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PHYSICAL ATTRACTIVENESS AS A SIGNAL OF BIOLOGICAL QUALITY

Markus J. Rantala

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University of Turku

Faculty of Social Sciences
Department of Psychology

Supervised by

Professsor Heikki Hämäläinen
Department of Psychology
FI-20014 University of Turku
Finland

Profofessor Antti Revonsuo
Department of Psychology
FI-20014 University of Turku
Finland

Dr. Katja Valli
Department of Psychology
FI-20014 University of Turku
Finland

Reviewed by

Professor Boguslaw Pawlowski
Department of Human Biology
University of Wroclaw
Poland

Dr. Jan Havliček
Department of Zoology
Charles University in Prague
Czech Republic

Opponent

Professor Boguslaw Pawlowski
Department of Human Biology
University of Wroclaw
Poland

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Dedicated to my children

ABSTRACT

It has been commonly thought that standards of beauty are arbitrary cultural conventions that vary between cultures and time. In my thesis I found that it is not so. Instead, I show that attractiveness and preferred traits serve as cues to phenotypic qualities that provide selective benefits for those who choose their mates based on these criteria. In the first study I show that attractive men have a stronger antibody response to the hepatitis b vaccine and higher levels of testosterone than their less attractive peers. Men with low levels of testosterone also tend to have high levels of the stress hormone cortisol, suggesting that their immune responses may have been inhibited by stress hormones. Thus, facial attractiveness may serve as an honest cue of the strength of immune defence in men. In the second study, I show that the attractiveness of the male body is also a cue of better immunity. In addition, I show that adiposity, both in men's faces and bodies, is a better cue of the strength of immunity and attractiveness than of masculinity. In the third study, I test the preferences of women from 13 countries for facial cues of testosterone and cortisol. I show that there is cross-cultural variation in women's preference for cues of testosterone and cortisol in male faces. I found a relationship between the health of a nation and women's preferences for cues of testosterone in the male face and the interaction between preferences for cues of testosterone and cortisol. I show also a relationship between preferences for cues of testosterone and a societal-level measure of parasite stress. Thus, it seems that societal-level ecological factors influence the relative value of traits as revealed by combinations of testosterone and stress hormones. In the fourth study, I show that women's immune responsiveness (amount of antibodies produced) does not predict facial attractiveness. Instead, plasma cortisol level is negatively associated with attractiveness, indicating that stressed women look less attractive. Fat percentage is curvilinearly associated with facial attractiveness, indicating that being too thin or too fat reduces attractiveness. This study suggests that in contrast to men, facial attractiveness in women does not indicate the strength of immune defence, but is associated with other aspects of long-term health and fertility: circulating levels of the stress hormone cortisol and the percentage of body fat. In the last study I show that the attractiveness of men's body odor is positively correlated with stress hormone levels, suggesting also that the attractiveness of body odors may signal the phenotypic quality of males to females. However, the attractiveness of men's body odor was not associated with testosterone levels. My thesis suggests that the standard of beauty is not in the eye of the beholder. Instead, our standard of beauty is hardwired in our brains by genes that are selected by natural selection and also influenced by current environmental conditions.

TIIVISTELMÄ

Lukuisat viimeaikaiset tutkimukset evoluutiopsykologian alalla ovat osoittaneet että kasvojen ja vartalon puoleensavetävyydellä on huomattava vaikutus ihmisen parinvalinnassa. Evoluutiopsykologit olettavat, että fyysinen puoleensavetävyys kertoo henkilön fenotyyppisestä- tai geneettisestä laadusta pariutumiskumppanina, mutta mitä tämä laatu on ja miksi puoleensavetävyys olisi rehellinen signaali laadusta, on jäänyt epäselväksi ja kiistanalaiseksi. Väitöskirjani ensimmäisessä osatutkimuksessa selvitin miesten immuunijärjestelmän tehokkuuden yhteyttä miesten kasvojen puoleensavetävyyteen tutkimalla kuinka voimakkaasti miesten immuunijärjestelmä reagoi hepatiitti B -rokotteeseen tuottamalla vasta-aineita virusta vastaan. Kokeessa havaitsin että naiset arvioivat komeimmiksi miehiä, joilla oli voimakkain immuunivaste ja korkein testosteronitaso. Toisessa osatutkimuksessa havaitsin, että myös miesten vartalon puoleensavetävyys on yhteydessä immuunipuolustusjärjestelmän tehokkuuteen. Lisäksi havaitsin, että vartalon rasvaprosentti on voimakkaammin yhteydessä vartalon puoleensavetävyyteen ja immuunijärjestelmän tehokkuuteen kuin vartalon maskuliinisuus. Kolmannessa osakokeessa tutkin eroaako naisten mieltymys testosteronitasosta ja stressihormonitasosta kertoviin miesten kasvonpiirteisiin maantieteellisesti. Tutkimuksessa esitin 13 eri maassa naisille kuvia miesten kasvoista, joita oli manipuloitu testosteronista ja stressihormonista kertovien piirteiden suhteen. Kokeessa havaitsin että köyhissä maissa, joissa terveydenhuolto on huono naiset suosivat voimakkaammin testosteronista kertovia piirteitä kuin paremman terveydenhuollon omaavissa maissa. Tutkimus viittaa siihen, että ympäristöolosuhteet vaikuttavat siihen, millaisista miestenkasvoista naiset pitävät. Neljännessä osakokeessa tutkin kuvastaako naisen kasvojen puoleensavetävyys hänen immuunijärjestelmänsä toiminnan tehokkuutta. Havaitsin, että toisin kuin miehillä, naisilla kasvojen puoleensavetävyydellä ei ole yhteyttä hänen kykyyn tuottaa vasta-aineita hepatiitti B -rokotetta vastaan. Sen sijaan huomasin, että miehet suosivat naisia jolla on alhainen stressihormonitaso. Myös naisen rasvaprosentilla oli vaikutusta puoleensavetävyyteen. Sekä liian alhainen että liian korkea rasvaprosentti heikensi puoleensavetävyyttä. Aikaisempien tutkimusten perusteella tiedetään sekä liian alhaisen, että liian korkean rasvaprosentin heikentävän naisen hedelmällisyyttä. Korkean stressihormonitason tiedetään myös heikentävän naisen hedelmällisyyttä, joten tutkimusten valossa näyttäisi siltä, että miehet ovat sopeutuneet suosimaan naisten kasvoissa piirteitä jotka kuvastavat hedelmällisyyttä, mutta ei hyvää immuniteettikykyä. Viimeisessä osatutkimuksessani havaitsin, että miesten hajun puoleensavetävyys ei ole yhteydessä heidän testosteroni- ja estradiolitasoihinsa. Sen sijaan naiset suosivat sellaisten miesten ominaishajua joilla oli korkea stressihormonitaso koetilanteessa. Väitöskirjatutkimukseni viittaavat siihen, että fyysisellä puoleensavetävyydellä on vankka biologinen pohja, eikä kauneuskäsitys ole vain sosiaalisesti rakentunut mielivaltainen konstruktion, kuten monet humanistit väittävät.

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LIST OF ORIGINAL ARTICLES

This thesis is based on the following publications and manuscripts, referred to in the text by their Roman numerals:

I. Rantala MJ, Moore FR, Skrinda I, Krama T, Kivleniece I, Kecko S, & Krams I. 2012. Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nature Communication* 3, 694

II. Rantala MJ, Coetzee V, Moore FR, Skrinda I, Kecko S, Krama T, Kivleniece I & Krams I. 2013. Adiposity found to be a more valid cue to immunocompetence than masculinity in human mate choice. *Proceedings of the Royal Society London B* 280, 20122495.

III. Moore, F. R., Coetzee, V., Contreras-Garduño, J., Debruine, L. M., Kleisner, K., Krams, I., Marcinkowska, U., Nord, A., Perrett, D. I., Rantala, M. J., Schaum, N. & Suzuki, T. N. 2013. Cross cultural analysis of women's preferences for cues to sex- and stress- hormones n the male face. *Biology Letters* 9, 20130050.

IV. Rantala MJ, Coetzee V, Moore FR, Skrinda I, Kecko S, Krama T, Kivleniece I & Krams I. 2013. Facial attractiveness is related to women's cortisol and body fat, but not with immune responsiveness. *Biology Letters* 9, 20130255.

V. Rantala MJ, Eriksson CJP, Vainikka A & Kortet R. 2006. Male steroid hormones and female preference for male body odor. *Evolution and Human Behavior* 27, 259-269.

1. INTRODUCTION

"Personal beauty is a greater recommendation than any letter of reference."
Aristotle (384– 322 BC)

1.1. Evolutionary psychology

A scientific fact is that we are not descended from apes. We are apes. We share 98.7% of our genetic material with our closest existing relative - the bonobo (pygmy chimpanzee) - (Prufer et al., 2012), which is more closely related to humans than it is to gorillas. This is due to the fact that the ancestor of humans split with the common ancestor of bonobos and chimps only between 4 to 7 million years ago. Another scientific fact is that we do not have any physiological traits that are not found in any other animals. Naturally, we are unusual and unique among other animal species in our own way, but so are bonobos or tapeworms. Although most of us can easily accept the fact that our physical traits are shaped by natural and sexual selection, it is much more difficult for people to accept the fact that also our mental traits are shaped by natural selection although nowadays the evidence is overwhelming (e.g. Buss, 2008; Cartwright, 2007). However, it is relatively easy for people to accept evolutionary thinking to explain the behavior of chimpanzee or fruitflies.

Evolutionary psychology (EP) is a branch of psychology that incorporates the effects of evolution to explain human behavior (e.g. Buss, 2008). EP predicts that our cognitive structure, like physiological structure, has been designed by natural selection to serve survival and reproduction (e.g. Buss, 2008). It seeks to identify which psychological traits are evolved adaptations (the functional products of natural

or sexual selection). Though applicable to any organism with a nervous system, most research in EP focuses on humans. EP is steadily increasing as an influence in the general field of psychology both in Finland and around the world. However, EP should not be seen as a sub-discipline of psychology or as an area of study, like vision, reasoning or social behaviour. Instead, EP is a way of thinking and can be applied to any topic in psychology or the social sciences. Thus, EP should provide a foundational and meta-theoretical framework that integrates the entire field of psychology and social sciences, in the same way it has for biology. Although evolutionary psychology has met severe criticism, it is usually targeted towards the predictions or definition of EP given by individual researchers (like Tooby & Cosmides (1987, 1992)) concerning the modularity of mind or about the environment of evolutionary adaptation (EEA), rather than towards mainstream thinking in EP (that dates back to Darwin) (see Ylikoski & Kokkonen 2009; Peters, 2013). Criticism towards the mainstream of EP is mostly ideologically rather than scientifically motivated, and is based on an incorrect nature vs. nurture dichotomy, or is based on misunderstandings of the discipline (e.g. Segerstråle, 2000, Pinker, 2002, Barkow, 2006). Evolutionary psychology contrasts sharply with the Standard Social Science Model (SSSM) which has been the dominant theoretical paradigm in psychology and social science during the 20th century (Barkow, Tooby & Cosmides 1992). SSSM views the human mind as a general-purpose cognitive device shaped almost entirely by culture, and often referred to as a "blank slate" (Pinker, 2002). Instead, evolutionary psychologists assert that the human mind is designed by natural selection during our evolutionary history and is full of psychological adaptations that help to resolve adaptive problems met by our ancestors (e.g. Buss, 2008).

People often think that our behavior is more cultural as opposed to biological, although they accept that human cultures are the products of evolved brains. The most frequently cited examples concerning the influence of culture on human behavior are our standards of beauty, which are commonly thought to vary between cultures and time. Traditionally social science has upheld that standards of beauty are arbitrary cultural conventions (e.g. Berry, 2000; Etcoff, 1999). After observing large cultural variation in beautification practices during his voyage around the world, Charles Darwin also became convinced that standards of beauty are cultural rather than

biological (Darwin 1871). However, rather than searching for differences between cultures, people should look for similarities. The growing field of evolutionary psychology reports a large body of evidence to suggest that standards of beauty are not arbitrary cultural conventions, pointing to, for example, cross cultural agreement in preferences for cues to health and fertility (Tovee, Swami, Furnham, & Mangalparsad, 2006). Furthermore, a number of studies suggest that facial preferences emerge early in childhood, before any cultural standards of beauty are likely to be assimilated and suggesting that we have a strong inborn universal standard of facial beauty (Rantala & Marcinkowska, 2011). Evolutionary psychologists interpret preferences as strategies that have evolved due to the selective benefits accrued to those who chose their mates based on these criteria (Rhodes, 2006). To argue that such preferences are adaptive, however, it is necessary to show that preferred traits serve as cues to fecundity, health or other traits that enhance fitness, and contribute to higher reproductive success. To date, despite the identification of traits that contribute to human attractiveness, our understanding of the underlying physiological or psychological qualities signaled by such traits remains limited. The aim of my doctoral thesis is to study whether sexually attractive faces, bodies or body odors are associated with the strength of immune defense or other traits that enhance fitness of a person that mates with an attractive person.

1.2. Sexual selection

In many species males have extravagant secondary sexual traits, like bright colours, antlers, horns and long tails. In the nineteenth century Darwin had presumed that they were the result of sexual selection and nowadays a considerable body of experimental and comparative evidence supports his hypothesis (Andersson, 1994). Darwin (1871) defined that sexual selection arises from the advantages that certain individuals have over other individuals of the same sex and species in relation to reproduction success. He divided sexual selection into two major categories: competition for mates and mate choice. In numerous species it has since been revealed that females base their choice on the degree of expression of the males' secondary sexual characters (Andersson & Simmons, 2006). Usually the advantages of female preference for more ornamented

males is clearly apparent, because females may acquire immediate benefits from their mate choice, such as better territory or other resources (Andersson 1994). However, the preference for an ornamented male is even stronger in species where males are not likely to provide anything more than their sperm to females. Thus, it has been thought that by preferring the most ornamented male females would aquire "good genes" for their offspring. However, what these "good genes" are has remained elusive (Puurtinen, Ketola, & Kotiaho, 2009).

1.3. Immunocompetence and sexual selection

Because parasites and pathogens are universal threats to all animals and sick animals are not able to develop as highly elaborated sexual ornaments as healthy ones, it has been suggested that the quality that the ornaments signal to females is resistance to parasites and pathogens (Hamilton & Zuk, 1982). Thus, the "good genes" that females would acquire for their offspring are the genes that make the offspring resistant against the parasites and pathogens that are most import in the current environment (Hamilton & Zuk, 1982). Folstad & Karter (1992) developed this idea a step further by presenting the immunocompetence handicap hypothesis (ICHH) which states that elaborate traits could be honest and reliable signals of immunocompetence. Their hypothesis suggests that the development of secondary sexual signals may be dependent on testosterone, so that high levels of testosterone are needed for the development of a larger ornament. The cost of expression of the ornament is incurred physiologically, as testosterone also corrupts the immune system (Folstad & Karter, 1992). Therefore, only males of high phenotypic and/or genetic quality can develop elaborated sexual ornaments and can afford to pay the cost of immunosuppression. Thus, only males in good condition or with high immunocompetence, or both, can afford to allocate resources to large ornaments, which should produce a positive correlation between immune defense and the expression of costly secondary sexual characters (Westneat & Birkhead, 1998). Females who choose to mate with males that have the most elaborated secondary sexual ornaments would enhance immunocompetence and viability of their offspring. Thus, a female would enhance her fitness by preferring males with large ornaments.

Although the immunocompetence handicap hypothesis sounds logical and has been adapted widely as an explanation of female preference for masculine traits in humans (Rhodes, Chan, Zebrowitz, & Simmons, 2003; Scott, Pound, Stephen, Clark, & Penton-Voak, 2010), the hypothesis does not stand up to closer scrutiny. For example, there is a mismatch between theoretical and empirical evidence. For example, although many studies have found that testosterone is immunosuppressive, there are also many studies that have failed to find the immunosuppressive effect of testosterone and some studies have even found the opposite effect (review in Roberts, Buchanan, & Evans, 2004)). In addition, the meta-analyses by Roberts et al. (2004) pertaining to the experimental manipulations of testosterone levels, found support for the immunocompetence handicap hypothesis only related to ecto-parasites in reptiles. To resolve this discrepancy between studies it has been suggested that the effect of testosterone on the immune system occurs indirectly through covariance with the stress hormone corticosterone (Evans, Goldsmith, & Norris, 2000; Møller, 1995). On the other hand, mathematical models (e.g. Getty, 2002; Kokko, Brooks, McNamara, & Houston, 2002) have found that the strength of the secondary sexual signals can be positively, negatively, or not related at all to viability and components of viability (e.g., immunocompetence), depending on the specific parameter values affecting selection. Negative associations tend to arise when sexual selection is extreme (e.g., in "winner takes all" scenarios). Humans may not have been characterized by such extreme sexual selection ancestrally, because we are not a lekking species. Thus, based on the mathematical models one might be able to argue that positive associations between viability and male attractiveness should be expected to exist in humans. In addition, the immunocompetence handicap hypothesis (Folstad & Karter, 1992) might be more easily applicable to the species that has a specific breeding period, when males are full of testosterone and stress hormones for only a short period of time. Since humans have no specific breeding period, men would be forced to pay the cost of high testosterone and stress hormone levels all year around. This would lead to selection to optimize the testosterone levels at levels that would maximize their long term fitness. Thus, one could expect positive correlations between testosterone levels, attractiveness and the strength of immune defense, because men would be selected to optimize their testosterone titers at the level that they were able to tolerate for a long period of time. Interestingly, although insects and spiders lack sex hormones many studies on them

have found positive correlations between expression of secondary sexual ornamentation and the strength of immune defence (reviewed in Lawniczak et al., 2007). Thus, the best support for the immunocompetence handicap hypothesis comes from studies on insects (Rantala, 2002).

1.4. Immunocompetence and sexual selection in humans

Although humans apparently lack elaborated secondary sexual ornaments, humans do have highly sexually dimorphic body shape and size. Humans also have sexually dimorphic faces. Male and female faces diverge at puberty. In males, testosterone stimulates the growth of the jaw, cheekbones, brow ridges, center of the face (from brow to bottom of nose) and facial hair (e.g. Verdonck et al. 1999). In females, growth of these traits is inhibited by estrogen, which may also increase lip size (Thornhill & Møller, 1997). Because sexual dimorphism increases at puberty, sexually dimorphic traits signal sexual maturity and reproductive potential (Thornhill & Gangestad, 1996). Thus, it has been suggested that women's preferences for male facial traits may be adaptations for identifying healthy mates with good genes. However, studies linking facial attractiveness and health measures in men have found only weak or no association between facial attractiveness and health (Kalick, Zebrowitz, Langlois, & Johnson, 1998; Langlois et al., 2000; Zebrowitz & Rhodes, 2004). Thus, my aim in the first study (I) was to test whether facial attractiveness in men is associated with a direct measurement of the strength of their immune system.

Women have smaller waist relative to hips (WHR) and larger breasts than men. Men have larger shoulders and narrower hips (SHR), making men's bodies more Y shaped than women's bodies. Women also have longer legs relative to height than men, and men are taller than women. These sex differences in human body shape and size are thought to result from sexual selection by enhancing success in male-male rivalry in men and fecundity selection in women (Carrier, 2007; Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004; Pawlowski, Dunbar, & Lipowicz, 2000). However, it is possible that these secondary sexual characteristics are preferred in inter-sexual selection because they signal the phenotypic quality of the bearer. For example, women with hourglass shaped bodies (large breasts and a narrow waist) have higher fecundity as assessed by

precise measurements of daily levels of 17-beta-oestradiol and progesterone than less curvaceous women (Jasienska et al., 2004). However, the attractiveness of men's bodies has received much less attention among evolutionary psychologists, although Wallace has made the suggestion that the attractiveness of the male body is a reliable indicator of male quality as an alternative to Darwin's good taste explanation (Cronin 1991). Recently, Brown et al. (2008) found by using a 3D optical body scanner, that men with an attractive body were more symmetrical than less attractive men, suggesting that the attractiveness of men's bodies indicates phenotypic quality. If parasite-mediated sexual selection plays a role in sexual selection in men, one could think that attractiveness of men's bodies could signal men's resistance against parasites and pathogens. However, to the best of my knowledge there are no studies to test whether the attractiveness of the male body signals the strength of immune defense. The aim of my second study (II) was to test whether the attractiveness of men's bodies is correlated with the strength of immune defense. Another aim was to study those traits which work as a cue of a strong immunity in the face and body.

Evolutionary psychologists have considered masculinity to serve as a secondary sexual cue to immunocompetence in human mate choice (Rhodes, 2006; Rhodes et al., 2003; Thornhill & Gangestad, 1999; Thornhill & Gangestad, 1993). Studies in many animals have found a positive link between the expression of secondary sexual ornaments and health (Møller, Christe, & Lux, 1999). In humans facial masculinity is perceived as healthy, suggesting that women interpret masculine traits as a sign of health (Rhodes et al., 2003). However, the relationship between masculinity and health measurements is not consistent across studies. Rhodes *et al.* (2003) found facial masculinity to be correlated modestly with actual health in adolescent males (Rhodes et al., 2003), and Thornhill & Gangestad (2006) found that men's facial masculinity correlated negatively with the incidence and duration of respiratory disease over the previous three years and a lower incidence of antibiotic use. However, masculinity was associated with stomach and intestinal infections. Although MHC heterozygosity (diversity at the major histocompatibility complex) is known to be associated with strength of immunity in humans and other animals Lie *et al.* (2008) did not find any significant relationship between facial masculinity and genetic diversity in MHC region of the male genome. However, whether masculinity is

associated with direct measurement of the strength of men's immune systems has not been tested.

Interestingly, although females of many species have been shown to prefer males with extravagant secondary sexual ornaments, the effect of facial masculinity on facial attractiveness in human males is not clear. Studies using normal faces have found that the rating of masculinity correlates positively with the attractiveness ratings of faces, but studies using photographic sex continua generally show a preference for feminized male faces (reviewed in Rhodes 2006). It has also been found that women vary greatly in the extent to which they prefer male masculinity: women with higher estradiol concentrations exhibit stronger preferences for the faces of men with higher testosterone concentrations than women with lower estradiol concentrations (Roney & Simmons 2008). Furthermore, in the fertile (late follicular) phase of the menstrual cycle, women have been found to have an increased preference for facial and bodily masculinity (e.g. Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001; Little *et al.* 2007; but see Rantala *et al* 2010). It has been found that masculine men are less likely to invest in offspring and relationships than feminine men (e.g. Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008), which may be why women find femininity in male faces more attractive at the non-fertile phase of their menstrual cycle. Thus, depending on women´s reproductive strategy women may prefer different degrees of masculinity in the male face. One possible explanation for the inconsistent findings on the effect of masculinity on facial attractiveness judgments in women may be due to a trade-off between the benefits (e.g. genetic quality) and costs (e.g. negative personality attributes) associated with masculinity (e.g. Pawlowski & Jasienska 2005, Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001; Little *et al.* 2007).

In humans like other animals, choosing the right partner is an important decision with large fitness consequences. Women can derive many benefits, like resources, "good genes", or parental care by carefully choosing their partner(s). Whether mate-choice decisions are modulated by cultural or prevailing environmental conditions, has received only very little attention by evolutionary psychologists. However, studies on other animals have shown that female preference for male traits can be affected by many environmental factors, such as predation risk, social factors, cost of sampling, resource

quality as well as female competition (Jennions & Petrie, 1997). Recently, DeBruine et al (2010) tested cultural variation in women's preferences for facial masculinity across 30 countries by presenting pairs of pictures that were masculinized or feminized. They compared a health index derived from the WHO's statistic for mortality rates, life expectancies and the impact of communicable diseases with women's preferences for facial masculinity. They found that women's preference for facial masculinity in men increased when the health index of the nation decreased (DeBruine, Jones, Crawford, Welling, & Little, 2010). It has been found that circulating testosterone levels is more closely related to adiposity than masculinity (Rantala et al., 2013), and both the testosterone levels and stress hormone levels of men do interact and have an influence on facial attractiveness (Rantala et al., 2012). Thus, the aim of my third study was to test whether women's preferences for cues of testosterone or cortisol change cross-culturally.

Secondary sexual characters may also be expressed in females, and males can also be choosy in their mate preferences, especially in those species demonstrating biparental care (Cluttonbrock & Vincent, 1991). However, little is known about the extent to which female ornamentation indicates benefits to males. Although the immunocompetence-handicap hypothesis was originally developed for males, it is possible that by preferring more ornamented females as mates, males may also benefit from securing a healthy partner and enhancing the immunocompetence of their offspring. However, there have been very few tests of relationships between female ornamentation and parasite resistance, with extant tests in avian species showing mixed results (Parn, Lifjeld, & Amundsen, 2005; Roulin, Riols, Dijkstra, & Ducrest, 2001).

Although humans appear to lack elaborate secondary sexual ornaments, we have sexually dimorphic facial characteristics that diverge from puberty. Because sexual dimorphism increases at puberty, sexually dimorphic traits signal sexual maturity and reproductive potential. Since in humans both sexes are choosy, one could predict that female facial attractiveness may also be associated with immune defense and sex hormone levels (Law Smith et al, 2012). However, to my knowledge studies testing the association between female facial attractiveness, immune defense and stress hormone levels are lacking. The aim of my fourth study was to test whether facial attractiveness in women is associated with the strength of their immune response, circulating levels of the stress hormone cortisol and adiposity.

Although good looks is an important criterion in mate choice for both men and women, it has been found that men rate the odor of women as almost as important as their visual appearance when choosing their mate (Herz & Cahill, 1997). In contrast, women's assessments of men's odours has shown to be more important than male looks, voice, wealth and all social factors except his pleasantness (Herz & Inzlicht, 2002). Women have been found to be more olfactory oriented in general, not only in mate choice context (Havlicek et al., 2008). It has been thought that odors play an important role in mate choice in many species because they do reveal the state of an individual's health (Kavaliers, Choleris, Agmo, & Pfaff, 2004; Penn & Potts, 1998), immunocompetence (Rantala et al., 2002; 2003a,b), social dominance (Havlicek, Roberts, & Flegr, 2005; Kortet & Hedrick, 2005), mate compatibility as a reproductive partner (Havlicek & Roberts, 2009), phase of menstrual cycle (Havlicek, Dvorakova, Bartos, & Flegr, 2006; Kuukasjärvi et al., 2004) and many other things (Havlicek & Lenochova, 2006; Roberts et al., 2011). Thus, women could use their sense of smell to choose a mate with preferable qualities. It has been found that androstenol, a steroid chemical precursor of androstenone, contributes importantly to human body odor in men, giving a musky smell (Gower & Ruparelia, 1993). Androstenol is produced in the adrenal glands and its metabolism follows a common steroidogenetic pathway (Dufort, Soucy, Lacoste, & Luu-The, 2001). Thus, we could expect that circulatory hormones could contribute to the attractiveness of body odors in men. The aim of the last study (V) was to test whether attractiveness of men body odour is associated with his sex hormone or stress hormone levels.

2. STUDIES

2.1. Study I.

Evidence for the stress-linked immunocompetence handicap hypothesis in humans.

To study whether facial attractiveness in men is associated with the strength of their immune system, we photographed and vaccinated 74 young men with hepatitis B vaccine. A month before and after the shot, we took a blood sample to measure the amount of hepatitis B antibodies (specific immune proteins that help the body defend against foreign invaders). In addition, we measured their plasma testosterone and cortisol levels. Women rated the attractiveness of the pictures. We found positive relationships between testosterone, facial attractiveness and immune response to a hepatitis B vaccine. In addition, we present evidence that these relationships are moderated by levels of cortisol, a naturally co-occurring stress hormone. Our results are the first to show that human female face preferences are correlated directly with a measure of male immune function, and we also provide evidence for a possible moderating role of glucocorticoids in relationships between testosterone, secondary sexual trait expression and immune function. Our study provides strong support for the hypothesis that perception of facial attractiveness is an adaptation for identifying higher-quality mates.

2.2. Study II.

Adiposity found to be a more valid cue to immunocompetence than masculinity in human mate choice.

To study which traits in men's face and body reveal immunocompetence we took facial and full body photographs of 69 Latvian men and young Latvian women rated for their attractiveness. We vaccinated the men with hepatitis B vaccine and measured the amount of specific antibodies produced and their plasma testosterone levels. In addition, we measured each participant's percentage body fat (a more accurate measure of adiposity than BMI) and a group of people rated the perceived masculinity of each man's face and body. Latvian women rated the attractiveness of the pictures of faces and bodies. We found that men's ability to produce antibodies against the hepatitis B vaccine was positively correlated with attractiveness of the faces and bodies, suggesting that the attractiveness of men's faces and bodies are both associated with the strength of their immune defense. Surprisingly, we found that masculinity was not related to both attractiveness and antibody response in either the body or the face. Instead, we found that adiposity, but not masculinity, mediates the relationship between men's immune responsiveness against hepatitis B antigenes (which is a direct measure of immune response) and both their body and facial attractiveness. Interestingly we also found that the circulating levels of testosterone in plasma is more closely associated with adiposity than masculinity in men. Our study suggests that adiposity is a more important cue to immunocompetence than facial or body masculinity in human mate choice.It is possible that masculinity plays more important role in intersexual interactions than on intersexual selection (see e.g.Hill et al. 2013).

2.3. Study III.

Cross cultural analysis of women's preferences for cues to sex- and stress-hormones in the male face.

To test cross-cultural variation in women's preference, we tested the preferences of 2842 women from 13 countries towards facial composite pictures constructed to differ in combinations of testosterone or stress hormone levels. We found statistically significant

relationships between a measure of the societal development (the United Nations human development index 2011, HDI) of countries and the mean preference of women for cues to testosterone in the men's face. In addition, we found the interaction between preferences for cues to testosterone and cortisol with the HDI of country. Interestingly, there was also a statistically significant relationship between preferences for cues to testosterone and a societal-level measure of parasite stress. We found a clear preference for low cortisol across countries and in no instance did women prefer high-cortisol faces. However, we found no between countries differences in preference for facial cues to cortisol. Our study suggests that ecological and cultural factors may cause cross-cultural differences in women's preference for cues of testosterone in men faces.

2.4. Study IV.

Association between women's facial attractiveness, immune responsiveness, cortisol levels and body fat.

To test whether facial attractiveness in women reflects the strength of their immune defense, we photographed young Latvian women, vaccinated them against hepatitis B and measured the amount of specific antibodies produced, plasma cortisol levels and the percentage of body fat. Next, Latvian men rated the attractiveness of the women's faces. Interestingly, and in contrast to men, we found that in women immune responsiveness (amount of antibodies produced) did not predict facial attractiveness. Instead, plasma cortisol level was negatively associated with attractiveness, indicating that stressed women look less attractive. We also found that fat percentage was curvilinearly associated with facial attractiveness, indicating that being too thin or too fat reduces attractiveness. Our study suggests that in contrast to men, facial attractiveness in women does not indicate immune responsiveness against hepatitis B, but is associated with two other aspects of long-term health and fertility: circulating levels of the stress hormone cortisol and percentage body fat. Thus, the study suggests that the standards of female beauty are not arbitrary cultural conventions as social scientists have long stated (e.g. Berry 2000, Etcoff 1999). My study also suggests that men seek to avoid cues for stress in potential mates (Moore, et al., 2011a,b)

2.5. Study V.

Male steroid hormones and female preference for male body odor

In this study we tested with a classical T-shirt sniffing experiment whether women's olfactory preferences for a man's scent could be correlated with his testosterone, estradiol, or cortisol concentrations in saliva. 19 young Finnish men wore a T-shirt for 5 h while watching movies. We collected three saliva samples taken from each male participant during the duration of the study. Later seventy-six young Finnish women sniffed the t-shirts and rated the intensity and attractiveness of the body odor. Surprisingly, we found that cortisol concentration in saliva correlated positively with the attractiveness but not with the intensity ratings of male T-shirt odor. However, neither testosterone nor estradiol was significantly associated with the ratings of attractiveness or intensity. Although, we found that women in the most fertile period of their menstrual cycle gave the highest attractiveness ratings to all men, the intensity ratings by women did not changed with her cycle. Surprisingly, the phase of their menstrual cycle did not effect on the preference for body odor according to men's' stress or sex hormone levels, instead women seemed to prefer males with high cortisol levels. Our study suggests that visual attractiveness and attractiveness of body odors are differently associated with stress and sex hormones.

3. GENERAL DISCUSSION

In my thesis I found that both facial and body attractiveness correlate positively with men's ability to produce specific antibodies against hepatitis B antigens, suggesting that men who are physically attractive to women have stronger immune defenses than their less attractive peers. Thus, my findings are consistent with studies on other organisms which have found that the expression of secondary sexual ornaments or general attractiveness of males to females is associated with the strength of their immune defence (Ahtiainen, Alatalo, Kortet, & Rantala, 2004; Bonato, Evans, Hasselquist, & Cherry, 2009; Dunn, Garvin, Whittingham, Freeman-Gallant, & Hasselquist, 2010; Mougeot, 2008; Rantala et al., 2000; 2002; Rantala & Kortet, 2003; Saino, Ferrari, Romano, Rubolini, & Moller, 2003; Saks, Ots, & Horak, 2003). Thus, the attractiveness of men is more than skin deep.

Interestingly, I found that obese men had lower immune responsiveness than normal weighted men. This finding is consistent with previous work showing that obesity is associated with a poor antibody responses to hepatitis B vaccine (Minana, Ganuza, Millan, & Fernandez, 1996; Weber, Rutala, Samsa, Santimaw, & Lemon, 1985) and that obesity is associated with incidence and the severity of many infectious diseases (Nieman et al., 1999). Thus, by preferring men with a lower BMI women may be selecting men with a stronger immune defense and better general health. Furthermore, one could expect that obesity reduces success in male-male competition. Therefore, unless there are compensatory mechanisms or environments in which the propensity for obesity might be advantageous, sexual aversion against obese men might be highly adaptive for women.

Previous studies have found that males with more attractive faces have higher genetic diversity within MHC (Lie et al., 2008; Roberts et al., 2005).We have also

found in this population that attractive men had higher genetic diversity within their major histocompatibility complex (MHC) (Hakkarainen et al., unpublished). MHC heterozygosity is especially important for immune function because MHC alleles encode peptides that bind to and present a restricted range of antigen-peptides to T-cells, thereby initiating a rapid immune response (Piertney & Oliver, 2006). MHC heterozygosity has been found to be positively correlated with resistance against viral infections, including hepatitis B virus (Thursz, Thomas, Greenwood, & Hill, 1997). If males with more attractive faces had higher genetic diversity within MHC then they would be able to detect hepatitis antigens faster and mount stronger immune responses than less attractive men. Thus, the association between strength of immune response and attractiveness that we report here might provide a mechanism for the relationship between genetic diversity and facial attractiveness found in previous studies. If the heterozygosity is the "good genes" that females choose (Brown, 1997), it would explain why unattractive bodies wouldn't just be selected out of the population. On the other hand, healthy life styles (Pölkki & Rantala, 2009), nutrition, social dominance and many other environmental factors like pollutants (Jerrett et al., 2010) may influence attractiveness, but they may also influence the strength of the immune system.

Recent mathematical models suggest that females may gain little or no fitness advantage by selecting for male immunocompetence (Adamo, 2004; Adamo & Spiteri, 2005). However, if the attractiveness of men does not signal general immunocompetence, but more specific resistance against those parasites and pathogens that are most common and important in the current environment, like Hamilton & Zuk's hypothesis predicts (Hamilton & Zuk, 1982), women may increase their fitness by mating with attractive men, because it would increase the strength of immunity of their offspring. On the other hand, in the case of humans and other species with biparental care, females would get also a direct benefit from mating with attractive males with strong immune defence since this could potentially provide more direct benefits in the form of resources, parental care or reduced risk of contagion due to their good health than less attractive males.

Secondary sexual characters may also be expressed in females, with males demonstrating choosiness in their mate preferences, especially in those species with biparental care (Cluttonbrock & Vincent, 1991; Kokko & Johnstone, 2002; Parker,

2006). However, little is known about the extent to which female ornamentation signals benefits to males. Although the immunocompetence-handicap hypothesis was originally developed for males, it is possible that by preferring more ornamented females as mates, males may also benefit from securing a healthy partner and enhancing the immunocompetence of their offspring. However, there have been fewer tests of the relationship between between female ornamentation and parasite resistance, with extant tests in avian species showing mixed results (Parn et al., 2005; Roulin, Jungi, Pfister, & Dijkstra, 2000; Roulin et al., 2001). For example, in the Barn owl, *Tyto alba*, Roulin et al (2001) found that immune responsiveness against a non-pathogenic antigen in cross-fostered nestlings was positively correlated with the plumage spottiness of the genetic mother but not of the genetic father, suggesting that female ornamentation signals genetic quality. Instead, in bluethroats *Luscinia s. svecica* Parn et al., (2005) found that female throat ornamentation does not reflect cell-mediated immune response. Surprisingly, although I found that men's facial attractiveness was associated with the strength of their immune system, I did not find any association between facial attractiveness and the strength of immunity in women. Instead, I found that facial attractiveness in women was associated with plasma stress hormone levels. Body fat was also linked to attractiveness, such that the thinnest and fattest women were seen as the least attractive. Since stress, obesity and being underweight causes fertility problems (Glaser & Kiecolt-Glaser, 2005; Richedwards et al., 1994), it seems that female beauty is a cue about high fertility and high reproductive value, but not good genes. This is consistent with the hypothesis that women try to maximize the quality of their offspring and men try to maximize the quantity (Symons 1979, Williams 1975).

It has been found that body mass index is strongly associated with facial adiposity (the perception of weight in the face), which predicts perceived health and attractiveness in faces (Hume & Montgomerie 2001; Coetzee *et al.* 2009). It has been shown that perceived facial adiposity is associated with cardiovascular health and reported infections (Coetzee et al. 2009). Thus, it has been suggested that facial adiposity may serve as a cue to health (Coetzee et al. 2009). Likewise, we found that adiposity had a substantial effect on attractiveness in both sexes even when the effect of all other factors was controlled.

At the first glance the association between the amount of antibodies produced and attractiveness ratings seems rather weak. However, there were substantial differences in attractiveness between men whose immune system recognized the antigen than those whose immune system did not recognize the antigen. It is possible that the ability to produce lots of antibodies might be more sensitive to nutrition and the current health state than the ability to recognize the antigen. It is important to note that our study was performed in a society with relatively good nutrition and medical care. It would be interesting to replicate the study in a society with poor nutrition and medical care. It has been previously demonstrated that human preferences for physically attractive mates are strong in the areas where parasite prevalence is high (Gangestad & Buss, 1993). Thus, one could expect that in the population with high parasite prevalence and poor medical care the association between the strength of the immune system and body attractiveness might be stronger than in our study. Likewise, in our evolutionary history parasite mediated sexual selection might have played a much more important role than in modern times (Rantala, 1999, 2007).

One could criticise our methods to measure the strength of the immune system because we measured only one parameter of the immune system, the ability to produce antibodies against a vaccine (Adamo, 2004). It is important to note that immunoecological studies on birds and other animals have commonly used the vaccination method to measure the strength of immune system for a long time (Kilpimaa, Alatalo, & Siitari, 2004; Peters, Delhey, Denk, & Kempenaers, 2004; Saino et al., 2003; Ujvari & Madsen, 2006). However, immunoecological studies in humans where the strength of immunity has been measured has been lacking. It is important to note that we measured men's ability to produce antibodies against the hepatitis-B virus, which is ecologically a very important pathogen for humans. This is because the current global estimate of the number of chronic Hepatitis B-infected individuals is 350 million, with it being the most common cause of chronic liver disease worldwide (Custer et al., 2004). Although the immune system of most people who become infected with hepatitis-B virus is able to clear the virus and subsequently become immune to the virus, the hepatitis-B virus may cause hepatic fibrosis and eventually cirrhosis, terminal liver disease. It has been estimated that 600 000 people die each year due to the acute or chronic consequences of hepatitis B (Custer et al., 2004). The Hamilton-Zuk hypothesis

(Hamilton & Zuk, 1982) predicts that sexual ornaments reveal males' resistance against the parasites and pathogens that are the most common and significant in the currently prevailing environment. Thus, we think that the use of immune responsiveness against hepatitis-B virus to measure the strength of men's immune system makes ecologically more sense if we are testing the Hamilton-Zuk hypothesis than if we would measure the ability to produce antibodies against evolutionary novel antigens or any indirect measure of the function of immune system. However, it would be interesting to know whether the attractiveness of men or women correlates with other components of the immune system, resistance against any other pathogens or resistance to parasites. Thus, more studies are needed in this field.

It has been previously demonstrated that human preferences for physically attractive mates are strong in the areas where parasite prevalence is high (Gangestad & Buss, 1993). This might be adaptive if physical attractiveness would signal the strength of the immune system. My studies strongly support the hypothesis that the perception of facial attractiveness in men may be an adaptation for identifying higher-quality mates, particularly ones with good disease resistance especially under poor economic conditions (Gangestad & Buss, 1993). In our study (IV) we found that women's preference for cues of testosterone and cortisol varies between countries. There was a relationship between preferences for cues for testosterone and a societal-level measure of parasite stress and also a societal-level measure of development. Thus, our findings suggest that ecological factors may shape mate preferences at a societal-level. This is consistent with studies that have found geographic variation in mate preferences which may reflect environmental conditions or cultural difference (DeBruine et al., 2010; Kushnick 2013; Marlowe, 2004; Rantala, Pölkki, & Rantala, 2010; Sear & Marlowe, 2009; Wetsman & Marlowe, 1999; Yu & Shepard, 1998). It would be interesting to test whether women's preferences for other traits associated with testosterone levels, like for example dominant behaviour (Mehta & Josephs, 2010) and voice qualities (Dabbs & Mallinger, 1999) also varies between societies in a similar way. This remains to be tested in future studies.

In study number V, I found that the attractiveness of men's body odor was neither associated with his saliva testosterone nor estradiol levels. Instead, the attractiveness of men's body odours were positively correlated with their saliva cortisol level. This

contrasts with my finding that saliva cortisol reduces the attractiveness of faces in all countries that participated the survey. It is possible that body odours signal different qualities to choosy females than is signalled by facial attractiveness. My results are surprising, because high cortisol levels make us sweat. Although sweat alone is not stinky, bacteria that lives on the skin changes it so that it starts to smell stinky (Stoddard 1991). However, in my study cortisol levels were not associated with intensity of body odor, so the effect of cortisol on body odor is probably not simply due to increased sweating. Thus, it seems that cortisol influence on scent is qualitative. It is also possible that in all men stress hormone levels were so low due to the experimental set up that it did have a negative effect on body odor in this study. Interestingly, Thornhill *et al.* (2013) carried out a similar study in USA and found that the attractiveness of men's body odor correlated positively with his testosterone levels. They speculated about the possible reason for the discrepancy by saying that this might be due to the differences in methods used or the difference in statistical power (Thornhill, Chapman, & Gangestad, 2013). However, it is possible that there are also societal level differences in women's preference for cues of testosterone in men's body odors. Since in study number III we found that in Finland women had the weakest preference for facial cues of testosterone in the world (see figure 1), it is possible that Finnish women also have the weakest preference for the scent of men with high testosterone levels. This would explain the discrepancy between our study and their study. This societal-level difference in women's preference for cues of testosterone would also explain why I found in studies (I and II) that Latvian women did prefer the faces and bodies of men with high testosterone levels, but in study (V) I found that testosterone levels were not associated with the attractiveness of a body when sniffed by Finnish women. This possible societal-level difference in women's preference for body odours remains to be tested in future studies.

4. CONCLUSIONS

Facial attractiveness is important for human mating behavior (Rhodes, Simmons, & Peters, 2005) and associated with reproductive success (Jokela, 2009). In my thesis I show that the physical attractiveness of men is associated with the strength of the immune system. Thus, in the light of my studies, it seems that parasite mediated sexual selection plays an important role in mate choice in modern humans, despite the advanced medical care which has made many previously common parasites and pathogens rare in modern society. My studies support the hypothesis presented by evolutionary psychologists that the perception of attractiveness is a sexually selected adaptation for finding good mates (Fink & Penton-Voak, 2002; Rhodes, 2006; Thornhill & Gangestad, 1999). Attractive men with a strong immune defence could provide potentially more direct benefits in the form of resources, parental care or reduced risk of contagion due to their good health than less attractive men for women. Likewise, facially attractive men with a strong immune defense could provide indirect genetic benefits to offspring, such as heritable resistance to parasites and pathogens. However, attractive men had higher plasma testosterone levels which potentially decreases their paternal investment due to higher mating effort (Booth & Dabbs, 1993). Thus, our study supports the hypothesis that women meet a trade-off between good genes and paternal care when selecting their mates, which might explain why women have the strongest preference for masculinity when they are most likely to conceive (Gangestad & Thornhill, 2008). In addition, my findings that facial attractiveness in women is associated with stress hormone levels and body fat percentage, suggest that perception of facial attractiveness in women is also a sexually selected adaptation for finding good mates (Fink & Penton-Voak, 2002; Rhodes, 2006; Thornhill & Gangestad, 1999), because both stress hormone levels and body fat percentage are associated with long term health and fertility (Campagne, 2006; Pisunyer, 1993). Thus, we could expect that those men in our evolutionary history who

married woman with facial features that is perceived as attractive probably got more offspring than those men who married woman with facial features that is perceived as unattractive. If the facial preference has heritable components, we could expect to find a correlation between facial attractiveness and traits associated with fertility and long term health, as I found in my thesis. Thus, my thesis suggests that the standard of beauty has deep biological roots.

There is also the applied side in my findings. The finding that physical attractiveness is associated with the strength of immune defense and hormone levels makes it possible to influence our own attractiveness by influencing the strength of our immune defence, testosterone levels or stress hormone levels. This can be done by living a healthy life style, avoiding stress and eating the right nutrients that enhance immunity or reduce stress hormone levels (e.g. Pölkki & Rantala, 2009; Puertollano, Puertollano, de Cienfuegos, & de Pablo, 2011). In addition, if facial and bodily attractiveness reveal a person's state of health, a medical doctor may use the physical appearance of patients to diagnose the ultimate factors behind possible health problems and instruct patients on life style changes rather than just offering cures for the currently showing symptoms of bad health.

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