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EVOLUTION AND SOURCES OF INDIVIDUAL VARIATION IN MATE PREFERENCES IN HUMANS

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1. INTRODUCTION TO SEXUAL SELECTION AND MATE PREFERENCES

“Millions of years ago, we evolved three basic drives: the sex drive, romantic love and attachment to a long-term partner. These circuits are deeply embedded in the human brain. They’re going to survive as long as our species survives.” Helen Fisher

Most likely ever since humans first engaged in creating art, the joy of infatuation, the sadness of unreciprocated love and the rage of jealousy have served as ceaseless springs of inspiration. As early as 40 000 years ago, the first representation of women’s bodies can be found in depictions of Venus in the form of little figurines. Great philosophers such as Sappho, Platoon and Kant conducted endless enquiries on the definition of beauty (Buggio et al. 2012). Ideal beauty has been *pursued* by artists in all described eras, from Boticelli’s perfectly symmetrical face of Venus, to Leonardo da Vinci’s unblemished facial proportions of Vitruvian Man (Dayan 2011). Countless poems and songs explain why love is the best (or the worst) thing that could ever happen to a human being (references to love may be found in any list of top music hits or on almost any randomly chosen music album). Human sexuality appears in the media, in songs and is a topic in everyday life discussions. Annually, billions of euros are spent on cosmetics, hair and nail care, diet products and cosmetic surgery (Sullivan 2001). Attractiveness is of major concern to both men and women (Little et al. 2011). It has been thoroughly investigated scientifically and discussed, and yet we still are only just beginning to understand the rules and bases by which people’s lives are made happy, sad, complicated or worth living. Why do we want to be with certain people and what are the biological – inherited from our ancestors - bases of those nerve-wracking processes?

Over millions of years, the behaviour of all living animals has been evolving. The genes that are passed from one generation to another mutate, drift and change their frequencies and combinations, what results in phenotype change. Two of the forces behind the process of evolution are natural and sexual selection (Darwin 1871). By these means, subsequent generations of organisms acquire traits that can enhance their survival and reproduction – such traits are defined as adaptations (Dobzhansky 1956). **Natural selection** is a process by which organisms that vary in multiple ways, vary also in their potential for survival based on the heritable characteristics enhancing their life performance (adaptations based on survival and fitness enhancement). Included in this process is **sexual selection**, whereby an individual who is most preferred by the other sex, or gains most access to the other sex, can have the highest access to fertilization, can pass on the greatest number of his genes and via this enhance his fitness (adaptations based on the mating success, Darwin 1871, West-Eberhard 1983,

but see Safran et al. 2013 for a fuller distinction between natural and sexual selection). The existing state of a certain feature that can be observed in nature is an outcome of natural and sexual selection, that can work in synergy (Safran et al. 2013), but whose mechanisms can *also* have antagonistic results (Johnston et al. 2013), and which are two of the evolutionary processes shaping the organisms (together with genetic drift, mutations and gene flow).

Aside from the obviously adaptive traits (feathers of birds, sharp canines of meat eating animals etc.), observers are often puzzled by the lack of apparent survival utility of certain features evident in the natural world (like a peacock's tail or stag's horns). Charles Darwin stated, that it is obvious such features could not have evolved merely due to the life enhancing advantages they bring to the owner (Darwin 1859), such as making hunters better in sneaking up on prey or making prey less visible to the predator. In the majority of species, males compete with each other for access to females (females are the choosy sex). The male that is the most successful in the all-male competition wins the opportunity to pass on his genes more frequently than weaker (or worse equipped) males. Hence, even without the direct effect of judging females (intersexual preference), features can arise based purely on their utility in the rivalry with same-sex competitors. Such evolutionary force is referred to as intrasexual competition and is one of two underlying forces of sexual selection. On the other hand, females of all species demonstrate profound preferences for certain features in males, features which can lack any function other than serving to impress the female. A peacock's tail is certainly not cryptic, nor does it enhance mobility or foraging skills. It evolved because throughout generations peacock hens preferred richer ornamentation in males. Males who were adorned with such had the possibility to leave more offspring behind than males with more cryptic plumage. It evolved through intersexual selection (preferential mate choice) – the second base force of sexual selection (Safran et al. 2013).

“Sexual selection depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring” Darwin 1859, chapter 4, page 88.

Since the mid-nineteenth century and following on from Charles Darwin's work, there have been a myriad of studies on sexual behavior in animals (humans included). Thanks to dedicated researchers and the development of greater and improved tools leading up to the present time, we have gained better insight into what is the innate, biological or evolutionary basis of animals' mating behaviors. To start with, one of the visible, salient issues is the fact that females and males differ. Due to differences in females' and males' physiology, both intra- and intersexual mechanisms will affect their features with varying force. All individuals strive to enhance the number of their offspring and their survival, however, for males and females it can be achieved in different ways. Robert Trivers in 1972 formulated the **Parental Investment Theory**,

defining the conditions under which sexual selection can evolve. As in the majority of species, females are the parent whose minimum investment in offspring is higher, and so it follows that they should be the choosier partner (Trivers 1972). What's more, only by multiple matings can males substantially increase the number of their offspring. For females, multiple matings can bring some advantages, however, this strategy will never have such a strong correlation with offspring number as for males (Larson et al. 2013). This basic difference in the minimum investment is the source of a multitude of later physiological and morphological differences, and contributes to the evolved adaptations that guide females in how to be choosy, and males how to impress females or how to deceive them.

“The course of true love never did run smooth”

William Shakespeare, A Midsummer Night's Dream – Act 1, Scene 2

Due to the sexual reproduction mechanism that *varies* between males and females **sexual dimorphism** arises, and emerges in accordance with the mating strategies manifested by different species (Dunn, Whittingham & Pitcher 2001). In cases of more long-term bonding, or monogamous species, where competition between sexual rivals is weaker, males will not differ greatly from females. In species, where the number of sexual partners vary greatly between individuals (their probability to sire offspring differs profoundly), competition will be much stronger, and in what follows males will need to be equipped with tools for that competition (Fraye & Wolpoff 1985). Humans are not easily classified into one group or the other –there is moderate sexual dimorphism and the debate on which is the predominant sexual strategy in humans is on-going (Bailey et al. 1994). (In support of a more monogamous point of view see Stewart-Williams & Thomas 2013). Sexual preferences also influence the intensity of sexual dimorphism in a species. Preferential mate choice, even in the absence of explicit sexual rivalry, can lead over generations to the emergence of exaggerated secondary sexual characteristics (Barber 1995). The plumage of birds-of-paradise is one of the most prominent examples of such exponential growth of sexual ornaments over the course of evolution (Irestedt et al. 2009). Thereupon, there are two main forces that drive a trait to be more sexually dimorphic: sexual rivalry and preferential mate choice.

Sexual dimorphism is visible in human faces (e.g. Bribiescas, Ellison & Gray 2012, Prokop & Hromáda 2013, Sagarin et al. 2012) - men having a wider jaw and cheekbones; a stronger brow and chin; less full lips; and less fat in their cheeks and lips than women (Thornhill & Grammer 1999). The proximate cause of women's femininity and men's masculinity is a result of exposure to hormones produced by the ovaries (among others estrogen) and by the testicles (testosterone) respectively (Bruckert et al 2006, Dabbs & Mallinger 1999, Penton-Voak & Chen 2004, Puts 2005). During pubertal development, craniofacial features develop differently in boys and girls, leading to pronounced sex differences in the size and shape of bodily and facial

features (Farkas 1987). Size and shape variance persists throughout an individual's life and cannot be explained merely by the body size difference between women and men (Bastir, Godoy & Rosas 2011). Women's estrogen-dependent body features correlate positively with reproductive fitness and health (Jasienska et al. 2004). As estrogen also affects facial growth (Enlow 1982), increased facial sexual dimorphism in women should lead to their higher perceived attractiveness, with facial dimorphism presenting cues to heritable fitness benefits (and hence causes attractiveness, e.g. Thornhill & Gangestad 1999). Furthermore, femininity is an honest signal of higher long-term reproductive value (Confer, Perilloux & Buss 2010) and women with higher levels of estrogen manifest a desire for a higher number of offspring than women with lower estrogen levels (Law Smith et al. 2012). Indeed, it has been observed that on average, men tend to prefer feminine women's faces (Perrett et al. 1998).

Masculinity in men is correlated with levels of testosterone. As the **immunocompetence handicap hypothesis** states, only men with good health or with strong immune defence or both can afford to develop testosterone based pronounced secondary sexual characteristics (for a review see Møller & Swaddle 1997). Positive relationships between testosterone, facial attractiveness and immune function (antibody response to a hepatitis B vaccine) in human males were strongly correlated (Rantala et al. 2012). What's more, testosterone is positively correlated with men's social status and dominance (Booth et al. 2006, Mazur & Booth 1998). Another hypothesis that could explain females' preference for exaggerated secondary sexual features in males is the sexy sons hypothesis (Weatherhead & Robertson 1979) or preference for "good genes" (Anderson 1994). The **good genes hypothesis** predicts that females will be attracted by honest signals of condition (Rowe & Hule 1996, Tomkins et al. 2004), such as exaggerated sexual dimorphism which would in turn increase offspring survival, viability and fecundity (Møller and Alatalo 1999, Kirkpatrick and Ryan 1991). The **sexy son hypothesis** predicts that females benefit from mating with polygynous males that will sire sons who inherit genes for the highest reproductive success (Gwinner & Schwabl 2005). Other features of a potential mate, such as position within the social hierarchy, care-giving, and other direct benefits (Price, Schluter & Hackman 1993) are of lesser importance (for theoretical criticism see Huk & Winkel 2007). Even if attractive males sire sons that will suffer from a higher than average mortality, being more attractive (Brooks 2000) means their net mating success can still be positive, and hence beneficial to females (for a discussion see Kokko 2001). Interestingly, a recent study has found that more masculine looking men have more masculine, but not more sexually attractive, sons (Cornwell & Perrett 2008).

As physical appearance provides information about health (Boothroyd et al. 2013), women's preference for masculinity in men may reflect a preference for a healthy mate (Rantala et al. 2013, Rhodes et al. 2003, Rhodes et al. 2007). On the other hand, preferring high masculinity in a potential mate also carries costs (Gangestad 1993). Masculine men provide less parental care (Boothroyd et al. 2008, Gray et al. 2002, Muller et al. 2009, Waynforth & Dunbar 1995), are more likely to cheat and get

divorced (Booth & Dabbs 1993) and exhibit more aggressive behaviours (Booth et al. 2006) than their more feminine peers. Moreover they are perceived as less caring and honest than men with more feminine traits (Perrett et al. 1998). Consequently women's preference for masculinity is a result of a trade-off between good genes and parental investment (or dominance/health and care-taking/resources), that will vary depending on the context and conditions (like the importance of developmental health versus parental care, Pisanski & Feinberg 2013).

“Cosmetics is a boon to every woman, but a girl's best beauty aid is still a near-sighted man” -Yoko Ono

Human mate preferences are no exception to the rules of sexual selection and all of the above described mechanisms (e.g. Pisanski & Feinberg 2013). The actual state of what we can observe in the contemporary mating arena is a result of, among others, millions of years of successful mating between our ancestors that has led us to prefer what we prefer now and to adjust our choices according to circumstances (for examples of genetic bases of variation in sexual preferences see Ackermann & Cheverud 2004). Sexual attraction is not entirely conscious process of mind, and can be interpreted as rather physiological-like reaction of our hard-wired bodies. There is a vast body of studies investigating what humans perceive as **attractive** or unattractive (for a review see for example Gallup & Frederick 2010, Pisanski & Feinberg 2013, Swami & Furnham 2008). Mate preferences are heavily influenced by physiological traits that putative partners possess (Barber 1995, Rhodes, Simmons & Peters 2005). Physical traits can give information on the genetic quality of an individual, or on his/her potential offspring's genetic quality (Pisanski & Feinberg 2013) and mate-relevant economic and social factors (for example, income or hunting abilities (Escasa, Gray & Patton 2010)). It has been shown that physical appearance influences people's choices more than any other factor (such as humour, wealth or intelligence) and this influence is stronger for men than for women (Eastwick & Finkel 2008, Luo & Zang 2009, Sprecher 1989). Certain physical features can be considered attractive among all human societies – there are standards of beauty that are present in all human populations world-wide (Buss 1989, Langlois et al. 2000, Shackelford, Schmitt & Buss 2005). A number of studies have shown that attractive people enjoy advantages that unattractive people cannot attain (Beall 2007, Berscheid & Walster, 1974, Bull & Rumsey, 1988, Eagly et al. 1991) and they may get better grades at school and earn higher salaries too (Synnott 2006). Even though such advantages mainly apply during the first formation of impressions, they can also extend into more profound interactions (Frieze, Olson, & Russell, 1991). Infants as early as in their third month of life attend more to faces that are judged to be more attractive (Ramsey et al. 2004, Samuels & Ewy 1985) and they are thought to be congenitally equipped with information and tools for face recognition and prefer face-like patterns (Morton, Johnson & Maurer 1990). Children judge faces that are more average (5-years-old judges) and symmetrical (9-years-old judges) as more attractive (Vingilis-Jaremko & Maurer 2013).

Furthermore, study of preferences of congenitally blind men showed that even without prior exposure to any visual stimulus, men prefer more feminine body shapes (lower waist to hip ratio) proving the innate bases of general sexual choices (Karremans, Frankenhuys & Arons, 2010). A population has never been found that rates men or postmenopausal women who are strongly asymmetric as more attractive than young, symmetric individuals. Many features of the face (symmetry, averageness, femininity, skin condition and fairness, fat distribution) are an honest cue to biological quality and are strictly connected with the attractiveness of an individual (Coetzee, Perrett & Steven 2009, Fink & Penton-Voak 2002, Grammer & Thornhill 2001).

Symmetry is considered to be attractive (Rhodes, Sumich & Byat 1999). Since random deviations from symmetry reflect perturbations in physiological development during the life-span and signal poor health, (Moller & Swaddle 1997, Polak 2003, Shackelford & Larsen, 1997, Thornhill and Gangestad, 1993, Thornhill and Gangestad, 1999) asymmetric individuals will be less desired than symmetric ones (Perrett et al. 1998) and average ones (Langlois & Roggman 1990). Indeed, Thornhill and Gangestad (1993, 1999) suggested that preference for averageness of the face might have evolved because it “denotes genetic heterozygosity, which could signal an outbred mate or provide genetic diversity in defence against parasites”. Averageness is understood as the magnitude of resemblance to the majority of other individuals within one’s group (Little et al. 2011) and is considered to be one of the major components of facial beauty (Honn & Goz 2007, Jefferson 1996). Hence, as average faces are considered to be attractive and symmetrical faces obviously tend to be closer to the average than asymmetrical ones, even when *omitting* the genetic bases and indications of health, symmetry contributes to the attractiveness (Baudouin and Tiberghien 2004, but see also Cellerino 2003). Attractiveness criteria are, therefore, expected to be wide-spread across cultures (Langlois et al. 2000) and even across different species (Tybur & Gangestad 2011). A number of studies showed a strong inter-national, inter-racial agreement on what is beautiful in general matters like symmetry and sexual dimorphism (Bernstein, Cunningham et al. 1995, Iwawaki, Eysneck & Gotz 1979, Langlois et al. 2000, Lin & McClellan 1982). However, the majority of those studies have been conducted in populations strongly influenced by Western culture (Sorokowski, Koscinski & Sorokowska 2013) and hence, they could have assimilated Western, unified standards through social learning (Little et al. 2011). Individuals sharing a social group (restricted for example by nationality or geographical location) can acquire common patterns of preferences towards a variety of stimuli, depending on the life condition. What’s more, as averageness is one of the components of beauty (Symons 1979, Thornhill & Gangestad 1993, 1999) and it is based on life-time exposure to our social group con-specifics (Leopold et al. 2001), we would expect that members of the same group will share a sense of averageness (and following from this, attractiveness, Laeng, Vermeer & Sulutvedt 2013). Nevertheless, it has been found that when it comes to features more complex than age, averageness and symmetry, cultures

vary considerably in the characteristics they consider to be attractive (Little, Apicella & Marlowe 2007, Penton-Voak, Jacobson & Trivers 2004).

Varying environments can have variable influence on mate preferences or fitness related traits (Andersson 1994), which can be locally adaptive and context-specific (Pisanski & Feinberg 2013). Depending on multiple factors, perceptions of which particular features, or which intensity of a certain characteristic is attractive (and most preferred or most frequently chosen) varies greatly (e.g. Buss 1989, DeBruine 2010a, Scott et al. 2010, Sorokowski, Koscinski & Sorokowska 2013). Some of the factors that influence the inter-individual variation in mating preferences are: mating context, self-perceived mating value, contemporary fertility, relationship status, life experience or health conditions and resource availability (Cohen and Belsky 2008). In addition, increased perception of attractiveness can be caused by repeated visual exposure to a certain characteristic (Peskin & Newell 2004, Winkler & Rhodes 2005) or can be a result of varied cultural trajectories and norms that differ regionally (Reischer and Koo 2004). Because of the multitude of factors influencing this complex mate game it is hard to classify them in one certain way.

An important *internal* cue being correlated strongly with sexual preferences and behavior are hormones. Recent studies have found that in both sexes preferences for facial traits in the other sex change with **hormone levels** (Jones et al. 2005, Roney & Simmons 2008; Welling et al. 2007; Welling et al. 2008). Men with higher levels of testosterone not only attend more to sexual stimuli (Rupp & Wallen 2007), but also they prefer more feminine women (Welling et al. 2008). In comparison, women's fluctuating preferences that depend on the menstrual cycle phase and changing levels of hormones are a far more investigated topic. Elevated progesterone during an infertile phase and pregnancy (Jones et al. 2005) is thought to lower preferences for masculinity. As masculinity in men is associated with less interest in long-term mating (Boothroyd, Lawson & Burt 2009), a drop in women's preference for masculinity maximises the chances of acquiring a stable, investing mate (Jones et al. 2005). Women in their fertile phase were found to give the highest general attractiveness rating to all men (Rantala et al. 2005), prefer more masculine manipulated faces (Frost 1994, Johnston et al. 2001, Penton-Voak & Perrett 2000, Penton-Voak et al. 1999), voices (Feinberg et al. 2006, Puts 2005) and bodies (Little, Jones & Burriss 2007, Pawlowski & Jasienska 2005) than in the infertile phase. Furthermore it has been found that women in their fertile phase preferred odours of men who were defined as more dominant (Havlicek, Roberts & Flegr 2005) and who were more symmetrical (Thornhill & Gangestad 1999, Thornhill et al. 2003). Such a peak in preference for masculinity when correlated with a peak in fertility is suggested to be of indirect genetic benefit to future offspring (Gangestad & Thornhill 1997). In some studies this well-established hypothesis was narrowed to short-term mating, whereby fertile women did choose men who were more masculine, but only when judging putative mates for a short-term liaison (Penton-Voak et al. 1999). However, such a fluctuating preference was not found when women judged realistic (not computer manipulated)

faces and bodies with varying symmetry and masculinity (Peters, Simmons & Rhodes 2009).

Another source of variation in sexual preferences intertwined with hormone levels is the **mating context** – the willing or possibility of a putative mate engaging and then investing in a sexual relation. Mating strategies of men and women differ greatly (basically due to the inequality of minimum parental investment that is inflicted by sexual relations). Depending on the amount of time and engagement one is willing to devote, mating strategies can be defined as short or long-term. In the short-term, engagement is brief, more sexually oriented, and destined to not last (but where the major benefit can be genetic quality of offspring). In a long-term strategy there is more investment from both parties, the relationship is long and presumably more monogamous (Buss & Schmitt 2003). Men and women pursue both long and short-term strategies, in conditions in which reproductive benefits outweigh the costs. However, due to the asymmetry of the minimum investment between the sexes, it is adaptive for men to devote more of their mating effort towards a short-term strategy, and for women towards a long-term one (Buss & Schmitt 1993). There is also another hypothesis pointing to the existence of a dual strategy in women. It suggests that women possess two overlapping strategies: to form long-term relationships with partners that bring investment and are stable in their relations, and on the other hand to seek good genes for their offspring from extra pair mates (Pillsworth & Haselton 2006). It has been suggested that this dual strategy depends on hormone fluctuations during the ovulation cycle (Larson et al. 2013), with women in their high-fertility phase preferring more masculine, “good genes” and more symmetrical men, than in their low-fertility phase (DeBruine et al. 2010b, Gangestad et al. 2007, Little, Apicella & Marlowe 2007, Rikowski & Grammer 1999, Thornhill et al. 2003, Thornhill & Gangestad, 2008).

The perceived attractiveness of a potential partner is influenced as well by the **relationship status** of both the rater and the rated person (O’Sullivan & Vannier 2013). Individuals currently in a relationship, lower their judgments of the attractiveness and desirability of other-sex faces. Additionally, women judge attached men as more attractive but as equally desirable (however, see Rupp et al. 2009). A person’s own relationship status also influences their preferences for sexual dimorphism. Women in a long-term romantic relationship tend to prefer more masculine men’s faces (faces bearing putative health cues, Thornhill & Gangestad 2006) than single women (Little et al. 2002, Quist et al. 2012, Sacco et al. 2009). As a dual mating strategy suggests, this might result in searching for an extra pair copulation, with a man with “good” more diverse genes providing the biological contribution for future offspring, whilst a long-term partner securing and providing the resources (Larson et al. 2013).

In addition to all of the above factors one is exposed to during one’s life-time, another important feature of a potential partner is similarity to facial templates that come from our early experience. These templates have been imprinted in our minds strongly enough to affect our later adult life mate choices. Imprinting is defined as a

learning process characterized by a relatively short sensitive phase occurring early in development, which has a long lasting effect (Hogan 2001, Le Grand et al. 2001, Lorenz 1937) and which occurs without external rewards, such as food or sexual satisfaction (ten Cate 1994). One of the variations of imprinting is **sexual imprinting** (Bateson 1966; Clayton 1989). This can be positive, such as when young animals learn the phenotype of one or both parents and use it as a model to assess future sexual partners (see e.g.: ten Cate, Verzijden & Etman 2006), or negative, such as (in reverse of the above example), when individuals learn to avoid conspecifics in adulthood that resemble those whom they had lived with closely when young (usually siblings and/or parents, Westermarck 1903/2005). Furthermore, in sexual imprinting a sensitive phase occurs before the maturation of an individual and hence before the final formation of a sexual behaviour system (Eibl-Eibesfeldt 1975, Immelmann 1980). A number of interspecific cross-fostering experiments investigating birds, mammals and fish that give biparental care suggest that species recognition may be learned through positive imprinting in early life. It was shown that during pair formation, adults tended to prefer sexual partners of the species that gave them parental care when they were young rather than other adults of their own species (ten Cate, Verzijden & Etman 2006). Likewise, studies using novel or artificially exaggerated ornaments have found positive sexual imprinting on these ornaments (ten Cate & Bateson 1989). However, some interspecific cross-fostering experiments with birds have found that exposure to conspecifics during first courtship can shift an initial preference for the foster species towards conspecifics (Bischof & Clayton 1991; Kruijt & Meeuwissen 1991, see also Kruijt & Meeuwissen 1993; Oetting, Prove & Bishof 1995). Thus, sexual imprinting may not be fixed during adolescence as previously thought, and can change due to social experience. Alternatively, in another study of birds it has been shown that a conspecific sexual preference can occur in individuals that have not socialized with any other individual (e.g. Gallagher 1977). This might suggest that animals have an innate conspecific sexual preference and sexual imprinting may merely refine this bias in natural conditions.

Findings from intra- and interspecific cross-fostering experiments in other animals might have been wrongly extrapolated to support the positive sexual imprinting hypothesis on traits that have continuous variation in humans (see Bereczkei et al. 2002; 2004). There are substantial theoretical problems in applying the positive sexual imprinting hypothesis to humans (explained more in-depth in Review Article Nb. I). Although positive sexual imprinting plays a role in species recognition (Hansen, Johannessen & Slagvold 2007) and in preferences for novel ornaments (for example in zebra finches, Witte & Caspers 2006), it seems that it does not affect mating preferences for traits that display a natural range of variation (Schielzeth et al. 2008). Positive imprinting was found in humans when examining non-phenotypical features, like smoking (Aronsson, Ghirlanda & Enquist 2011), or contemporary features like pregnancy or lactation (Enquist et al. 2011). On the other hand, positive sexual imprinting would increase the risk of inbreeding, because it would increase the

attractiveness of individuals related to self. Study **II** was designed to study this issue. However, negative sexual imprinting (and inbreeding avoidance) in humans is hard to study because there are few real life studies from the last century. There has been some more theorising recently in this area but it has involved using mathematical methods or visual stimuli studies based on self (not kin) similarity only. I address these issues in my study and article **III**, where I study preference for faces that resemble self and actual sibling faces.

In my thesis I examined other sources that influence variation in human mate preferences, such as sexual dimorphism. The prevalent and most accessible form for conducting studies on humans is by using a questionnaire. Due to the latest abundance of computers and advanced technologies, researchers have been given more possibilities to gain insights into the human mind. One such relatively new technique is tracking the gaze of individuals while presenting them with sexually relevant stimuli. As covert shifts of attention are immediately followed by overt gaze shifts toward preferred stimuli (Henderson 1992), **eye-tracking** is a valid tool for investigating autonomic, subconscious immediate reactions toward sexual stimuli (as opposed to self-reports, diaries and verbally communicated information). Studying gaze patterns has been shown to serve as a direct method for investigating sexual preferences and attention (a.e. Lykins, Meana & Strauss 2008). Tsujimura et al. (2009) showed that both men and women spend more time attending to the face than the body of individuals depicted in sexual stimuli, further consolidating the importance of the face in mate choice. Eye-tracking has been profitably applied to the investigation of sexual preferences and attention across multiple studies, facilitating the measurement of attention to different body parts, such as the waist, hips, breasts, pubic area and face (Dixson et al. 2011, Suschinsky, Elias, & Krupp 2007), and to erotic and non-erotic stimuli (Lykins, Meana and Strauss 2008). I have used this physiological measure of attraction in Study **IV** to study women's preferences for masculinity in different mating contexts.

Additionally, individual's sexual preferences rely strongly on life circumstances, such as the **health of the nation** where an individual has been brought up, the economic situation of the society and the sex ratio etc. (DeBruine 2010a, Pisanski & Feinberg 2013). Preferences can fluctuate depending on the economic situation of the country, health conditions, parasite prevalence, the distribution of economic resources, gender equality and other country-wide characteristics. Moreover if in different human populations a typical face shape or facial proportions vary, then individuals could materialize a preference for the face most typical in this particular population – hence their preference would vary accordingly (Symons 1979). It has been found that women's preference for sexual dimorphism is positively correlated with the national health of the country they live in. It was suggested that this variation in preferences is based on a trade-off between the low investment of masculine men and the heritable benefits to offspring (DeBruine et al. 2010a). Although it has been suggested that national income inequality and homicide rates are a better explanation of the variability

of such preferences, (Brooks et al. 2011) the National Health Index can explain better the geographical variation in women's masculinity preference (DeBruine et al. 2011). There were very few real life studies conducted hitherto in the underrepresented cross-cultural studies of men's preferences (Pisanski & Feinberg 2013), hence I designed the study Nb. V to fill this gap.

Both men and women attend more to the face than to the body, and ratings of facial attractiveness more closely mirror ratings of overall physical attractiveness than do ratings of body attractiveness – hence the focus on facial preferences in my studies. What's more, all studies in this thesis were conducted using facial pictures and not derived from direct cephalometric measurements. As has been found in previous studies, “both liner and angular measurements useful for characterizing facial morphology can be reliably measured from facial photographs” (Zhang et al. 2007). By choosing **photographs** and not direct measurements it was possible to increase the number of participants of each study, and so, increase the reliability of the outcomes. In studies where computer manipulations of the pictures were needed (Study III, IV and V), the PsychoMorph programme was used, which is designed for facial picture transformations (Tiddemann, Burt and Perrett 2001). This software maps the facial characteristics of a face and saves it as a net of coordinates – or a template. Having created templates for a number of faces, we could then calculate the differences between certain point's location on different base pictures. The programme can apply or subtract a percentage of this difference between pictures used and apply them either to one of the base pictures or to another picture. Due to continuous scale of morphing we can adjust the similarity to base pictures and set them manually for a desired percentage. (In different studies we used slightly different methods of morphing).

What's more, conducting the majority of the studies **on-line** allowed for a high degree of anonymity, which can elicit a more candid response to questions on emotions than paper and pencil methods or interview methods (Locke & Gilbert 1995, Millstein & Irwin 1983, Turner et al. 1998). Also, online studies are a convenient, user-friendly, comfortable and secure tool for data gathering (Prokop 2013), which was crucial in a cross-cultural study. Thanks to using on-line questionnaires we were also able to gather a larger sample in an efficient and cheap way (Birnbbaum 2004). Therefore, participants for our study were recruited via on-line forums and university mailing lists. It can be postulated that some respondents might deliberately provide inaccurate information via online-questionnaires (Brewin et al. 1993, Maughan & Rutter 1997). However, it has been shown that web-questionnaire data is not more affected by unreliable responses than are other types of questionnaires (Gosling et al. 2004) and, hence, our data should not bear larger bias than any other type of study on humans. All participants we included in the studies were heterosexual as assessed via the Kinsey Scale of Sexual Orientation (Kinsey, Pomeroy & Martin 1948).

2. AIM OF THE THESIS

The aim of this thesis was to *study* inter-individual differences in human sexual preferences and their sources. The sexual preferences of contemporary humans are a fascinating window into our evolutionary past, and can serve to provide a fuller understanding of the origins of humans beings and our cultures. The sexual behavior of humans is an interesting, common topic that is becoming increasingly discussed as time progresses. All studies within the thesis were designed to create together as broad as possible approach for the research of facial sexual preferences. For my thesis I wanted to place the greatest focus on studying the repetition of methods applied in different, changing circumstances (like cross-country researches) and on utilizing interdisciplinary and diverse methods by employing state of the art scientific techniques (e.g. using physiological measures like gaze tracking, morphing pictures and conducting cross-continental survey on-line) in order to verify existing hypotheses and test new ones.

This thesis was designed to sum up existing evidence (Article No. **I**) and re-investigate previous hypotheses. My aims were to study the mechanisms underlying a positive sexual imprinting-like mechanism within new circumstances (Study No. **II**); to add important input to the existing pool of evidence concerning the existence of negative sexual imprinting (with an innovative usage of real sibling pictures in study No. **III**); to investigate physiological measures of sexual attention with modern equipment (eye-tracking sexual dimorphism preference in study No. **IV**); and to verify the existing hypothesis on global variation in sexual preferences and their correlation with the health of the particular societies (study No. **V**).

Review article on sexual imprinting in humans (I)

Sexual imprinting mechanisms involve a process by which individuals learn to recognise a phenotype of an individual with whom they lived closely during childhood (usually a member of the family), and use this template in their later mate choices (Bateson 1966, Clayton 1989, for review, see ten Cate and Vos 1999). In this review article we gathered existing literature on sexual imprinting mechanisms and their influence on mate choice in humans. Despite a number of studies that identify the effects of positive sexual imprinting in animals (ten Cate and Bateson 1989; Kendrick, Hinton & Atkins 1999, Plenge, Curio and Witte 2010, Witte, Hirschler & Curio 2000; Witte and Sawka 2003, Witte and Caspers 2006), it would be erroneous to directly interpolate this mechanism into human behavior.

Existing articles concerning humans mentioned in the review article often do not exclude the heritable preferences effect (Bereczkei et al. 2002), nor are they without

design flaws (Berezkei et al. 2008, 2009, Wiszewska, Pawlowski & Boothroyd 2007) and they do not account for several alternative plausible explanations of the obtained results (Jedlicka 1980, Jedlicka 1984, Little et al. 2003, Wilson & Barrett 1987). Flawless validation of sexual imprinting in humans that would exclude confounding reasons for attraction (e.g. heritable preferences) could be based only on adoptive families. However, the opposite mechanism (negative sexual imprinting) gained some support in natural experiments, showing that individuals prefer to mate with unrelated individuals. (For evidence in non human animals see: Hill 1974, Hughes et al. 1999, Gavish, Hoffma & Getz 1984, Kelley, Graves & Maguran 1999, Kruczek 2007, Penn & Potts 1998. For evidence in humans see: Bevc & Silverman 2000, McCabe 1983, Shepher 1983, Walter and Buyske 2003, Wolf 1985 but see also Shor & Simchai 2009). In this article we suggest that imprinting is a valid and important mechanism, but that plausibly its chief purpose is for species-recognition and, therefore, it might be inaccurate to assume its influence on sexual preference in cross-fostering animal experiments (the source of the majority of evidence for sexual imprinting). We point out that understanding sexual imprinting rigidly would lead us to assume that an individual imprints on all features of the closest individual (often the parent), including detrimental features, and thus such preferences would disappear over the course of generations due to the lowered fitness of the offspring of the individuals that imprint these features. What's more, acknowledging the existence of negative sexual imprinting in humans requires that caution be applied, as there might be other kin-recognition mechanisms that may play a role in mate choice, beside the proximity to the other in early infancy and childhood (Lieberman, Tooby & Cosmides 2007, Lieberman 2009). We postulate, that positive and negative sexual imprinting should not be perceived as competing explanations - that final sexual preference should be rather perceived as the outcome of these two antagonistic forces.

Sexual imprinting on parents study (II)

The aim of this study was to test the sexual imprinting hypothesis by measuring the facial resemblance between a 'subject's spouse' spouse and their other-sex parent. Based on hair and eye colour (Laeng, Mathisen & Jonsen 2007, Little et al. 2003, Penton-Voak et al. 2003) and age preferences (Heffeman & Fraley 2013, Wilson & Barret 1987, Zei, Astofli & Jayaker 1981) it has been suggested that individuals choose partners that resemble their parents. There are a number of studies investigating sexual imprinting theory in humans. Among others, there have been studies that have looked at the similarity between a woman's husband and an adoptive father (Berezkei, Gyuris & Weisfeld 2004) and the correlation between a women's father's characteristics and her sexual preferences (Wiszewska, Pawlowski & Boothroyd 2007). However, often studies cannot exclude all plausible explanations of the similarity between a spouse and a parent, such as an individual's inherited sexual preferences or preference for familiar features (Rantala & Marcinkowska 2011). Following other authors (e.g., Schmitt et al.

2012), in our study we wanted to replicate and re-evaluate sexual imprinting hypotheses (from retracted study, see Bereczkei et al. 2009; retraction and publishers note) using improved methods and in different populations. We took pictures of 70 participants, their long term (minimum 6 months) partner and other-sex parent. Then participants completed a short form of the EMBU test, which measured their relations with parents during the first ten years of life on three scales: emotional warmth, over-protection and rejection (Arrindell et al. 1998). Random raters were shown tableaux with a picture of the other-sex parent of the individual and four other facial photographs including the partner of the individual and three random facial pictures (sex and age matched, see Fig. 1). Raters were asked to judge the similarity between the parent and the four stimuli facial pictures. We computed whether the similarity between a parent and partner was different from random (25% accurate selections by random raters) and checked whether this similarity correlated with the relation with the parent when young.

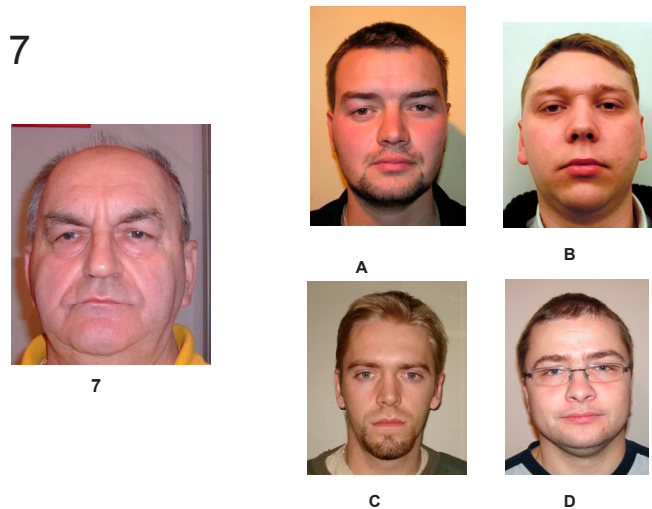


Fig. 1. Example of a slide shown to random judges with a question, “Please pick a picture (from A to D) that resembles the most picture number 7”.

Our study found that men’s partners statistically resembled significantly more their mothers than randomly chosen women ($t(30) = 2.84, p = 0.008$), whereas for women there was no detectable similarity between their father and partner ($t(37) = 0.94, p = 0.356$, Fig. 2). None of the scales measuring the quality of the relation between participants and their parents was correlated significantly with this facial resemblance. Based on the results of our study we can say that men tend to pair with women who resemble their mother more commonly than we would expect by chance. Women’s partners however did not resemble their fathers. The pattern found in men can support the positive sexual imprinting-like mechanism on facial traits of the other-sex parent.

However, since the relationship with the mother did not predict the facial resemblance between mother and spouse, we suggested that the resemblance might also be the result of heritable components for facial preferences or of increased familiarity with a parent's face (template) that enhanced later-on attractiveness judgments of potential mates similar to the template (Zajonc 1968).

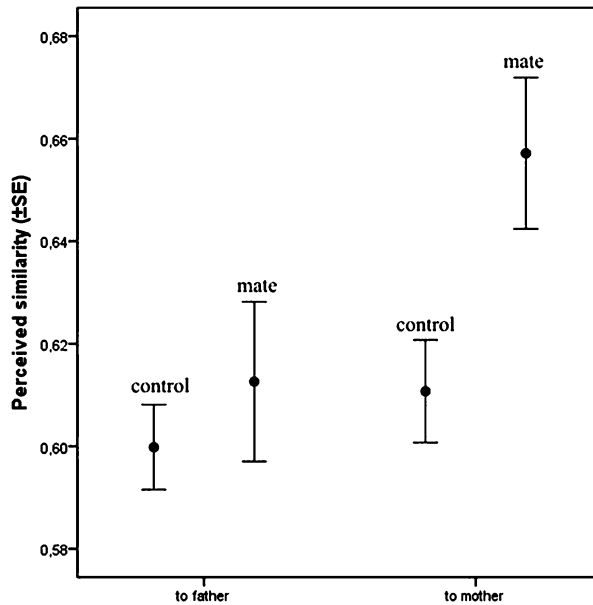


Fig. 2. Facial resemblance (\pm SE) assessed by randomly chosen referees (of both sexes) between the partner, control and participant's other-sex parent.

Asymmetry of obtained results between women and men can be caused by the fact that women show stronger inbreeding avoidance than men (Walter & Buyske 2003) – in other words, they need to be more cautious about kinship when choosing a putative mate. Trivers' parental investment theory (1972) states that females should show greater inbreeding avoidance than males because of the greater costs they can suffer as a consequence of inbreeding depression, i.e. the lowering of children's fitness (Postma, Martini & Martini 2010). Our results support the idea that a sexual imprinting-like mechanism existing in humans manifests in men only, because in women it is suppressed by inbreeding avoidance.

Sexual imprinting on siblings study (III)

Mating between close relatives (inbreeding) can be costly for the offspring's fitness (Postma, Martini & Martini 2010). Humans should be equipped with a special mechanism that allows for the development of a strong sexual aversion towards

individuals with whom they have lived closely in infancy and early childhood (usually biological siblings) – otherwise known as the “Westermarck effect” or negative sexual imprinting (Westermarck 1903). The aim of our study was to test the existence of sexual imprinting (negative or positive) by examining preferences for faces differing in resemblance to self and to sibling. Our hypothesis, based on negative sexual imprinting theory, was that any similarity to self and one’s real-life sibling will render other-sex faces less attractive. Furthermore, based on the fact that women’s minimum investment in offspring is higher (Trivers 1972) and that the costs of bearing a child suffering the negative consequences of inbreeding depression will be higher for women than for men (Fessler & Navarrete 2004), we predicted that this aversion to similarity will be stronger for women than for men.

Participants completed a short socio-demographic questionnaire assessing their parents’ ethnicity, age, years of co-habitation with the sibling, marital status and they judged a photo slide show consisting of the facial stimuli. Photos were taken with different cameras, but with standardized settings (i.e., same size of the picture, time of exposure, and brightness of the background). Stimuli pictures for the questionnaire were created with PsychoMorph software (Tiddeman, Burt & Perrett 2001). We created stimuli pictures by calculating the shape difference between a participant’s own or a sibling face and the same-sex base face and applying 50% of this difference to the other-sex face (Penton-Voak et al. 1999, Fig. 3). Participants judged all pictures on a 7 point Likert scale answering a question, “How sexually attractive do you find this person?”



Fig. 3. The example of other-sex transformations: a – participant, b – transformation of the participant and an average male, c – average male, d – transformation of the sibling of the participant and average male, e – sibling of the participant.

Men rated sibling similar pictures as significantly more attractive than non-kin pictures ($t_{19} = 2.21$, $P = 0.039$). In contrast, women rated sibling similar pictures as significantly less attractive than non-kin ($t_{43} = -2.66$, $P = 0.011$, Fig. 4). This asymmetry in sexual aversion is congruent with the hypothesis of parental investment theory of inbreeding avoidance, whereby as the costs of inbreeding depression are

greater for women than for men, women have become better equipped for detecting kinship. Men also found sibling similar pictures more attractive than non-kin pictures. Since daughters resemble their mothers, men's attraction found in this study can be explained by positive sexual imprinting like theory (preference for phenotypes similar to ones other-sex parent, Marcinkowska and Rantala 2012). Interestingly, self-similarity did not alter the attraction rating in the same manner; not significant ($t_{19} = 1.64, P = 0.118$), or almost significant ($t_{19} = 0.10, P = 0.92$) difference of preference between non-kin and self-similar picture was recorded for men and women respectively.

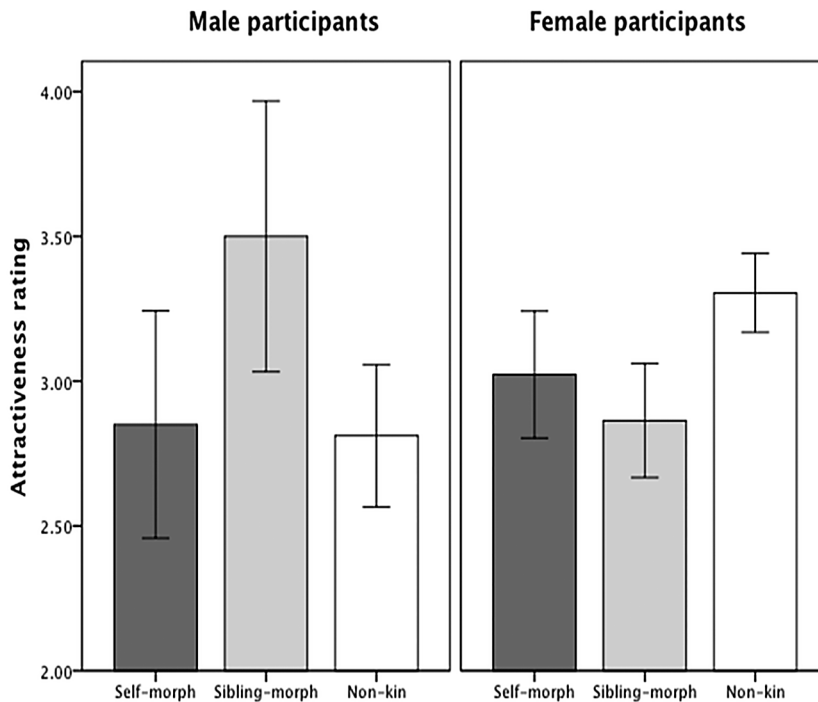


Fig. 4. Facial preference towards stimuli morphs (self-similar, sibling-similar and non-kin similar) for male and female participants.

Mating strategies are an adaptive behavior functioning in the present but shaped in the past – when phenotype matching could not be based solely on similarity to self, as mirrors were not accessible (pointed out also in Cornwell & Perrett 2008). We suggest that similarity to a sibling, rather than self-referent comparison, is a more ecologically valid kinship recognition tool. Results of this study suggested that a positive sexual imprinting like mechanism can be extended to siblings, but interestingly, this effect of increased attractiveness of a kin face was not detected for self-similar faces.

Gaze patterns study of women's facial preferences (IV)

Men's facial attractiveness is suggested to be an honest cue to health (Boothroyd et al. 2013, Rantala et al. 2013, Rhodes et al. 2003), personality (Penton-Voak et al. 2006) and intelligence (Zebrowitz et al. 2002). One of the important characteristics influencing women's perception of men's attractiveness is facial sexual dimorphism. Despite a vast body of research, women's preference for sexual dimorphism remains unclear, with some studies showing women's preference for masculine men's faces (i.a. Cornwell & Perrett 2008, DeBruine et al. 2006, Morisson et al. 2010, Penton-Voak et al. 2001), some for feminine faces (i.a. Berry & McArthur 1985, Penton-Voak et al. 1999, Penton-Voak et al. 2003, Welling et al. 2007) and some showing neither (i.a. Glassenberg et al. 2010). In addition, due to the varying costs and benefits of choosing masculine men in differing mating contexts (long-term vs. short-term) or characteristics of the referee (single vs. in a relationship, usage of hormonal contraception), preferences for masculinity may be fluctuating. In this study we wanted to investigate women's preference for sexually dimorphic men's faces with two parallel methods: a conscious and a non-conscious one. Each participant was presented with 40 slides with two transformations created with PsychoMorph software (Tiddemann, Burt & Perrett 2001), that differed only in masculinity, and was asked to choose the more sexually attractive face (Fig. 5). As a conscious measure we used two-alternative forced choice preferences (following DeBruine et al. 2010a, Jones et al. 2005, Welling et al. 2007).

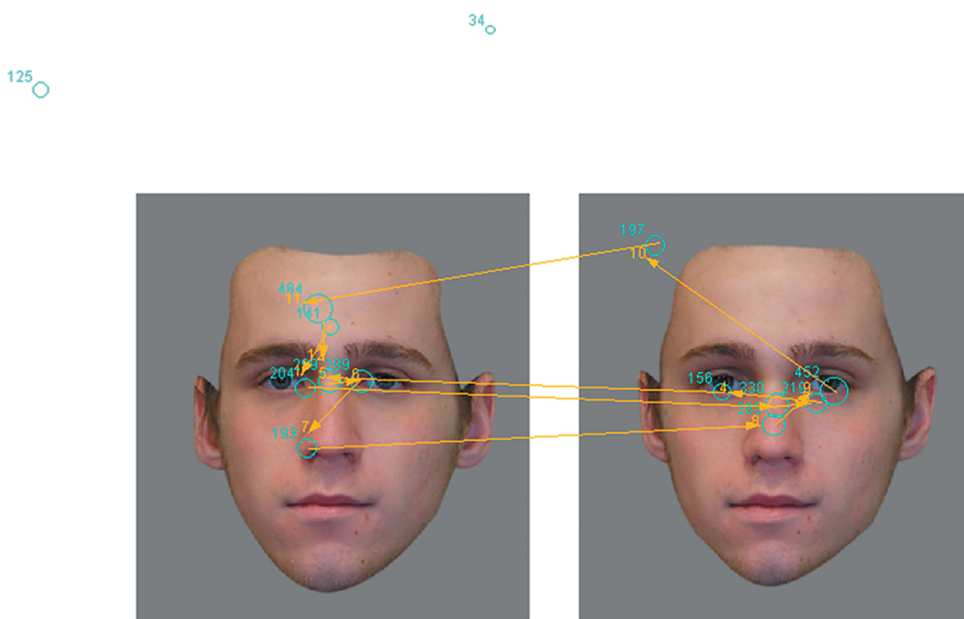


Fig. 5. Example of feminized (left) and masculinized (right) faces with a depiction of recorded gaze shift and fixations

To measure non-conscious preferences we used an eye-tracking camera that recorded saccade eye-movements (Dixson et al. 2011) when choosing more attractive faces. Relevant for perception (and the directing of attention which follows on), eye-movements can be divided into saccades and fixations (Fromberger et al. 2011). Saccades are the rapid eye-movements during which the acquisition of information is not possible and fixations are the periods in which the eye is still and the acquisition of information occurs (Henderson & Hollingworth 1999). The length of time a person fixates on a stimulus, and the number of fixations they make, can be used as a measure of interest in, or attention to that stimulus (Vo et al. 2012) and they correlate with genital arousal and self-reports of attraction (Harris et al. 1996). Eye-tracking has been found to serve as a valid physiological tool for investigating sexual preferences and attention (Lykins, Meana & Strauss 2008). We have found that women choose more feminine than masculine male faces in both the long ($t(92) = 6.05, p < .001, r = .53$) and short-term ($t(92) = 4.74, p < .001, r = .44$). Results of self-reported preferences were consistent with fixation count and fixation duration. This finding supports the hypothesis that women express an overall preference for feminine men's faces. Consistently with previous findings, we have found that partnered women prefer femininity when judging attractiveness for long- rather than short-term relationship.

Masculine men are perceived as more dishonest, interested in short-term relations (Perrett et al. 1998), engage more in such relationships (Rhodes, Simmons & Peters 2005) and have weaker preference for long-term relationships (Boothroyd, Lawson & Burt 2009) than their feminine peers. Based on those tendencies, it might be adaptive for women to choose more feminine men as long term mates. Mating context and relationship status had no significant overall effect on either fixations or on conscious choice, which accords with the findings of previous studies. However, we did find a trend in the influence of relationship context and status on visual attention, but only in women who did not use hormonal contraception. Single women fixated on facial stimuli more frequently during short-term relationship trials, whereas partnered women fixated more frequently during long-term trials (regardless of the masculinity of the presented face). As eye movement is a subconscious action, this study constituted extra evidence of women's preferences for more feminine men.

Population differences in mate preference (V)

Cross-cultural data provides us with an in-depth possibility to examine evolutionary psychology predictions on mate choices (Pisanski & Feinberg 2013). A number of studies have found cross-cultural variation in the sexual preferences of women (e.g. DeBruine et al. 2010a, Moore et al. 2013). In this study we tested the following two hypotheses: (a) men from different countries differ in their preference for sexual dimorphism in women and, (b) this variation is associated with harshness of the environment indicated by the national health indices. We gathered 2142 respondents from 28 countries (aged 18 – 45). The survey consisted of a short socio-demographic

questionnaire followed by a slide show, during which participants, by forced choice, needed to choose a more sexually attractive Caucasian women's faces. The language of the survey was either English, or the most common locally used language. Facial stimuli pictures were manipulated with PsychoMorph software (Tiddemann, Burt & Perrett 2001) by adding or subtracting 50 per cent of the linear difference between an averaged male and female face to the base picture, hence making it more masculine or feminine (following among others DeBruine et al. 2010a, Welling et al. 2007). Preference for facial femininity was calculated as the proportion of feminized pictures being chosen over masculinized ones (0 – all masculine choices, 1 – all feminine, Jones et al. 2005). We did not find any difference in femininity preference between participants of Caucasian and non-Caucasian origin. We did find a significant preference for feminized pictures over the masculinized ones in all examined countries. Moreover, the residents of different countries diverged in their femininity preference ranging from 0.525 in Nepal to 0.778 in Japan (Fig. 6). The National Health Index explained 50.4% of this variation. Neither the mean age of participants nor the Gross National Income met the 0.15 significance level for entry into the model.

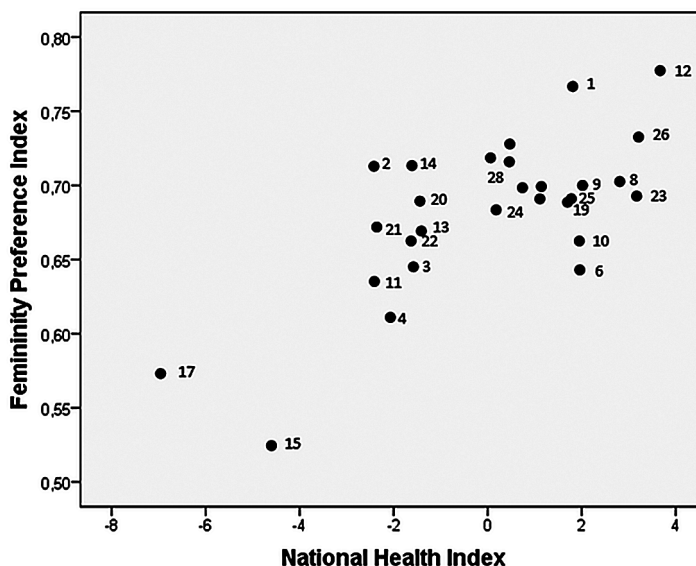


Fig. 6. Relationship between Femininity Preference Index and National Health Index. 1 – Australia, 2 – Brazil, 3 – China, 4 – Colombia, 5 – Croatia, 6 – Czech Republic, 7 – Estonia, 8 – Finland, 9 – France, 10 – Germany, 11 – Islamic Republic of Iran, 12 – Japan, 13 – Latvia, 14 – Mexico, 15 – Nepal, 16 – New Zealand, 17 – Nigeria, 18 – Poland, 19 – Portugal, 20 – Romania, 21 – Russian Federation, 22 – Saudi Arabia, 23 – Singapore, 24 – Slovakia, 25 – Spain, 26 – Sweden, 27 – United Kingdom, 28 – United States of America.

We suggested two possible mechanisms that underlie this result. Firstly, it can be related to varying testosterone levels. It is possible that in countries with poorer health conditions, during their life-time men are exposed to more pathogens, which as a result

lowers their testosterone levels in adulthood (Boonekamp et al. 2008). As testosterone level is positively correlated with preference for sexual dimorphism (Welling et al. 2008) this would explain lowered preference for feminine women in countries with the worst levels of health. Secondly, lowered preference for femininity in harsh environment can be caused by the direction of preference towards woman's dominance. As femininity is correlated with lower ratings of dominance (Perrett et al. 1998), drop of men's preference for sexual dimorphism in harsh conditions can be a result of directing preferences towards cues for effective resource acquisition and holding potential rather than high fertility. This result explanation follows previous research in rural Jamaica and Bangladesh, which showed that men in harsher environments show unusually weak preference for femininity (Penton-Voak, Jacobson & Trivers 2004, de Barra et al. 2013). This was the first ever study to examine men's preferences for sexual dimorphism cross-culturally and to understand this highly significant result further studies are needed.

3. DISCUSSION

As “mating effort is a finite resource” (Jones et al. 2008), mechanisms to choose, attain and maintain a relation with a good mate have to be efficient and not random. For both sexes, general physical attractiveness is better predicted by facial rather than body image ratings (Alvarez & Jaffe 2004, Peters, Rhodes & Simmons 2007), and hence sexual preferences can be best measured by judgements of facial stimuli. In my thesis I underline the importance of taking into account all possible factors, and explanations of existing mechanisms in human preferences (article I). I investigated previous hypotheses about positive (study II) and negative sexual imprinting, by placing emphasis on using novel methods, in the form of photos of real siblings (study III). I also used an innovative approach to individuals’ sexual dimorphism preferences by using an eye-tracking camera (study IV) and by gathering a global sample of participants (Study V). I have found that variations in human sexual preferences are not random; rather, they are often systematic and they follow specific predictions as to the putative mate’s sexual dimorphism and similarity to kin and his/her sexual dimorphism.

I have found that a positive sexual imprinting like mechanism is visible in men’s choices of an actual partner and in their sexual preferences. In my studies, I have empirically shown that men tend to bond with women who resemble their mother, and prefer women’s faces that resemble their sibling. I have not found such a tendency in women, hence my studies only partly support previous studies on sexual imprinting in humans (e.g. Aronsson, Ghirlanda & Enquist 2001, Bereczkei et al. 2002, Bereczkei, Gyuris & Weisfeld 2004, Boothroyd and Perrett 2008, Enquist et al. 2001, Little et al. 2003, Perrett et al. 2002, Zei, Astolfi & Jayakar 1981). Women’s partners did not resemble their fathers more than might be expected by chance, and neither did they judge kin similar faces as more attractive than non-kin ones. It is interesting to note that there is a strong **sexual asymmetry** in sexual-imprinting like mechanisms. As stated by Parental Investment Theory (Trivers 1972), women bear higher minimum proximate costs caused by the inbreeding depression and this increases their aversion towards sexual activities with males similar to kin (Hang 1999, Tooby 1977). The results of my studies (II, III) corroborates those of previous studies conducted with different stimuli (Walter & Buyske 2003) to show that sexual aversion towards kin is stronger in women than in men.

It is important to note that as the **relationship with the parent** did not predict the facial resemblance between the partner and the mother of participants, facial resemblance noticed by raters in my studies might also be a result of the heritable components of facial preferences. Face recognition mechanisms are heritable (Zhu et al. 2009) and so humans can be born with a schematic idea of a human face, which later on in early life can be supplemented via exposure to other human faces (Laeng,

Vermeer and Sulutvedt 2013). Sexual preferences then can have a genetic base, and hence it is possible that sons of men preferring, for example, round-faced women, would prefer round-faced women merely due to the genes that they have inherited from their fathers. Provided both father and son are of sufficient mating quality to be able to pursue and secure a mate they have chosen, then mothers would resemble spouses. Unfortunately, I was not able to rule out genetic effects because I could not include enough adoptive families in my studies. However, if the similarity between fathers and sons-in-law was too weak to be noticed in non-adoptive families, it is of low probability that in adoptive families the effect would be stronger.

Another caveat concerning studies on sexual imprinting is the difficulty to distinguish between preferring similarity to the other-sex parent and preferences for **familiar, similar to self** individuals. On one hand, it was shown that individuals prefer putative mates that are similar to themselves (Alvarez & Jaffe 2004, Bovet et al. 2012, Mateo & Johnston 2003, Nojo, Tamura & Ihara 2012) and that couples resemble each other more than two randomly picked people (Hinsz 1989, Zajonc et al. 1987). Such assortative mating (or homogamy (Fisher 1918, Bovet et al. 2008)) is also common among non-human animals (Thiessen & Gregg 1980). Furthermore, due to mere exposure to a certain face, individuals gain preference for the template they are familiar with (Moreland & Zajonc 1982/2009, Zajonc 1986). Individuals who cohabited with their parents during childhood and saw their parents' faces often throughout many years, can then in adult life choose individuals similar to those faces mainly because they seem familiar. On the other hand, extreme outbreeding – mating with a strongly unrelated individual – can have detrimental results (Liljedal, Rudolfson & Folstad 2008, Ochoa & Jaffe 1999), and so it would not be adaptive to pick highly dissimilar individuals (Lie, Simmons & Rhodes 2010). Hence the outcome should be a trade-off in similarity. Mating with an individual that is similar to one's self genetically can increase genetic compatibility (Tregenza & Wedell 2000) and reproductive success (for a study on a human population see Helgason et al. 2008). In fact it was suggested that similarity to self should be achieved by adding 22% of the self-template into an averaged facial picture (Laeng, Vermeer & Sulutvedt 2013) because then similarity to self is subtle enough not to be consciously apprehended (Fraley & Marks 2010), yet depicted enough to increase perceived attractiveness.

The situation is similar when examining **negative sexual imprinting**. Bearing in mind the impossibility of organising real life-long experiments on humans, it is highly improbable to gather a sample that would allow us to exclude confounding factors. Even in the famous case of the Kibbutz in Israel (where children of the same age group were brought up together in groups, Wolf 1985, Wolf 2004a) or the Sim-pua marriages in Taiwan (where girls as young as one year old were placed in the household of the future husband, Wolf 2004b), researchers were unable to state unequivocally that there was a clear inbreeding mechanism (criticism in Shor & Simchai 2009). When investigating judgements of sexual attractiveness of putative kin, researchers usually use their own pictures of the individuals. They assume that since siblings share on

average 50% of their genes, similarity to self should have the same results as similarity to a sib (DeBruine 2004). But our study did not support this assumption. We have found that similarity to self and similarity to a real-life sibling altered the attractiveness judgement in a different way. For neither men nor women did we find that pictures morphed with self were more attractive than random faces (result opposite to DeBruine 2004). However, with men the similarity of judged pictures to the real sibling did enhance their judgement of attractiveness. It is interesting to note that no study before has used the pictures of actual siblings of participants, assuming that any alteration of preference should be the same for similarity to self and to a sib. I may only hypothesise that since the majority of research is conducted on students in university laboratories, it is harder for researchers to gather pictures of real siblings. On the other hand, researchers could have also assumed that, due to the genetic bases of phenotype expression, individuals should always be sufficiently similar to his/her sibling to produce the same reaction towards a face that has been manipulated. As shown in my study, this is not the case. I would strongly encourage future researchers who examine the Westermarck effect, inbreeding avoidance mechanisms or negative sexual imprinting to conduct studies on the actual siblings of participants.

I support a trend for re-examining existing or suggested hypotheses with new methods. With the development of **computer techniques** that can be used for the research of human sexual preferences, new tools are being proposed. For example, to obtain a closer similarity to real life circumstances Tigue et al. (2012) used rotating three-dimensional facial images to test whether men's attractiveness ratings of women's faces from 2D and **3D** images differed. Study confirmed that the attractiveness ratings of 2D and 3D stimuli are highly correlated. As the majority of studies till now have been based on 2D stimuli (Little, Jones, & DeBruine, 2011), it was of great worth to re-test the well-established assumptions with a new, only recently accessible tool (such as 3D computer graphics). Although this research did not depict an observation of a novel preference in the field, it is an important mainstay for future studies on facial preferences. It shows that 2D images contain enough information about 3D structural elements of the face to assess attractiveness accurately (Tigue et al. 2012). Additionally, women's faces were rated significantly more attractive in 3D images than in 2D images, from which we can infer that for facial cues less salient than femininity or symmetry, 3D stimuli might be a better choice. Another example is the usage of **video-clips** and *comparing* whether the judgement of attractiveness of static and moving stimuli is strongly correlated (i.e. Rhodes et al. 2011, Roberts et al. 2009, Saxton et al. 2009) or whether the artificial parallel manipulation of multiple cues to dimorphism affects attractiveness judgements (O'Connor et al. 2011, O'Connor et al. 2013). The results of these studies are not innovative *sensu stricte*, however they confirm with a new method the correlation of preferences for cross-modal cues (interaction between dimorphism of face and voice) with mate quality (Fraccaro et al. 2010). In my studies, I have used only 2D visual stimuli due to limited laboratory resources and the *trade-off* with number of participants (and countries/cultures) taking part in the study. Often

participants completed the survey using a poor internet broadband connection, and in some work fields (in the study Nb V especially) there was no internet access at all so that responses had to be gathered from printed questionnaires. In such cases I was unable to use either 3D or video stimuli. However, this fact should not be viewed as a drawback to any of my above described studies because, as shown in multiple articles, 2D static facial pictures do correlate strongly with more complex (meaning 3D and dynamic) stimuli, and they are a valid measurement of attractiveness judgement.

Due to rapidly advancing technology we can manipulate facial stimuli, both static and dynamic, in two or three-dimensions, and we can also follow the attention, or observe attraction judgments of the participant in addition to simply using written questionnaires. When completing a survey, participants can alternate their answers for multiple reasons: they might not want to share issues too private; they might want to lie on purpose; they might want to make themselves feel better about themselves etc. Bypassing the written questionnaire and recording directly the preference or judgment would allow us to obtain more objective results. Gaze tracking is also a new technology, providing a tool that allows us to measure participants' attention. Gazes serve both to facilitate the allocation of mating effort (Conwey et al. 2008) and to gather information. However, in using eye-tracking to understand mating strategies, more studies are needed to understand the difference between attraction and fear, and to understand better what characteristic of the gaze (fixation count, time, dwell time etc.) is the best predictor of attention or attraction. In our eye-tracking experiment we were only able to hypothesise whether a difference in the fixation count of women judging men's faces constitutes indecisiveness due to insufficient up-to-date literature. At the present time, studies explaining particular characteristics of gaze and their functions are lacking. A series of studies simultaneously conducting eye-tracking and verbal interviews with a participant could help us better understand these mechanisms. For example, exposing participants to a range of stimuli (and not only sexually relevant stimuli) and asking them about their impressions and evaluations, while simultaneously tracking their gaze could give us a basis to better understand all possible variations of pupil dilation, fixation duration and counts and dwell time.

Another insightful and, in my opinion, a crucial tool for forming a strong hypothesis is a cross-cultural wide gathering of responses. To my knowledge, the cross-cultural study (V), conducted as a part of this thesis, is one of the largest up to date records on men's sexual preferences. Having such a numerous range of samples (when it comes both to participants and countries) is an indisputable strength of this data set. Controlling country-specific systematic variation in sexual preferences is an indisputable and strong base for further analysis of less salient and intra-individual variation. I also recommend the future usage of physiological measures in cross-cultural studies (to omit self-judgment bias and participants manipulating their responses). This is particularly important when bearing in mind that the ideals of beauty are strongly influenced by changes in socio-economic status and fashion (Pettijohn & Jungeberg 2004), and hence can change preferences temporarily and

geographically (Buggio et al. 2012). In this respect, future studies could show the underlying biological bases that are later on modulated by life experience and culture.

Studying human attractiveness and, following on from this, the features that underlie attractiveness can also be of aid when investigating the relationship between phenotype (what we can observe in a human body), genotype (what we inherited from our ancestors) and environmental factors (what happens during our life time). In **real life applications**, the investigation of attractiveness features can lead us to understand how certain traits are associated with specific diseases - especially hormone related conditions – as these may share a common origin (Buggio et al. 2012). Peculiarly, bearing in mind the prevalence of beauty topics in everyday human culture, a major part of the human population is unable to accurately rate their own attractiveness (Alam, Jeffrey & Dover 2001). In fact, both women and men show surprisingly low correlations between self-ratings and objective measures of attractiveness (Feingold 1992). Body image distortion (purportedly facilitated by the Western media's promotion of particular aesthetic ideals (Becker 2004)) can lead to body dissatisfaction, which in turn can trigger eating disorders (Stice & Shaw 2002). Nevertheless the hypothesized relation between body dissatisfaction and eating disorders and the exact mechanisms through which the media exercises an influence on body dissatisfaction is still being investigated (Ferguson, Winegard & Winegard 2011). One hypothesis from an evolutionary perspective is that eating disorders can be defined as adaptive and yet are self-destructive mechanisms occurring in response to particular environmental factors and cognitive processes (Behar 2012). Despite the multitude of contributing factors to the risk of eating disorders, the socio-cultural factors moderating that risk are incompletely understood (Becker 2004). Research on human facial cognition and sexual preferences can help us to better understand the mechanisms triggering or underlying ever more prevalent body image diseases (Becker 2004).

Following on from these assumptions, studies into human sexual preferences may not appear to be of direct benefit to our species or to individuals' survival in the same way that cancer treatment research or famine problem studies are. However, sexual preference studies contribute to a greater pool of evidence that facilitates the understanding of our own behaviours and minds.

4. CONCLUSION

In my thesis I studied the sexual preferences of humans using different methods and different approaches, which together created a coherent and state of the art perspective on human mating. Modern humans are the result of mate choices made by our most successful ancestors, who managed throughout evolutionary time with their set of adaptive skills to survive, attract a mate, sire offspring and take care of its well-being. As descendants of those successful individuals we inherited a set of mate preferences, which have been proven to be adaptive over time and which we use in our lives in the contemporary world. With the studies constituting my thesis, I have examined reasons for their variation - the plasticity of mate preferences - and the multiple factors in operation. I have corroborated some already established hypotheses, such as the existence of sexual-imprinting like mechanisms in men, which I have analysed by using photographs of actual partners and the novel method of photographing the actual siblings of the individuals I studied (study **II** and **III**). I have added a further valid point to the physiological measures of female attraction towards masculine men – by simultaneously measuring the conscious response and subconscious eye movement I found that women prefer more feminine men’s faces (study **IV**). I have also conducted the first ever study into men’s global preferences for facial femininity, which showed that men in poorer conditions of health prefer less feminine women (study **V**). I have offered possible explanations for this but further analysis is needed to understand the underlying biological mechanisms of this variation and to exclude all confounding factors. Through my studies I have proven the existence of a systematic variation in preferences between different individuals (Articles II, III, IV), and between groups of individuals (Article V). I have proven that, although subjected to evolutionary forces, variation remains.

Face perception and preferences are of key importance for the further understanding of general human sexual preferences. The body of evidence gathered in this thesis contributes to a fuller, more inter-disciplinary perception of an evolutionary attitude towards human behavioural ecology. With the specific focus on sexual selection being evermore popular and crucial for the understanding of deeply complex *Homo Sapiens* behaviour, I have expanded the existing evidence for inter-individual variation in humans. All of the articles contribute to a body of evidence promoting understanding of the evolutionary bases of our daily behaviour and are a useful base for future research.

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ORIGINAL ARTICLES

- I Rantala M.J. & Marcinkowska U.M. The role of positive and negative sexual imprinting on mate choice in humans. (*Behavioral Ecology and Sociobiology* 2011)
- II Marcinkowska U.M. & Rantala M. J. Sexual imprinting on facial traits of opposite-sex parents in humans. (*Journal of evolutionary Psychology* 2012)
- III Marcinkowska U.M., Moore F.H. & Rantala M.J. An experimental test of Westermarck effect: sex differences in inbreeding avoidance (*Behavioral Ecology* 2013)
- IV Burris R., Marcinkowska U.M. & Lyons M.T. Gaze properties of women judging the attractiveness of masculine and feminine male faces (*Evolutionary Psychology* 2014)
- V Marcinkowska U.M, Kozlov M.V, Cai H., Contreras-Garduño J., Dixson B.J., Oana G.A., Kaminski G., Li N.P., Lyons M.T., Onyishi I.E., Prasai K., Pazhoohi F., Prokop P., Rosales Cardozo S.L., Sydney N., Yong J.C., Rantala M.J. 2014 Cross cultural variation in men's preference for sexual dimorphism in women faces (*Biology Letters* 2014)