). Many derived proportions of the human hand have also been suggested to be a pleiotropic result of selection on the foot for terrestrial locomotion (Rolian, Lieberman, & Hallgrímsson, 2010) as hands and feet are serially homologous structures that share similar developmental pathways.

Importantly, in fistfights the primary target is the face (Brink, Vesterby, & Jensen, 1998), and bones of our faces break much more frequently than do bones of the hand during fights, indicating that the fist is a sufficiently effective weapon (Carrier & Morgan, 2014).

Buttressing features of facial morphology

When men fist fight in modern societies, the face is indeed the usual primary target and co-evolution of protective buttressing of this primary target can be expected. Studies focusing on the locations of injuries that result from assaults and interpersonal violence found that the face was the most common site (Brink et al., 1998; Shepherd et al., 1990) and fractures most frequently occurred in the mandibles, nasal complex, zygoma arches, maxillae, and supraorbital arches. The bone structures that suffer from the highest fracture rates are the parts of the skull that exhibit the greatest increase in robusticity during the evolution of genus Homo (see Carrier & Morgan, 2014). These bones are also the most sexually dimorphic parts of the human skull (Enlow, Hans, & McGrew, 1996). The increase in facial robusticity in our ancestors was seen as functionally related to a diet that included hard, difficult to crush objects (Strait et al., 2009). However, later it was shown that our ancestors experienced relatively low strain during chewing, and wear patterns on the teeth suggest that the diet of our ancestors included very few or no hard objects (Daegling et al., 2013).

An alternative hypothesis for the development of our typical facial features and their robusticity is based on the need to protect the face from injury during fighting (Carrier & Morgan, 2014). The protective buttressing hypothesis provides an evolutionary explanation for many of the features that distinguish our ancestors' face and masticatory system from other species'. Orthognathic facial shape, expansion, and bunodont form of postcanine teeth, increased robusticity of the orbits, excessively stronger masticatory system including the mandibula, zygomatic arch, and anterior pillars of the maxilla, and increased size of the jaw adductor muscles are the traits that tentatively represent functional features of protective buttressing of the face against injury during fighting (Carrier & Morgan, 2014).

However, one feature of the human face appears inconsistent with the protective buttressing hypothesis: the extraordinarily large, fragile, and prominent nose which is easy to break (Horns et al., 2015; Mikalsen, Folstad, Yoccoz, & Laeng, 2014). It was suggested that the nose actually evolved as an amplifier of the individual's quality, and less crooked hence more attractive noses cue higher quality (Mikalsen et al., 2014). However, archaeological evidence suggests that nasal fractures related to physical aggression are not universal, but instead rather culturally contingent (Walker, 2001). It seems more likely that popularity of sports such as boxing influences the assault patterns and data from coroner records support that there is a positive correlation between popularization of modern pugilism and the proportion of facial injuries caused by techniques learned through viewing and participating in martial arts and sports (Walker, 2001).

The pronounced sexual dimorphism in body size and upper body strength, plantigrade foot posture, hand morphology, and protective buttressing of our faces all seem to be adaptations for intraspecific fighting in humans. Moreover, the protective buttressing hypothesis is also consistent with the main argument of the following chapter, that is, modern humans can accurately assess a male's strength and fighting capacity from facial shape (e.g. Sell, Cosmides, et al., 2009; Třebický et al., 2013). A man may be therefore considered as more formidable simply because his face is more resistant to injuries and knockouts.

Perception of formidability

Assessing various behavioural characteristics and intentions of others is a key adaptive problem that cognition evolved to address (Galperin, Fessler, Johnson, & Haselton, 2013). Understanding others can help one to forecast others' future behaviour and adjust oneself accordingly. Being able to assess mating interests, trustworthiness, willingness to cooperate, or formidability of conspecifics is of high importance for individuals' fitness, therefore to possess neuro-cognitive mechanisms that work for perceiving and responding to these characteristics and intentions would be very effective. Such mechanisms should swiftly recognize cues in others relying minimally on direct interaction, and should be sensitive to cues that are related to fighting ability (Stoker et al., 2016).

According to Zero acquaintance paradigm (Albright, Kenny, & Malloy, 1988) - the context in which perceivers are given no opportunity to interact with targets that they have no prior knowledge about – they are able to form impressions even when they are presented with thin slices of stimuli containing limited number of information/cues. This is carried out by first impressions (i.e., Bar, Neta, & Linz, 2006) - impressions that can be formed very quickly, based on whatever information is available. Such first impressions are often formed by using, among other features, the visual appearance of faces, frequently independent of emotional cues. Any impact that such stimulus generates in perceivers can then be attributed primarily to the presented cues, like physical features of the target's face. A substantial body of evidence shows that people spontaneously and almost immediately (Willis & Todorov, 2013) attribute various characteristics to others based on their facial appearances such as sexual orientation (i.e., Rule, Ambady, Adams, & Macrae, 2008), trustworthiness (Stirrat & Perrett, 2010), intelligence (Kleisner, Chvátalová, & Flegr, 2014), physical strength (Holzleitner & Perrett, 2016a; Sell, Cosmides, et al., 2009), and aggressive behaviour (Carré, McCormick, & Mondloch, 2009), relying on which we guide our social interactions.

On average, these impressions are rather accurate (Todorov, Olivola, Dotsch, & Mende-Siedlecki, 2015), although it should be noted that the variance explained in the studies remains rather low, and as they are based on stereotypes, they may not fit to all individual cases and may misguide one's behaviour.

It was for instance reported that perceived intelligence correlates to some extent with actual IQ measure (Kleisner et al., 2014), personality characteristics like agreeableness and socio-sexuality are concordantly perceived from faces (Kramer, Gottwald, Dixon, & Ward, 2012), body size (Schneider, Hecht, Stevanov, & Carbon, 2013) or physical illness (Tskhay, Wilson, & Rule, 2016) can by accurately assessed by using facial cues. Regarding perception accuracy related to fighting ability, converging lines of evidence show that people judged as more powerful reported being higher in assertiveness, aggressiveness, and power (Berry, 1991), those who were judged as stronger and better fighters were physically stronger (Sell, Cosmides, et al., 2009), better fighters are correctly distinguished from others (Little, Třebický, Havlíček, Roberts, & Kleisner, 2015; Třebický, Havlíček, Roberts, Little, & Kleisner, 2013), and even criminals who were judged as more violent were more likely to have been confined for violent crimes (Stillman, Maner, & Baumeister, 2010). This evidence suggests that perceivers may be inferring these traits based on static facial morphology cues that are reliably linked to the corresponding aspects of human psychology.

According to the Kernel of truth hypothesis (Berry & Finch Wero, 1993), there might be a positive relationship between stereotypical attributes (e.g., personality characteristics) that people make based on whatever source of information is available (i.e., appearance or facial morphology) and the actual psychological profile of the perceived individual. Such associations may arise as a consequence of several processes which, for instance, include the self-fulfilling prophecy model (Merton, 1948) which is the tendency to act in a way to fulfil other people's beliefs about us. According to this model, facial structure, among other characteristics, may not have an inherent link to behaviour, but rather serve as a social cue that shapes interactions with others over time. An alternative scenario is proposed by the repeated emotional expressions model. According to this model, during the course of life facial structures are shaped by the most frequently expressed emotions, so a frequently frowning person might look uneasy and angry over time, even though not having any negative emotions at the time (Rubešová & Havlíček, 2011). Furthermore, morphological and personal/temperamental characteristics can be affected by a shared underlying biological mechanism. For instance, testosterone levels affect muscle mass growth, development of sex-specific facial morphology, and aggression-related behaviours (Archer, 2006).

Perception of numerous socially relevant characteristics that are important in social contexts (e.g., confrontations and negotiations), are frequently determined by physical traits like conspecifics' body size. In many species, direct visual inspection of others' physical size is well documented (Arnott & Elwood, 2009) primary determinant of social dominance and formidability (Třebický & Havlíček, 2017). For example, various avian species are able to recognize fighting ability of other members of their species without engaging in contest (Fretwell, 1969; Senar & Camerino, 1998), paper wasps are able to detect combative abilities from facial patterns of one another (Tibbetts & Lindsay, 2008), and perceived fighting ability depends on size in lizards (Frýdlová, Šimková, Janovská, Velenský, & Frynta, 2017) and presence and size of weapons in hermit crabs (Neil, 1985). Also, non-human primates use cues such as testicular size and colour changes in sexual skin to assess dominance hierarchy (Ghazanfar & Santos, 2004).

Recently, behavioural scientists proposed that humans are likely to possess cognitive mechanisms that assess fighting ability (Arnott, 2017; Johnson, 2016a; Sell, Cosmides, et al., 2009). Physical stature (e.g., body bulk) is a significant predictor of physical fighting ability among adolescent boys (Beaver, Connolly, & Schwartz, 2015), and men with greater body size and upper body strength reported more frequent involvement in physical aggression (Archer & Thanzami, 2007). Majority of research on cues of threat potential in humans has investigated the relationships between measures of men's threat potential such as body size, upper-body strength, or actual fighting ability and assessments of their facial traits (Arnott, 2017; Puts, 2010; Sell, 2017; Sell, Hone, & Pound, 2012; Třebický et al., 2013). Several studies have reported positive correlations between measures of men's upper-body strength and ratings of their faces for dominance, strength, and ascribed fighting ability (Fink, Neave, & Seydel, 2007; Holzleitner & Perrett, 2016b; Sell, Cosmides, et al., 2009; Windhager, Schaefer, & Fink, 2011). Other studies found that faces of taller men are perceived as more dominant (Burton & Rule, 2013; Re, Debruine, Jones, & Perrett, 2013; Watkins et al., 2010). Cross-cultural research also supports these findings. Ratings from distinct cultures including hunter-horticulturalists, industrialists, and pastoralists, show that cues of physical strength and aggression are present in the face and that these cues can be extracted and assessed rapidly and accurately (Sell et al., 2010; Sell, Cosmides, et al., 2009; Short et al., 2012, Třebický et al., 2013; Zilioli et al., 2014).

There is important evidence showing that attributions of several characteristics related to the fighting ability (e.g., strength or aggressiveness) match with the actual performance and behavioural tendencies of given individuals. A recent study by Han et al. (2017) showed that men's perceived "facial threat potential" (a composite measure derived from Principal Component Analysis of dominance, strength, and weight ratings based on their faces) was positively related to their scores on the "actual threat potential" (constructed as PCA of men's handgrip strength, weight, and height). Man's handgrip strength (a measure of upper body strength) is positively correlated with women's ratings of their dominance (controlling for age and body weight) (Fink et al., 2007). Also, perceived strength is correlated with actual muscle performance (Holzleitner & Perrett, 2016b; Sell, Cosmides, et al., 2009). Peer ratings of each other's fighting ability are tracked by rating of dominance from facial images by strangers (Doll et al., 2014).

Measures of formidability

One limitation of previous studies concerning assessment and measures of formidability (i.e. Han et al., 2017; Sell, Cosmides, et al., 2009) is that they rely on body strength or body size as a measure or rather a proxy for fighting ability. While physical strength is undoubtedly a large component of fighting ability, there are many additional sources of variation in the ability to fight. These studies are rather studying a threat potential, which is highly interesting by itself, however even high threat potential does not need to translate into actual strong fighting ability. The ideal situation for a researcher would to use the outcomes of the actual fights to measure the fighting ability of the participants, nonetheless this presents a considerable logistic and ethical problem as some fights may result with injuries.

Several researchers (Baker & Schorer, 2013; Kraus & Chen, 2013; Little et al., 2015; Palmer-Hague, Zilioli, Jagore, & DeLecce, 2015; Pollet, Stulp, & Groothuis, 2013; Třebický et al., 2015, 2013; Zilioli et al., 2014) have overcome this issue by using available data on fighting ability from databases of mixed martial arts contests. Mixed martial arts (MMA) is an increasingly popular physically demanding combatant sport in which individuals fight using various techniques like punching, kicking, wrestling, takedowns, chokes, and joint locks from diverse martial arts and sports to defeat their opponents. Even though MMA seems to have relatively few restrictions (in reality having highly strict rules), and is referred to as "ultimate fights" or "bloody sports", it serves as the best available model of hand-to-hand fights. Some authors refer to Ultimate Fighting Championship ® (the largest professional Mixed Martial Arts organization) as Quasi-Darwinian environment (Zilioli et al., 2014) in which fighters differ in their abilities to win and fighters who lose several times are eliminated/selected out of the UFC. Unfortunately, using data from this kind of competitive sports is still far from ideal. Compared to general population in which selection pressures of intra-sexual competition would be applied, the sample of MMA fighters consists of elite athletes who are highly skilled in hand-to-hand fights and individual bouts are fought only within designated weight classes.

In most cases of hand-to-hand confrontation little-to-no experience or formal training in fighting can be expected, and therefore more random factors that influence the outcome of a physical fight must be at play. The fighting ability is undoubtedly a complex skill affected by various characteristics including body size, reach, strength, dexterity, speed, hand–eye coordination, proper technique, and aggressiveness, among others. However, the available evidence indicates that body size and upper body strength might carry special significance. Body size is an observable biological indicator of the formidable individual, at least among adolescent males (Beaver et al., 2015). Kinanthropometric analysis, for instance, shows that body size is positively related to punching force one can generate (Carrier, 2011). Certain performance measures such as handgrip strength have also been shown to be related to overall physical fitness and fighting performance (Windhager et al., 2011). However, our knowledge in this area is far from definite and contribution of other characteristics may vary according to the form of the fight (e.g., reach might be relatively more important in cold weapon combats compared to the others). Hence, data available from Mixed Martial Arts need to be taken with adequate caution in mind.

Perception of actual fighting ability based on Mixed martial arts data

Recently, we have tested the role that facial perception plays in assessment of aggressiveness and fighting ability by investigating the association between both perceived aggressiveness and perceived fighting ability based on fighters' faces and their actual fighting success in MMA (Třebický et al., 2013). More than 600 individuals from the Czech Republic rated a random subset of 50 images from 146 selected portrait photographs of UFC fighters for perceived aggressiveness and additional 278 individuals rated the same photos for perceived fighting ability. Independently of the rater's sex, perceived aggressiveness was positively associated with the proportion of fights won, after we controlled for the effect of weight, which also independently predicted perceived aggressiveness. Perception of fighting ability was confounded by weight, and an association between perceived fighting ability and actual fighting success was restricted only to the fighters in heavy-weights category.

Our study focused on routinely studied paradigm of personality perception, the Zero-acquaintance paradigm (Albright et al., 1988), where raters assess the characteristics of only one target individual at a time. Although inter-personal conflicts are frequently solved in a similar fashion, on man-to-man level, other men's presence during brawls is not uncommon and judging potential opponents on a relative scale – who would or who won the fight given two men - would prepare the way for selectivity in prospective encounters. Therefore, in our subsequent study we used the forced choice test paradigm (in which the rater is usually presented with two target stimuli at a time and his task is to choose one stimuli considering a given question) to test whether people can predict winners of mixed martial arts bouts based only on facial cues at greater than chance level (Little et al., 2015). Our results showed that the raters could accurately distinguish the winner of two UFC fighters who fought each other greater than chance level based on their faces. Our data demonstrated that both men and women perceive the winners of the fights differently from the losers. Specifically, winner's faces were more likely to be seen as able to win the fight, physically stronger, more aggressive, more masculine, more aggressive, and more attractive to women than losers' faces. Thus, our findings are in line with the notion that humans possess the perceptual/cognitive ability to assess fighting ability in other humans, which can be expected in species that engage in such behaviour (Parker, 1974).

Errors in formidability assessments

When assessing other's formidability and evaluating own costs and benefits of a potential confrontation, miscalculations might lead to costly expensive consequences to fitness. According to the "adaptive rationality" approach, our mind was shaped by selection to enhance our fitness rather than to always yield accurate judgments (Haselton & Buss, 2009). The evolution of such an effect can be subsumed within Error Management Theory (Haselton & Buss, 2000), which predicts that false-positive and false-negative errors might have highly biased consequences in terms of survival and/or fitness. The costs of false-negative attributions to dangerous opponents might be disproportionally higher than false-positive attributions of fighting ability to harmless individuals.

Sex differences in formidability assessment

Because men are substantially stronger than women (Lassek & Gaulin, 2009), and deploy physically aggressive strategies more often (Archer, 2004), cognitive specializations for formidability assessment could be expected to be better developed in men compared to women. Although women are far less likely to participate in aggressive encounters (Archer, 2004), to accurately predict the outcomes of male conflicts would be relevant for both men and women. Fighting ability can be considered as an honest cue to male mate quality, so it is likely that it would affect women's judgments about who to mate with (Johnson, 2016b). Also, as women are frequent victims of inter-sexual violence (Felson, 1996), they are expected to be sensitive in assessing with whom not to get involved with. Given these pressures, it would be surprising if both men and women did not have adaptive specializations for detecting relevant cues of these characteristics. The existing evidence strongly supports the idea that men and women perform equally well in assessing fighting ability from visual cues, even though men are much more likely to engage in and be victims of aggression (Little et al., 2015; Sell, Cosmides, et al., 2009; Třebický et al., 2013). Moreover, women appear to prefer men with greater fighting ability (Fink et al., 2007).

Inter-individual differences in formidability assessment

Results of previous studies indicate that accuracy in assessing fighting ability varies considerably among individuals (Třebický et al., 2013). This might either be a result of idiosyncratic variations or might be systematically related to specific characteristics of the perceiver. The latter is predicted by the recalibrational theory of anger (Sell, 2011) which predicts that an individual with a relatively low fighting ability potential (e.g., short stature, small body mass etc.) will be more attentive to the cues of fighting ability of the opponent to avoid potential costs of the encounter (Sell, Cosmides, et al., 2009). In other words, without an accurate estimate of one's own fighting ability, knowledge of another's would be of little use. Thus, it is expected that individuals are equipped with mechanisms for assessing their own fighting ability. It is of crucial importance to adequately assess formidability of a potential opponent relative to one's own powers. Inadequacy of such assessments might have profound consequences, as overestimation of own powers might lead to loss of resources, and underestimation of the opponent's powers may result in one's injury or even death.

If relative formidability is primarily represented in terms of size and strength (Sell, Cosmides, et al., 2009; Třebický & Havlíček, 2017), then a man's own body parameters like strength should inversely predict his assessments of a prospective opponent's fighting abilities.

Available evidence supports that men have cognitive mechanisms allowing them to accurately assess men's strength from visual cues, and make judgments about others' fighting ability on this basis (Sell, Cosmides, et al., 2009) while accurately assessing their own strength as well (Sell, Tooby, & Cosmides, 2009), suggesting that assessment of rival physical threat varies as a function of one's own strength. Doll and colleagues (2014) showed that individuals' ratings of their own fighting ability correspond closely to those of their peers. In another study, men's own physical strength was inversely related to his estimates of potential opponents' strength (Fessler, Holbrook, & Gervais, 2014). Similarly, shorter men are more likely to perceive masculinized faces as dominant than taller men (Watkins et al., 2010) who are less vulnerable to assault and better built to inflict higher damage (Carrier, 2011).

Facial morphology related to perceived formidability

Perception of formidability and related attributes, such as aggressiveness and dominance, is stereotypically associated with some facial (and bodily) morphological characteristics and behavioural expressions. In the scholarly literature, the stereotypical attribution of personality characteristics from outer traits (appearance, behaviour, clothes, etc.) is commonly labelled as the Halo effect (Thorndike, 1920). A key set of traits that affect social attributions is usually associated with sexual dimorphism. Individuals with highly developed male-typical facial features are then consistently and stereotypically perceived as more masculine (Penton-Voak & Chen, 2004), dominant, and aggressive (Perrett et al., 1998; Rhodes, 2006). Consequently, these features may affect experience and attributions in social interactions. For example, ratings of facial dominance of men predicted their later progress in military career (Mueller & Mazur, 1996).

A growing body of research aims to identify facial morphological traits related to various characteristics (from body size to behavioural and personality characteristics). These studies investigate which visual cues people use to estimate those characteristics from the face and subsequently test how accurately visual cues relate to relevant morphological structures. For example, in the case of body size, taller people are generally reported to have more elongated faces than shorter ones (Windhager et al., 2011). Facial elongation (i.e., full length of the face divided by its width) increases starting from infancy to adulthood as the lower jaw develops and starts protruding, making the face less round and more oval. Furthermore, heavier men and women have wider and more square faces, and heavier men also have rounder lower facial regions (Coetzee, Chen, Perrett, & Stephen, 2010). Adiposity produces a typical facial shape because a large percentage of facial lipid tissue is allocated in the cheek area (buccal fat pads), thus providing a visual cue for body size (Coetzee, Perrett, & Stephen, 2009). Available evidence also indicates that people use the abovementioned or related facial cues to assess others' body weight and height, and they are fairly accurate in their judgments. Individuals with wider, more square faces, and rounder lower faces are correctly judged as heavier (Coetzee et al., 2010), while people with longer faces are judged as taller (Re, Hunter, et al., 2013). It was found that low brows, large chins, wide noses, and narrow mouths are morphological traits related to perceived dominance and strength in both natural and computergenerated faces (Toscano, Schubert, & Sell, 2014), and that physical strength (i.e., handgrip, shoulder width) is associated with rounder faces with wider eyebrows, and more prominent jaws (Windhager et al., 2011). Another study employed computer generated facial stimuli varying in muscle movements that constitute angered facial expressions for assessment of physical strength (Sell, Cosmides, & Tooby, 2014). Their results showed that each of the major components of the angry face (lower brow ridge, higher cheekbones, wider nose, higher mouth, thinner lips, protruding lips, and larger chin and chin bun) independently increases perceived strength. While these studies demonstrate that there are specific facial morphological features associated with formidability-related traits and that people pay attention to these traits, they do not demonstrate whether these particular features are indeed present in more successful fighters.

To test a possible relationship between perception, facial shape, and actual fighting success, we used the available dataset of professional MMA fighters and their portrait photographs (Třebický et al., 2013).

Facial features were analysed by using the geometric morphometric methods (GMM). The GMM represents a toolbox of analytical methods for the multivariate statistical analysis of Cartesian coordinate data of landmark positions. The landmarks (anatomically or geometrically homologous points) and semi-landmarks (denote curves and outlines of a given shape) are manually digitized on photographs of people's faces. Landmark configurations are then superimposed using the Generalized Procrustes Analysis (GPA), which standardizes the size, position, and orientation of the objects. To determine the shape variation related to the perceived characteristics, GPA shape coordinates are regressed onto the examined trait using shape regression. Visualisation of these shape regressions can be displayed by thin-plate splines as deformation grid from the overall mean configuration (the consensus) of the landmarks.

Results of these analyses showed systematic differences in structural configurations of facial features, perceived aggressiveness, and actual fighting success. Shape regressions revealed that aggressive-looking faces are generally wider and have broader chins, more prominent eyebrows, and larger noses than less aggressive-looking faces. However, the association between facial configuration and fighting success was restricted to heavyweight fighters. The shape changes associated with high fighting success strongly resemble transformations predicted along the attribution of aggressiveness. However, estimated configurations of aggressiveness also show certain inconsistencies with prediction of fighting success. For example, the thinner chin and mouth associated with the estimated configuration of high fighting success do not correspond to attribution of high aggressiveness associated with a broad chin (Třebický et al., 2013).

The Facial Width-to-Height ratio

In the last decade, there was a boom of research focusing on one very particular morphological measure in human face, the facial width-to-height ratio (fWHR or relative facial width) (Weston, Friday, & Lio, 2007), and it has been the subject of intense investigation as a cue to numerous behavioural and personality characteristics since then (for recent meta-analyses see Bird et al., 2016; Geniole, Denson, Dixson, Carré, & McCormick, 2015; Haselhuhn, Ormiston, & Wong, 2015; Kramer, 2017). This ratio is measured by dividing the facial width by the upper facial height. First it was introduced as a measure used on skeletal remains (Weston et al., 2007), where the ratio is delineated as bizygomatic width divided by distance between prosthion and nasion. However, the vast majority of research on fWHR uses frontal facial photographs, where only projection of some anthropometrical points is available, and thus the procedure of fWHR ratio measurement is slightly altered. Most commonly, it is delineated as the distance between projection of right and left zygions (zy'-zy') and the distance between the centre most superior point of the upper lip (labrale superius, ls) and projection of nasion (ns') in the middle of the brows (i.e. Carré et al., 2009; Třebický et al., 2015).

Because the growth trajectories of bizygomatic width change during pubertal growth independently of the height of the upper face and body height, the fWHR was formerly considered as a sexually dimorphic trait (Weston et al., 2007). This claim has been challenged due to the inconsistent results of several subsequent studies using data from various populations (i.e., Lefevre et al., 2012; Özener, 2012), suggesting that if fWHR is sexually dimorphic it might hold only for some non-Western populations. According to the recently published meta-analyses, men do have larger fWHR (measured both from skulls and photographs) than women, although this effect is very small and when each population is separately analysed, the differences remain significant only in samples from Eastern Asia (Kramer, 2017).

It has been speculated that the relationship between within-sex variation in fWHR and many behavioural characteristics might reflect a common association with a third variable, such as organizational effects of testosterone which influences the development of craniofacial morphology, the physique, and the central nervous system as a part of the sexual differentiation during adolescence (Carré & McCormick, 2008a). Indeed, initial research found significant (but weak) associations between fWHR in men and baseline levels of testosterone, as well as acute changes in testosterone levels in response to potential mate exposure (Lefevre, Lewis, Perrett, & Penke, 2013). However, other studies found null or mixed results (for review see Bird et al., 2016). A recent re-evaluative study failed to find a significant link of fWHR to neither men's circulating testosterone levels nor their reactive testosterone levels following competition (Bird et al., 2016).

Nevertheless, a rapidly growing body of research links men's facial width-to-height ratio to a wide range of behaviours. For instance, researchers have demonstrated that a greater fWHR is associated with lifetime reproductive success (Loehr & O'Hara, 2013), achievement drive in US president candidates (Lewis, Lefevre, & Bates, 2012), and the number of nominations and the award probability in nominees and laureates of the Nobel Prize in Literature (Lebuda & Karwowski, 2016). Also, men with wider faces are better negotiators in competitive bargaining (Haselhuhn, Wong, Ormiston, Inesi, & Galinsky, 2014), and companies led by CEOs with greater fWHRs achieve superior financial performance (however, this only applies to the companies that are managed by cognitively simple leadership styles) (Wong, Ormiston, & Haselhuhn, 2011). Men with greater fWHR are less cooperative in the context of intra-group competition, however more cooperative in the context of inter-group competition (Stirrat & Perrett, 2012). A substantial body of evidence shows that male fWHR correlates with characteristics that are considered as socially undesirable including higher prejudice (Hehman, Leitner, Deegan, & Gaertner, 2013), anti-social and unethical behaviour (Geniole, Keyes, Carré, & McCormick, 2014; Haselhuhn & Wong, 2012), lower trustworthiness (Stirrat & Perrett, 2010), greater psychopathic traits (Anderl et al., 2016), and also lower attractiveness (Geniole et al., 2015). Interestingly, fWHR does not seem to predict as many behavioural or psychological characteristics in women compared to men (Carré & McCormick, 2008; Haselhuhn, Wong, Ormiston, Inesi, & Galinsky, 2014; Stirrat & Perrett, 2010; but see Geniole et al., 2015; Lefevre, Etchells, Howell, Clark, & Penton-Voak, 2014 for exceptions).

Differences in fWHR are perceived rapidly (Carré, Morrissey, Mondloch, & McCormick, 2010), and they are conspicuous even in bearded men (Geniole & McCormick, 2015). Furthermore, the fWHR is positively associated with dominance even in capuchin monkeys (Lefevre, Wilson, et al., 2014). Male monkeys with lager faces behave more assertively (Wilson et al., 2014), thus they are more likely to achieve alpha-male status (Lefevre, Wilson, et al., 2014). Humans can accurately assess this trait in non-human primates as well (i.e. Kramer & Ward, 2012), suggesting that the fWHR, and the sensitivity to it, might be a part of an evolved cuing system in human and non-human primates.

The facial width-to-height ratio is an intensively studied trait in the context of antagonistic encounters in particular. fWHR in men is related to dominance perceived in self and others (Mileva, Cowan, Cobey, Knowles, & Little, 2014), sport performance (Třebický et al., 2015; Tsujimura & Banissy, 2013; but see Kramer, 2015) and physical strength (Windhager et al., 2011). Stirrat and colleagues (2012) found that narrow-faced men were more likely than wider-faced men to die by contact violence compared to other causes of death or homicide. Several studies also reported that relative facial width is positively related to aggressive behaviour and perceived aggressiveness (Carré & McCormick, 2008b; Carré et al., 2009; Lefevre & Lewis, 2013; Welker, Goetz, & Carré, 2015; but see Gómez-Valdés et al., 2013; Özener, 2012), even in cross-cultural context (Short et al., 2012). Despite somehow mixed findings in the literature, results of meta-analyses demonstrate a robust positive link between fWHR and aggression, suggesting that the fWHR may serve as a reliable cue to one's propensity for aggressive behaviour, but it is important to note that the effect sizes are small (Geniole et al., 2015; Haselhuhn et al., 2015).

Zilioli et al. (2014) employed faces of professional MMA fighters as stimuli and reported that fWHR is associated with fighting performance and judgments of formidability. They showed that fighters with greater fWHR had longer fighting careers, and both higher numbers and proportions of wins in their career (independently of their BMI). Coincidentally at the same time, we tested a similar hypothesis (Třebický et al., 2015) as a follow- up to our previous research that examines other aspects of facial appearance and success in MMA fighters (Třebický et al., 2013). Specifically, we tested whether variation in fWHR is associated with actual fighting performance, perception of aggressiveness, and fighting ability. While drawn from an overlapping database, in comparison to Zilioli et al.'s (2014) study, our stimuli set consisted of a smaller sample of portrait photographs (for details see Třebický et al., 2015). Our results also revealed a correlation between fWHR and fighting performance with a comparable effect size to Zilioli et al.'s (2014). Interestingly, in our study both perceived aggressiveness and fighting ability were positively correlated with fighter's fWHR and body weight, but not with fighter's height.

However, there were some methodological differences between the two studies. Zilioli et al. (2014) employed pairs of composite images varying in the level of fWHR and fighting experience for perceptual tests. They used a forced- choice paradigm which is highly sensitive to detect subtle effects. However, a disadvantage of this approach is that it uses only extreme forms from the overall variation and may therefore overestimate the actual effect. In contrast, we used a variety of non- manipulated faces which captures the natural variability more widely. However, such a test might be somewhat less sensitive to detect possible effects. Thus, the two approaches are complementary.

Overall, the body of converging evidence supports that relative facial width can act as a cue to formidability in men and may play an important role in intra- sexual selection, as well as suggesting that human perception may have evolved to be attentive to such cues.

Influence of third variables on results of relative facial width studies

Weston, Friday, and Lio (2007) had originally found that fWHR is independent from body size. Therefore, this variable has been frequently overlooked in previous studies. However, several subsequent studies suggested that the link between fWHR and aggression (Carré & McCormick, 2008b) or sport performance (Tsujimura & Banissy, 2013) might be an epiphenomenon of body size (Deaner, Goetz, Shattuck, & Schnotala, 2012; Geniole et al., 2015; Mayew, 2013). It has also been shown that variation in body dimensions is related to the face size, including fWHR (Coetzee et al., 2010). For this reason, in our study of the professional MMA fighters (Třebický et al., 2015) we tested the relationship between body size and fWHR and did find that fWHR is positively correlated with height and weight. Subsequent analyses of our data revealed that perceived aggressiveness was significantly and independently correlated with both fWHR and weight, while fighting ability was correlated with weight, but not with fWHR. Another line of evidence shows that fWHR as a facial feature is not stable in time and decreases with age (Hehman, Leitner, & Freeman, 2014), and aging-related changes in fWHR (e.g., facial elongation) mediated the relationship between target age and multiple aging-related perceptions (e.g., decrease in physical and social abilities, ascribed wisdom). Taken together, these results indicate that variables describing body size and age should be controlled in future studies since some of the previous fWHR associations can be explained by differences associated with size and age, rather than relative facial morphology itself.

Additionally, the association between FWHR and social behaviour may be moderated by social or contextual factors. One potential moderator of the relationship between fWHR and aggression is social status. As previous studies demonstrated, subjective social status moderates the effect of fWHR on aggressive behaviour (Goetz et al., 2013). Specifically, fWHR was positively correlated with aggression, but only in men that report low subjective social status. These findings indicate that men with relatively wider faces are not generally more prone to aggressive behaviour, but it is the relatively low social status that triggers the willingness to engage in aggressive behaviour.

In a well-designed study, Hehman and colleagues (2013) showed that even slight (both forward and backward) head tilts significantly alter perceived fWHR and assessed formidability. Moreover, individuals with smaller baseline fWHRs, who would be particularly likely to benefit from augmenting their perceived fWHR, increased their fWHR more than individuals with larger fWHRs by tilting their heads more sharply. These results present that individuals behaviourally manipulate their perceived fWHR in order to appear more intimidating.

In a typical setup where facial stimuli are presented, the vantage point of the rater is centred and aligned with the facial stimuli. However, we do not usually view faces of others from levelled vantage points. Humans show a relatively significant height dimorphism and since men are typically taller, they view women's faces from slightly above, while women tend to view men's faces from slightly below (Burke & Sulikowski, 2010). One study manipulated the vantage point of perception and showed that participants tend to overestimate the body weight for the faces presented from a lower vantage point and underestimate it for the faces presented from a higher vantage point (Schneider, Hecht, & Carbon, 2012). This seemingly minor difference between the laboratory setting and real-life situations might consequently lead to misleading results.

The majority of the studies on facial perception employ portrait photographs as stimuli. Although several previous studies have reported careful methodological processes of photograph acquisition (e.g., Peron & Morosini, 2012; Verhoff, Witzel, Kreutz, & Ramsthaler, 2008), the employed methodology varies across individual studies which may in turn impede assessment of the validity and an accurate replication of previous findings. This may lead to overall small effect-sizes reported by meta-analyses as in the case of fWHR studies (Geniole et al., 2015).

A key technical aspect affecting the photographs acquired for morphological and perceptual studies, which is frequently not reported, is the focal length of the lens. Focal length represents the distance between lens optics and camera sensor, provides variance in viewing angle resulting in different degrees of image distortion. Due to these distortions, artefacts in size and shape representations in photographs can occur. In our methodological study (Třebický, Fialová, Kleisner, & Havlíček, 2016), we investigated the possible influence of focal length on depicted facial shape by measuring facial width-to-height ratio and employing geometric morphometrics as well as perception of facial images. We found that fWHR, as measured from the photographs, significantly varied across the focal lengths used (50 mm, 85mm and 105mm full-frame equivalences), and fWHR that was taken at 50 mm was significantly the smallest. Results of the geometric morphometric analyses similarly showed significant differences in overall facial shape between the focal lengths that were used (at the 50mm focal length as compared to the longer focal lengths: overall rounded face, larger and wider set eyes, wider set eyebrows, rounded, longer and broader nose, taller forehead, rounded chin, and ears obscured by the cheeks). Further, facial photographs that were taken with the longest focal length (105 mm) were judged as the most attractive, dominant, and masculine/feminine. In contrast, photographs taken with a shorter focal length were perceived as the least attractive, dominant, and masculine/ feminine.

Changes in facial dimensions, shape, and facial perception that we found in our study appear to be a consequence of the variation in perspective distortion produced by the different focal lengths. These findings show that certain camera settings can considerably influence how the taken photographs are perceived. Such distortion of the facial shapes may increase the possibility of making type I (falsely positive results) and/or type II (falsely negative results, e.g., floor or ceiling effect) errors.

In sum, our study provides additional evidence that the methodology of photograph acquisition should be controlled as it can influence the results of perceptual and morphological studies.

Multilevel approach to assessments of formidability

Current body of research shows many pieces of evidence about which factors affect assessments of formidability. Nevertheless, it is not yet fully understood how these assessments work in real-life situations. To account for this issue, we propose a model of multi-level assessments of formidability that tries to cover processes responsible for the fight-or-flight decision when faced with a potential antagonist. In our study (Třebický et al., 2013), perceived aggressiveness and perceived fighting ability were moderately correlated, and the data indicated that the two variables might be underpinned by slightly different cognitive processes. First, judgments of fighting ability seem to focus on general probability of winning a fight, which is substantially related to size and weight (Deaner et al., 2012; Třebický et al., 2015). This is further supported by the fact that heavyweight contestants were seen as much better fighters than lightweight contestants. This might be the reason why we found no association between perceived fighting ability and actual fighting success in the overall sample of fighters who fight only within individual weight class.

Relying on the abovementioned findings, we can conclude that overall assessment of fighting ability might involve several more specific attributions. We suggest that assessment of potential opponents acts on multiple levels. Based on the knowledge of one's own formidability, a resource holding power (Parker, 1974) of each competitor is evaluated regarding the potential costs and benefits of confrontation, so that the welfare trade-off ratios (Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008) which help to recalibrate appropriate level of anger of rivals could be calculated (Sell, 2011). The first step, in such a multilevel fight-or-flight decision-making process, might depend predominantly on the overall size of the opponent, as suggested by the ratings of fighting ability in our study (Třebický et al., 2015). If one of the competitors is substantially larger (e.g., taller, more muscular, or bulkier), the smaller one surrenders and withdraws from the conflict, as his chances of winning are rather small. When the rivals have roughly equal sizes, a further level of assessment takes place - which might be related to the perception of bargaining potential such as the assessment of aggressiveness from facial features (Třebický et al., 2013). The more aggressive-looking competitor might be recognized before the actual confrontation, and the less competitive one surrenders. If both competitors feel equally formidable, the confrontation may get escalated. However, in situations in which even the less formidable competitor has little to lose (or would lose for sure if he would not defend himself) and a lot to gain, he can escalate the conflict which would be otherwise omitted.

In terms of decision making models, this would correspond to "The fast and frugal tree" model where an individual follows a decision-tree with an exit option after each attribute (Martignon, Vitouch, Takezawa, & Forster, 2003). Although, to my best knowledge, this claim has not been tested so far.

Conclusions

The main aim of this thesis was to test whether morphological features in men's faces may serve as potential reliable cues to the actual formidability and whether our visual perception is sensitive towards such cues. Based upon converging results of our empirical studies (Little, Třebický, Havlíček, Roberts, & Kleisner, 2015; Třebický et al., 2015; Třebický, Havlíček, Roberts, Little, & Kleisner, 2013), we can conclude, that in selected samples of professional mixed martial art fighters, facial morphology is a predictive cue of actual performance in physical fights, and that raters, irrespective of their sex, are sensitive toward these cues.

In our first study (Třebický et al., 2013), we showed, that ratings of perceived aggressiveness positively correlate with actual performance of given fighters. Holistic facial shape analyses showed systematic differences in structural configurations of facial morphology in successful competitors, compared to unsuccessful ones and between fighters perceived as more aggressive compared to less-aggressive ones. Visualisation of shape regressions indicates that aggressive-looking faces are overall wider, have a broader chin, more prominent eyebrows and larger noses than less aggressive-looking faces. The shape changes associated with high fighting success strongly resemble transformations predicted by perception of aggressiveness, although having rather a thinner chin and mouth. In this case, the association between facial configuration and fighting success was restricted to heavyweight fighters. The second study (Little et al., 2015) focused on different paradigm of facial perception. Instead of presenting one face at a time, we showed pairs of competitors with known outcome of their competition. This scenario specifically tests not how single rater assesses the formidability of potential competitor (probably relatively to self-perceived formidability), but whether we are able to assess these traits across dyads of other individuals. Result of this study shows, that raters were able to choose the winner of consequent fight with accuracy higher than chance. The winners were rated as better fighters, as stronger, more dominant and attractive, compared to losers. The third study (Třebický et al., 2015) aimed to test, if a simple descriptor of facial morphology, relative facial width (fWHR) is a sufficient predictor of perceived formidability and fighting performance. In line with comparable studies (Zilioli et al., 2014) in our sample both perceived aggressiveness and fighting ability were positively correlated with fighter's fWHR and with their body weight, as well.

Evidence provided in our studies is important contribution to emerging body of research concerning evolution of neuro-cognitive and behavioural processes finetuned toward perception and adequate behavioural responses toward potential opponents (i.e. Sell, 2017). The main drawback of previous studies was their focus only on proxies to one's formidability, like physical strength or propensity for aggressiveness (Han et al., 2017; Sell et al., 2009). Our studies provide results about actual fighting ability in two complementary scenarios of potential opponent assessments.

Although, intra-sexual competition in men is a widely investigated area in behavioural sciences, we are still at realms of rather skin-deep understanding to how the assessments of potential opponents take place. Variety of third variables affecting perception of others and its accuracy are coming at play, like social status (Welker, Goetz, & Carré, 2015) of the perceiver, or physical size of rated individual (Deaner, Goetz, Shattuck, & Schnotala, 2012; see also Hehman, Leitner, & Gaertner, 2013). For this reason, we propose that the assessment of potential opponents acts on multiple levels, then simply based on first impressions. In this multilevel 'fight or flight' decision making model, individuals assess their potential competitors following a decision-tree with an exit option after each attribute. At the first level, the decision-making process might depend predominantly on the overall size comparisons (Třebický et al., 2015). Further levels than might depend on perception of other's formidability related measures, like facial morphology (Třebický et al., 2013).

Current literature also suggests that other morphological or behavioural cues might provide additional information about one's formidability, like skin coloration (e.g. levels of facial redness) (for review see Rowland & Burriss, 2017; Stephen, Oldham, Perrett, & Barton, 2012) or vocal characteristics (Pisanski, Cartei, McGettigan, Raine, & Reby, 2016). Another drawback of the current state of research is the focus on thin slices of information provided by a single cue rated on a single behavioural/personality characteristic. However, our perception is not limited to gathering information through just one perceptual channel, e.g. just with our sight and we do ascribe many characteristics based on a single slice of information. Utilizing multiple cues assessment and/or multiple characteristics rating, and testing the agreement between modalities and scales, and their subsequent interplay remains a challenge for future studies.

Finally, most of the studies conducted so far aimed on only one a specific scenario of physical confrontations, where only two opponents confront. Though, physical encounters among men are not limited solely to the two individual opponents and may frequently involve other, the allies. Of high adaptive importance would be ability to assess the prowess of a potential opponent as that of a potential ally, in terms of deciding whether to enter the fight and pursue relevant joined activities. Assessments of formidability are therefore not relevant solely in the context of a potential opponent, but also in the context of selection of allies.

Even though substantial body of evidence available, we are still at a pioneering phase of discoveries regarding intra-sexual competition in men.

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Part 2

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Declaration of publication co-authorship

This is to confirm that PhD candidate Vít Třebický, M.A. significantly contributed to the following publication: *Třebický, V., Kleisner, K., & Havlíček, J. (2012). Evolutionary concepts of human physical attractiveness: The case of male physique. Anthropologie, 50(1), 33–45.*

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EVOLUTIONARY CONCEPTS OF HUMAN PHYSICAL ATTRACTIVENESS: THE CASE OF MALE PHYSIQUE

ABSTRACT: Perception of certain body traits as attractive or unattractive has a profound effect on our everyday life. Here we employ sexual selection models which aim to explain why perception of specific traits as attractive might have evolved to conceptualize evidence on male body attractiveness. One line of reasoning considers attractive traits to be markers of individual qualities. We specifically focus on two concepts: I) developmental stability and heterozygosity and II) immunocompetence and sexual dimorphism and their link to attractiveness of the human male physique. The available data on preferences for the majority of traits of the human male physique show inverted U curved patterns, which are indicative of a trade-off. Further, we show that several key links between physical appearance and the quality of a mate still need to be established in humans.

KEY WORDS: Attractiveness – Male body – Cue – Health – Fitness – Quality

INTRODUCTION

Charles Darwin (1859) in his classical treatise claimed that male traits, like a colourful plumage, serve as displays of arbitrary beauty for charming females and that these traits bear no signs about the biological quality of a male. He also assumed that humans have no universal measure of attractiveness and that the criteria by which male beauty is assessed are purely arbitrary and often change in time within a single population and markedly differ between populations (Darwin 1871). In contrast, his contemporary, Alfred Russell Wallace (1892), argued that females are more influenced in their choice by qualities affecting the survival of a male, by means of attraction to traits which serve as a cue to the real quality of a male. In the recent decades, the distinction between the Darwinian aesthetical beauty and Wallace's cues of quality has recaptured the attention of evolutionary scientists. At the end of the 1970s, researchers began to interpret perception of physical attractiveness in humans from an evolutionary perspective, that is, as a result of natural and sexual

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selection (e.g., Symons 1979). Subsequent research has shown that it is highly plausible that human criteria of mate selection do not qualitatively differ from those of other species. In other words, they were selected in our evolutionary past and are responsible for our perception of attractiveness and related preferences (Grammer *et al.* 2003). However, it has also turned out that neither the perception of attractiveness nor the traits considered attractive are so strictly defined as implied by Darwin's (1859) or Wallace's (1892) suggestions, especially in humans.

The main aim of this paper is to show that in spite of an enormous body of literature about physical attractiveness published during the past two decades, several theoretical issues remain to be resolved. Here we exclusively focus on evolutionary-informed theories of human physical attractiveness. These are briefly introduced and it is assessed how well-founded they are on empirical findings. Thus, we do not aim to provide a comprehensive review on physical attractiveness, but rather we focus on critical appraisal of the main evolutionary concepts of physical attractiveness. To make the paper concise, we present these concepts using studies on preferences of human male bodily traits. Thus, the extensive body of literature on facial attractiveness is not considered here as it would exceed the limits of this work. For similar reasons, we do not deal here with studies on women's physical attractiveness. These issues have recently been reviewed elsewhere (for a current review of the literature on facial attractiveness see Little *et al.* 2011). Although there is ample evidence that physical attractiveness plays an important role in various social interactions ranging from how well children are treated, job interviews to juridical outcomes, its primary scope lies in romantic relationships. Due to the central role of reproduction in evolutionary theorizing, not surprisingly the majority of evolutionary theories of physical attractiveness revolve around its role in mate attraction. Thus, we too follow this line and deliberately focus mainly on the mate choice context, although we acknowledge the significance of physical appearance in other social contexts as well.

TRAITS CONSIDERED ATTRACTIVE AS CUES OF QUALITY

For the development of any trait acquisition of energy from the environment is needed as proposed by the life-history theory (Roff 1992). The theory assumes that the amount of energy available is limited and each individual must allocate a proportion of the energy to activities which increase his or her chance to survive. This is especially to reach sexual maturity, to reproduce and enhance the chances of survival of offspring, and further factors that generally lead to increased fitness. (Throughout the paper we use the term "fitness" to express a degree to which a given genotype contributes to the gene pool of the next generation, while the term 'physical fitness' is meant to describe parameters of physical performance of an individual such as strength, endurance, etc.). Such a trade-off between the investment into survival, growth, sexual maturity or traits related to attractiveness is thought to be an important drive of the selection of attractive traits and preference for them.

It is assumed that the tendency to be attracted to individuals of the opposite sex exhibiting certain traits provides the individuals so inclined with the advantage of higher reproductive success (Gangestad, Scheyd 2005). Several models have been proposed to explain how such preferences might have arisen.

In a model first introduced by Fisher (1930), a trait that becomes preferred develops by chance and preference for the most frequent trait is maintained within a population in such a way that offspring of one sex are expected to inherit the trait and offspring of the other sex inherit the preference for a such trait. Thus, the model assumes a genetic linkage between the genes affecting the preference and the genes responsible for the development of the preferred trait (Fisher 1930). However, this does not assume a link between the trait and the quality of the individual who possesses it. For that reason, the model is frequently referred to as the "sexy sons" or, more precisely, "sexy offspring" hypothesis. It should be noted that Fisher's model does not imply any positive relation of fitness and viability of an individual, which in turn could have been possibly reduced by prior investing into "sexy traits".

Another model (or, more correctly, a set of models), explaining how the preferences relate to the fitness of an individual, is frequently referred to as "honest signalling". One potential account of how honest signals have arisen, first introduced by Zahavi (1975), is a model of handicap. According to this model, only individuals of superior quality can afford to develop a trait which reduces their chance of survival and thus can serve as a quality signal. In other words, the trait poses a handicap to its bearer (e.g., deer's antlers). Later it was specified that for such a trait to limit its bearer, its cost must be high, however it must not reduce the fitness of its bearer in such a way that it would be lower than that of individuals without the handicap (Getty 2002). In the other account of honest signals, the quality of an individual is presented by the degree of development of the trait. In other words, a more developed trait shows the higher quality of the given individual, however, this relation is not necessarily linear (Getty 2002). This other account of honest signals focuses on the often-cited relation between attractiveness and the assumed parasite load present in a given individual, as proposed by Hamilton and Zuk (1982).

Although Fisher's runaway selection (Fisher 1930) is frequently presented as an alternative to the models of honest signals, mathematical modelling shows that every trait ultimately becomes costly (Kokko *et al.* 2003). As the cost of maintaining the trait which has evolved through runaway selection rises, the trait becomes an indicator of quality of the particular individual.

The above-reviewed models refer to an organism's quality in general terms. However, preferences might be related to specific qualities such as health, physical fitness etc. Below we focus on a hypothesis proposing such a specific link.

DEVELOPMENTAL STABILITY AND HETEROZYGOSITY

Throughout the evolutionary past of humankind, similarly to other species, infections and parasites have played an important role as they reduce an individual's fitness. It was therefore proposed that individuals will choose mates who show heritable cues of health (Hamilton, Zuk 1982). However, later it was argued that viability and reproductive success might be, to some extent, independent and thus the actual health status of individuals with preferred traits could be higher, the same or even worse than that of individuals lacking such traits (Getty 2002).

In the course of ontogeny, individuals face various adverse environmental effects caused by pathogens, factors affecting the rate of somatic mutation, availability of caloric intake and so on. The ability of an organism to successfully cope with such effects is commonly referred to as developmental stability and its heritability is thought to be relatively high. Developmental stability is assumed to be phenotypically represented by a high degree of bilateral symmetry of an individual's morphology (Møller, Swaddle 1997). A low level of developmental stability is expected to be related to a high level of fluctuating asymmetry (Gangestad *et al.* 1994), i.e., non-directional deviations from perfect symmetry in paired morphological traits (Benderlioglu *et al.* 2004).

Fluctuating asymmetry correlates with the speed of growth, fecundity and survival in many species (Parsons 1990). In humans, it has been previously found that fluctuating asymmetry is associated with the health of an individual, low resting metabolic rate (Manning *et al.* 1997), muscle soreness and shortness of breath (Shackleford, Larsen 1997) or chromosomal abnormalities, including Down's syndrome (Thornhill, Møller 1997). It is therefore expected that males with a lower level of fluctuating asymmetry are more frequently preferred as mates.

The results of previous studies in humans show that low fluctuating asymmetry is positively associated with an overall number of sexual partners in men (Thornhill, Gangestad 1994) and with the age of first sexual intercourse (Thornhill, Gangestad 1994). The level of fluctuating asymmetry thus appears to affect women's preferences and deviations from symmetry significantly change ratings of attractiveness. The effect of fluctuating asymmetry of the male body on ratings of physical attractiveness was tested in a sample of raters from England and Srí Lanka (Dixson *et al.* 2003). The results showed that a silhouette with a natural level of fluctuating asymmetry was rated by women as significantly more attractive than silhouettes manipulated to perfect symmetry in both population settings. Dixson's results are in line with those of studies in which perfectly symmetrical faces and bodies of men were not preferred (Swaddle, Cuthill 1995, Thornhill, Gangestad 1994). On the proximate level, it was suggested that traits which are too symmetric appear "unnatural" to raters and hence less attractive. In contrast, on the ultimate level, traits which are too asymmetric may indicate a poorer quality of the genotype of an individual.

However, it is unclear whether the variance in fluctuating asymmetry or resistance to adverse environmental influences reflected by fluctuating asymmetry is heritable (Thornhill, Gangestad 1994). Moreover, the link between developmental stability and parasitism is based on the correlative nature of several studies and the causation thus cannot be easily inferred (Møller 2006).

Fluctuating asymmetry in many species is also related to hetero- and homozygosity (e.g., Mitton 1984). It is thought that heterozygosity allows an individual to easily compensate for negative environmental and genetic influences during development, resulting in a lesser degree of deviation from perfect symmetry. The most up-to-date research on heterozygosity in humans has focused on its relation to the immune system and genes of the Major Histocompatibility Complex (MHC) in particular (Roberts, Little 2008). Products of the MHC genes participate in detection of alien agents in an organism (Hedrick 1994) and heterozygosity within the MHC loci is advantageous because the expression of MHC genes is co-dominant and an individual heterozygous in the MHC loci should potentially have a more efficient immune system. Heterozygosity in MHC loci is partly heritable (Mitton *et al.* 1993), therefore the offspring should have a similar advantage (McClelland *et al.* 2003).

Thus, heterozygosity might present one of the ways by which individuals develop more stable and morphologically more symmetric and average traits (e.g., Mitton 1984). Albeit the evidence for the relation of fluctuating asymmetry and heterozygosity is still inconsistent (Kartavtsev 1990, Livshits, Smouse 1993, Zink *et al.* 1985), fluctuating asymmetry alone appears to be a heritable trait without any necessary linkage to developmental stability or heterozygosity (Thornhill, Gangestad 1994). The patterns of fluctuating asymmetry might underestimate those of developmental stability, for asymmetries only weakly correlate with developmental stability (Gangestad, Thornhill 1999, Van Dongen 1998, Whitlock 1996, 1998). Importantly, fluctuating asymmetry (as a marker of developmental stability) cannot differentiate between environmental and genetic factors contributing to the resulting values of fluctuating asymmetry. Let us consider two individuals who live under the same environmental conditions. Their developmental stability may not be the same because of the differences in the individuals' genotype. In contrast, two individuals with an identical genotype may vary in their fluctuating asymmetry as a result of different environmental conditions they have been living in. It is then questionable what the level of fluctuating asymmetry alone actually says about the quality of an individual, without the knowledge of his hetero- or homozygosity and/or developmental stability, expressed, for example, in terms of his health history.

SEXUAL DIMORPHISM

It has been proposed that the expression or development of sexually dimorphic traits serve as cues to immunocompetence of an individual (Folstad, Karter 1992). The development of many sexually dimorphic traits is responsive to changes in the levels of sex hormones, which are thought to adversely affect the function of the immune system (Thornhill, Gangestad 1993). Therefore it is assumed that only high-quality individuals may afford to develop distinctive sexually dimorphic traits without reducing the function of the immune system below the limits of viability. Testosterone adjusts the use of energy and can allocate it for the development of traits like mate-seeking behaviour or intra-sexual competition (Gangestad *et al.* 2007). Such traits might further include the amount of muscle mass, physical strength or motivation to mate. These traits will not develop without allocating the energy which would otherwise be used to maintain the level of immunocompetence (Gangestad *et al.* 2007). A high level of masculinization in men may thus serve as a cue to a high quality of the immune system and selection may favour the women who prefer these traits. This way they gain advantage in the form of higher reproductive success (Fink, Penton-Voak 2002, Frederick, Haselton 2007, Provost *et al.* 2008). It was recently reported that facial attractiveness positively correlates with the antibody levels after hepatitis B vaccination; a marker of the total of the immune function (Rantala *et al.* 2012). However, similar results regarding the physique are currently not available. Further, it is important to stress that 20 years since the publication of the Immunocompetence handicap theory (Folstad, Karter 1992), convincing evidence about the adverse influence of sexual hormones on immunity is still missing or is not clear for many species, including humans (for review see Roberts *et al.* 2004).

It is well known that mate choice in humans partly relies on morphological traits of the opposite sex (Barber 1995, Hatfield *et al.* 1966) and some of them might be a result of sexual selection (Dixson *et al.* 2007). This may account for certain features of the human male physique, especially the upper body and a greater amount of muscle mass (Lassek, Gaulin 2009), which are sensitive to testosterone (Swami, Tovée 2005).

The largest differences in body constitution between men and women arise during puberty and early reproductive age, stimulated by levels of sex hormones regulating lipid tissue distribution (Vague 1956). Steroid hormones form either android (high testosterone level) or gynoid (high level of oestrogen) fat distribution, which can be assessed by measuring the waist-hip ratio index (WHR). WHR thus appears a cue to the action of steroidal hormones, sexual maturity and risk of cardiovascular or metabolic disorder (Björntorp 2009, Deridder *et al.* 1990, Evans *et al.* 1983). Previous studies have found that men's silhouettes with male-typical WHR (from 0.90 to 0.95) are rated by women as the most attractive (Singh 1995), with a positive correlation between attractiveness ratings of men's WHR and perceived health (Furnham *et al.* 1997). On the other hand, silhouettes out of the male-typical WHR range are rated as more likely to be older, with poorer health and shorter life span (Han *et al.* 1999).

Several studies examined preferences for male body shape in a cross-cultural perspective, assuming greater preference for endomorphic (i.e., stout) body builds in countries with poorer socio-economic conditions. Such a body build might be a marker of higher mate quality, which could be especially valuable in adverse environment. To test this hypothesis, Furnham and Nordling (1998) recruited raters from Denmark and Portugal, two European populations varying in net income. However, they did not find any convincing differences in body shape preferences between the two populations. Female raters from both settings rated the "V" body shape as the most attractive. This is characterised by large and broad shoulders, medium-sized waist and a small gluteo-femoral area. Perhaps the two populations the participants were recruited from in this study did not show enough variation in terms of economy (Furnham, Nordling 1998).

Moreover, other studies which employed the Waist-to-Chest Ratio (WCR) confirmed that a "V"-shaped upper body positively correlates with ratings of attractiveness. Nevertheless, the WCR (where WCR < 1 results in a "V"-shaped body) was the primary determinant of attractiveness only in western and urban samples of raters. Raters of rural origin (e.g., in Malaysia) preferred bodies with a more tubular body shape (WCR ≅ 1) (Swami, Tovée 2005). The best predictor of attractiveness in this sample was the BMI, explaining about 50% of variability (Swami, Tovée 2005).

The effect of overall variability of the male physique on female-rated attractiveness of the male body in several different countries (England, Srí Lanka, Cameroon, China, USA, and New Zeeland) was tested by Dixson and colleagues. They found that the mesomorphic physique (muscular body type) was rated as the most attractive in all the populations except China, where the average male somatotype was rated as the most attractive (Dixson *et al.* 2007), while the endomorphic physique (stout body type) was rated as the most unattractive in all the tested populations (Dixson *et al.* 2003, 2007a, 2007b, 2010). However, the somatotypes not only allow us to classify body constitution variability but they can also be used for physical fitness (e.g., strength, endurance) and health assessments as well (Carter, Heath 1990). Physical performance and health in the endomorphic somatotype are on average lower with a higher risk of cardiovascular disorders (Bolonchuk *et al.* 2000, Katzmarzyk *et al.* 1998). In contrast, the mesomorphic somatotype on average excels in physical performance tests and exhibits cardiovascular health up to a certain level (Carter, Heath 1990).

The above-reviewed female preferences have been shown to have their implications for real-life behaviour as men with the preferred physique and a high level of physical fitness indicate a younger age of first sexual intercourse and a higher number of sexual partners (Faurie *et al.* 2002, Frederick, Haselton 2007, Gallup *et al.* 2007, Hughes, Gallup 2003). In the light of the results on women's preferences for the male physique and sexual behaviour of men with such a physique, the level of physical fitness could be seen as a more reliable marker of attractiveness (Hönekopp *et al.* 2007) than cues of immunocompetence (Folstad, Karter 1992).

Besides body build, another sexually dimorphic trait that is assumed to explain most of the variance in ratings of physical attractiveness of the human male physique is body height (Pawłowski, Kozieł 2002). The life history theory considers differences in adult body height to be a result of different strategies of allocation of available energy during the development (Sear 2010). Every organism optimizes allocation of the available energy into growth and the immune system or reproduction and the pattern of this allocation is reflected in the adult height (Sear 2010). One key moment of the individual's ontogeny is that of the timing of the termination of growth and the start of reproduction since humans, like many other species, separate the period of growth from that of reproduction, both of which are costly (Sear 2010). Individuals developing in adverse or unpredictable environmental conditions are expected to finish growth and start reproduction earlier, which results in a smaller body size, compared to that of individuals who develop in more favourable and predictable environmental conditions, who can thus afford to allocate energy to a prolonged period of growth and postpone reproduction; a strategy which results in a bigger body size.

Studies conducted so far have focused on how sexual dimorphism in stature (SDS), i.e., differences in height between partners, affects mate preferences. The results indicate that women prefer men who are relatively taller than themselves (Pawłowski 2003, Salska *et al.* 2008, Swami *et al.* 2008). These preferences are influenced by women's own height (Pawłowski 2003); short women prefer a greater difference in the SDS whereas tall women prefer a smaller difference in the SDS (Pawłowski 2003). This adjustment can increase the pool of potential partners with regard to the distribution of height within the given population in contrast to preference for partners with a certain height, which would lead to a reduction of the pool of potential partners (Pawłowski 2003). Further, the variability in height is related to the risk of chronic health problems (Park *et al.* 2003) and disorders such as pituitary gigantism or Marfan's syndrome (Salska *et al.* 2008). Since height is a heritable trait (Silventoinen *et al.* 2001) it may be a cue to one's fitness and to the efficiency of the individual's immune system (Judge, Cable 2004, Sorokowski, Pawłowski 2008).

Importantly, recent studies in Himba (Namibia) (Sorokowski *et al.* 2011) and Datoga (Tanzania) (Sorkowski, Butovskaya 2012) people show that the pattern commonly found in the Western populations cannot be considered universal, as in the Himba sample, the preferred body height of a partner was similar to height of the rater and in the Datoga sample, women preferred much taller or much shorter partners. While preferences in the mentioned populations basically follow the one reported in the Western samples, nevertheless the "male-taller norm" is less pronounced here. Up to date, it is not clear what influences the preferences for a potential partner's body height, as body height is affected not only by genetic differences but also by environmental influences. It can be suggested that body height preferences may be influenced by cultural/stereotypical, environmental, and/or ecological conditions which need to be further investigated, e.g., by comparing height preferences and gender roles in the selected populations or testing ecological demands on body height dimorphism.

The size and height of an individual are commonly seen as characteristics that play a significant role in terms of reproductive success (Pawłowski *et al*. 2000), socio-economic status (Silventoinen *et al.* 1999), intra-sexual competition (Carrier 2011), and hence fitness. Pawłowski *et al.* (2000) have shown that taller men have higher reproductive success and it has been assumed that shorter men are disadvantaged in mate choice (Nettle 2002, Pawłowski *et al.* 2000), probably due to inter-sexual competition as taller men are perceived as healthier (Silventoinen *et al.* 1999) and more attractive (Pawłowski 2003), or due to the intra-sexual competition as taller men have the advantage of greater striking force (Carrier 2011) and perceived dominance (Watkins *et al.* 2010). However, a positive correlation of height and reproductive success cannot be considered universal, as results follows a rather curvilinear association between height and a number of children, with men of average height attaining the highest reproductive success (Stulp *et al.* 2012).

INDIVIDUAL DIFFERENCES IN PREFERENCES

The majority of the above-reviewed studies focused on a general pattern of preferences for specific features of the male body. However, the life-history theory posits that the outcome of trade-offs between growth and reproduction, for instance, varies across individuals depending on their current condition. As a consequence of such a variation, we may also expect inter-individual variation in mate preferences. In other words, preferences are expected to be relatively flexible in a condition-dependent manner. Unfortunately, the literature on the inter-individual variability in preferences for the male physique is rather limited.

One's own mate value appears to be an influential factor in mate preferences. More specifically, there is a robust body of evidence that physical attractiveness is an important determinant of the female mate value (Weeden, Sabini 2005). Thus, predictors of women's body attractiveness such as WHR, BMI (Furnham *et al.* 2002, Swami *et al.* 2006) and body height (Pawłowski, Koziel 2002) may modulate female preferences for the male physique (Björntorp 1997, Tovée *et al.* 2012, Weeden, Sabini 2005).

Nonetheless, only few studies considered the influence of a rater's own attractiveness on perception of body attractiveness of others. It has been shown that women who perceive themselves as attractive prefer a more masculine male body build (Little *et al.* 2007) and women with a BMI within a range that is considered attractive perceive the mesomorphic body build as more attractive (Třebický 2012). However, more studies are definitely needed as individual variation in traits related to fertility and fecundity might play a significant role in women's preferences. These would include the effect of fecundity markers such as age, breast symmetry, average levels of oestrogen hormones and so on.

Another factor which shows individual variation in preferences is fluctuation across the menstrual cycle (i.e., fluctuations of actual fertility). During the follicular phase of the cycle, when probability of conception is highest, women in general prefer more masculine faces (Jones *et al.* 2008, Little *et al*. 2007, Peters *et al.* 2009). In a similar fashion, they prefer greater development of other sexually dimorphic traits such as body height (Pawlowski, Jasienska 2005), masculine body shapes (Little *et al.* 2007) and the mesomorphic component of the somatotype (Třebický 2012). An alternative explanation stresses increased preferences for less masculine facial traits during the non-fertile phase (Jones *et al.* 2005). This preference might help find a mate exhibiting a greater tendency towards nursing behaviour and less prone to infidelity (Jones *et al.* 2005). It is thought that due to their association with a higher testosterone level, individuals with masculine traits may potentially tend more towards aggressive behaviour (Benderlioglu *et al.* 2004) and partnership instability (Burnham *et al.* 2003).

Thus, variation in preferences across the menstrual cycle might reflect variation in preferences for direct and indirect benefits and might ultimately lead to maximization of potential benefits from mating (Penton-Voak *et al.* 1999).

DISCREPANCY BETWEEN PREFERENCES AND ACTUAL MATE CHOICE

Throughout this paper we have almost exclusively focused on preferences. Aside from a scarce evidence from speed dating sessions (Stulp *et al.* 2012) and silhouette preferences (Třebický 2012), it seems that preferences are hardly ever actually explored in mate choice and should not be equated with actual mate choice. In contrast to preferences, mate choice is limited for several reasons. Firstly, a mate with the preferred trait may not be available, interested or could be subject to intense competition. Secondly, mate selection is a complex process and multiple traits are considered. A single individual rarely, if ever, possesses the exact combination of the most desired traits. Consequently, other traits may outweigh the most desired trait under consideration. For these reasons, we may frequently observe a discrepancy between the most preferred trait and quality of the trait in the actual partner.

For example, and as shown above, male height is related to mate choice in Western societies. However, recent studies indicate that mating with taller men is not cross-culturally universal and, as recent results from the Hadza people (Tanzania) show, there is no evidence for a general male-taller norm. In contrast to Western societies, mating appears not to be affected by men's height in the Hadza sample (Sear, Marlowe 2009).

One may ask about the rationale of the research on preferences when its findings may not reflect the actual mate choice. The primary significance of the research on preferences is that it allows us to explore perception irrespective of the actual real-life settings. Such studies may give us significant insights into the evolved psychological mechanisms and test evolutionary-inspired hypotheses. Further, studying the discrepancy between preferences and the actual mate choice allows us to test the relative significance of individual traits. The traits which are crucial in mate selection will be reluctantly compromised and vice versa.

IMPLICATIONS

As has been shown above, women exhibit consistency in their preferences for men's physique, which may present a cue to a higher level of muscularity or sexual dimorphism, physical fitness and health. A moderate degree of development of muscularity and height appears to be the most attractive. Previous studies on attractiveness have often considered only linear effects. In contrast, the inverted-U hypothesis suggests that preferences for an extreme degree of trait development might be limited and follow a more curvilinear pattern, i.e., ratings increase up to a certain point but the traits which exceed a certain limit are rated as less attractive (Frederick, Haselton 2007). Such inverted U patterns of ratings can be seen in the ratings of height (Pawłowski 2003), muscle development (Frederick, Haselton 2007, Lynch, Zellner 1999), fluctuating asymmetry (Dixson *et al.* 2003) or the composition of a somatotype (Třebický 2012). Although the mesomorphic component of a somatotype positively affects attractiveness ratings, its effect is neither absolute nor linear (Třebický 2012).

A great degree of development of masculine traits is related to high levels of testosterone (Bhasin 2003), which is assumed to reduce the immunity of an individual (Folstad, Karter 1992, Thornhill, Gangestad 1993). In contrast to the expected linear relationship of the development of a trait and its attractiveness, in the immunocompetence handicap theory (Folstad, Karter 1992) heterozygous individuals are expected to exhibit better immunocompetence and because heterozygosity is manifested in phenotypic averageness, one might assume that the traits exhibiting a degree of development that falls within the range of the population norm should be rated as the most attractive (Thornhill, Gangestad 1993, Watson, Thornhill 1994). It is then advantageous for individuals of the opposite sex to prefer masculine traits in mates which are developed slightly more than is the population average (as described by the inverted U pattern), and achieve the most beneficial trade-off between the ability of a man to hunt, fight or defend and the weakest adverse effect of testosterone on the immune system possible (Barber 1995). Individuals should avoid mating with others who are out of the population norm in terms of trait development; accordingly, such a degree of development may serve as a cue to a disadvantageous genotype. However, the adverse effect of the sexual hormone on the function of the immune system in humans is yet to be fully established.

Results of the above-reviewed studies which employed attractiveness ratings also indicate that women prefer traits of the male physique which might provide a cue to physical fitness (e.g., the mesomorphic somatotype and tallness) (Thomis *et al.* 1998). Women should be attracted to such traits whereas their offspring may profit not only from the indirect benefits but also from the direct ones.

A common denominator of all cues of quality mentioned above is health (Weeden, Sabini 2005) which is usually related to immunocompetence, heterozygosity, developmental stability and fitness in many species (Møller, Swaddle 1997). The concept of health encompasses not only the actual absence of disease, but also effectiveness of the immune system, lower incidence of pathogen-induced diseases, better ability to allocate the available energy during development, and may be a cue to health during growth and maturity. Health does not necessarily imply a longer life span of an individual or higher physical fitness, though. Traits related to the reproduction potential of an individual are expressed in the concept of health disproportionally (Weeden, Sabini 2005). Getty (2002) and Kokko and Johnstone (2002) emphasize that health or survival only have an important place in the modern theory of evolution as long as they contribute to an increase in the reproductive success. Hence there is no evidence of a direct and linear relation between health and physical fitness. Healthy individuals are not necessarily more physically fit, but physically fitter individuals are supposed to be healthier. A greater mesomorphic component is related not only to higher physical fitness but also to lower prevalence of cardiovascular disorders (Carter, Heath 1990, Katzmarzyk *et al.* 1998, Malina *et al.* 1997). The relation between physical attractiveness and health is likely to be subtle, especially in the Western, Educated, Industrialized, Rich and Democratic (WEIRD) individuals who participate in most of behavioural studies (Henrich *et al.* 2010) in which the evidence is often mixed or missing (Geary 2005, see also review by Weeden, Sabini 2005). It is likely that the relation between traits of attractiveness and sexual hormones or the efficiency of the immune system is not fully expressed and thus not easily detected in populations that are not under environmental stress (Geary 2005). Traits assumed to be indicators of environmental stress (e.g., fluctuating asymmetry) are likely to be more distinct indicators of physical attractiveness and health in populations which are more at risk of parasite infection or poorer caloric intake (Grammer *et al.* 2005). Therefore, attempts to explain evolutionary processes which are based solely on results from the Western samples should be treated with caution as reproductive strategies may differ depending on the specific environmental conditions.

It is generally assumed that the above-discussed sexually dimorphic traits are products of inter-sexual selection. This might seem self-evident due to the fact that men and women in the Western societies are virtually free to choose mates on the basis of beauty and physical fitness. These criteria and conditions are so pervasive today that it is tempting to think of them as being characteristic of the human evolution. But are these preferences really the primary force? It was recently argued by Puts (2010) that inter-sexual selection has been the primary mechanism of sexual selection in men, which contradicts the mainstream theoretical predictions. In particular, male intra-sexual selection might override other mechanisms of sexual selection (e.g., mate choice, sperm competition) by excluding rivals by force from opportunities to mate and it is thought to be the main form of mating competition in men.

Men are larger, stronger, faster, and more physically aggressive than women (see Puts 2010 for a review). Men report engaging in and inclinations to engage in, more physical aggression than women (Buss, Perry 1992) and perpetrate more offensive physical aggression in all societies studied (Ellis *et al.* 2008). Relatively greater male upper-body muscle mass and strength suggest an evolutionary history of fighting in men (Sell *et al.* 2009). Thus men's anatomy and behaviour predicts male intra-sexual competition to be the primary mechanism shaping the human male phenotype. Further, several masculine traits are perceived as attractive (e.g., muscular physique), however a higher degree of development of these traits increases perceptions of dominance more substantially than it increases ratings of attractiveness and masculinity. This has been found to produce smaller positive effects on attractiveness to women than on dominance judged by men (Puts *et al.* 2006). Thus, masculine traits appear to be probably designed for intra-sexual competition rather than for attraction of potential mates. Body size, strength and aggression are probably helping modern-day men to win mating opportunities in much the same way they helped their ancestors, rather than to increase their attractiveness for the opposite sex. Therefore, preferences for the physique with cues to a high level of physical fitness could be adaptive for women as men with such a physique might be successful in intimidating potential rivals in the intra-sexual competition (Barber 1995, Gangestad *et al.* 2007) and men with a higher level of physical fitness are perceived as better fighters (Sell *et al.* 2009). In sum, this suggests that neither intra-nor inter-sexual selection have been the single selection pressure, but they have interacted in shaping the human male phenotype.

Finally, we would like to point out several methodological issues which might have affected the outcome of some of the above-reviewed studies. The major is the inconsistency and the form of the stimuli employed for studying physical attractiveness. The stimuli frequently capture the variability of the human male physique insufficiently (e.g., Dixson *et al.* 2003) or unnaturally. They often take on the form of line drawings originally based on real male body variability, but with unnatural manipulations (e.g., Dixson *et al.* 2003) or the form of line drawings based solely on draughtsmen's interpretations resulting in low validity forms (Lynch, Zellner 1999). Another common form of the stimuli employed are digitally morphed images or composite images produced by overlapping several individual photographs. Even here the resulting validity might be limited. The resulting morphs or composites based on the correlative nature of studies may be outside the range of possible morphological variability. For example, in a study by Little *et al.* (2007) masculine and feminine morphs of bodies were created. However, the feminine body morphs were not based on the shapes of male bodies rated as feminine, but rather they were based on ratings of female body shapes, and thus could not capture the variability of the male physique.

CONCLUSION

Research on physical attractiveness has been one of the central topics in current human ethology, behavioural ecology and evolutionary psychology as it might have significant impact on one's reproductive success. It is expected that the perception of attractiveness is sensitive to traits linked with biological or other qualities of the given individual. However, in spite of an enormous body of literature on physical attractiveness, core evolutionary inspired theoretical concepts are rather vaguely phrased and several theoretical issues still remain to be resolved.

The aim of the paper was to briefly demonstrate these theoretical concepts and review empirical findings of the studies on preferences of selected human male body traits. In particular, we discussed theories of developmental stability, its relation to fluctuating asymmetry and heterozygosity. A modest level of symmetry appears to be perceived as the most attractive, individuals showing a lower level of fluctuating asymmetry are rated as more attractive similarly as heterozygote individuals. Although body symmetry appears to be related to developmental stability, and might be a marker of heterozygosity, these three concepts cannot be freely interchanged as they refer to distinctive qualities. Subsequently, we discussed theories on immunocompetence and sexual dimorphism and its expression in overall body build and body height. In general, only slightly more athletic and taller men higher development of body build and body height are perceived as the most attractive. Further, individuals of greater physical fitness show higher level of body build and/or height development. These associations suggest that body attractiveness might cue to physical fitness rather than supporting immunocompetence theory which still lacks robust empirical evidence in humans. Finally, a vast majority of human male body features shows that a moderate development appears to be the most attractive and that preferences for these traits seem to follow a curvilinear pattern.

Due to the central role of reproduction in evolutionary theorizing, a majority of the evolutionary theories of physical appearance focus on its role in mate attraction. However, some of the human male body features might have arisen as a result of intra-sexual competition. As men are on average stronger, more physically aggressive, and more frequently engage in physical contests than women in all societies studied so far, it suggests a relatively high level of male intra-sexual competition in human evolutionary history. Further, more developed male-typical traits increases perception of dominance more substantially than it increases ratings of attractiveness. It could be assumed that men's anatomy and behaviour predicts male intra-sexual competition to be the highly influential mechanism shaping the human male phenotype. Thus, both inter- and intra-sexual selection should be considered in the context of human male body build.

Most of the studies so far explored a general pattern of the preferences; however, life-history theory proposes that one may expect individual variations in preferences related to the actual conditions of the given individual. On similar note, we currently need more studies based on raters from non-Western countries as cultural and environmental variables may contribute to the variations in preferences. Thus, both individual- and society-level differences should be explored in future studies. Finally, one should note that preferences cannot be equated with actual mate choice as the mate choice in contrast to the preferences might be restricted by various factors such as availability of the preferred partner, importance of the preferred trait and so on.

In conclusion, we hope that the paper will contribute to unravelling the blurred theoretical issues and help future researches on physical attractiveness to follow new avenues for further research.

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Signals of Body Size

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Synonyms

Cues to body size; Cues to height; Cues to size; Cues to weight; Signaling body dimensions

Definition

The perception of cues related to visual and acoustic body size provides socially relevant information linked to an individual's fitness.

Introduction

The body size of individuals varies and is associated with sexual maturity, health, dominance, strength, and overall genetic quality. Physical size is a crucial determinant of various socially relevant characteristics of an individual across many species. The perception of conspecifics' body size is thus involved in various social contexts including physical confrontations.

The main components of body size are body weight, height, and muscularity. These factors have been shown to be linked to success in physical confrontations. Potential competitors can thus base their fight-or-flight decisions on body size assessments (Sell et al. 2010).

ĉBody size-related cues can be perceived by several modalities. Multimodal perception can provide Overlapping information and thus reduce the risk of inaccurate assessment. Alternatively, each modality can provide additional information, thereby helping to increase the accuracy of judgement. Acoustic and visual assessment of others prior to close contact is common in many species, since it helps to reduce the risk inherent in direct physical contact. Since the accuracy of assessment of physical characteristics solely from visual cues may suffer due to obstacles in the environment, excessive distance, and/or low luminescence, acoustic cues can supplement or replace solely visual information.

In humans, assessments of others are initially guided primarily by visual and acoustic cues. Our physical appearance and voices are socially rich stimuli which attract attention and offer plenty of cues to socially relevant qualities.

Acoustic Cues to Body Size

Apart from conveying linguistic information, human voice carries cues to various physical, social, and fitness-related characteristics of

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speakers such as age, sex, and body size (Pisanski et al. 2014).

Fundamental frequency (F0) and formant frequencies (FF) are the two most studied features of the human voice. According to source-filter model of speech production, which is based on the basic idea that voice/sound is produced by expelling air from the lungs (the source) through vocal folds, vocal tract, and the mouth (the filter) where it is modulated into speech. F0 and FF are anatomically and functionally independent (Fant 1960). Fundamental frequency is determined mainly by the length and the mass of vocal folds, which vibrate during phonation-modulating flow of air expelled from the lungs. Produced sounds are then perceived as having a certain pitch. Increase in the folds' thickness results in a lower F0 and a lower perceived voice pitch.

Formant frequencies (FF), on the other hand, i.e., the spectral characteristics of speaker's voice perceived as the voice timbre, are determined mainly by speaker's supra-laryngeal voice tract length (VTL) and its resonance. Formants are more anatomically constrained than F0 by the length and dimensions of the vocal tract, which is related to skull size and body height (Fitch 2000).

F0 and FF are associated with individuals' stable characteristics due to the exposure to testosterone during development and are consequently anatomically related to physical size (Rendall et al. 2005). In boys, elevated levels of circulating testosterone during puberty lead to a lengthening and permanent thickening of vocal folds, which result in a lower F0 (Jenkins 1998). Further, the descent of larynx results in a lowering of formants and narrowing of formant dispersion (formants being produced closer together). The acoustic effect of these changes is that the voices of adult men are lower-pitched and deeper or, in other words, more resonant and rather monotonous than the voices of women or prepubescent children. Longer vocal tract and thicker vocal folds thus produce lower FFs and lower F0, which can thus serve as potential cues to a bigger body size.

Research which tested the role of F0 and FF as indicators of size has generally confirmed that both independently predict variation in body size among different species (Pisanski et al. 2014; Rendall et al. 2005), meta-analyses of acoustic predictors of human voice showed only weak or marginally negative relationships between both F0 (accounting for less than 2% of the variance) and FF (accounting for up to 10% of the variance) and the height or weight within each sex (Pisanski et al. 2014).

Listeners demonstrate sensitivity to variations in F0 and FF and a high consistency in associating lower F0 and FFs with larger speakers. Their judgments, however, tend to be incorrect with respect to speakers' actual size (Pisanski et al. 2014). This relatively low accuracy in assessing body size from voice might be due to the presence of other characteristics unrelated to height or weight, which, too, affect the quality of human voice.

Current research indicates that men with a lower voice pitch are significantly stronger than those with high-pitched voices, and that raters are able to estimate strength from vocal cues accurately and independently of their height or weight assessments (Sell et al. 2010). Some studies which investigated the relationship between voice acoustics and muscularity suggest a negative correlation between F0 and men's shoulder-to-hip ratio (i.e., lower FF indicates individuals with larger upper body musculature). Other studies, however, did not confirm this association (Pisanski et al. 2016).

Human voice also provides cues to speaker's current state. Certain psychological states, such as self-confidence, fear, or rage, can modulate the position of the larynx and change the tension of the vocal folds, thereby affecting also the resulting F0. The F0 can be modulated to deceive others and to disguise or exaggerate the characteristics of an individual (Fitch 2000). This feature is not unique to humans. It has been suggested that its original selective advantage may have been in enabling individuals to simulate the vocalizations of larger conspecifics, thus exaggerating their own size, and reducing the degree to which FF accurately indicate body mass and shape (Pisanski et al. 2016).

Most recently, scholars have been focusing on some less variable voice parameters, such as non-mean-based F0 measures (measuring voice pitch deviation from its baseline), voice jitter (frequency perturbation), shimmer (amplitude perturbation), and harmonic-to-noise ratio (which is related to the mass and oscillating properties of the vocal folds). These characteristics are supposed to be sexually dimorphic, related to body size and shape via shared influence of sex hormones on these vocal properties, and linked to the development and distribution of lipid and muscle mass (Pisanski et al. 2016).

Visual Cues to the Body Size

In many species, direct visual inspection of the physical size of others is the primary determinant of social dominance. It is therefore not surprising that individuals try to appear physically larger to make a more intimidating impression. Interestingly, direct observations of overall body size of others and the effect of nonverbal behavior on the perception of body size have not yet been thoroughly tested in humans. Available evidence suggests that changes in apparent physical size (e.g., elevation by standing on a platform) affect the perceived height of the individual in question (Schwartz et al. 1982). Perceived body height can also be manipulated by altering other perceptual cues to size, such as the size of background features, which then increase or decrease the apparent size of individuals (Marsh et al. 2009). Moreover, nonverbal cues such as expansive body posture or posture openness can also make the displayer appear physically larger in eyes of others (Marsh et al. 2009).

Based on facial traits, we spontaneously attribute various personality characteristics. High levels of testosterone are thought to be an important determinant of both the body size and changes to the shape of face during puberty, because testosterone has a strong anabolic effect on the musculoskeletal system, thus influencing various features including the volume of lean body mass and differences in muscle strength. Through the mechanism of hormone action, facial morphology thus seems to be connected to both muscularity and overall body size.

Several studies have investigated a relation between testosterone levels and facial appearance. Their aim was to identify visual cues used to estimate height and weight from the face. Generally, taller people are reported to have more elongated faces than shorter ones (Windhager et al. 2011). Facial elongation (full length of the face divided by its width) increases from infancy to adulthood as the lower jaw develops and starts protruding, making the face less round and more oval. Heavier men and women have wider and more square faces, and heavier men have also rounder lower facial regions (Coetzee et al. 2010). These facial shape cues can be quantified by width-to-height ratio, perimeter-to-area ratio, or cheek-to-jaw-width ratio (for a review see Coetzee et al. 2010). Adiposity produces a typical facial shape because large percentage of facial fat is allocated to the cheek area, buccal fat pads, thus providing a visual cue to body size (Coetzee et al. 2009).

Available evidence indicates that people use the abovementioned or related facial cues to assess body weight and height of others, and they are fairly accurate in their judgments. Individuals with wider, squarer faces, and rounder lower faces are correctly judged to be heavier (Coetzee et al. 2010), while people with longer faces are judged as being taller (Re et al. 2013). We should, however, bear in mind that visual cues in 2D images (portrait photographs) are fairly limited, especially for volumetric weight estimates (Coetzee et al. 2010). Moreover, we do not usually view faces from the perspective of a typical facial stimuli presentation, i.e., a vantage point centered on and aligned with their faces. Humans show relatively significant height dimorphism and since men are typically higher, they view women's faces from slightly above, while women tend to view men's faces from slightly below (Burke and Sulikowski 2010). When this vantage point is manipulated, participants tend to overestimate body weight for faces presented from a lower vantage point and underestimate it for faces presented from a higher vantage point (Schneider et al. 2012).

Conclusion

Assessment of body size is an important part of first impression formation. It is involved in various social interactions including physical confrontation. Most previous research on perception of body size focused on vocal and facial cues. It has been shown that the main vocal parameters affecting the perception of body size are fundamental frequency and formant frequencies. However, attribution of body size based on these vocal cues tends to be inaccurate. On the other hand, people are usually relatively accurate when judging body height and weight from facial images. The main facial cue related to body weight is a rounder lower facial region, while body height is associated with elongation of the face. Interestingly, relatively little is known about behavioral cues to body size. Further, to our best knowledge, no studies have as yet tested cross-modal integration of individual body size-related cues.

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Cross-References

- ► Aggression
- ► Communication, Cues, and Signals
- ► Cue Detection
- ► Evolution of Fighting Assessment Abilities
- ► Fighting Assessment
- ► Physical Size
- ► Physically Strong
- ► Vocal Attractiveness
- ► Vocal Indicators of Dominance
- ► Voice Pitch

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He developed the study concept, contributed to the study design, performed data collection, contributed to the manuscript writing and subsequent revisions.

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Perceived Aggressiveness Predicts Fighting Performance in Mixed-Martial-Arts Fighters

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Abstract

Accurate assessment of competitive ability is a critical component of contest behavior in animals, and it could be just as important in human competition, particularly in human ancestral populations. Here, we tested the role that facial perception plays in this assessment by investigating the association between both perceived aggressiveness and perceived fighting ability in fighters' faces and their actual fighting success. Perceived aggressiveness was positively associated with the proportion of fights won, after we controlled for the effect of weight, which also independently predicted perceived aggression. In contrast, perception of fighting ability was confounded by weight, and an association between perceived fighting ability and actual fighting success was restricted to heavyweight fighters. Shape regressions revealed that aggressive-looking faces are generally wider and have a broader chin, more prominent eyebrows, and a larger nose than less aggressive-looking faces. Our results indicate that perception of aggressiveness and fighting ability might cue different aspects of success in male-male physical confrontation.

Keywords

fighting ability, aggressiveness, mixed martial arts, geometric morphometrics, competition, face, perception, aggressive behavior, face perception, facial features, evolutionary psychology

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Humans are especially attentive to facial cues and spontaneously attribute age, sex, emotional state, and personality characteristics according to facial traits (Bar, Neta, & Linz, 2006; Willis & Todorov, 2006). A key set of traits affecting facial perception are associated with sexual dimorphism. Individuals with highly developed male-typical facial features are consistently perceived as masculine (Penton-Voak & Chen, 2004), dominant, and aggressive (Perrett et al., 1998; Rhodes, 2006). Consequently, these features may affect experience and attributions in social interactions. For example, ratings of facial dominance in men predict their career progress (Mueller & Mazur, 1996) and age of first sexual intercourse (Mazur, Halpern, & Udry, 1994).

Particular attention has focused on the facial width-to-height ratio (fWHR). Trajectories of bizygomatic width change during pubertal growth independently of the height of the upper face and body height (Weston, Friday, & Lio, 2007). There is growing evidence linking fWHR to male aggressive and dominant behavior in both controlled conditions and naturalistic settings (Carré & McCormick, 2008; Carré, McCormick, & Mondloch, 2009; but see Deaner, Goetz, Shattuck, & Schnotala, 2012). Furthermore, fWHR predicts cause of death by contact violence: Higher fWHR is less frequently associated with violent death (Stirrat, Stulp, & Pollet, 2012).

Human perception may have evolved through natural selection to be especially sensitive to cues of aggression and competence in fighting (Carré & McCormick, 2008). Anticipation of both cues of aggression in facial expressions (Ekman et al., 1987) or body posture (Duclos

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et al., 1989) and probability of winning seems to be critical for making decisions about whether to flee or fight, influencing risk of injury or death. The perception of aggression cues is especially significant in male-male interactions, in which conflicts are frequently resolved through physical contest. Therefore, men are expected to be more attentive than women to the potential dangerousness of their opponent (Sell et al., 2009).

Previous research has shown that people make relatively accurate inferences about men's physical strength from static images (Sell et al., 2009). In particular, Sell et al. report correlations between measurements of upper-body strength and ratings of fighting ability. Although Sell et al.'s study and the fWHR studies indicate that facial cues may be linked to potential fighting success, there is currently no direct evidence for such a link. Furthermore, participants in previous studies were not facing a real antagonist in an actual direct physical confrontation.

To address the relationship among perception, face shape, and fighting success in the present study, we used data that directly reflected the results of fights among professional fighters. We tested whether the perception of aggressiveness predicts the results of direct physical confrontations because human perception may have evolved to be specifically sensitive to cues of threat and aggression. Fighting ability depends on many factors alongside aggression, so being seen as a powerful fighter does not necessarily equal being seen as aggressive. Therefore, we further collected ratings of perceived fighting ability to test whether people are able to infer actual fighting ability.

To do this, we used the results of past fights among professional mixed-martial-arts (MMA) fighters and their facial photos, which were rated in an online survey. In addition, by use of geometric morphometric (GMM) techniques, we searched for the specific facial traits associated with actual fighting ability and compared them with traits responsible for perceived aggressiveness.

Method

Participants

In total, 618 individuals from the Czech Republic (216 men, mean age = 26.98 years, *SD* = 6.35; 402 women, mean age = 26.18 years, *SD* = 6.22) rated photographs of fighters for perceived aggressiveness, and a further 278 (98 men, mean age = 28.31 years, *SD* = 9.99; 180 women, mean age = 27.1 years, *SD* = 7.52) rated the same photos for perceived fighting ability. All participants gave informed consent to participate in the study.

The stimulus set consisted of 146 photographs selected from 336 portraits of MMA fighters that are freely accessible on the official Web site of MMA division Ultimate Fighting Championship (UFC; www.ufc.com; photos downloaded in July 2011). To avoid potential confounding effects on raters' perceptions, we selected only images fulfilling the following criteria: (a) apparent non-African or non-Asian origin, (b) facing directly into the camera, (c) absence of beard or moustache, and (d) hair not obscuring the face. The images were subsequently standardized regarding the position of the face in the image (e.g., same position in vertical axis), and the background color was changed to gray (hex #808080 in red, green, blue color space).

For each fighter, we obtained data on his age (M = 29.77 years, SD = 4.6), weight class (bantamweight, up to 61.2 kg: n = 14; featherweight, up to 66 kg: n = 14; lightweight, up to 70.3 kg: n = 34; welterweight, up to 77.1 kg: n = 32; middleweight, up to 83.9 kg: n = 19; light-heavyweight, up to 93.0 kg: n = 19; heavyweight, up to 120.2 kg: n = 14), number of fights in the UFC (range = 1–38, M = 8.78, SD = 7.02), and number of wins in the UFC (range = 0–27, M = 5.86, SD = 5.19). To assess whether the tested effect varied across the weight classes, we merged the seven weight classes into three: lightweight (up to 70.3 kg), middleweight (70.4–83.9 kg), and heavyweight (over 83.9 kg).

To account for varying numbers of fights among fighters, we computed fighting success as the proportion of wins relative to the total number of fights. There are no official rules for selection of a particular individual for a fight in the UFC, and the fights are arranged by managers of the individual fighters (R. Andrš, personal communication). It seems unlikely that such a selection process might systematically bias the effect under investigation. To estimate the possible effect of facial damage on judgment of photos, one of the authors (V. T.) assessed each photo for marks of apparent damage using binary coding (0 = damage absent, n = 34; 1 = damage present, n = 112).

Procedure

Each participant reported his or her sex and age and then rated either aggressiveness or fighting ability of a set of 50 randomly selected photographs, presented in random order. Aggressiveness ratings were done using a 7-point scale (from 1, *not aggressive at all*, to 7, *very aggressive*). For fighting ability, participants judged whether the depicted person was a good fighter (from 1, *not at all*, to 7, *excellent*). Each participant's ratings were converted to z scores to account for differences in scale use, and a mean standardized score was calculated for each photograph.

GMM analyses

We used a GMM approach to investigate which facial features of the 146 MMA fighters are responsible for the perception of aggressiveness and fighting success. The GMM technique is a set of analytical procedures for multivariate statistical analysis of shape. Its mathematical and theoretical background is well understood, and it has been widely used in biological applications (for a recent review, see Baab, McNulty, & Rohlf, 2012). GMM's main strength is that it takes into account information about the spatial relationships among the measured variables that is preserved during analysis, and this information can be later visualized in the form of thin-spline deformation grids.

The 71 landmarks (including 36 semilandmarks) were digitized in tpsDig2 software (Version 2.14; Rohlf, 2009a). Landmarks are anatomically (or at least geometrically) corresponding points that can be delineated in different individuals, whereas semilandmarks denote curves and outlines. The definitions of landmarks and semilandmarks were adopted from previous studies (Kleisner, Kocnar, Rubesova, & Flegr, 2010; Kleisner, Priplatova, Frost, & Flegr 2013; Schaefer, Lauc, Mitteroecker, Gunz, & Bookstein, 2006).

All configurations of landmarks and semilandmarks were superimposed using a generalized Procrustes analysis (GPA), which standardizes the size of the objects and optimizes their rotation and translation so that distances between corresponding landmarks are minimized. We used principal component analysis (PCA) to translate original data (shape coordinates) into orthonormal principal components; this approach ensures the multivariate normality. The PCA scores matrix represented by all principal components and carrying the information about face shape was saved and used for further analyses. Both GPA and PCA were carried out in tpsRelw (Version 1.46; Rohlf, 2008).

For testing the effects of perceived aggressiveness, fighting success, and weight on shape coordinates, we performed permutational multivariate analysis of variance using distance matrices with 9,999 permutations (the Adonis function in the Vegan package in R; Oksanen et al., 2011); the Euclidean method was used as a distance measure. We ran a multiple multivariate regression with principal component scores as the response variable and with scores of perceived aggressiveness, fighting success, and weight as explanatory variables. The shape changes associated with perceived aggressiveness were visualized by a thin-plate spline interpolation function, available in tpsRegr (Version 1.36; Rohlf, 2009b), as a deviation from the overall mean configuration (the consensus) of landmarks.

Statistical analysis

The effect of fighting success on perceived aggressiveness and perceived fighting ability was tested using general linear models (the "lm" function in R) using the mean z score of perceived aggressiveness or fighting ability as the response variable, fighting success of the rated fighter as the explanatory variable, and fighter's age, fighter's weight, and rater's sex as confounding variables. The association between bivariate variables was assessed by Pearson's correlation, in which data were normally distributed; otherwise, we used either Pearson's correlation with bootstrapping with 10,000 iterations or Kendall's test for ordinal data. Statistical plausibility of linear models was evaluated by F tests. Effect sizes were expressed by partial R^2; we report adjusted R^2 in all results.

Results

Correlational and linear regression analyses

All correlational analysis were performed using the full photo set ($N = 146$). First, we tested the effects of potentially confounding variables, such as fighter's age and rater sex, on perceived aggressiveness and perceived fighting ability. Fighter's age was not significantly correlated with perceived aggressiveness ($r = .13$, $p = .128$). However, there was a significant positive correlation between age and perceived fighting ability ($r = .358$, $p < .001$). Judgments of aggressiveness ($r = .93$, $p < .001$) and fighting ability ($r = .95$, $p < .001$) by male and female raters were highly correlated; therefore, we analyzed the ratings of both sexes together. We also found a significant positive correlation between the ratings of aggressiveness and perceived fighting ability ($r = .483$, $p < .001$).

Subsequently, we found a significant positive association between perceived aggressiveness and fighting success ($r = .203$, $p = .014$). In contrast, there was no significant association between perceived fighting ability and fighting success ($r = .069$, $p = .409$). Linear regression showed a similar result after age was added as a covariate, $F(1, 143) = 0.969$, $p = .326$, $R^2 = .007$; the effect of age was significant ($p < .001$).

However, both perceived aggressiveness ($r = .31$, $p < .001$) and perceived fighting ability ($r = .296$, $p < .001$) were also positively correlated with weight; therefore, we added weight into the linear regression models. In this analysis, perceived aggressiveness was independently predicted by both fighting success, $F(1, 143) = 4.91$, $p = .028$, $R^2 = .033$, and weight, $F(1, 143) = 13.68$, $p < .001$, $R^2 = .089$. To test for the interaction between weight and fighting success, we fitted a model with both the main effects and the interaction of weight and number of wins. Comparing the two models, we found that the more complex model including both main effects and the interaction did not fit the data better than a simple model with two main effects (p = .331). The more parsimonious model with weight and fighting success as main effects was thus preferable.

After weight was added as a covariate in the linear regression, perceived fighting ability was predicted by weight, $F(1, 143) = 13.29$, $p < .001$, $R^2 = .085$, but not by fighting success, $F(1, 143) = 0.242$, $p = .624$, $R^2 = .002$. This might be due to a ceiling effect of attributed weight. In other words, raters might have primarily used cues of weight to attribute fighting ability (Deaner et al., 2012), which in turn obscured the effect of fighting success, as the actual fights take place within defined weight categories. We therefore tested the hypothesis that heavyweight fighters are seen as better fighters than those with lighter weights. We ran a one-way ANOVA with perceived fighting ability as the dependent variable and weight category as a factor. The effect of weight category was significant, $F(2, 143) = 5.97$, $p = .003$, $R^2 = .077$. Pairwise comparisons (tests of least-significant differences) showed that heavyweights were seen as significantly better fighters than lightweights (p = .001), but the differences between ratings of middleweight and heavyweight fighters (p = .074) and between middleweight and lightweight fighters (p = .078) were close to significant.

Subsequently, we tested the correlation between perceived fighting ability and actual fighting success separately for individual weight categories. We found a close-to-significant correlation between perceived fighting ability and fighting success in heavyweights (n = 33, r = .301, p = .088), but there was no significant correlation in middleweight (n = 51, r = −.127, p = .375) and lightweight fighters (n = 62, r = .076, p = .558). Finally, facial damage showed a significant positive correlation with perceived fighting ability (n = 146, τ = .196, p = .004) but not with perceived aggressiveness (n = 146, τ = .073, p = .28).

GMM analyses of aggressiveness

We used multivariate regressions to test for possible associations among perceived aggressiveness, fighting success, and facial configuration. The regression of shape data (represented by multiple PCA scores) on perceived aggressiveness showed a significant relationship between perceived aggressiveness and facial shape, $F(1, 144) = 2.42$, $p = .024$, $R^2 = .017$. Controlling for the effect of the weight, we found that the effect of face shape was close to significant, $F(1, 143) = 1.97$, $p = .055$, $R^2 = .013$, whereas weight was significantly related to facial shape, $F(1, 143) = 2.74$, $p = .015$, $R^2 = .019$. To test for the interaction between weight and perceived aggressiveness, we fitted a model with both the main effect and the interaction of weight and aggressiveness. The interaction was significant, $F(1, 142) = 2.48$, $p = .027$, $R^2 = .017$, which indicates that facial features responsible for attribution of aggressiveness are associated with weight distribution. Therefore, for explorative purposes, we separately tested for the same effect in both extremes of weight distribution. We found a significant effect of perceived aggressiveness in heavyweights, $F(1, 31) = 2.13$, $p = .037$, $R^2 = .064$; the same effect was not significant for lightweights, $F(1, 60) = 1.78$, $p = .071$, $R^2 = .029$.

The regression of shape data on fighting success was not significant, $F(1, 144) = 0.65$, $p = .743$, $R^2 = .004$, but weight had a significant effect on facial morphospace, $F(1, 144) = 2.72$, $p = .013$, $R^2 = .019$. When we ran the same analysis for both extremes of weight distribution, we found a significant effect of fighting success in heavyweights, $F(1, 31) = 2.18$, $p = .033$, $R^2 = .065$; however, no similar effect was found in lightweights, $F(1, 60) = 0.83$, $p = .558$, $R^2 = .014$.

To compare facial traits associated with perceived aggressiveness and fighting success, we used the tps interpolation function to visualize the results of shape regressions. Deviations from the mean facial configuration linked with the perception of aggressiveness included dilations and contractions of the grid in the bizygomatic range and around the eyes and jaw (Fig. 1). The aggressive-looking faces were generally wider and had a broader chin and larger nose than the nonaggressive-looking faces. The grid was markedly contracted around the eyes, showing an effect of deep-set eyes beneath prominent eyebrows. Significant shape differences associated with higher fighting success in heavyweights included a narrower chin, wider bizygomatic range, and a more horizontally depressed grid around the eyes (Fig. 2). The morphology of fighting success was also characterized by a bigger nose and mouth with a distinct philtrum, compared with a typical losing fighter's face.

Discussion

It has been suggested that fighting ability might be inferred from facial cues (Sell et al., 2009). In this article, we present the first direct evidence that the perceived aggressiveness of fighters' faces is linked to their success in actual physical confrontations. Although perceived aggressiveness was also associated with weight, our results show that the two effects are independent. Perceived fighting ability was predicted only by weight, and its link to fighting success was restricted to heavyweights. We further found systematic differences in structural configurations of faces with high and low perceived aggressiveness. However, the association between facial configuration and fighting success was restricted to heavyweight fighters.

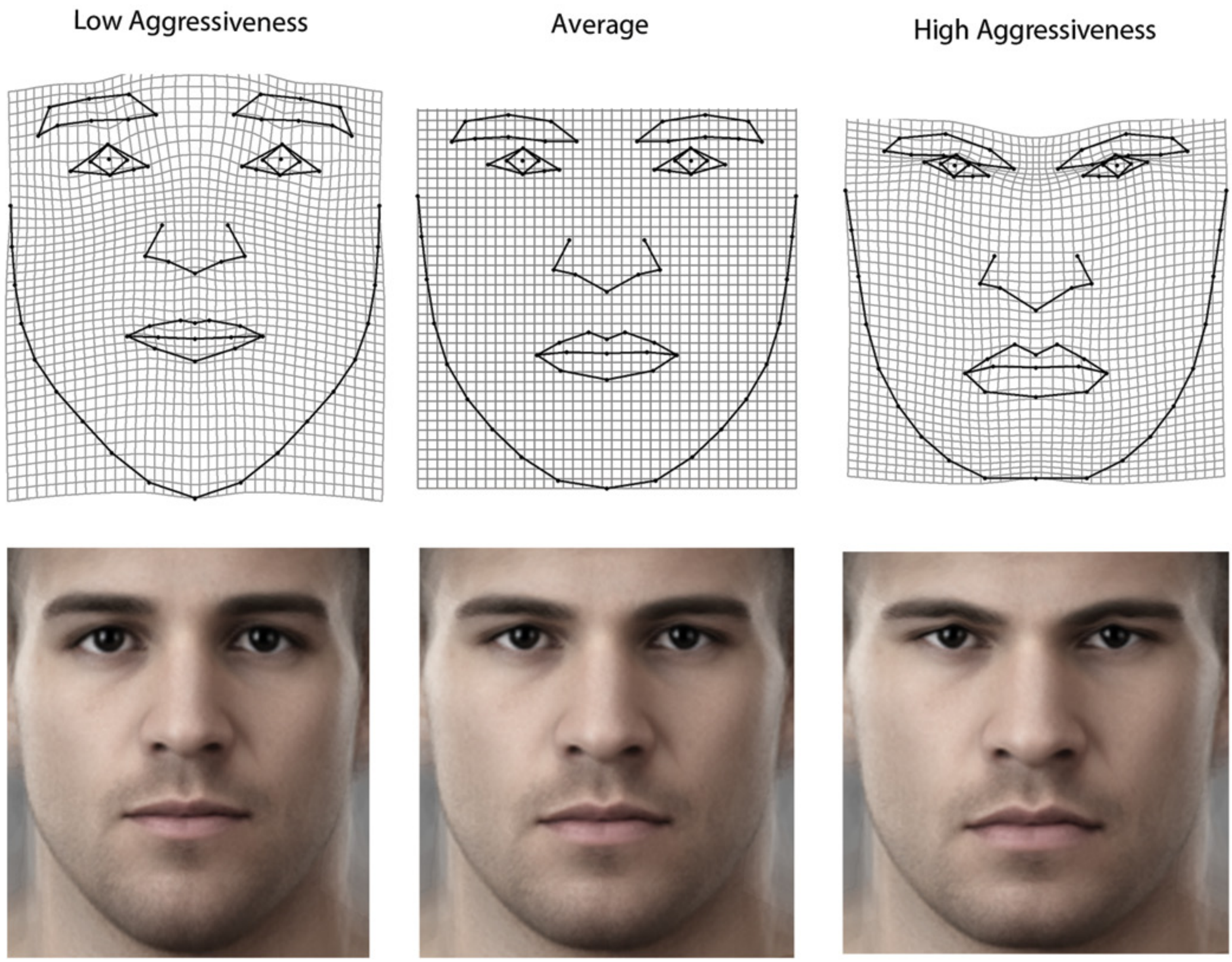

Fig. 1. Visualization of the shape regression on perceived aggressiveness by thin-plate spline-deformation grids (top row) and composite visualizations (bottom row), based on mean results for all fighters. Results are shown separately for low and high perceived aggressiveness, with the average reference shown for comparison; the effects were magnified 3 times for better visibility. The composite visualizations are based on landmark configurations estimated by shape regression; the effects are shown within the observed range.

Although there was a moderate positive correlation between perceived aggressiveness and perceived fighting ability ($r = .48$), our results indicate that the two variables might be underpinned by slightly different cognitive processes. First, judgments of fighting ability seem to focus on general probability of winning a fight, which is substantially related to size and weight (Deaner et al., 2012). This is supported by the fact that heavyweight contestants were seen as better fighters than lightweight contestants. Perhaps this is why we found no association between perceived fighting ability and actual fighting success in the overall sample of fighters who fight within individual weight categories—in combat sports (including MMA), weight categorization avoids large disparities in weight between contestants. In contrast, ratings of aggressiveness might focus on the probability of winning a fight that would actually take place. More specifically, individuals assessing the chances of winning a fight as low might flee or attempt reconciliation, thus avoiding likely losses. We think it likely, therefore, that most fights occur where competitors are relatively equally matched, and in such contexts, people employ judgments of aggressiveness to predict fight outcomes.

We employed GMM analysis to reveal the facial features linked to perception of aggressiveness. It is apparent that higher aggressiveness corresponds to facial morphology with lower level of fatty deposits, especially in the cheeks and chin area. This is probably

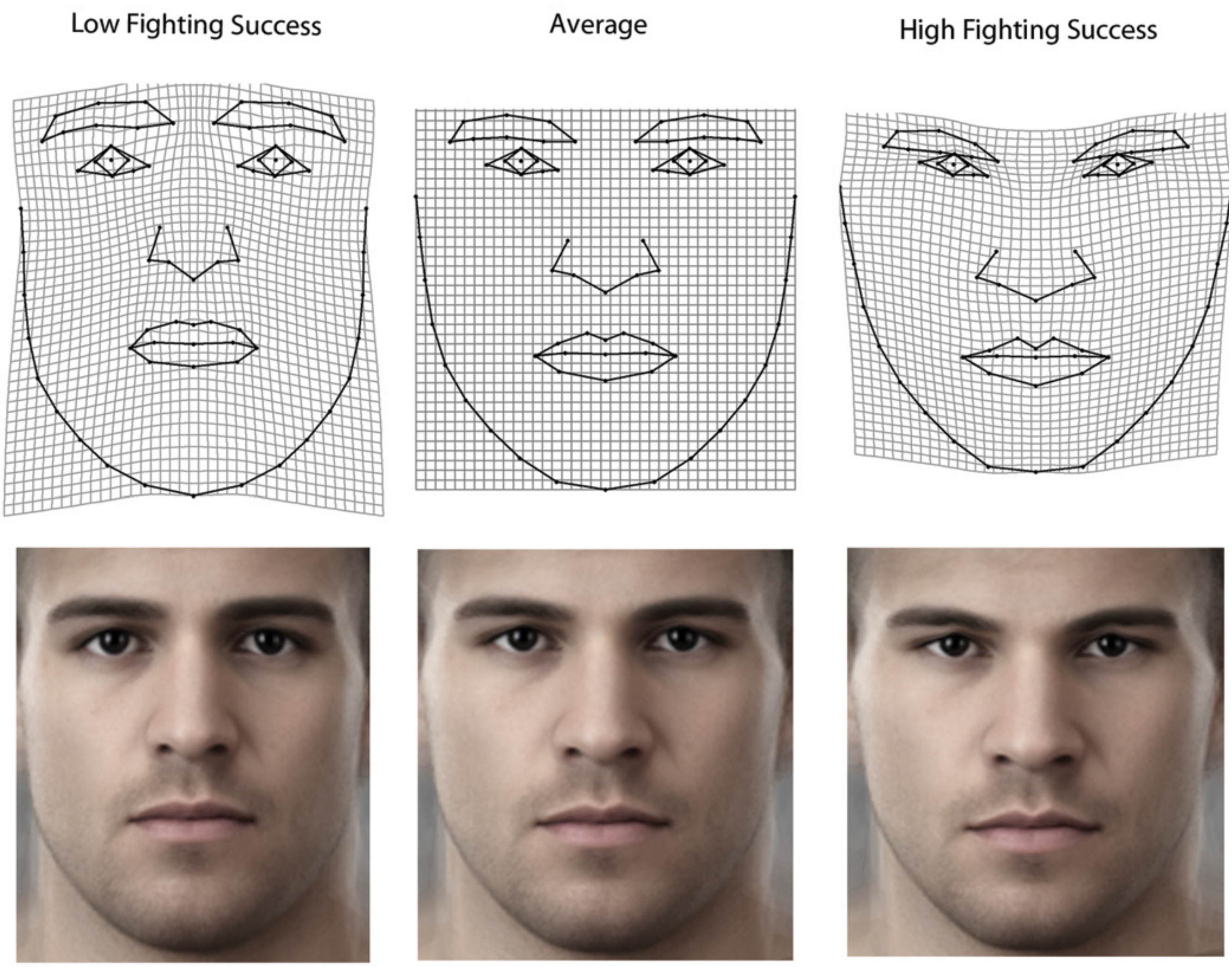

Fig. 2. Visualization of the shape regression on fighting success by thin-plate spline-deformation grids (top row) and composite visualizations (bottom row), based on faces of heavyweight fighters. Results are shown separately for low and high fighting success, with the average reference shown for comparison; the effects were magnified 3 times for better visibility. The composite visualizations are based on landmark configurations estimated by shape regression; the effects are shown within the observed range.

due to successful fighters maximizing overall physical performance, reducing subcutaneous fat. Another possibility is that, by removing body fat, a fighter may not increase his fighting ability per se but can increase his win/loss record by pairing himself with smaller opponents who have less muscle. This may also explain why better fighters had different faces only among heavyweights (the only weight category in which the trade-off is relaxed). Apart from soft tissue, we observed a significant effect of apparent "aggressive gaze," which is achieved by the horizontally narrowed eye area, probably due to the developed masculine features such as prominent superciliary arches. In certain respects, our results parallel those of Carré et al. (2009), who found that fWHR is a reliable cue to propensity to aggression. The deformation grids (Fig. 1) modeling the shape changes associated with perceived aggressiveness show proportional increases of bizygomatic width and smaller distance between the eyes and mouth. Nevertheless, the GMM analysis also showed that differences are not restricted to the area captured by fWHR. Other facial traits, including the shape of the nose, mouth, chin, and, especially, eye area all significantly contribute to perceived aggressiveness and potentially reflect the probability of winning. Our results were not entirely explained by cues associated with a history of fighting, such as scars and wounds, as our measure of facial damage was not related to perceived aggression.

To explore the facial features that perceivers use to infer aggressiveness, we compared, again using GMM analyses, similarities in perceptual morphospace and morphospace linked to fighting success for heavyweight classes (Figs. 1 and 2). These comparisons revealed the extent to which the perception of aggressiveness corresponds to the actual success in fights. The shape changes associated with high fighting success strongly resemble transformations predicted along the attribution of aggressiveness. However, estimated configurations of aggressiveness also show certain inconsistencies with prediction of fighting success: For example, the thinner chin and mouth associated with the estimated configuration of high fighting success does not correspond to the prediction of attribution of high aggressiveness associated with a broad chin.

One may wonder why the link between facial configuration and fighting success is restricted to heavyweight fighters. However, fighting success is a complex measure, and it is conceivable that proportional significance of aggressiveness varies across weight classes. Testosterone-linked characteristics such as muscle mass, power, and aggression might be relatively more important for successful attack techniques among heavyweights, whereas in lightweights, characteristics that are only loosely linked to testosterone, such as dexterity and speed, might be proportionally more significant (Sterkowicz-Przybycien, 2010). As the level of muscularity and masculinity—and also aggressive behavior—correlates with testosterone levels, specific facial configuration in heavyweights may be due to the effect of testosterone and other hormones affecting growth (Lassek & Gaulin, 2009). Similarly, the negative relationship between the ratio of the second and fourth fingers, thought to be an indicator of prenatal testosterone levels, and the fighting performance of Japanese sumo wrestlers supports this view (Tamiya, Lee, & Ohtake, 2012).

One might also question how far findings based on a specific sample such as MMA fighters can be generalized. Individuals involved in professional MMA adhere to specific daily training and dietary routines, and our findings could reflect these specific conditions. However, as the fighters are rewarded according to fighting success, they are presumably highly motivated to win, and differences in their physical fitness are rather subtle. These facts diminish the chances of finding the predicted effects, and it is conceivable that in real-life settings, the judgments based on appearance might actually be more predictive than reported here. Another defining factor of the fighters in the MMA sample is that their encounters are limited to predefined weight classes. At face value, this seems to be far from ancestral conditions. In contrast, one may argue that real fights occur only rarely between antagonists that are highly unequal in weight and strength. In most such cases, the weaker side would likely choose a strategy that avoids physical confrontation. In this respect, combats within weight classes may more closely resemble real-life situations.

From an evolutionary perspective, our results indicate selective pressures in ancestors of modern humans to be perceptually sensitive to facial cues associated with aggression and fighting ability. If aggressive-looking people are in fact more likely to be better competitors, and perhaps more likely to engage in aggressive behavior, it would be highly adaptive to recognize such a potentially dangerous antagonist in order to avoid physical confrontation and minimize the risk of injury and possible death. However, our results also show that inferences of fighting success and aggressiveness based on facial shape might hold only within a specific spectrum of individuals. Similarly, Zebrowitz and Rhodes (2004) reported congruent attributions of health and intelligence only in the lower half of the attractiveness distribution; however, raters inappropriately employed similar cues in the other half of the distribution as well. Zebrowitz and Rhodes explain this by an overgeneralization effect. The evolution of such an effect can be subsumed within error-management theory, which predicts that false-positive and false-negative errors might have highly biased consequences in terms of survival or fitness (Haselton & Buss, 2000). Here, the costs of false-positive attributions of aggressiveness to harmless individuals might be disproportionally higher than false-negative attributions to dangerous opponents. However, the degree and direction in disproportion of costs between false-positive and false-negative attributions remains to be empirically tested. Males might be expected to be more sensitive to aggressiveness judgments, as they frequently use force to settle intrasexual conflict. In contrast, for women, it should also be advantageous to assess a potential male aggressor, as such attributions can reflect males' capability to protect themselves and their offspring from other men. This is supported by our results, as we did not report any significant sex difference in perception of aggressiveness or fighting ability, and the ratings of men and women were highly correlated (r = .93 and r = .95, respectively).

In conclusion, our results support the hypothesis that humans are able to infer aggressiveness from the face of potential opponents. Such an ability exploits the correlates between the facial traits responsible for perception of aggressiveness and those facial features that reflect the actual likelihood to succeed in male-male physical confrontation.

Author Contributions

V. Třebický, J. Havlíček, and K. Kleisner developed the study concept. All authors contributed to the study design. Data

collection was performed by V. Třebický and K. Kleisner; K. Kleisner performed the data analysis. V. Třebický, J. Havlíček, and K. Kleisner drafted the manuscript, and S. C. Roberts and A. C. Little provided critical revisions. All authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Editor's choice

Original Article

Human perception of fighting ability: facial cues predict winners and losers in mixed martial arts fights

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In antagonistic encounters, the primary decision to be made is to fight or not. Animals may then possess adaptations to assess fighting ability in their opponents. Previous studies suggest that humans can assess strength and fighting ability based on facial appearance. Here we extend these findings to specific contests by examining the perception of male faces from paired winners and losers of individual fights in mixed martial arts sporting competitions. Observers, unfamiliar with the outcome, were presented with image pairs and asked to choose which of the 2 men was more likely to win if they fought while other observers chose between the faces based on masculinity, strength, aggressiveness, and attractiveness. We found that individuals performed at rates above chance in correctly selecting the winner as more likely to win the fight than the loser. We also found that winners were seen to be more masculine, stronger, and more aggressive than losers. Finally, women saw the winners as more attractive than the losers. Together these findings demonstrate that 1) humans can predict the outcome of specific fighting contests based on facial cues, 2) perceived masculinity and strength are putative cues to fighting success available from faces, and 3) facial cues associated with successful male–male competition are attractive to women.

Key words: **competition, face appearance, fighting, intrasexual, violence.**

INTRODUCTION

Across many animal species, fighting as a form of intrasexual selection (competition between members of the same sex) is common and has led to the evolution of animal weapons, such as horns and antlers, particularly in males (Andersson 1994). Adaptive decisions, or fitness-enhancing decisions, rely on balancing the net benefits against the net costs of particular actions (Krebs and Davies 1998). In antagonistic encounters with other individuals of the same species, the primary decision to be made is to fight or not. The benefits to be gained, such as territory, must be weighed against the costs, the potential for injury or even death.

Although the benefits of fighting will vary across species and environment, the same costs are applicable to many species, and critically, the costs vary greatly depending on whether an animal is likely to be the winner or loser of the fight. We can then expect that animals that engage in intraspecies fighting will possess perceptual/cognitive adaptations to assess the risks involved in this behavior by assessing fighting ability in their opponents (Parker 1974; Enquist and Leimar 1983) using cues that are potentially related to fighting ability such as body size, strength, and weaponry (Krebs and Davies 1998). Indeed, there is evidence that animals make decisions about fighting based on the assessment of the relative fighting abilities of their opponents (Gosling et al. 1996; Hazlett 1996) and that specific traits in some species can be related to fighting success. For example, in terms of visual perception, variable black facial patterns in paper wasps are related to both body size and social dominance (Tibbetts and Dale 2004) and red chest coloration in gelada baboons is related to troop status, with leader males having the reddest chests (Bergman et al. 2009). Individuals could base their decisions to fight on appearance-linked cues to fighting ability allowing them to compete when likely to win and to avoid costly agonistic interactions when likely to lose.

In humans, there is evidence that male–male competition is important across various different cultures. For example, as noted by Sell et al. (2009), fighting ability is associated with access to resources in the Yanomamo of Venezuela (Chagnon 1983), the Achuar of Ecuador (Patton 2000), and the Tsimane of Bolivia (von

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Rueden et al. 2008). In other cultures, sports involving ritualized combat between men are common and take many forms, such as Sumo in Japan and stick-fighting in the Suri of Ethiopia. These ritualized forms of combat have a long recorded history, including fencing in the 16th century Germany and gladiatorial combat in Ancient Rome. In line with this evidence for physical combat between men, also noted by Sell et al. (2009, 2012), there are a range of anatomical and physiological sex differences that appear to reflect adaptation to male–male competition in humans, including sex differences in height and upper body strength (Plavcan and Van Schaik 1997; Puts 2010).

Given evidence for intrasexual conflict in humans and following theoretical predictions for adaptations to assess fighting ability (Parker 1974; Enquist and Leimar 1983), previous researchers have suggested that humans possess adaptations to infer fighting ability, specifically that fighting ability might be inferred from facial, body, and vocal cues (Sell et al. 2009, 2010). For example, people make relatively accurate inferences about men's physical strength from static facial images (Sell et al. 2009) and voice recordings (Sell et al. 2010), and measurements of physical strength are associated with ratings of fighting ability (Sell et al. 2009). One study has shown that self-rated fighting ability is positively related to acquaintance-rated fighting ability, which in turn is positively related to unfamiliar-person-rated fighting ability based on face photographs (Doll et al. 2014). This work is suggestive of cues to fighting ability being available in faces, but it is important to note that self-ratings and acquaintance ratings are likely to be noisy measures of real fighting ability. Focusing on human facial cues, masculinity in male faces has been associated with perceived dominance (Perrett et al. 1998) and physical strength is positively related to ratings of facial masculinity (Fink et al. 2007). Recent studies have also highlighted that face measurements are associated with aggression in men. For example, facial width scaled for face height is correlated with perceived aggression (Carré et al. 2009), related to self-reported dominance and, relating to real behavior, aggressive behavior in sport (Carre and McCormick 2008; Třebický et al. 2015; Zilioli et al. 2015). Further, one study examining forensic data from skeletons has shown that men with narrow faces are more likely to have died from contact violence than their wider faced peers (Stirrat et al. 2012).

While the accurate assessment of strength and its association with fighting ability (Sell et al. 2009), links between facial measurements and aggression (Carre and McCormick 2008), and that studies have associated fighting success with facial measurements showing that men with wider faces relative to height are more likely to win in mixed martial arts (MMA) competition (Třebický et al. 2015; Zilioli et al. 2015) are all in line with the notion that humans can assess fighting ability from facial cues, they do not provide direct evidence for this notion. One study has, however, examined fighting success based on instances of real fights in MMA sporting contests. Calculating fighting success as the ratio of wins to losses across a fighter's Ultimate Fighting Championship (UFC) fighting career, it was found that the perceived aggressiveness of fighters' faces was linked to their success in actual physical confrontations, although perceived fighting ability and differences in facial shape were only associated with fighting success in heavyweight fighters (Třebický et al. 2013). This suggests that perceived aggression may be an underlying cue to fighting success rather than the cognitively complex inferred fighting success. However, fighting success across fights is somewhat different to assessing fighting outcomes from faces in particular contests between pairs of fighters. In other words, only one face is relevant when assessing general fighting ability, whereas, in specific contests, individuals can compare the traits of 2 protagonists. This comparison may enable greater accuracy in judgment. Being able to predict the outcome of contests between 2 individuals may be adaptive because it allows for discrimination between individuals within a group in order to select successful allies or mates. The cue used to discriminate between pairs of others could also be used to assess a person's relative fighting ability. For example, an individual may be able to compare their own estimated ability to a competitor's ability based on appearance to predict their own chances of successfully winning a fight.

In the current study, we examined individual's abilities to directly assess the outcome of particular fights. Although previous results suggest that individuals can assess the fighting ability of particular fighters from their faces based on their overall success across a number of fights (Třebický et al. 2013), here we focused on a more fine-grained analysis in which face images of fighters were presented as pairs such that observers were tasked to judge the difference in perceived traits of the winners and losers of specific fights. We asked observers to judge between the winners and losers of fights for a variety of traits to test ideas relating to intrasexual and intersexual selection. First, we addressed accuracy in judgment by asking observers to choose who they think would win in a fight. Accuracy at this level would indicate that observers are able to assess the relative fighting ability of 2 fighters to correctly predict the outcome. Second, we examined specific cues from faces that may underlie accuracy: perceived masculinity, strength, and aggressiveness. Third, we addressed attractiveness to the opposite-sex because, while perception of fighting ability is often considered the domain of intrasexual selection, it may also be related to intersexual selection. In terms of attractiveness to the opposite-sex, there are benefits that could be associated with preferring better fighters: 1) indirect benefits, genetic benefits that are passed to offspring such as genes associated with health, strength, or high quality immune systems and 2) direct benefits, benefits that are directly passed to mates or offspring such as resources or protection from other males. We then also asked a sample of women who they thought was more attractive out of the pair.

METHODS

Participants acting as observers

There were 5 different studies in which participants chose between pairs of faces for different traits. Independent groups of participants judged between faces for: who would win in a physical fight (N = 69, men = 32, women = 37, mean age = 29.7, standard deviation [SD] = 10.7, 95% confidence interval [CI], lower: 27.1, upper: 32.2), who is more masculine (N = 33, men = 11, women = 22, mean age = 25.6, SD = 8.1, 95% CI, lower: 22.7, upper: 28.5), who is stronger (N = 30, men = 10, women = 20, mean age = 30.3, SD = 12.7, 95% CI, lower: 25.5, upper: 35.0), who is more aggressive (N = 30, men = 12, women = 18, mean age = 27.4, SD = 8.2, 95% CI, lower: 24.3, upper: 30.4), and who is more attractive (N = 34, women = 34, mean age = 29.0, SD = 11.3, 95% CI, lower: 25.1, upper: 33.0). Participants were selected for being older than 16 years of age. For attractiveness judgments, only women reporting to be heterosexual were selected for analysis. Participants were recruited for the study online via a research-based website and the study was conducted online.

Stimuli

The original study population consisted of 285 MMA fighters for which facial photographs and details of their previous fight (opponent and win/loss), as well as facial photographs of their opponent, were available from the official Web site of the MMA division of the UFC (www.ufc.com; database accessed in June 2012). Because this represented the total pool of fighters, excepting unselected fighters for which data or photographs were unavailable, it was possible to match the 285 fighters with their opponent in their most recent fight. Out of the 285 fighters, we created 156 pairs of fights based on the most recent matches for the fighters. From these pairs, 42 pairs were excluded from the analyses because they contained a duplicate fighter from one of the preceding fight pairs.

The final set of images used were of 228 fighters which made up 114 unique pairs representing fights between 2 different fighters. Using the available database, for each pair, 1 fighter was classified as the winner and 1 as the loser.

For each pair of fighters, we obtained data on their weight class, which was the same for each fighter making up the pair. To reduce the number of classifications and increase the sample size of final groupings, we averaged the 7 available weight classes into 3 groupings: lightweight (bantam weight, feather weight, light weight, $N = 48$ pairs), middleweight (welter weight, middle weight, $N = 42$ pairs), and heavyweight (light heavy weight, heavy weight, $N = 24$ pairs).

The stimulus set comprised the official front-on photographs available from www.ufc.com. These photographs appear to have approximately similar lighting and background with individuals posing with an approximately neutral expression. To equate size of the face in the image, all images were aligned to standardize the position of the pupils in the image.

Procedure

Participants were administered a short questionnaire assessing age, sex, and sexual orientation (only used for women rating attractiveness), followed by a forced-choice face test. There were 5 different forced-choice face tests for which the stimuli and procedure were identical except that participants in each test were given different instructions on what type of discrimination they were asked to do. Different participants took part in each of the tests based on random allocation to tests.

In the forced-choice tests, the 114 pairs of winners and losers of MMA fights as described above were shown with both order and side of presentation randomized. Participants were asked to choose 1 face from the pair for a particular trait. Clicking a button below the face selected moved participants on to the next face trial. There was no time limit for responses and both faces remained on screen until participants selected a face.

Specific questions for the 5 tests were:
"Which person is more likely to WIN in a physical fight?"
"Which person is more MASCULINE?
"Which person is PHYSICALLY STRONGER?"
"Which person is more AGGRESSIVE?"
"Which person is more ATTRACTIVE?"

Statistical analyses

The dependent variable was the choice by each participant of the winner or loser for each pair of fighters for 114 pairs. If the participant selected the winner from the pair, this was scored "1" and if the participant selected the loser from the pair, this was scored "0".

First, general linear mixed model (GLMM), or multilevel modeling, analyses were conducted using R (R Core Team 2013); specifically, we used the "glmer" function available in the "lme4" package (Bates et al. 2014). Such models allow simultaneous analysis of participant and stimulus effects negating the need to collapse across either. Participant (1|subject) and face pair (1|fight) were specified as random factors in the model. The nature of data entered here was binary (0/1), and so a binomial model was specified using the "glmer" function which fitted the model using maximum likelihood with Laplace approximation. The model as specified in R was as follows:

$$\left(\text{modelA} = \text{glmer}\left(\begin{array}{l}\text{pickwinner} \sim (1\,|\,\text{subject}) + (1\,|\,\text{fight}),\\ \text{data} = \text{fight},\ \text{family} = \text{binomial}\end{array}\right)\right)$$

In this model, where "pickwinner" was whether the subject correctly chose the winner, we tested for a significant effect of the intercept which would indicate a difference from chance (0).

A second model was specified in which sex of participant and weight category were added as fixed effects to the above model:

$$\left(\text{modelB} = \text{glmer}\left(\begin{array}{l}\text{pickwinner} \sim (1\,|\,\text{subject}) + (1\,|\,\text{fight}) +\\ \text{sexparticipant} + \text{weightcategory},\\ \text{data} = \text{fight},\ \text{family} = \text{binomial}\end{array}\right)\right)$$

Models were compared using the "Anova" function. A nonsignificant difference between models would indicate that adding sex of participant and weight category did not impact significantly on the original model.

To follow-up these analyses, we additionally included a by-participant and by-face analysis using 1-sample *t*-tests to test if choice of winner over loser was significantly different from chance. Impact of weight category was tested in the by-face analysis using Anova and impact of sex of participant was tested in the by-participant analysis using independent samples *t*-tests.

RESULTS

General linear mixed models

Separate models were computed for: who would win in a physical fight, who is more masculine, who is stronger, who is more aggressive, and who is more attractive.

The first model indicated that choice of "Which person is more likely to WIN in a physical fight" was a significant predictor of winning a match ($Z = 2.35$, $P = 0.019$). Adding sex and weight category to the model created a model that was not significantly different from the original model (chi square = 1.66, df = 3, $P = 0.645$).

The second model indicated that choice of "Which person is more MASCULINE?" was a significant predictor of winning a match ($Z = 2.00$, $P = 0.038$). Adding sex and weight category to the model created a model that was not significantly different from the original (chi square = 2.54, df = 3, $P = 0.469$).

The third model indicated that choice of "Which person is PHYSICALLY STRONGER?" was a significant predictor of winning a match ($Z = 2.00$, $P = 0.045$). Adding sex and weight category to the model created a model that was not significantly different from the original for strength (chi square = 2.27, df = 3, $P = 0.518$).

The fourth model indicated that choice of "Which person is more AGGRESSIVE?" was a significant predictor of winning a match ($Z = 2.57$, $P = 0.010$). Adding sex and weight category to the model created a model that was not significantly different from the original for aggressiveness (chi square = 6.17, df = 3, $P = 0.104$).

The last model indicated that choice of "Which person is more ATTRACTIVE?" was a nonsignificant predictor of winning a match ($Z = 1.76$, $P = 0.079$), although the P value was close to 0.05. Adding weight category to the model created a model that was not significantly different from the original for attractiveness (chi square = 0.43, df = 2, $P = 0.808$).

In all of the above models, winners were selected more often than losers. A summary of model statistics for each question is presented in Table 1.

To examine the equivalence of the GLMM analysis with methods involving calculation of means, because these types of analysis are common in the literature, we carried out further analyses in which mean choice was calculated for each face pair and for each participant. We note that variance across fighters is most important to the question of whether individual fighter's faces contain cues to fighting success and so the GLMM above and the by-face pair analyses are more appropriate to answer this question.

By face pair

Mean choice of winner versus loser was calculated for each face pair and face pair was used as the unit of analysis and compared with chance with 1-sample t-tests. This was done separately for: who would win in a fight, who is more masculine, who is stronger, and who is more attractive. We additionally tested for effects of weight category using 1-way Anovas.

One-sample t-tests indicated that winners were chosen significantly more often than losers for winning in a physical fight ($t_{113} = 2.36$, $P = 0.020$, $D = 0.44$), being more masculine ($t_{113} = 2.17$, $P = 0.032$, $D = 0.41$), and being more aggressive ($t_{113} = 2.74$, $P = 0.007$, $D = 0.52$). Although winners were chosen more often than losers, this was not significantly different from chance for being stronger ($t_{113} = 1.97$, $P = 0.052$, $D = 0.37$) and being more attractive ($t_{113} = 1.71$, $P = 0.091$, $D = 0.32$).

One-way Anovas (dependent variable = mean choice of winner, fixed factor = weight category) indicated no significant effect of weight category for judgments of winning in a physical fight ($F_{2,111} = 0.72$, $P = 0.491$, $\eta_p^2 = 0.013$), masculinity ($F_{2,111} = 1.15$, $P = 0.319$, $\eta_p^2 = 0.020$), strength ($F_{2,111} = 0.32$, $P = 0.724$, $\eta_p^2 = 0.006$), aggressiveness ($F_{2,111} = 2.37$, $P = 0.099$, $\eta_p^2 = 0.041$), or attractiveness ($F_{2,111} = 0.14$, $P = 0.871$, $\eta_p^2 = 0.002$).

By participant

Mean choice of winner versus loser was calculated for each participant, and participant was used as the unit of analysis and compared with chance with 1-sample t-tests. This was done separately for: who would win in a fight, who is more masculine, who is stronger, and who is more attractive. We additionally tested for effects of sex of participant using independent samples t-tests.

One-sample t-tests indicated that winners were chosen significantly more often than losers for winning in a physical fight ($t_{68} = 7.86$, $P < 0.001$, $D = 1.91$), being more masculine ($t_{32} = 4.93$, $P < 0.001$, $D = 1.74$), being stronger ($t_{29} = 6.57$, $P < 0.001$, $D = 2.44$), being more aggressive ($t_{29} = 5.34$, $P < 0.001$, $D = 1.98$), and being more attractive ($t_{33} = 6.96$, $P < 0.001$, $D = 2.42$).

Independent samples t-tests indicated no significant effect of sex of participant for judgments of winning in a physical fight ($t_{67} = 0.69$, $P = 0.493$, $D = 0.17$), masculinity ($t_{31} = 0.31$, $P = 0.762$, $D = 0.11$), strength ($t_{28} = 1.46$, $P = 0.156$, $D = 0.55$), or aggressiveness ($t_{28} = 0.97$, $P = 0.342$, $D = 0.37$).

Correlations among judgments

Using data by face pair, we ran Pearson product-moment correlations to examine relationships between the different attributes. Correlations can be seen in Table 2. Significant positive correlations were found among the judgments of winning in a physical fight, masculinity, strength, and aggressiveness (all $r > 0.490$, all $P < 0.001$). None of these variables, however, was significantly related to attractiveness judgments (all $P > 0.05$).

Previous authors have argued that masculinity in male faces may not be attractive because it is associated with negative attributions, such as aggressiveness (Little et al. 2011; Puts et al. 2012). We tested this idea by examining the relationship between choice as more masculine and choice as more attractive while controlling for both choice as more aggressive and stronger. To examine how women's preferences were related to these traits independently, we entered perceived masculinity, strength, and aggression as predictors of women's attraction in a linear regression. This revealed a significant overall model ($F_{3,110} = 6.23$, $P < 0.001$,

Table 2

Intercorrelations among perceived traits based on the choice of a face out of a pair for each question

	Masculine	Strong	Aggressive	Attractive
Win fight	0.783**	0.815**	0.720**	0.150
Masculine		0.743**	0.699**	0.175
Strong			0.490**	0.139
Aggressive				−0.120

**Significant at $P < 0.01$.

Table 1

Model summaries for choice of the winner as more likely to win, more masculine, stronger, more aggressive, and more attractive of 114 pairs of fighters

	Winner	Masculine	Strong	Aggressive	Attractive
Estimate	0.203	0.183	0.238	0.238	0.193
Mean	0.550	0.546	0.559	0.559	0.548
Standard error	0.086	0.088	0.119	0.092	0.110
Z/P value	2.35/0.019	2.08/0.038	2.00/0.045	2.57/0.010	1.76/0.079
Participant, N	69	31	30	30	34

Estimate is the probability of picking the winner on the logit scale and the standard error reported is that of the estimate.

R^2 = 0.145) in which masculinity was significantly positively (beta = 0.514, P < 0.001), aggressiveness was significantly negatively (beta = −0.474, P < 0.001), and physical strength was not significantly (beta = −0.011, P = 0.932) associated with women's choices for attractiveness.

DISCUSSION

Our data demonstrated that both men and women perceive winners of fights differently from losers. Specifically, from the mixed model analyses, winner's faces were more likely to be seen as able to win the fight, physically stronger, more aggressive, more masculine, more aggressive, and more attractive to women than loser's faces (although this last effect was nonsignificant, P = 0.079). We found no significant effects of sex of observer or weight category of fighter for these judgments. Similar effects were seen in by-participant and by-face pair analyses, although effects were strongest in the by-participant analyses. This difference is the result of greater variance between face pairs than between observers in terms of choices. For example, while the mean choice is identical (M = 0.543), for choice of winner as winning in a physical fight, the SD was lower across participant (SD = 0.05) than across face pair (SD = 0.20).

Given the potential importance of male intrasexual selection in human evolution (Chagnon 1983; Plavcan and Van Schaik 1997; Patton 2000; von Rueden et al. 2008), our data are in line with the notion that humans possess perceptual/cognitive adaptations to assess the risks involved fighting by assessing fighting ability in other humans, as expected in a species that engages in such behavior (Parker 1974; Enquist and Leimar 1983). Although previous researchers have suggested that humans possess adaptations to detect fighting ability based on perceptions of strength (Sell et al. 2009, 2010) and correspondence between self-rated and acquaintance-rated fighting ability (Doll et al. 2014), here we show direct evidence that humans can predict the actual outcome of specific fights based on facial information, in line with a previous demonstration that the perceived aggressiveness of fighters' faces was linked to their career fighting success (Třebický et al. 2013). Although humans do not necessarily have obvious evolved phenotypic weaponry, such as horns or antlers seen in nonhuman species (Krebs and Davies 1998), humans may display cues to their fighting abilities and possess adaptations to help guide their choice to fight specific individuals (Parker 1974; Enquist and Leimar 1983).

We tested for sex differences in each judgment but found no significant effects. It might be expected that men would pay more attention to cues to male–male competitive ability because such contests are more relevant to them, but our data suggests that women perform similarly in discriminating winners from losers on the basis of facial appearance (see also Třebický et al. 2015). We note, however, that our sample sizes were relatively small for examining sex differences because this was not the main aim of the study. Sex differences may indeed be found using larger sample sizes or in alternative situations that emphasize the relevance to men over women, such as in real-life competitive situations.

We note that across all types of judgments, the perceptual difference between winners and losers was relatively small. Given the number of other variables that could determine the winner and loser of these fights, we think it would be surprising if facial cues accounted for the majority of the variance, and of course, small advantages can prove important over evolutionary time scales. There are also other reasons why the effects seen here are likely to be modest. In our study, observers were limited to seeing static 2D face information. Stronger relationships between facial appearance and fight outcome may be possible under different experimental conditions, for example, if participants were given 3D face images or were exposed to the faces for more time. Given our interest was in static facial cues, we excluded lots of potential cues to fighting ability. In real-life fights, body size and dynamic cues are available which may increase accuracy. Additionally, the fighters here belong to a relatively homogenous group of highly trained athletes and are therefore well matched. This is an interesting case in discriminating winners and losers as this is likely to be a harder task than predicting who will win in less balanced fights. Indeed, fighters here were also further matched in terms of weight category specifically designed to create more even odds. In real fighting situations, where weight, as a proxy for muscle mass or strength, is more uneven, we might predict greater success in predicting the outcomes of fights.

In terms of specific cues to fighting success, winner's faces were generally seen as more masculine and stronger than loser's faces. Facial masculinity is then a potential cue to fighting ability and is also positively related to perceived dominance (Perrett et al. 1998), real physical strength (Fink et al. 2007), and testosterone levels, although the relationship with testosterone may be somewhat more complex than a simple linear relationship (Pound et al. 2009). Judgments of perceived physical strength from faces have been previously highlighted as a proxy for judgments of fighting ability (Sell et al. 2009), with perceived strength relating to actual measured strength (Sell et al. 2009). There are also links between facial measurements and aggression (Carre and McCormick 2008) and one previous study has shown that fighters with more aggressive appearing faces are more likely to have higher success in their fights over the careers (Třebický et al. 2013). Given these traits are potentially interlinked, they could all relate to fighting success via the same mechanism. For example, underlying levels of testosterone could underpin facial cues to masculinity, strength and aggression. Of course these traits may be also associated with fighting success for different reasons. For example, strength may be a good predictor of who wins fights because it is linked directly to the outcome of competition, but in more evenly matched fights, cues to behavioral aggression may also be used to predict winners independent of strength (see also Třebický et al. 2013). In fact, there may be shared and unshared factors relating to fighting success for each of these 3 factors.

In predicting women's preferences, the zero-order correlations indicated nonsignificant correlations between other judgments and attractiveness judgments. However, when controlling for other judgments in the regression analysis, masculinity was positively related, aggressiveness negatively related, and strength was unrelated to faces being selected as attractive to women. This is suggestive that while women found winner's faces as more attractive than losers, this was due to differences in perceived masculinity. This further highlights that masculinity and aggressiveness, while having similar effects on perceived intrasexual competition abilities (winning fights), have quite different effects in term of intersexual selection (their attractiveness to women). Indeed, the benefits of avoiding aggressive male partners are clear despite the fact that such males may be successful in intrasexual competition. Here, controlling for perceived aggressiveness and strength, the relationship between judgments of masculinity and attractiveness increased from r = 0.175 to 0.514 (Z = 2.92, P = 0.004). Previous studies have shown that women moderate their preferences for masculine facial cues according to their recent experience of visual environmental cues of direct male–male competition and violence. In these previous studies, women preferred more masculine male faces after exposure to cues of direct male–male competition and violence (Little et al. 2013), which is consistent with idea that women here preferred the faces of men who were most likely to be successful in male–male competition. Perhaps such preferences reflect that ideal men should be able to compete successfully but not actively seek out conflict (indicated by high perceived aggression). In this way, women may select men who can defend themselves, their partner, and their offspring from other men but who do not continually seek conflict. Indeed, it has previously been argued that women may face a trade-off in selecting masculine appearing partners because, while such partners may be more dominant, masculine partners may not possess behavioral traits, such as cooperativeness or faithfulness, that are desirable in a long-term partner (Little et al. 2011; Puts et al. 2012). In such preferences, it is difficult to tease apart the role of indirect from direct benefits. This is because preferences for successful competition can relate to both. For example, preferring men who are likely to win in fights can lead to direct benefits in terms of resources as such men may most successfully defend or acquire resources. However, such preferences can also lead to potential indirect benefits by passing genes for the successful defense or acquisition of resources on to male offspring, if these factors are heritable. In other words, if women prefer traits that are associated with the ability to provide direct benefits and mate with these men, the factors associated with ability to provide direct benefits may also be passed to her offspring thereby providing indirect benefits (see Kokko et al. 2003). It is then likely that both direct and indirect benefits from men play a role in generating preferences for the faces of men likely to win fights.

In summary, we found that individuals performed at rates above chance in correctly selecting the winner as more likely to win the fight than the loser. We also found that winners were seen to be more masculine, more aggressive, and stronger than losers. Finally, women saw the winners as more attractive than the losers. The effect sizes for each of these relationships were generally small but could have potentially important evolutionary consequences. Together these findings demonstrate that 1) humans can correctly predict the outcome of specific fighting contests, 2) perceived masculinity/strength/aggressiveness are all putative cues to fighting ability available from faces, and 3) facial cues associated with successful male–male competition are attractive to women.

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Further Evidence for Links Between Facial Width-to-Height Ratio and Fighting Success: Commentary on Zilioli et al. (2014)

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Recent research has reported an association between facial width-to-height ratio (fWHR) and both fighting performance and judgments of formidability in a sample of mixed martial arts (MMA) combatants. The results provide evidence of fWHR being associated with sporting performance and aggression in men. However, it has been argued that the effect of fWHR might be a by-product of associations between body size and behavioral measures. Here we tested whether fWHR is associated with perceived aggressiveness, fighting ability and success in physical confrontation, while controlling for body size, also in a sample of MMA fighters. We found that perceived fighting ability was predicted by weight but not by fWHR. In contrast, both fWHR and body weight independently predicted perceived aggressiveness. Furthermore, we found positive associations between fWHR and fighting performance which appear to be independent of body size. Our findings provide further support for the proposal that fWHR is associated with fighting ability and perceived aggression, and that these effects are independent of body size. Therefore, fWHR might be considered as a viable and reliable marker for inference of success in male intra-sexual competition. Aggr. Behav. 9999:XX–XX, 2014. © 2014 Wiley Periodicals, Inc.

Keywords: formidability; perception; fWHR; aggression; fight

A growing body of evidence indicates an association between facial morphology and some aspects of human psychology. Such morphological and personality/temperamental characteristics can be affected by a shared underlying biological mechanism. For instance, testosterone levels during puberty affect both muscle growth and aggression-related behaviors (Tremblay et al., 1998).

An extensively studied morphological trait that is also associated with behavior is facial width-to-height ratio (fWHR). fWHR has been shown to be positively associated with anti-social behavior (Haselhuhn & Wong, 2012; Stirrat & Perrett, 2010), self-perceived and other-perceived dominance (Mileva, Cowan, Cobey, Knowles, & Little, 2014), perceived aggressiveness (Lefevre & Lewis, In press; Short et al., 2012), actual aggressive behavior (Carré & McCormick, 2008; Carré, McCormick, & Mondloch, 2009), sport performance (Tsujimura & Banissy, 2013; Třebický, Havlíček, Roberts, Little, & Kleisner, 2013), strength (Windhager, Schaefer, & Fink, 2011), the probability of being killed in violent physical encounters (Stirrat, Stulp, & Pollet, 2012) and lifetime reproductive success (Loehr & O'Hara, 2013).

Testosterone levels appear to influence growth trajectories of craniofacial shape during puberty (Verdonck, Gaethofs, Carels, & de Zegher, 1999) and recently it was found that fWHR variation in adult men is related to reactive testosterone levels (Lefevre, Lewis, Perrett, & Penke, 2013). As testosterone levels also correlate with various aspects of aggressive behavior (for review see Archer, Graham-Kevan, & Davies, 2005), testosterone may represent a shared underlying mechanism that

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explains covariance between these morphological and behavioral characteristics.

Recently, Zilioli et al. (In press) reported an association between fWHR, fighting performance and judgments of formidability, employing faces of professional mixed-martial arts (MMA) fighters as stimuli. They showed that fighters with greater fWHR had longer fighting careers, and both higher numbers and proportions of career wins, independent of their BMI. Further, Zilioli et al. collected assessments of formidability using two pairs of composite facial images, in which the first pair varied in experience and the second pair in bizygomatic breadth. Composites of the more experienced and wider-faced fighters were assessed as more formidable and judged as tougher opponents.

Coincidentally, we recently tested a similar hypothesis (Třebický, Fialová, Kleisner, & Havlíček, 2013) as a follow-up to our previous research examining other aspects of facial appearance and success in MMA fighters (Třebický, Havlíček, et al., 2013). Specifically, we tested whether variation in fWHR is associated with actual fighting performance, perception of aggressiveness and fighting ability, while controlling for potentially confounding effects of body height and weight, in a sample of professional MMA fighters from the same organization, UFC®.

While drawn from an overlapping database, in comparison to Zilioli et al.'s study, our stimuli set consisted of a smaller sample of portrait photographs ($N = 146$) as we only used images of fighters that fulfilled the following criteria: (i) being of apparent non-African or non-Asian origin, (ii) facing directly into the camera, (iii) with an absence of beard, moustache or hair obscuring the face, in order to minimize the effects of these potentially confounding variables. We also obtained data about fighter's age ($M = 29.77$ years, $SD = 4.6$), height ($M = 179.5$, $SD = 8$), weight ($M = 79.08$, $SD = 14.55$), number of fights ($M = 8.78$, $SD = 7.02$) and wins ($M = 5.86$, $SD = 5.19$) in the UFC. Subsequently, we calculated their fighting performance (proportion of wins to fights) and measured their fWHR as per Carré & McCormick (2008). The images were rated online for aggressiveness by 618 individuals (216 men) and for fighting ability by 278 individuals (98 men) from the Czech Republic. For details of ratings see Třebický, Havlíček, et al. (2013). As fighters' weight, height, and fighting performance were not normally distributed, we used Kendall's correlations.

Although Weston, Friday, and Lio (2007) originally found fWHR to be independent of body size, several subsequent studies have suggested that the link between fWHR and aggression or sport performance might be an epiphenomenon of body size (Deaner, Goetz, Shattuck, & Schnotala, 2012; Mayew, 2013). It has also been shown that variation in body dimensions are related to the size of the face, including fWHR (Coetzee, Chen, Perrett, & Stephen, 2010). For this reason, we tested the relationship between body size and fWHR and did find significant positive correlations between fWHR and fighter's height ($\tau = .171$, $P = .003$) and weight ($\tau = .210$, $P < .001$) in our sample ($N = 146$). Similar to Zilioli et al.'s results for the association between proportion of wins and fWHR ($r = .139$), we found a positive correlation between fWHR and fighting performance of comparable effect size ($\tau = .114$, $P = .046$), but not with body height ($\tau = .021$, $P = .73$) or weight ($\tau = .03$, $P = .625$). Interestingly, in Zilioli et al.'s sample, the positive relationship was restricted to the Caucasian looking fighters. As the authors noted, the null results in non-Caucasian fighters might be due to the small number of non-Caucasians in the UFC and thus there was low power for detecting a possible effect. Alternatively, the fWHR-related effects might be restricted to individuals of European origin. Also, other performance/aggression related studies have been performed predominantly on Caucasian samples (Carré & McCormick, 2008; but see Tsujimura & Banissy, 2013 who used an Asian sample of baseball players) suggesting bias towards Caucasian competitors in fWHR studies. Further studies should therefore examine the relationship between fWHR and formidability related characteristics in non-Caucasian samples.

In our study, both perceived aggressiveness and fighting ability were positively correlated with fighter's fWHR ($\tau = .161$, $P = .004$; $\tau = .157$, $P = .005$, respectively), body weight ($\tau = .189$, $P = .002$ and $\tau = .153$, $P = .01$, respectively), but not with fighter's height ($\tau = .08$, $P = .171$ and $\tau = .072$, $P = .215$, respectively). In comparison, Zilioli et al. in their study 2b reported a substantially stronger positive correlation ($r = .46$) between toughness ratings of the individuals faces and fWHR. This stronger effect might reflect their selection method as they employed only the faces extreme in respect to facial width and fighting experience (see below for more detailed discussion). The effect of fWHR on perception of aggressiveness and fighting ability was further examined by GLM with height and weight as covariates (covariates were added only if these characteristics were found to be significantly associated with the relevant measures). The GLM analysis revealed that perceived aggressiveness was significantly and independently correlated with both fWHR ($F_{(1, 143)} = 7.108$, $P = .009$, $\eta^2 = .047$) and weight ($F_{(1, 143)} = 6.335$, $P = .013$, $\eta^2 = .042$) while fighting ability was correlated with weight ($F_{(1, 143)} = 4.018$, $P = .047$, $\eta^2 = .027$) but not with fWHR ($F_{(1, 143)} = 2.649$, $P = .106$, $\eta^2 = .018$).

Zilioli et al. employed two pairs of composite images varying in the level of fWHR and fighting experience for perceptual tests. They used a forced-choice paradigm which is highly sensitive to detect subtle effects.

However, a disadvantage of this approach is that it uses only extreme forms from the overall variation and may therefore overestimate the actual effect. In contrast, we used a variety of non-manipulated faces which captures natural variability more thoroughly. However, such a test might be somewhat less sensitive to detect possible effects. Thus, the effect size for the correlation between the toughness ratings and fWHR, based on the forced-choice paradigm reported by Zilioli et al. in their study 2b, was substantially stronger ($r^2 = .34$) than the effect size for the correlation between perceived aggressiveness and fWHR ($\eta^2 = .047$) in our sample. We note that the values of r^2 and η^2 are equivalent and for comparison we computed r^2 from the Cohen's d reported by Zilioli et al. by employing an effect size conversion formula (Borenstein, Hedges, Higgins, & Rothstein, 2009).

The two approaches are complementary, and because the results converge it gives us more confidence that relative facial width acts as a cue to formidability. However, our results also indicated some influence of body weight in the perception of aggressiveness, independently of fWHR. In contrast, assessments of fighting ability were driven solely by body weight. This suggests that studies testing the potential association between morphological and formidability-associated characteristics should control for the effect of confounding morphological variables such as body height or weight (Sell, Cosmides, Tooby, Sznycer, von Rueden, & Gurven, 2009).

As noted above, both our study and that of Zilioli et al. find that fWHR, but not body height and weight, was positively correlated with performance, at least when competitors were relatively matched for weight. This is not to say that body weight is irrelevant (Sell et al., 2009), because MMA fights take place between fighters in specified weight categories. Further research is needed to test possible interactions between fWHR, body size and performance in other samples. Interestingly, we also found no significant association between performance and fighters' height, which is correlated with upper arm length and could thus provide advantage through longer reach and greater striking force (Carrier, 2011).

Our results showing that fWHR is associated with the perception of facial aggressiveness, and that perception of fighting ability is only correlated with body weight, might have interesting theoretical consequences. One may speculate that the assessment of potential opponents acts on multiple dimensions. The first step, a "fight or flight" decision, might depend predominantly on the overall size of the fighters, as suggested in our ratings of fighting ability. However, when the rivals are of comparable size, a further level of assessment takes place which is related to the perception of aggressiveness, affected by fWHR as well as other bodily and behavioral traits (Třebický, Havlíček, et al., 2013). Future studies might also test whether context affects the relative significance of attributed characteristics. For instance, fWHR may play a different role when assessing formidability of potential opponents and when judging suitability of potential allies.

In conclusion, our independent study, based on a similar sample of professional MMA fighters but with different methodology, shows parallel results to Zilioli et al.'s recent study. This mutually converging evidence supports the notion that relative facial width can act as a cue to formidability and may play an important role in intra-sexual selection, as well as suggesting that human perception may have been selected to be attentive to such cues.

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He developed the study concept, contributed to the study design, performed data collection and statistical analyses, contributed to the manuscript writing and subsequent revisions.

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PLOS ONE

RESEARCH ARTICLE

Focal Length Affects Depicted Shape and Perception of Facial Images

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Abstract

Static photographs are currently the most often employed stimuli in research on social perception. The method of photograph acquisition might affect the depicted subject's facial appearance and thus also the impression of such stimuli. An important factor influencing the resulting photograph is focal length, as different focal lengths produce various levels of image distortion. Here we tested whether different focal lengths (50, 85, 105 mm) affect depicted shape and perception of female and male faces. We collected three portrait photographs of 45 (22 females, 23 males) participants under standardized conditions and camera setting varying only in the focal length. Subsequently, the three photographs from each individual were shown on screen in a randomized order using a 3-alternative forced-choice paradigm. The images were judged for attractiveness, dominance, and femininity/masculinity by 369 raters (193 females, 176 males). Facial width-to-height ratio (fWHR) was measured from each photograph and overall facial shape was analysed employing geometric morphometric methods (GMM). Our results showed that photographs taken with 50 mm focal length were rated as significantly less feminine/masculine, attractive, and dominant compared to the images taken with longer focal lengths. Further, shorter focal lengths produced faces with smaller fWHR. Subsequent GMM revealed focal length significantly affected overall facial shape of the photographed subjects. Thus methodology of photograph acquisition, focal length in this case, can significantly affect results of studies using photographic stimuli perhaps due to different levels of perspective distortion that influence shapes and proportions of morphological traits.

Introduction

Human face research has received immense attention in fields ranging from social psychology to behavioural neuroscience and economics. Studies on perception of human faces involve various social contexts such as mate choice, cooperation, and parental care [1]. These studies have many practical implications; for instance, it has been shown that facial appearance affects electoral success, career progress, and child treatment [2]. Further, perceived characteristics are frequently associated with facial appearance [3]. For instance, it was recently found that facial width-to-height ratio (fWHR) is related to perceived aggressiveness [4–6], dominance [7,8],

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and trustworthiness [9]. Moreover, perceptions of certain psychological characteristics such as dominance [10], intelligence [11], and aggressiveness [12] can be, to some extent, predicted from overall facial morphology as analysed by geometric morphometrics.

The majority of studies on facial perception employ portrait photographs as stimuli. The facial images can be either obtained from free access sources [12–16] or taken for the purpose of the specific study [17–20]. There are several major factors affecting the resulting stimuli including exposure (e.g., under- or overexposure of images or inappropriate depth of field), optical aberrations of the lens used (e.g., radial and perspective distortions) [21,22], colour representations and lighting set up (e.g., number and type of lights and light modifier used) [23]. For instance, recent studies reported that variation in colours of facial photographs affects assessments of health, attractiveness, aggressiveness, and dominance [20,24]. Similarly, the position and posture of the target during image acquisition influences fWHR as measured from the photograph [25] or perceived body size [26]. Although several previous studies have reported carefully the standardized procedures for photograph acquisition (e.g., [27,28], employed methodology varies across individual studies. Further, detailed descriptions of photograph acquisition and standardization within a study is often missing which may impede assessment of validity and accurate replication of previous findings.

A key factor affecting the resulting photographs, which is frequently not reported in previous studies, is focal length. Focal length represents the distance between lens optics and camera sensor and provides variance in viewing angle and zoom (from wide angle fish eye lens to narrow telephoto lens) resulting in different degrees of image distortion. The most common image distortions are radial distortions, where straight lines are rendered as curved lines (i.e., barrel and pincushion distortion) [21], and perspective distortions, which are determined by the viewpoint from which the photograph is taken in relation to the target (i.e., nearby elements are rendered larger than distant ones) [22]. Due to these distortions, artefacts in size and shape representations in photographs can occur.

Here, we investigated the possible influence of focal length on perception of facial images through the assessment of selected interpersonal characteristics. Further, we tested the potential effect of focal length (50 mm, 85 mm, 105 mm) on depicted facial shape by measuring facial width-to-height ratio and employing geometric morphometrics.

Methods

Ethics statement

The study was approved by the Institutional Review Board of Charles University, Faculty of Science (approval number 2013/11). All participants gave written informed consent prior to taking part in the study.

Participants

Targets. In total we obtained facial images of 23 target men (mean age = 23.83, SD = 4.38) and 22 target women (mean age = 22.91, SD = 4.38). The targets were recruited via social networks (e.g., Facebook) and advertisement at a part-time jobs webpage (www.jobs.cz) and were reimbursed with 100 CZK (approximately €4).

Raters. We recruited 369 students (176 males) from Charles University in Prague to rate a set of photographs on one of the selected characteristics (i.e., attractiveness, dominance, and femininity/masculinity). Attractiveness of the male photographs was assessed by 25 male (mean age = 21.72, SD = 2.42) and 30 female raters (mean age = 21.2, SD = 1.34). Attractiveness of the female photos was assessed by 30 male (mean age = 23.5, SD = 3.45) and 34 female raters (mean age = 22.47, SD = 3.08). Dominance of the male photographs was assessed by 30 male (mean age = 23.33, SD = 2.85) and 34 female raters (mean age = 22.53, SD = 2.08). Dominance of the female photos was assessed by 27 male (mean age = 21.85, SD = 3.19) and 30 female raters (mean age = 21.53, SD = 1.96). Masculinity of the male photos was assessed by 30 male raters (mean age = 22.97, SD = 3.01) and 33 female raters (mean age = 22.61, SD = 2.38). Finally, femininity of the female photos was assessed by 34 male (mean age = 22.56, SD = 2.35) and 32 female raters (mean age = 22.31, SD = 2.07). Raters were not reimbursed for their participation.

Photograph acquisition

Three facial photographs of each target varying in focal length (50 mm, 85 mm, 105 mm) were taken using a DSLR camera (Nikon D90) equipped with APS-C sensor (crop factor 1.5×). Crop factor indicates how many times smaller the sensor is compared to the full frame (FF) sensor (the size of a full 35mm analogue film frame). Exposure was set to ISO 100, shutter speed 1/100s, aperture F8 and 2/3 of strobe power. We used ISO 100 to maintain the highest image quality and the lowest amount of digital noise, and shutter speed 1/100s to freeze potential motion while giving enough time for synchronizing the shutter curtains with the strobe lights [29,30]. Aperture F8 was selected to obtain the sharpest possible results with the lens used (see below) and give sufficient depth of field, i.e., the target's face from nose tip to ear ridges was sharp without needing to change settings while taking each photograph from different distances (different distances produce variance in the depth of field). The focusing point was set on the left eye in AF-S mode. White balance was set manually using a grey background to ensure constant colour representation. Photographs were processed into JPEG files in the camera with the Nikon STANDARD colour scheme.

All images were taken from a tripod (Velbon Sherpa) with the height set for each photograph depending on the height of the target, keeping the target´s face in middle of the frame. Similarly, the distance between the camera and the target was individually adjusted for each shot so that the head of the target filled the same portion of the frame (using grid lines in live view mode) [31,32].

To test the effect of the focal length we selected the closest FF equivalents of 50 mm, 85 mm, and 105 mm focal lengths. The 85 mm and 105 mm focal lengths are the most frequently used for portrait photography [30] and do not exceed ordinary space requirements between the target and the camera, concurrently giving the same field of view. Moreover, 50 mm lenses are frequently used as standard or prime lenses, as they are believed to be equivalent in focal length to the human eye and are adept at creating natural-looking images (e.g., [21]). However, to our knowledge, it appears that there is no solid evidence supporting this notion. We used a zoom type lens Nikon AF-S DX Zoom Nikkor 18–135 mm f/3.5–5.6 G IF-ED, which allowed us to set all three focal lengths without needing to switch lenses. To use the closest FF equivalent focal length on an APS-C sensor camera, one needs to multiply the focal length stated on the given lens barrel by the crop factor of a given camera (e.g., 1.5× for Nikon APS-C). The closest possible focal lengths were: 32 mm as 50 mm FF equiv. 48 mm; 56 mm as 85 mm FF equiv. 84 mm; and 70 mm as 105 mm FF equiv. 105 mm, respectively.

The targets were asked to stand 1.5 m from a plain grey background (Storm Gray, BD Company). Two studio strobes (Menik MD300, 300W, GN 54) with white reflective umbrellas (ø102 cm) as light modifiers were used to illuminate the targets. Lights were arranged in 40° angles on each side and were 1.85 m from the target, 1.8 m height and at 35° angle incline giving even illumination (Fig 1). Light conditions in the room were controlled by the use of non-translucent curtains and all ambient lights were switched off to remove any additional lighting variables.

The targets were instructed to remove any facial cosmetics and adornments (e.g., jewellery or glasses) and their hair was pulled back from the face and held by a headband. We instructed

Fig 1. Lighting setup diagram. Visualisation was generated by the online free service Sylights.com.

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them to keep a "neutral" facial expression, and look directly into the camera. In case of targets´ head not facing the camera directly, they were further instructed to adjust their head position accordingly (e.g., to move their chin up or down). All photographs were subsequently post-produced regarding the position of the face in the image (same position of the eyes in vertical and horizontal axis) using image manipulation software GIMP, ver. 2.8.

Rating sessions

Rating sessions were held in a lecture room equipped with 25 identical desktop computers and 22" DELL P2210 LCD screens (set on 50% level of contrast and brightness) under standardized light conditions. Qualtrics survey building engine (www.qualtrics.com) was used to present photographs in full screen mode. Photographs were presented in a randomized order using a forced-choice test, where raters were simultaneously shown all three photographs (taken with different focal lengths) of each target. The sides of the three photographs were fully randomized (i.e., different for each target for each rater). Photographs were judged for their attractiveness, dominance, and femininity/masculinity, characteristics frequently used in facial research (for recent reviews see [33,34]). We asked raters to order the triads of the photographs with respect to given characteristic (e.g., 1 –the least attractive, 2 –medium attractive, 3 –the most attractive). Each rater assessed photographs of all 45 targets.

Facial width-to-height ratio measurements

To investigate whether the ratio between selected facial features differs depending on the focal length used, bizygomatic width (facial width), and distance between the upper lip and brow (facial height) [4,5] was measured using tpsDig2 software, ver. 2.14 [35]. The fWHR was then calculated by dividing the facial width by the facial height. Measurements of fWHR were calculated by two independent experimenters (JF and VT). Inter-rater agreement for fWHR in images varying in focal length varied between Cronbach's α = 0.963–0.972, indicating excellent reliability [36].

Geometric morphometrics

Geometric morphometrics were applied to examine whether different focal lengths affect facial morphology in portrait photographs.

The 82 landmarks (including 42 semi-landmarks) were digitized by tpsDig2 software, ver. 2.14 [35]. Landmarks are represented as points that are anatomically (or geometrically) homologous in different individuals, while semi-landmarks serve to denote curves and outlines. The definitions of landmark and semi-landmark locations on human faces were based on previous work [11,12,37]. Semi-landmarks were slid by tpsRelw (ver. 1.49) software. All configurations of landmarks and semi-landmarks were superimposed by Generalized Procrustes Analysis (GPA), implemented in tpsRelw, ver. 1.53 [35]. This procedure standardized the size of the objects and optimized their rotation and translation so that the distances between corresponding landmarks were minimized. Subsequently, to visualize the effect of distortion produced by focal lengths, the original photographs of men and women were unwarped to consensual configuration of a particular focal length. The composite images were generated by tpsSuper 1.14 [38].

Statistical analysis

To assess differences between judgements given to the images taken with varying focal lengths, we calculated the proportion (from 0 to 1) of the images taken with given focal length selected as the most attractive/dominant/masculine-feminine. As the judgements were collected using a forced-choice paradigm, they are not independent and only data on the first choice (e.g., the most attractive) were analysed. The proportion for each judgement type was then compared to a random distribution (equal to 0.333) using a one-sample Wilcoxon Signed Rank Test.

Differences in mean proportions of the first choice between images taken with individual focal lengths were compared using Kruskal-Wallis H test. Subsequently, we used Mann-Whitney U tests as post-hoc tests to compare each pair of focal lengths (50 mm × 85 mm; 50 mm × 105 mm; 85 mm × 105 mm). Bonferroni adjustment was used to correct for the effect of multiple comparisons in the Mann-Whitney U tests, with a threshold for significance of 0.017 (i.e., 0.05/3) [39,40]. Effect sizes are reported in the form of Cohen's *d*.

A repeated measures ANOVA was employed to investigate differences in fWHR between images taken with different focal lengths. Overall effect size is reported in form of partial eta squared (η^2), effect sizes of subsequent Bonferroni post-hoc tests are again reported in the form of Cohen's *d*.

To test for shape differences that resulted from using various focal lengths, we performed permutational multivariate analysis of variance using distance matrices with 9,999 permutations (the Adonis function in the Vegan package in R [41]); the Euclidean method was used as a distance measure and the parameter 'strata' was set to constraint permutation within the groups of landmark configuration of the same photographed subject. We ran a multiple multivariate regression with principal component scores as the response variable and with focal length as an explanatory variable. Effect sizes are reported as R2.

All analyses were performed using IBM SPSS ver. 22 and R software for statistical computing [42].

Results

Perceived characteristics

To test for the potentially confounding effect of rater sex on the assessed characteristics, we performed an independent sample t-test. No significant differences between men and women were found on any of the rated characteristics for female or male faces: female attractiveness $t_{(190)} = 0.023$, $p = 0.982$; female dominance $t_{(169)} = 0.365$, $p = 0.715$; female femininity $t_{(196)} < 0.001$, $p = 1$; male attractiveness $t_{(163)} = 0.395$, $p = 0.694$; male dominance $t_{(187)} = 0.039$, $p = 0.969$; male masculinity $t_{(187)} < 0.001$, $p = 1$.

Subsequently, we compared the proportion of the first choices for each focal length against random distribution for each type of judgement, for results see Table 1. The differences in mean proportion of the first choices (for each characteristic) between focal lengths were analysed using Mann-Whitney tests (Table 2). We found significant effect of focal length on judgements of all characteristics for both target sexes. Figs 2, 3 and 4 represent the proportion of the first choices for each focal length with respect to their attractiveness, dominance, and femininity/masculinity, respectively. More specifically, the mean proportion of the first choices given to images taken with 50 mm focal length was the lowest for all assessed characteristics and significantly differed from both 85 mm and 105 mm focal lengths. The mean proportion of the first choices given to images taken with 105 mm focal length was the highest; however, the mean proportion of the first choices given to images taken with 105 mm focal length did not significantly differ from those given to images taken with 85 mm focal length for female attractiveness, female dominance, and male attractiveness ratings.

Facial width-to-height ratio

Repeated measure ANOVA showed that fWHR in female targets significantly varied across the individual focal lengths ($F_{(2,42)} = 120.511$, $p < 0.001$, $\eta^2 = 0.852$). Subsequent Bonferroni post-hoc tests revealed significant differences between 50 mm (mean = 1.716, SD = 0.023) and 85 mm (mean = 1.797, SD = 0.024) ($p < 0.001$, $d = 3.446$), 50 mm and 105 mm (mean = 1.1797, SD = 0.022) ($p < 0.001$, $d = 3.599$), but not between 85 mm and 105 mm ($p = 1$, $d = 0$).

In a similar fashion, fWHR in males also significantly varied across the individual focal lengths ($F_{(2,44)} = 176.419$, $p < 0.001$, $\eta^2 = 0.889$). Bonferroni post-hoc tests revealed significant differences between 50 mm (mean = 1.695, SD = 0.024) and 85 mm (mean = 1.787, SD = 0.026) ($p < 0.001$, $d = 3.677$), 50 mm and 105 mm (mean = 1.803, SD = 0.025) ($p < 0.001$, $d = 4.407$), and 85 mm and 105 mm ($p = 0.016$, $d = 0.627$).

Table 1. Comparison of the proportion of first choices for each focal length against random distribution (i.e., 0.333).

		One-Sample Wilcoxon Signed Rank Test	
	Focal length (mm)	Z	p
Female attractiveness	50	207	< 0.001
	85	1 684	< 0.001
	105	1 567	< 0.001
Female dominance	50	275	< 0.001
	85	751	0.548
	105	1 507	< 0.001
Female femininity	50	392	< 0.001
	85	1 768	< 0.001
	105	1 519	< 0.008
Male attractiveness	50	3	< 0.001
	85	1 351	< 0.001
	105	1 424	< 0.001
Male dominance	50	76	< 0.001
	85	1 130	0.403
	105	1 956	< 0.001
Male masculinity	50	173	< 0.001
	85	1 057	0.737
	105	1 942	< 0.001

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Table 2. The differences in mean proportion of first choices for attractiveness, dominance and femininity/masculinity between focal lengths.

	Focal length (mm)	M	SD	Kruskal-Wallis H Test*		Mann-Whitney *U* test								
						50×85			50×105			85×105		
				χ^2	p	*U*	p	*d*	*U*	p	*d*	*U*	p	*d*
Female attractiveness	50	0.1922	0.1419	69.114	<0.001	517.5	<0.001	1.696	582	<0.001	1.578	1874.5	0.405	0.148
	85	0.4099	0.1149											
	105	0.3969	0.1262											
Female dominance	50	0.2288	0.1429	58.25	<0.001	948	<0.001	0.775	413	<0.001	1.689	724	<0.001	1.095
	85	0.3261	0.1242											
	105	0.4577	0.1338											
Female femininity	50	0.2253	0.1607	45.158	<0.001	816	<0.001	1.288	1002.5	<0.001	1.056	2100.5	0.723	0.062
	85	0.391	0.0994											
	105	0.3835	0.1521											
Male attractiveness	50	0.1345	0.1396	100.737	<0.001	74.5	<0.001	2.912	78	<0.001	2.885	1208.5	0.067	0.354
	85	0.3505	0.1131											
	105	0.5106	0.1392											
Male dominance	50	0.1108	0.1766	107.739	<0.001	516	<0.001	1.669	154	<0.001	2.647	771.5	<0.001	1.248
	85	0.3359	0.0945											
	105	0.5531	0.145											
Male masculinity	50	0.0806	0.0821	116.152	<0.001	438	<0.001	1.836	227.5	<0.001	2.400	444.5	<0.001	1.814
	85	0.43	0.1176											
	105	0.4703	0.1301											

* df = 2 for all comparisons

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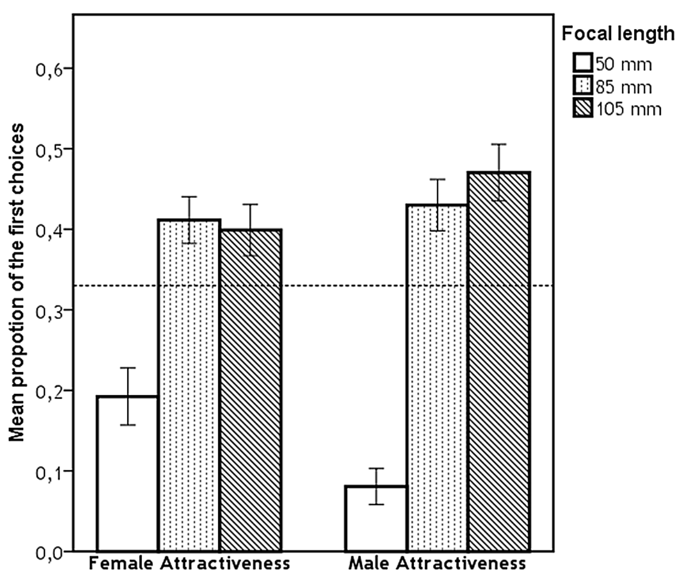

Fig 2. Proportion of first choices for each focal length with respect to their attractiveness. Dashed line represents the proportion of ratings expected by chance (i.e., 0.333), error bars represent 95% CI.

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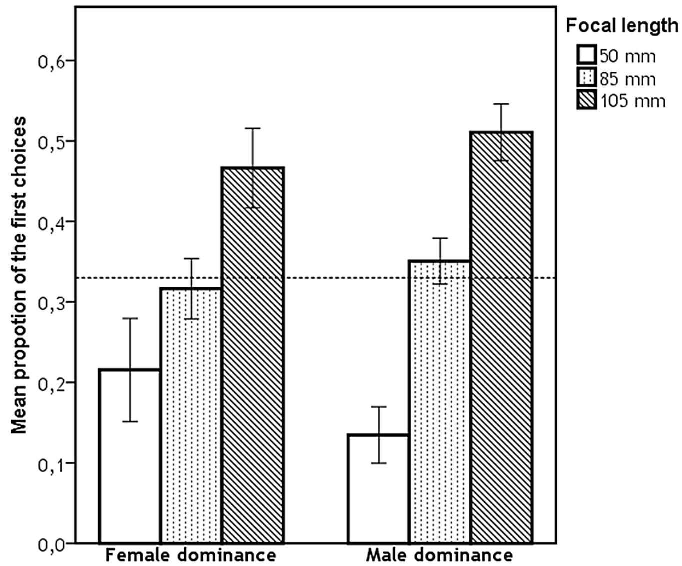

Fig 3. Proportion of first choices for each focal length with respect to their dominance. Dashed line represents the proportion of ratings expected by chance (i.e., 0.333), error bars represent 95% CI.

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Geometric morphometrics

Using permutational multivariate ANOVA we found statistically significant shape differences in female targets between the faces of the same individuals taken at different focal lengths ($F_{(1,64)} = 2.539$, $p = 0.004$, $R^2 = 0.038$). The differences between focal length pairs were significant in all three combinations: 50 mm × 85 mm ($F_{(1,42)} = 1.814$, $p < 0.001$, $R^2 = 0.041$); 50 mm × 105 mm ($F_{(1,42)} = 2.463$, $p < 0.001$, $R^2 = 0.055$); 85 mm × 105 mm ($F_{(1,42)} = 0.41$, $p < 0.001$, $R^2 = 0.01$).

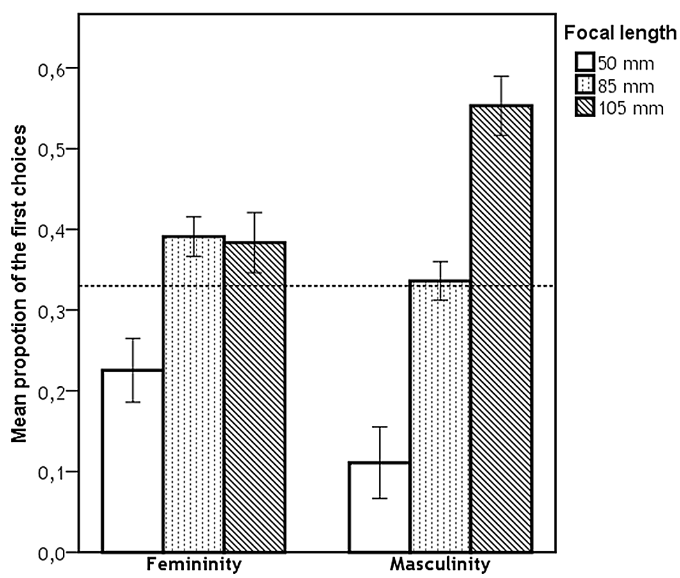

Fig 4. Proportion of first choices for each focal length with respect to their femininity/masculinity. Dashed line represents the proportion of ratings expected by chance (i.e., 0.333), error bars represent 95% CI.

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A similar pattern was found for the male targets ($F_{(1,66)} = 2.765$, $p < 0.001$, $R^2 = 0.04$). Subsequent comparison of focal length pairs again showed significant differences for all three combinations: 50 mm × 85 mm ($F_{(1,44)} = 1.739$, $p < 0.001$, $R^2 = 0.038$); 50 mm × 105 mm ($F_{(1,44)} = 2.721$, $p < 0.001$, $R^2 = 0.058$); 85 mm × 105 mm ($F_{(1,44)} = 0.23$, $p = 0.007$, $R^2 = 0.005$) (Fig 5).

Discussion

The main aim of our study was to test for possible effects of variation in focal length on perceptual judgements and shape distortions of male and female facial photographs. Photographs were taken of the same individual at focal lengths of 50 mm, 85 mm, and 105 mm equivalents. We found that facial photographs taken with 105 mm focal length equivalent were judged by both male and female raters as the most attractive, dominant, and masculine/feminine, irrespective of the target's sex. In contrast, photographs of both males and females taken with 50 mm focal length equivalent were perceived as the least attractive, dominant, and masculine/feminine. The differences in perception were further supported by our shape analysis. We found that fWHR, as measured from the photographs, significantly varied across focal lengths in both male and female faces; fWHR taken at 50 mm was significantly smaller than the two greater focal lengths (85 mm and 105 mm). Results of the geometric morphometrics analyses similarly showed significant differences in overall facial shape between the focal lengths used in both sexes. In both male and female faces the following pattern was observed for images taken at the 50 mm focal length as compared to the longer focal lengths: overall rounded face, larger and wider set eyes, wider set eyebrows, rounded, longer and broader nose, taller forehead, rounded chin and disappearing ears obscured with cheeks (Fig 3).

The changes in facial dimensions, shape, and facial perception found in our study appear to be a consequence of variation in perspective distortion produced by the different focal lengths. In objects captured with shorter focal lengths, perspective distortion produces an appearance expanded in its depth, which makes faces look rounded and facial traits closer to camera are perceived seemingly bigger (e.g., nose) while more distant traits look smaller (e.g., ears). The faces captured with the shortest focal length appear overall to be rounded due to the vertically oblong shape of the human head, which produces the most noticeable radial distortion at the sides of head. In contrast, objects captured with longer focal lengths look compressed in depth, which makes faces look flatter [32]. The resulting effect shows smaller facial width-to-height ratio for faces captured with shorter focal lengths [19].

For several characteristics (attractiveness in both female and male photographs and femininity in female photographs) the differences between judgements of the facial photographs taken with 85 mm and 105 mm were not significant. This effect might be a result of a smaller range between particular focal lengths and consequently less pronounced perspective distortion. Our analysis of facial shape supports this interpretation, as the observed effect sizes were rather small. Similarly, fWHR measurements of female faces did not significantly differ between photographs taken with 85 mm and 105 mm. Further, male faces have, on average, substantially more distinctive facial traits compared to females (e.g., more pronounced zygomatic arches, eye ridges, broader chin), hence their photographs might be more affected by distortions. Alternatively, the perception of some characteristics might be of greater importance in social interactions than others. Therefore, smaller differences in facial shape might not be reflected in attributed characteristics.

Here we employed a forced-choice paradigm, i.e., raters were simultaneously shown all three photographs of each target and they were asked to order the triads of photographs with respect to a given characteristic (e.g., attractiveness). The advantage of this approach is its higher sensitivity allowing for detection of subtle effects, on the other hand this setting may

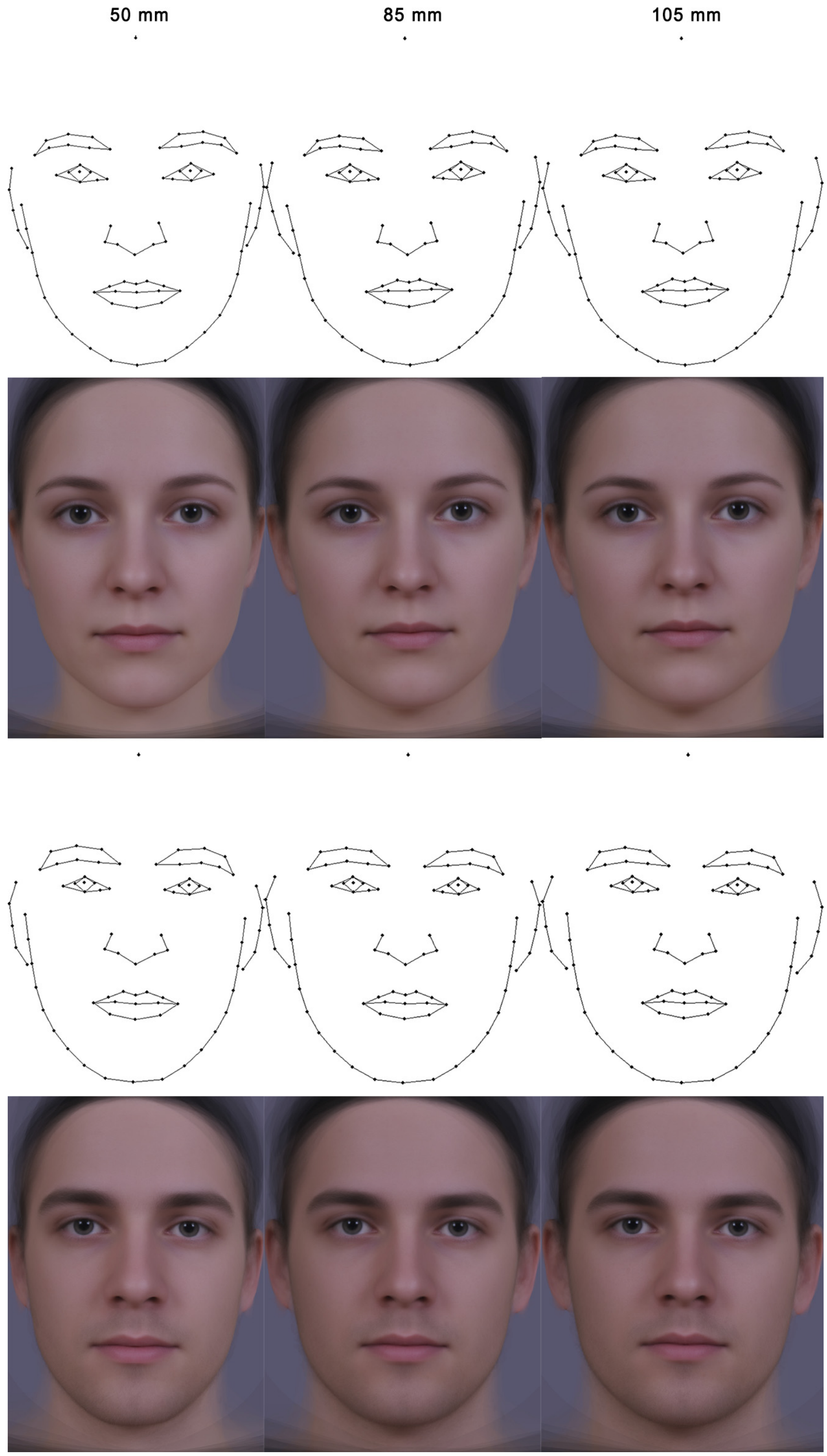

Fig 5. Consensual configurations and composites of female and male images for the 50 mm, 85 mm and 105 mm focal lengths.

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overestimate the actual effect. Another rating paradigm which is frequently employed in the face research is rating of each targets´ face on Likert scales one by one. However, this approach is somewhat less sensitive in detecting subtle effects. Future studies should therefore test whether a similar pattern as observed in the current study can be generalized to the other rating paradigm.

Apart from the focal length, several other important factors may affect the resulting portrait photographs; including target to camera distance [19,28,31]. As 3D objects (e.g., faces) are captured in form of 2D images on a plain (e.g., camera sensor) via perspective projection, the resulting image changes with a distance from the centre of projection, even when equated for its size [19,31]. The target to camera distance could be set by determining a field of view (or angle of view), which is a function of sensor size, focal length, and target to camera distance. Although there is no general consensus on ideal target to camera distance [28], the results of Bryan et al. [19] show considerable impact of this variable on perceived characteristics. They found that faces captured from a shorter distance (45 cm) were rated as less attractive and less trustworthy as compared to the images taken from a longer distance (135 cm). A possible explanation lays in interpersonal distance as a variable influencing social behaviour [43]; Bryan et al. [19] hypothesized that the distance-dependent perspective projection of a face might serve as a cue for social judgments and faces photographed from within personal space were judged more negatively on certain characteristics. The same principle applies to the distance between the rater and the assessed image. Positioning the rater at a distance from the image that equals the target to camera distance should give an accurate impression of the scene. However, raters are usually not positioned in the centre of projection when viewing the images which may in turn bias their impression [31]. Moreover, it appears that people tend to prefer shorter viewing distances for images captured with longer focal length and longer distances for the images captured with shorter focal lengths [31].

Previous research has further shown that colour representation [24,44,45] and head position [25] influence the resulting image. Specifically, changes in face colour affect perceived health and attractiveness with higher judgements of redder faces [24,44–46] (but see Burriss et al. [23]), while downward head tilt is perceived as more intimidating through the manipulation of fWHR [25]. However, downward tilt also increases attractiveness of female faces in mate choice context [47,48].

In our study we found that certain camera settings, in this case focal length, can considerably influence perception of resulting photographs. Distortion of the facial shape may increase the chance of both type I (falsely positive results) and/or type II (falsely negative results, e.g., floor or ceiling effect) errors. For instance, false positive results might occur by taking one set of the photographs with a certain focal length and another set with a different focal length, therefore introducing systematic error. This may occur in studies using images downloaded from the internet, where the image acquisition settings may vary in systematic fashion. For instance, studies measuring fWHR from downloaded images may reflect systematic differences in image acquisition rather than actual differences in facial proportions (e.g., successful athletes in combat sports might be depicted as tougher by adjusting camera settings compared to their less successful counterparts). In contrast, using a rather wide lens may skew the ratings of some positively perceived characteristics such as trustworthiness or attractiveness to the lower end of the scale, which might obscure the chances of finding an actual effect.

Our results thus indicate that the focal length should be adjusted according to aims of a particular study. Based on our findings and previous work it seems that longer focal lengths (e.g., 85 mm full frame equivalent) produce more positively judged images [30,49] which might be an advantageous approach in attractiveness studies as it diminishes chances of the floor effect. On the other hand, longer focal lengths entail higher demands on target to camera distance to obtain a suitable field of view and accordingly increase space requirements. Selection of an adequate focal length is thus frequently a trade-off between the lens and space available for image acquisition.

In sum, our study provides additional evidence that the methodology of photograph acquisition can influence the results of perceptual studies. We showed that facial photographs taken with various focal lengths differ in their proportions as demonstrated by the fWHR, overall facial shape as analysed by the GMM and perceived characteristics judged by independent set of raters. These results highlight the importance of adopting a standardized methodology for photograph acquisition, at least within each particular study. This is often not possible in the case of photographs downloaded from online sources. Interestingly, although this approach is methodologically questionable, it is an increasingly popular method within various branches of psychological science due to its easy availability. Further, we urge researchers capturing images in the lab to report details of image acquisition parameters and settings such as camera brand and type, sensor size (crop factor), lens and focal length, exposure parameters (F-stop, shutter speed and ISO), light source(s), modifier(s), and scene setup (e.g., distance from photographed target). Providing such details would enable a more rigorous analysis of the discrepancies between individual studies–a standard that is currently not yet achieved even in some prestigious academic journals.

Supporting Information

S1 Dataset. Data from ratings and fWHR measurements (.XLSX). Data on GMM are available from the authors.
(XLSX)

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Author Contributions

Conceived and designed the experiments: VT JF JH. Performed the experiments: VT JF. Analyzed the data: VT JF KK. Contributed reagents/materials/analysis tools: VT JF KK. Wrote the paper: VT JF KK JH.

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