Kandrik, Michal. (2016) *Variation in men's mate preferences and mating strategies*. PhD thesis.

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Variation in Men’s mate preferences and mating strategies

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MA Honours, MSc

Submitted in fulfillment of the requirements for the
Degree of Doctor of Philosophy

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October 2016

Abstract

The vast majority of research investigating mating strategies and mate preferences focused on variation among and within women. However, there are strong theoretical reasons to expect systematic differences in men's mating strategies and mat preferences as well. In this thesis I present four empirical chapters investigating variation in men's mating strategies and face preferences. The first empirical chapter investigates the regional variation in men's and women's sociosexual orientation across US states, using improved measures of sociosexuality and multilevel modeling. I show that scarcity of female mates, but not health risks or wealth predict people's sociosexual orientation. Women and men in states, where female mates were scarce reported being less willing to engage in uncommitted sexual relationships. In my second empirical chapter I present a study investigating the relationship between men's hormone levels and men's preferences for healthy color cues in faces. I show that men with the combination of high testosterone and low cortisol show the weakest preferences for yellower and darker skin; a color profile associated with carotenoid coloration. The third chapter tests for within-subject effects of hormones on men's perceptions of vocal characteristics. I show that within-subject changes in men's hormone levels were not associated with preferences for sexually dimorphic acoustic properties in women's or men's voices. In the final chapter I present a study testing for relationships between men's facial appearance and their hormone levels and show that men's rated facial dominance is lowest among men with high cortisol and low testosterone, but that men's rated facial attractiveness and health are unrelated to their hormone levels.

The findings of this thesis demonstrate that there is meaningful systematic variation in men's mating strategies at a regional level and that men's face preferences are associated with their trait hormone levels in an adaptive fashion. I also show that previously reported within-subject hormonal modulation of femininity preferences in human faces does not occur for human voices. Lastly the results of my final experimental chapter suggest that adult hormone levels may not be as important for men's facial appearance as previously thought.

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Publication statement

Parts of this thesis were published or are currently under review

Kandrik, M., Jones, B. C., DeBruine, L. M. (2015). Scarcity of female mates predicts regional variation in men's and women's sociosexual orientation across US states. *Evol. Hum. Behav.*, *36*, 206 – 210.

Kandrik, M., Hahn, A. C., Fisher, C. I., Wincenciak, J., DeBruine, L. M., Jones, B. C. (2017). Are physiological and behavioral immune responses negatively correlated? Evidence from hormone-linked differences in men's face preferences. *Horm. Behav., 97*

Kandrik, M., Hahn, A. C., Wincenciak, J., Fisher, C. I., Pisanski, K., Feinberg, D. R., DeBruine, L. M., Jones, B. C. (2016). Are men's perceptions of sexually dimorphic vocal characteristics related to their testosterone levels? *PLOS ONE*, *11,* doi: /10.1371/journal.pone.0166855.

Kandrik, M., Hahn, A. C., Han, CH., Wincenciak, J., DeBruine, L. M., Jones, B. C. (*under revision*). Do salivary testosterone and cortisol levels predict men's facial appearance? *Adapt. Hum. Behav. Physiol.* Invited revision.

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Acknowledgment

It is an understatement to say that the last three years were intense. It has been a truly transformative time, and I could not have gotten through it without the support of others. I would therefore like to take this opportunity the express my gratitude to some folks that have come to mean a whole lot to me.

First I would like to thank Lisa DeBruine and Ben Jones for their guidance, patience, generosity and support. Thank you for directing the Face Research Lab the way you do, and giving me something to aspire to.
I would also like to thank Amanda Hahn, Claire Fisher, Iris Holzleitner, Hongyi Wang, Joanna Wincenciak, Vanessa Fasolt, Danielle Morrison, Ant Lee and Chengyang Han for all the good times, and the team spirit you contributed to in and out of the lab. You all have made me feel like I was a part of something and like I belonged and it means a lot.

Thank you to my Mum and Dad and my brother Matej for always supporting me and going out of your way to help me pursue my ambitions and dreams.

Thank you to Marek, Lisa and Theo Zemanik and the Melvin family for always treating me like one of your own and being my family away from home.

Thank you Jeanne, for your words of encouragement, for proofreading, for sharing ideas, for believing.

Lastly I would also like to thank the ESRC and ERC who funded my PhD and my research.

Authors declaration

I, Michal Kandrik, hereby certify that this thesis has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

Date: 24 October 2016 Signature:

Chapter 1: Introduction

1.1 Variation in mate preferences and mating strategies

One of the most consistently reported sex differences between women and men is in willingness to engage in uncommitted sexual relationships (Schmitt, 2005). This difference is mainly explained by the differential costs of reproduction in women and men, such that women, whose reproductive costs are high, show on average much more restricted willingness to engage in uncommitted sex. On the other side, men's reproductive costs are relatively low, and they are more open to uncommitted sex on average (Penke & Asendorph, 2008; Schmitt. 2005; Simpson & Gangestad, 1991). Because of these differential reproductive costs we might expect women to be choosier and more sensitive to cues of quality in potential mates on average, in order to maximize their reproductive fitness, while we might expect men to pursue as many mating opportunities as possible to maximize their reproductive fitness. However while there are some large differences between the sexes, there is also a considerable amount of variation in both mating strategies and mate preferences within sexes (Gangestad & Simpson, 2000).

The dominant model explaining variation in mate preferences and mating strategies is the Trade-off theory by Gangestad and Simpson (2000).
This theory posits that people's mate preferences and mating strategies should be adaptive in response to their environment, in order to maximize their reproductive efforts. In women, these trade-offs mainly occur between obtaining the mate with best possible heritable genetic fitness and a mate who will provide the most parental investment. However, men displaying characteristics associated with good condition tend to be perceived negatively as good parents (e. g., Perrett et al., 1998), and men with higher testosterone levels (putative proxy of good condition) tend to show less interest in parental effort (Mascaro, Hackett & Rilling, 2013). To date, the majority of the research investigating factors influencing variation in mate preferences and mating strategies focused on women. However it is reasonable to expect that men should also vary in their mate preferences and mating strategies, as men also face trade-offs, such as investment of time and energy between mating and parenting effort. Men's resolution of these trade-offs might be influenced by

women's mating strategies as well as men's own physical condition and status, as only high-quality men might be able to maximize their reproductive fitness by pursuing multiple mating opportunities, while men of relatively lower quality might maximize their reproductive fitness by committed investment in their relationship and offspring (Gangestad & Simpson, 2000).

One measure of mating strategies is sociosexual orientation. It indexes individuals' willingness to engage in uncommitted sexual relationships. It is measured by the Sociosexual Orientation Inventory (Simpson & Gangestad, 1991), which was later revised by Penke & Asendoprf (2008). The revised Sociosexual Orientation Inventory (SOI-R) is composed of 3 subscales measuring sociosexual desires (e.g., In everyday life, how often do you have spontaneous fantasies about having sex with someone you have just met), attitudes (e. g., Sex without love is ok) and behaviors (e.g., With how many different partners have you had sex on *one and only one occasion*?). It has a high test-retest reliability, and higher scores on the SOI or SOI-R reflect people's greater reported willingness to engage in uncommitted sexual relationships. The SOI-R also improves on the SOI by replacing opened questions on sexual behavior in the original SOI with multiple choice answers which reduce the skew of the data by truncanting the scores associated with very high number of previous sexual partners, and one-night stands (Penke & Asendorpf, 2008) .

Below I will discus previous research investigating variation in people's mating strategies and mate preferences at regional level, individual level, and within-individual level.

1.2 Regional variation

1.2.1 Variation in health risks

Based on the trade-off theory, mate preferences and mating strategies should be affected by both benefits and costs related to mating strategies. One potential cost is health risks. The effects of increased health risks on people's mating strategies should reflect greater need for biparental care to increase offspring viability, and also people's increased avoidance of contagious pathogens detrimental to their fitness (Barber, 2008; Schaller & Murray, 2008; Schmitt, 2005; Thornhill et al., 2010). Studies investigating regional variation in health risks such as pathogen stress or infant mortality and sociosexuality find that people in regions where health risks were high reported being less willing to engage in uncommitted sexual relationships (Schaller & Murray, 2008; Thornhill et al., 2010; Schmitt, 2005, but see Barber, 2008). Studies investigating health risk dependent regional variation in women's mate preferences reported that women in countries where health is particularly poor show stronger preferences for men's faces exhibiting cues to good condition such as masculinity (DeBruine et al., 2010a, 2011, Moore et al., 2013; but see Scott et al. 2010) In men, Marcinkowska et al., (2014) reported a negative correlation between an index of national variation in health and men's preferences for women's facial femininity. This finding may reflect that men in countries where health is particularly poor resolve the mate preference trade-off between preferring mates displaying cues to fertility and mates displaying cues of higher viability in favor of more masculine, dominant women who may have higher resource acquisition and resource holding potential, and are therefore more likely to survive (Marcinkowska et al., 2014).

1.2.2 Variation in mating markets

Variation in mating markets, more particularly in the composition of the mating market, affects mating strategies because of the sex difference in mating strategies explained earlier. This enables people of the sex that is more scarce to be better able to pursue their preferred mating strategy while the people of the sex that is more abundant in the population might have to adjust their mating strategy in order to secure a mate. On a regional level, research has shown that variation in mating markets (e.g., sex ratio) predicts sociosexuality for both men and women (Schimtt, 2005). Furthermore, other indirect indices of mating strategies such as choosiness in mate preferences (Stone et al., 2007), use of financial resources (Griskevicius et al., 2012), and various marriage statistics (Kruger, 2009; Lichter et al., 1992; South & Trent, 1988) were also linked to variation in the composition of mating markets.

1.2.3 Variation in resource availability

Some of the variation in mating strategies is also explained by resource availability. Indeed in countries where resources are scarce, committed parental investment may be crucial for offspring survival. Previous studies have reported positive associations between people's willingness to engage in uncommitted sexual relationships and various indices of resource scarcity (e.g., gross national product, gross domestic product per capita, etc.) (Barber, 2008; Lippa, 2009; Schmitt, 2005). Also some studies reported relatively stronger positive associations between women' sociosexuality and resource availability than men's sociosexuality and resource availability, potentially reflecting greater importance of resources for women's greater engagement with offspring care (Barber; 2008; Lippa, 2009; Schmitt, 2005;).

1.3 Trait level variation

1.3.1 Sociosexuality

Previous studies have shown that women's preferences for masculine or symmetric men are positively associated with their sociosexuality (Waynforth et al., 2005). However, a more recent study by Sacco et al. (2012) showed that this effect is only present in single women but not partnered women. Lee et al. (2014) found that men's and women's sociosexual negatively predicted their preferences for feminine women and masculine men, respectively, while men's sociosexual desire positively predicted their preferences for attractive and feminine women. However, other studies reported weak or no relationships between people's SOI-R scores and preferences for partners with exaggerated sexually dimorphic characteristics (Glassenberg et al., 2010; Welling et al., 2013). Kandrik, Jones & DeBruine (2014) showed that, among romantic couples, SOI-R scores predicted couples' perceptions of own-sex faces (i.e. men's perceptions of men's faces and women's perceptions of women's faces) but not other-sex faces, suggesting that people who are particularly willing to engage in uncommitted sexual relationships may be more sensitive to cues of quality in potential competitors for mates.

1.3.2 Own condition

Some aspects of variation in preferences for mates can be explained by individual level variation in own condition or own market value. Women of high market value (or women who perceive themselves to be particularly attractive) may be better able to attract and retain commitment and investment from masculine men. These effects have been demonstrated in preferences for masculinity in men's faces (Little et al., 2001, Little & Mannion, 2006), and voices (Vukovic et al., 2008). Similar effects of own condition were also reported for men’s preferences for female femininity. Kandrik & DeBruine (2012) showed that perceptions of one’s own attractiveness predicted general preferences for other-sex faces with exaggerated sex-typical characteristics in both men and women, while Burris et al. (2011) showed that men who perceived themselves to be more attractive showed stronger preferences for feminine women, but only in a context of a short-term relationship.

1.3.3 Pathogen threat

Another important factor affecting individual variation in mate preferences is pathogen threat and individual sensitivity to pathogens. Pathogens are considered to be one of the major selection pressures in human evolutionary history (Fumagalli et al., 2011), as contracting infectious diseases can rapidly reduce fitness of individuals or their offspring. It is reasonable to assume that mate preferences and mating strategies might in part reflect adaptations to minimize exposure to infectious disease. Multiple studies have shown that pathogen disgust sensitivity (the extent to which individuals report being disgusted by pathogen sources) positively predicts women’s preferences for masculine men’s faces and bodies (DeBruine et al., 2010b, Lee et al., 2015; Tybur et al., 2009), and men’s preferences for feminine women’s faces and bodies (Jones et al., 2013; Lee et al., 2015). Importantly these effects were independent of people’s sexual disgust sensitivity and moral disgust sensitivity suggesting that these effects are not artefacts of other aspects of disgust sensitivity. One important caveat is that majority of these studies investigated these effects using relatively young and homogeneous samples of participants and used images of young people. Lee and Zietsch (2015) tested for the same effects in more heterogeneous samples and stimuli, and only found the reported effects in one out of three studies. Lee and Zietsch (2015) found a positive association between women’s pathogen disgust and their masculinity preferences, when young women were judging faces of young men, This may reflect that pathogen disgust is particularly sensitive to qualities of potential mates, or that facial masculinity in older men is not necessarily associated with good condition, or that older women who are less likely to reproduce do not necessarily need to consider heritable immunocompetence associated with masculine face shape. Taken together the findings of Lee and Zietsch (2015) highlight the need to further examine these effects with more diverse participant populations and stimuli.

1.3.4 Resource availability

Researchers investigating individual differences in people's mate preferences also noted the importance of effects of resource availability, with the main hypothesis suggesting that people who are experiencing resource scarcity should show stronger preferences for partners exhibiting cues of access to resources. On a biological level, body fat deposits are considered to be an honest cue to access to resources (e.g., Swami & Tovée, 2007), and studies have shown that men's and women's socio-economic status (SES), a proxy for resource availability, negatively predicts men's and women's preferences for cues to body mass index (BMI) in other-sex individuals (Lee et al., 2015), women's preferences for men's masculinity (Lee et al., 2014, 2015) and men's preferences for women's breast size (Swami & Tovée, 2013).

1.4 State-level variation

1.4.1 Previous visual experience

Previous research has identified that recent exposure to faces influences perception of subsequent faces (Buckingham et al., 2006; Little et al., 2013, Jones et al., 2008a). This research on visual adaptation has shown that exposing participants to faces with particular facial characteristics (e.g., increased or decreased sexual dimorphism) causes changes in the perception of novel faces such that faces which are similar to the previously seen faces are perceived as more normal or attractive, and that these effects tend to be specific to the sex of face seen in the adaptation period (Little et al., 2013). While these findings overall suggests that adaptation recalibrates preferences to relative to population average based on previous visual experience, Jones et al (2008a) showed that these adaptation effects are modulated by facial attractiveness of images used in the adaptation phase as well as participant's attention. More recently, Little et al. (2014) also reported a sex difference in the effects of recent visual experience, whereby women's preferences for familiar men's faces (i.e., previously seen faces) were stronger than their preferences for unfamiliar men's faces (i.e. faces seen for the first time). By contrast, men's preferences were stronger for novel, unfamiliar women's faces than for familiar women's faces, potentially reflecting adaptive preferences for maximizing men's mating opportunities.

While the research above reported adaptation effects on preferences of faces of the same sex as the adaptation faces, Little & Mannion (2006) showed that these effects of visual experience also affect women's self perceptions, and their preferences for masculine men, such that women who were exposed to a series of images of particularly attractive women's faces, reported lower self-rated attractiveness and showed weaker preferences for masculine men's faces that did women who were exposed to relatively unattractive women's faces.

1.4.2 Pathogen threat

Previous research also identified that current pathogen threat salience influences people's preferences for sexually dimorphic faces. Little et al. (2011b) first primed participants with either images depicting pathogen threat, or similar images in which pathogen threat wasn't apparent. This study showed that people who were in the pathogen priming condition showed increased preferences for opposite sex faces with exaggerated sex-typical characteristics, while people who were in the no pathogen condition did not show a similar increase in preferences. Further corroborating evidence comes from Lee and Zietsch (2011), who showed that women who were primed with pathogen prevalence showed stronger preferences for men's traits associated with good genes (e.g., muscularity, confidence, intelligence).

1.4.3 Resource scarcity

Resource scarcity has also been implicated in within-subject changes in preferences. This research has shown that women primed with resource scarcity show stronger preferences for male characteristics associated with good parental quality (e.g., kindness, emotional warmth, commitment, high earning potential), since offspring survival may be more strongly dependent on biparental care under such conditions (Lee & Zietsch, 2011). Other studies showed that a physiological cue to resource scarcity (i.e., hunger) affected men's preferences for women's body size and breast size, showing that men who were hungry showed stronger preferences for women with larger breasts and higher BMI, than did satiated men (Swami & Tovée, 2013). However it is important to note that these studies used between-subject designs, where equivalence among experimental groups is assumed but not necessarily demonstrated.

1.5 Effects of hormones on mating strategies and mate preferences

1.5.1 Estradiol and progesterone

A large amount of studies suggests that women's preferences for masculine traits in men shift between the fertile and non-fertile phases of their menstrual cycle. Past research has shown that during the fertile phase, naturally cycling women (i.e. women not using hormonal contraceptives) show stronger preferences for more masculine faces (Little & Jones, 2012; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000), voices (Feinberg et al., 2006, Puts, 2005), body shape (Little et al., 2007c), and body odor (Grammer, 1993). Previous studies have also identified shifts in mating strategies, whereby women in the fertile phase of their menstrual cycle show greater interest in pursuing short-term/ extra pair mating opportunities (Gangestad et al., 2002). These findings are in line with the trade-off theory: they suggest that women are seeking genetic benefits for potential offspring when fertile, but show a preference for partner characteristics associated with greater commitment and parental investment (Gilderlseeve et al. 2014a) when conception is unlikely. Other researchers noted that during the fertile phase of the menstrual cycle women also tend to look more attractive (Roberts et al., 2004). Yet, there is still much controversy as to the extent (and indeed existence) of these menstrual cycle shifts, and their ultimate mechanisms (DeBruine et al., 2010c; Gildersleeve et al., 2014a, 2014b, Harris, 2011, 2013; Wood 2014; Wood et al., 2014). At least in part, this controversy may be due to the use of suboptimal methods for estimating the fertile window of women's menstrual cycle. Majority of previous studies have relied on counting methods, which do not accurately reflect the great variation in menstrual cycle length and precise timing of ovulation, both within and between women (Marcinkowska et al., 2016).

The menstrual cycle is characterized by fluctuations in sex hormone levels, in particular estradiol and progesterone. Ovulation (i.e. the fertile phase of the menstrual cycle) occurs following a peak in estradiol levels, while the post-ovulatory phase is characterized by relatively lower levels of estradiol and high levels of progesterone (e.g., Marcinkowska et al., 2016). These fluctuations are considered to be the proximate mechanisms via which women's shifts in mate preferences and mating strategies occur. Relatively few studies investigated women's mate preferences using actual hormone values (Feinberg et al., 2006; Marcinkowska et al., 2016; Pisanski et al., 2014a; Roney & Simmons, 2008). These studies showed that women's preferences for men's facial characteristics associated with high testosterone were positively associated with their estradiol levels, both between and within women (Roney & Simmons, 2008). However, more recently Marcinkowska et al. (2016) reported no relationship between women's estradiol levels and their preferences for men's facial masculinity. Women's preferences for men's vocal masculinity were positively associated with within-subject variation in estradiol (Pisanski et al., 2014a). One study also investigated the extent to which estradiol and progesterone affect facial processing, reporting that estradiol to progesterone ratio was positively associated with the reward value of attractive female faces and faces with exaggerated sexually dimorphic characteristics (Wang et al., 2014).

Research investigating the effects of estradiol and progesterone on women's appearance found that within-subject changes in estradiol positively predict changes in facial redness, possibly reflecting the vasodilatory effects of estradiol (Jones et al., 2015). Other researchers reported negative associations between women's composite measure of vocal and facial attractiveness and their progesterone as well as a negative relationship between women's attractiveness and the interaction between progesterone and estradiol (Puts et al., 2013). Earlier research on between-subject differences in women's attractiveness and hormone levels reported positive associations between women's facial attractiveness and estradiol (Law Smith et al., 2006), and estradiol to testosterone ratio (Probst et al., 2016).

1.5.2 Testosterone

Testosterone is the primary androgen (class of steroid hormones involved in development and maintenance of masculine features). It is produced within the hypothalamo-pituitary-gonadal axis, particularly by the Leydig cells in men's gonads. Testosterone levels follow circadian rhythm such that the highest levels are observed in the morning, and gradually decrease during the day (Dabbs, 1990). Research into the effects of testosterone on men has identified three main sensitive periods –perinatal, puberty and adulthood. In human males, perinatal testosterone levels are associated with organizing the male typical architecture of body and brain, as well as distributing hormone receptors (Mazur & Booth, 1998). At puberty men’s gonads rapidly increase testosterone production, which activates structures and receptors organized by the perinatal testosterone levels, and starts rapid masculinization (e.g., muscle growth, body hair, enlargement of genitalia and larynx resulting in voice deepening). Testosterone levels reach their peak in early adulthood and then slowly decline with age (Dabbs, 1990). In adulthood, it is particularly circulating testosterone levels that are important for a range of sexual and social behaviors (Mazur & Booth, 1998).

The development of male secondary sexual characteristics is dependent on testosterone levels in multiple species (Andersson, 1994). Testosterone also has immunosuppressive effects on males (see Foo et al., 2016, for a recent meta-analytic review), therefore the development and display of exaggerated masculine characteristics is considered as an honest signal of male physical condition (Boothroyd et al., 2013; Rhodes et al., 2003; Thornhill & Gangestad, 2006).

Further research on the effects of testosterone on men’s mate preferences demonstrated that within-subject changes in men’s testosterone levels are associated with increased preferences for feminine women’s faces (Welling et al., 2008), but not masculine men’s faces, thus suggesting that these effects reflect changes in mating-related motivations rather than a general bias for increased sexual dimorphism. Similarly, a recent study using experimentally manipulated facial images found that men’s preferences for feminine women’s faces increased after being administered testosterone (Bird et al., 2016). Furthermore, men’s testosterone levels have been shown to increase after brief interactions with young women (Roney et al., 2003, 2007), and these increases were positively correlated to women’s ratings of men’s displays of interest (Roney et al., 2003, 2007). Studies investigating the role of testosterone in women’s mate preferences and mating strategies reported that early follicular testosterone levels were positively associated with women’s preferences for masculine men’s faces (Bobst et al., 2014), and within-subject changes in testosterone modulate intrasexual competitiveness (Hahn et al., 2016), as well as the reward value of attractive faces (Wang et al, 2014) and infant faces (Hahn et al., 2015).

Early research investigating possible links between testosterone and perceptions of men's facial appearance reported that the faces of men with higher basal testosterone levels were perceived to be more masculine and dominant (Penton-Voak & Chen, 2004; Roney et al., 2006; Swaddle & Reierson, 2002) and more attractive as short-term partners (Roney et al., 2006). However, other studies did not observe significant associations between men's basal testosterone and their facial attractiveness, dominance or masculinity (Hönekopp et al., 2007; Neave et al., 2003; Pound et al., 2009; Whitehouse et al., 2015). In women, similarly to men, the evidence for an association between testosterone and facial attractiveness is ambiguous, with evidence either pointing to a negative association (Wheatley et al., 2015) or no association at all (Gonzalez-Santoyo et al., 2015).

1.5.3 Cortisol

Like testosterone, cortisol plays an important role in immune function regulations. While short-term increases in cortisol tend to activate immune responses (see Martin, 2009, Sapolsky et al., 2000 for a comprehensive review), chronically elevated cortisol levels are immunosuppressive and considered to be a biomarker of stress (Hellhammer et al., 2009; Martin, 2009; Sapolsky et al., 2000). Cortisol has been linked to mate preferences in both non-human animals and humans. Pflüger et al. (2014) showed that in male Japanese macaques (*Macaca fuscata*) cortisol predicted male preferences for facial color cues associated with female fertility. Jones et al (2013) showed that men's trait cortisol levels positively predicted their preferences for femininity in women's faces, suggesting that men who might be particularly stressed show stronger preferences for mates displaying cues of good health.

Some research linked cortisol also to aspects of facial appearance, suggesting that trait cortisol levels negatively predict women's dominance (Gonzalez-Santoyo et al., 2015) and attractiveness (Rantala et al., 2013). However, a recent study by Han et al. (2016) failed to find associations between women's trait cortisol levels and their appearance. In men, effects of cortisol on facial appearance were mostly considered together with interactions with testosterone levels (Rantala et al., 2012, Moore et al., 2011a, 2011b). This is because the hypothalamo-pituitary-adrenal axis producing cortisol has inhibitory effects on the hypothalamo-pituitary-gonadal axis producing testosterone. Therefore the effects of testosterone and cortisol are interactive, and not additive (Handa et al., 1994). Research investigating the potential moderating role of cortisol on the relationship between men's facial appearance and testosterone levels has also produced mixed results, however. Rantala et al. (2012) found that the faces of men with high testosterone levels were perceived to be more attractive and that this relationship was strongest among men who also had low cortisol levels. Moore et al (2011b) did not replicate these findings. Moreover, Moore et al. (2011a) reported a negative relationship between men's cortisol and facial attractiveness, but no relationship between testosterone and men's facial attractiveness, or the interaction between cortisol and testosterone and men's facial attractiveness. Moore et al. (2011a) also found that neither ratings of men's facial health nor ratings of their facial masculinity were related to men's testosterone or cortisol levels, nor an interaction of these two hormones. These inconsistent effects of cortisol could occur due to different methodologies as Moore et al. (2011b) sampled salivary hormone levels and took facial photographs in the morning and afternoon, while Rantala et al. (2012) sampled salivary hormone levels and took facial photographs in the morning and Moore et al. (2011a) sampled salivary hormone levels and took facial photographs in the afternoon only. This is problematic as both testosterone levels and cortisol levels change diurnally with relatively high levels in the morning, and continually decrease throughout the day (Papacosta & Nassis, 2011) and it remains an empirical question whether men's appearance in photographs (e.g., potential changes in head posture or demeanor) changes with hormone levels. Alternatively, some of these results may be due to large uncontrolled differences between individual stimuli as faces indeed vary across many dimensions (Moore et al., 2011a, 2011b). Moore et al. (2011a, 2011b) hence investigated the effects of testosterone and cortisol using prototype faces composed of men with high levels of both testosterone and cortisol, low levels of both hormones, or a combination of high testosterone and low cortisol and vice versa. Between these two studies women tended to prefer faces displaying cues to low cortisol. However, even when using a more powerful technique where individual differences and idiosyncrasies are averaged out and face shapes associated with particular hormonal profiles remain, the evidence for a role of testosterone and cortisol in men's facial appearance is mixed at best.

1.6 The importance of facial appearance for mate choice

Faces play a central role in human social interactions and facial appearance informs many socially relevant judgments. People are experts at perceiving faces, with the ability to make very rapid and consistent judgments about peoples' attractiveness, trustworthiness, likeability or aggressiveness after very brief exposure to faces (Todorov et al, 2009; Willis & Todorov, 2006). Facial appearance has been shown to influence multiple outcomes, such as hiring recommendations (Zebrowitz et al., 1991), or electoral outcomes (Little et al., 2007a), and most crucially choice of romantic partners and mates (e.g., Little et al,. 2011, Jones, 2014, DeBruine 2014). People want a mate who is among other characteristics healthy, fertile and committed. Below I review some of the most prominent research on aspects of facial appearance related to mate choice.

1.6.1 Facial averageness

Facial averageness can be thought of as the extent to which a face resembles the majority of faces in a population, and is thought to reflect underlying genetic quality (Mitton & Grant, 1984; Thornhill & Gangestad, 1993). Indeed it has been positively associated with heterozygosity at the major histocompatibility complex (MHC), which codes for proteins involved in immune function (Lie et al., 2008) as has been facial attractiveness (Roberts et al., 2005). Moreover, individuals may prefer facial averageness because faces that are far away from average are likely to have higher mutation loads (Thornhill & Gangestad, 1993).

Multiple studies have found that average faces are judged as more attractive than relatively less average faces, using both measured averageness (Grammer & Thornhill, 1994, Komori et al., 2009; Rhodes et al, 2001a) as well as computer graphic methods to manipulate facial averageness (DeBruine et al., 2007; Jones et al., 2007; Perrett et al., 1994; Rhodes & Tremewan, 1996; Saxton et al., 2011), and these findings have been replicated across cultures (Appicella et al., 2007; Rhodes et al., 2001b). Studies using experimentally manipulated faces also showed that the effects of averageness on attractiveness are independent of effects of symmetry, even showing that facial averageness may be more important than facial symmetry (Baudoin & Tiberghein, 2004; Valentine et al., 2004, but see Komori et al., 2009).

A recent study in twins directly examined the relationship between facial averageness and genes by quantifying the genetic component associated with facial averageness (Lee et al., 2016). They found that genes only accounted for 24% of variation in facial averageness and majority of variation in averageness was due to environmental factors and measurement error. Furthermore, facial averageness was not related to the shape component of facial attractiveness, suggesting a possible role of other non-shape variables, such as color or texture that might mediate the relationship between facial averageness and attractiveness.

1.6.2 Facial symmetry

Apart from facial averageness, people also prefer faces that are symmetrical. Development of symmetrical face is also thought to reflect good underlying genetic quality, low mutation load, and/or good developmental stability (Møller, 1997, Møller & Swaddle, 1997). The extent to which individuals are able to maintain symmetrical development can be measured via fluctuating asymmetry (FA), which are randomly distributed deviations from symmetry across an individual’s face and/or body (Gangestad & Thornhill, 1999).

While there are multiple studies showing positive relationships between facial symmetry and indices of health, such as lower incidence of higher respiratory tract infections (Thornhill & Gangestad, 2006), and other putative cues of good condition such as exaggerated sexually dimorphic characteristics (Gangestad & Thornhill 2003), the largest study to investigate the association between facial asymmetry and health outcomes to date failed to find relationships between facial symmetry at the age of 15 years and early childhood health, in a cohort of 4732 individuals (Pound et al., 2014). Both studies using unmanipulated images as well as studies where facial symmetry was manipulated using computer graphics methods show that symmetry is positively associated with attractiveness (Jones et al., 2001; Little & Jones, 2006; Little et al., 2008a; Gangestad & Thornhill, 2003; Penton-Voak et al., 2001, Perrett et al., 1994).

Little & Jones (2003) also showed that preferences for facial symmetry are not due to more general perceptual bias, but indeed reflect possible mate choice adaptations. In their study Little & Jones presented participants with pairs of upright or inverted faces manipulated in facial symmetry and found that participants showed increased preferences for symmetry in upright but not inverted faces. This pattern of results cannot be accounted for by a general perceptual bias for symmetrical shape.

1.6.3 Facial sexual dimorphism

Human adult faces are highly sexually dimorphic; there are large differences in shape of male and female faces, such as larger and more prominent jawbones and cheek bones (e.g., Enlow, 1982). This differentiation and development of secondary sexual characteristics in faces occurs during puberty, and is closely related to levels of androgen hormones such as testosterone (Anderson, 1994). These sexually dimorphic characteristics are thought to be attractive because they may advertise individuals’ genetic quality, which may bring heritable survival and reproduction benefits to offspring (Debruine, 2014). This is because sexually dimorphic trait development, particularly in men, is positively associated with testosterone, and testosterone has been shown to be immunosuppressive among many species including humans (see Foo et al., for a recent meta-analytic review), therefore only individuals in particularly good physical condition can bear the handicap of testosterone immunosuppression while maintaining good health and develop exaggerated sexually dimorphic characteristics (Folstad & Karter,1992). Indeed some studies have shown that men with masculine faces reported lower frequency of upper respiratory tract diseases (Thornhill & Gangestad, 2006), and Rhodes et al. (2003) showed that young men who were perceived as masculine also tended to have better actual health.

Studies investigating whether sexually dimorphic face shape is indeed found attractive have consistently shown this to be the case for feminine women’s faces, which are perceived to be more attractive than relatively less feminine women’s faces by both men and women (Little et al., 2011a; Perrett et al., 1998; Welling et al., 2008). Women with feminine faces also reported to have better health (e.g., lower frequency of upper respiratory tract infections)

(Thornhill & Gangestad, 2006), and feminine face shape has been positively associated with maternal desires (Law Smith et al., 2012), and reproductive potential (e.g., higher estrogen levels, earlier sexual activity, more long term relationships) (Law Smith et al., 2006; Rhodes et al., 2005).

Evidence for the attractiveness of masculine male faces is more mixed, with some studies showing that women prefer masculine men's faces (DeBruine et al., 2006; Johnston& et al., 2001; Little et al., 2007b; Little et al., 2008a, 2008b), some studies showing that women prefer feminine men's faces (Little et al., 2001; Little et al., 2002; Penton-Voak et al., 1999, 2003; Perrett et al., 1998; Rhodes et al., 2000; Welling et al., 2007), and some studies showing no relationship between men's masculinity and attractiveness (Cornwell et al., 2004; Swaddle & Riersen, 2002). These inconsistent results are more likely due to between-individual differences and within-individual changes in preferences discussed in the previous sections, than due to methodological differences between studies (DeBruine et al., 2010d). Men with masculine faces also tend to be perceived as more aggressive (Puts, 2010), less committed partners that are not likely to invest in a relationship or offspring (Booth & Dabbs, 1993; Fleming et al., 2002), and more likely to cheat on their partners (Rhodes et al., 2005). That the importance of relationship commitment differs across contexts and ecologies may partly explain why women's preferences for male facial masculinity are inconsistent across studies.

1.6.4 Facial coloration

While facial averageness, symmetry and sexual dimorphism are thought, to some extent, to signal overall long-term condition of an individual, facial coloration can be a cue of both long-term and current condition (Scott et al., 2010; Little et al., 2011a, Stephen et al., 2011). Indeed it is easy to come up with examples when facial coloration can be quite diagnostic of the presence of disease, such as flushing in fever, blanching in septic shock, or extreme yellowness in jaundice. Some of the earlier research on effects of facial coloration has shown that apparent health rated from skin patches (rectangular areas of cheek skin) was positively correlated with attractiveness of male faces (Jones et al., 2004). Other studies showed that, at least in part, health perceptions can be explained by color homogeneity (evenness) (Matts et al., 2007; Fink et al. 2012), such that melanin homogeneity predicted both perceived and chronological age, while hemoglobin homogeneity predicted attractiveness and perceived health (Fink et al., 2012).

More recent research investigated effects of facial coloration on perception using computer graphic methods, where facial coloration was manipulated along the 3 primary color axes of human visual system (red/green, yellow/blue and light/dark, CIE, 1976). This research has shown that increasing redness, yellowness, and lightness in faces increased perceptions of health (Stephen et al., 2011) and attractiveness (Stephen et al., 2012a). However the color increase was negatively associated with base skin color suggesting that extreme color values can be perceived as unhealthy and/or unattractive (Stephen et al., 2009a, Stephen et al., 2009b). Aside from perceptions of health and attractiveness, red facial coloration has also been associated with perceptions of dominance, particularly in men (Stephen et al., 2012b), paralleling similar effects from non-human animals (Setchell et al., 2008).

A particularly important cue to health is carotenoid coloration (Jones et al., 2016, Lefevre et al., 2013, Lefevre & Perrett, 2014), as carotenoids play a vital anti-oxidative role in immune function (Hughes, 1999). This coloration is characterised by yellower, darker appearance, and has been linked to a diet rich in fresh fruit and vegetables (Allaluf et al., 2002; Whithead et al., 2012a, 2012b). Lefevre & Perrett (2014) have also shown that carotenoid skin coloration is preferred over sun tan (melanin) coloration and these effects are specific to facial coloration (Lefevre et al., 2013). However the effects of carotenoids on skin lightness are inconsistent across previous studies with some studies showing increases in skin lightness following beta-carotene supplementation while others showed no changes in skin lightness in the face, but overall decreases in skin lightness across the body (Whitehead et al., 2012a, 2012b) and studies using experimental manipulations of carotenoid skin coloration decreased facial lightness (Lefevre et al., 2013; Lefevre & Perrett, 2014). More recently Henderson et al. (2017) reported changes in decreases in skin lightness and redness following an infection. Taken together these results warrant further investigation into both color cues of health appearance as well as underlying mechanisms facilitating skin color changes associated with acute illness, and more general poor health.

1.6.5 Facial adiposity

Aside from facial coloration cues, recent research identified facial adiposity (facial fatness) as an important cue to health. Facial adiposity is positively related to overall body weight, body fat percentage, and BMI (Coetzee et al., 2009, Tinlin et al., 2013). Having a high body fat percentage, and to lesser extent having high BMI and body weight can have multiple deleterious effects on individuals' health (Mokdad et al., 2003; Must et al., 1999; Pi-Sunyer, 1993). Similarly to bodies (Furnham et al., 2006, Swami et al., 2008), faces high in adiposity tend to be perceived as less healthy (Coetzee et al., 2009, Fisher et al., 2013, Fisher et al., 2014), although too low levels of adiposity are also perceived as less attractive and healthy, particularly when combined with color cues of poor health (Fisher et al., 2014). Other studies found evidence that facial adiposity may positively predict actual health (e.g., frequency and duration of colds, blood pressure)(Coetzee et al., 2009; Tinlin et al, 2013) and health outcomes such as arthritis, diabetes and longevity (Reither et al., 2009). Moreover facial adiposity has been recently linked to immunocompetence adiposity was consistently related to perceived attractiveness (Rantala et al., 2013), as men with low facial adiposity showed stronger immune response (antibody production) to a hepatitis B vaccine. The results of this study showed that in men, adiposity and masculinity were independently related to immunocompetence, but only adiposity was consistently related to perceived attractiveness (Rantala et al., 2013).

1.6.6 Expression and gaze

While majority of the research on facial attractiveness has investigated effects associated with relatively stable characteristics (e.g., averageness, symmetry, skin coloration), other work has focused on effects of more transient characteristics such as facial expressions of emotion or gaze direction on facial attractiveness. This work has shown that people show stronger preferences for faces with direct gaze (a putative cue of social interest and/or attention) than faces with averted gaze and that these effects are stronger for opposite-sex faces (Conway et al., 2010; Conway et al., 2008). Furthermore tthese effects of gaze on attractiveness have also been shown to increase activation in the brain's reward circuitry (Kampe et al., 2001). Other aspects of facial appearance can modulate these preferences, however. For example Conway et al. (2008) showed that single women show stronger preferences for direct gaze in feminine male faces in a long-term relationship context but not a short-term relationship context, demonstrating effects of both sexual dimorphism and relationship context on preferences for direct gaze. Furthermore, facial expressions of emotion have also been shown to modulate people's preferences for direct gaze in faces. Jones et al. (2006) showed that men's and women's preferences for attractive faces were strongest when the faces were smiling and had direct gaze, potentially reflecting mechanisms that facilitate effective allocation of effort towards high quality potential mates or social partners that appear to be most likely to reciprocate (see also Conway et al. 2008; Main et al., 2010).

1.7 Importance of voices in mate choice

Like faces, human voices play a very important role in social communication, with some authors regarding spoken language as the defining human characteristic (Pinker, 1994). Similarly to faces, voices are highly sexually dimorphic, showing one of the largest sex differences (Puts et al. 214). Men speak with lower pitch (fundamental frequency), which is a consequence of their larger vocal chords resonating at lower frequencies (Titze, 1989, 1994). Men also speak with lower and more closely spaced formant frequencies, which are a consequence of a longer vocal tract (Childers & Wu, 1991).

Past research revealed that men show stronger preferences for feminine compared to masculine female voices (Apicella & Feinberg, 2009; Collins & Missing, 2003; Feinberg et al., 2008a; Jones et al., 2008b; Jones et al., 2010; Puts et al., 2011). Similarly to feminine female face shape, feminine female voices (voices with higher pitch) have been positively associated with fertility (Bryant & Haselton, 2009; Puts et al., 2011, but see Puts et al., 2012), reproductive potential (Awan 2006, Röder et al., 2013), and are also perceived as more attractive to men by other women (Puts et al., 2011). These preferences are modulated by cues of positive social interest - Jones et al.

(2008b) demonstrated that men show the stronger preferences for feminine women’s voices uttering “I really like you” than for feminine women’s voices uttering “I really don’t like you”.

Past research also revealed that women show stronger preferences for masculine male voices, using both correlational paradigms (Collins, 2000, Hodges-Simeon et al., 2010, Puts, 2010) and by experimentally manipulating (lowering the pitch, or format frequencies, or manipulating format dispersion) acoustic properties of men’s voices (Feinberg et al., 2005; Feinberg et al., 2006; Feinberg et al., 2008b; Jones et al., 2010). Like masculine face shape, masculine voices are thought to be cue to physical condition and possible heritable benefits in men (Puts et al., 2013). Both men’s and women’s masculine voices are also perceived as more dominant (Jones et al., 2010; Puts, 2010), and vocal masculinity has been linked to men’s actual threat potential and formidability as indexed by their physical strength and fighting ability (Hodges-Simeon et al.; *in press;* Puts et al, 2011; Sell et al., 2010).

1.8 Current studies

In this thesis I present 4 empirical chapters investigating variation in men’s mating strategies and faces preferences, building up on previous studies and more importantly, improving on limitations of previous research. The first empirical chapter investigates the regional variation in men’s and women’s sociosexual orientation across US states, using improved measures of sociosexuality and multilevel modeling. In my second empirical chapter I will present a study investigating the relationship between men’s hormone levels and men’s preferences for healthy color cues in faces using robust estimates of men’s facial coloration preferences and robust estimates of men’s hormone levels. My third empirical chapter tests for within-subject effects of hormones on men’s perceptions of vocal characteristics using a longitudinal design, where men’s preferences for vocal characteristics and men’s hormone levels were measured on 5 separate occasions. In the final chapter I present a study testing for relationships between men’s appearance and their hormone levels, using robust estimates of men’s trait hormone levels.

Chapter 2: Scarcity of female mates predicts regional variation in men’s and women’s sociosexual orientation across US states

Preface

This chapter is adapted from:

Kandrik, M., Jones, B. C., DeBruine, L. M. (2015). Scarcity of female mates predicts regional variation in men’s and women’s sociosexual orientation across US states. *Evol. Hum. Behav.*, *36*: 206-210.

All data and analyses scripts are available online with the journal at: http://www.sciencedirect.com/science/article/pii/S1090513814001391

Abstract

Previous studies have linked regional variation in willingness to engage in uncommitted sexual relationships (i.e., sociosexual orientation) to many different socio-ecological measures, such as adult sex ratio, life expectancy, and gross domestic product. However, these studies share a number of potentially serious limitations, including reliance on a single dataset of responses aggregated by country and a failure to properly consider intercorrelations among different socio-ecological measures. We address these limitations by (1) collecting a new dataset of 4,453 American men’s and women’s sociosexual orientation scores, (2) using multilevel analyses to avoid aggregation, and (3) deriving orthogonal factors reflecting US state-level differences in the scarcity of female mates, environmental demands, and wealth. Analyses showed that the scarcity of female mates factor, but not the environmental demand or wealth factors, predicted men’s and women’s sociosexual orientation. Participants reported being less willing to engage in uncommitted sexual relationships when female mates were scarce. These results highlight the importance of scarcity of female mates for regional differences in men’s and women’s mating strategies. They also suggest that effects of wealth-related measures and environmental demands reported in previous research may be artifacts of intercorrelations among socio-ecological measures or, alternatively, do not necessarily generalize well to new datasets.

2.1 Introduction

Some previous research suggests that environmental demands may be important for regional variation in individual mating strategies, such as willingness to engage in uncommitted sexual relationships (i.e., sociosexual orientation, Simpson & Gangestad, 1991). For example, people in countries with higher parasite stress (Barber, 2008; Schaller & Murray, 2008; Thornhill et al., 2010) or with higher incidence of low birth weight and child malnutrition, higher infant mortality rates, and shorter life expectancy (Schmitt, 2005) report being less willing to engage in uncommitted sexual relationships.

These links between sociosexual orientation and environmental demands could occur because engaging in uncommitted sexual relationships increases exposure to infectious diseases and such behaviors will be more costly in more demanding environments (Schaller & Murray, 2008). Alternatively, they may occur because committed relationships reduce the negative consequences of demanding environments on offspring viability by increasing the amount of parental investment available, meaning that preferences for committed relationships are likely to be higher in regions with greater environmental demands (Schmitt, 2005). That these links between environmental demands and sociosexual orientation tend to be stronger among women than men (Schaller & Murray, 2008; Thornhill et al., 2010; Schmitt, 2005, but see Barber, 2008) may reflect that the fitness costs incurred in demanding environments, such as increased risk of contracting infectious diseases, are greater for women than for men and that the fitness benefits of engaging in uncommitted sexual relationships are greater for men than for women (Schaller & Murray, 2008; Thornhill et al., 2010).

In addition to links between environmental demands and sociosexual orientation, several lines of evidence suggest that the scarcity of female mates in the local population may be an important factor. For example, in countries with a higher ratio of men to women, higher fertility and teen pregnancy rates, or lower mean age at marriage for women, people report being less willing to engage in uncommitted sexual relationships (Schmitt, 2005, see also Barber, 2008). Men's sociosexual orientation tends to be less restricted than women's (Simpson & Gangestad, 1991; Penke & Asednorpf, 2008). Consequently, scarcity of female mates in the local population may predict *women's* sociosexual orientation because women are better able to pursue their preferred mating strategy when intrasexual competition for mates among women is less intense and they can be more selective in their mate choices (Schmitt, 2005). Scarcity of female mates in the local population may predict *men's* sociosexual orientation because men are more likely to align their mating strategy with those that are preferred by women when intrasexual competition for mates among men is more intense and men may need to be willing to alter their preferred mating strategy in order to obtain mates (Schmitt, 2005). Consistent with this interpretation, women do show greater selectivity in their mate preferences (Pollet & Nettle, 2008; Watkins et al., 2012) and men are more willing to commit to and invest in monogamous relationships (Pedersen, 1991; Pollet & Nettle, 2009) when women are relatively scarce. Recent research also demonstrates that, across bird species, pair bonds are more stable when sex ratios are male-biased (Liker et al., 2014).

In addition to scarcity of female mates and aspects of environmental demand, such as parasite stress and other health risks, people report being more willing to engage in uncommitted sexual relationships in wealthier countries (Schmitt, 2005). This effect of wealth may occur because individuals in wealthier countries tend to have more resources to invest in their offspring and, consequently, biparental care is less important for offspring viability (Schmitt, 2005). In one study, wealth was related to women’s, but not men’s, sociosexual orientation (Barber, 2008), potentially reflecting women’s greater engagement with offspring care.

Although the studies described above suggest that socio-ecological factors predict regional differences in sociosexual orientation (Barber, 2008; Schaller & Murray, 2008; Thornhill et al., 2010, Schmitt, 2005), they have a number of potentially important limitations.

First, the studies all analyzed scores on Simpson and Gangestad’s (1991) Sociosexual Orientation Inventory (SOI) that were taken from the same dataset, which was collected by Schmitt (2005). Consequently, it is important to establish which of these results generalize to other, independent datasets.

Second, because they rely on a single dataset using Simpson and Gangestad's (1991) SOI, all of the studies analyzed global sociosexual orientation only. More recently, Penke and Asendorpf (2008) have argued that sociosexual orientation consists of three components (attitudes, desires, and behaviors) and developed a revised Sociosexual Orientation Inventory (SOI-R) to measure each of these components, in addition to a global measure of sociosexual orientation. Socio-ecological factors need not necessarily have identical effects on the three different components. For example, because attitudes and desires are not constrained in the same way that behaviors are (Penke & Asendorpf, 2008), links between socio-ecological conditions and sociosexual orientation may be more apparent when measured via attitudes and desires than when measured via behaviors.

Third, the studies all correlated measures of socio-ecological conditions with aggregated SOI scores for each country. This approach has recently been criticized because aggregating data in this way may give a misleading impression of responses typical of individuals in each region (Pollet et al., 2014). This concern can be addressed through the use of multilevel analyses, in which individual participants' data are grouped, but not aggregated, by region (Pollet et al., 2014). Multilevel analyses also account for differences in the number of samples in each region and the variance of scores in each region. These problems arising from the analysis of aggregated data also extend to prior research linking regional differences in sex ratio to other aspects of mating strategy, such as choosiness in mate preferences (Stone et al., 2007), access to financial resources (Griskevicius et al., 2012), and various marriage statistics (Kruger, 2009; Lichter et al., 1992; South & Trent, 1988).

Fourth, although measures of the scarcity of female mates, environmental demands, and wealth are often intercorrelated (Barber, 2008; Schmitt, 2005), the studies have not always controlled for the possible effects of these intercorrelations. For example, Schmitt (2005) presents only simple correlations between socio-ecological factors and sociosexual orientation, while Thornhill et al. (2010) only considered the possible effects of parasite stress. Schaller and Murray (2008) demonstrate that the effect of disease prevalence on women's sociosexual orientation was not due to the possible effects of wealth and life expectancy, but did not consider the possible effects of measures of the scarcity of female mates. Barber (2008) tested for independent effects of several aspects of environmental demand, scarcity of female mates, and wealth, reporting evidence that some of these measures have independent effects. However, these analyses also suggested that controlling for multiple, correlated socio-ecological factors can dramatically alter the nature of their effects. For example, the effect of infectious disease on women's sociosexual orientation was significant and negative in a simple correlation analysis, but significant and positive when effects of other measures were controlled (Barber, 2008). Consequently, it is unclear whether scarcity of female mates, environmental demands, and wealth do have independent effects on regional variation in sociosexual orientation.

To address the problems described above, we tested for possible relationships between sociosexual orientation and regional variation in scarcity of female mates, environmental demands, and wealth in a new dataset of men and women from 50 U.S. states (and Washington DC). First, we used principle component analysis to investigate the factor structure of measures of state-level variation in scarcity of female mates (i.e., adult sex ratio, fertility rate, teenage pregnancy rate, women's age at first marriage), environmental demands (i.e., infant mortality, low birth weight, life expectancy at birth, children living in poverty), and wealth (gross domestic product per capita, Human Development Index). These specific variables were selected because they are the closest US state-level analogues to the measures of country-level variation that were analyzed by Schmitt (2005). This initial analysis produced a three-factor solution in which the factors primarily reflected state-level variation in scarcity of female mates, environmental demands, and wealth (see Table 2.2). We then used multilevel analyses to test for independent relationships between these factors and participants' scores on Penke and Asendorpf's (2008) revised Sociosexual Orientation Inventory (SOI-R). Each of the three different components of sociosexual orientation (attitudes, desires, and behaviors) was analyzed, in addition to the global measure.

2.2 Methods

2.2.1 Participants

A total of 3209 heterosexual women (mean age = 23.4 years, *SD* = 5.94 years) and 1244 heterosexual men (mean age = 25.9 years, *SD* = 7.59 years) participated in the online study (total N = 4453). Online data collection has been used in many previous studies of sociosexual orientation (Penke & Asendorpf, 2008) and regional differences in both mate preferences (DeBruine et al., 2010a; DeBruine et al., 2011) and mating-related attitudes (e.g., Price et al., 2014). Participants were recruited by following links from social bookmarking websites (e.g., stumbleupon.com) and were not compensated for their participation.

2.2.2 Revised Sociosexual Orientation Inventory (SOI-R)

All participants completed the SOI-R, a questionnaire that measures individual differences in willingness to engage in uncommitted sexual relationships and has good test-retest reliability and good external validity (Penke & Asendorpf, 2008). Items on the SOI-R are drawn from three subscales indexing individual differences in behavior (e.g., “With how many different partners have you had sexual intercourse on one and only one occasion?”), attitudes (e.g., “Sex without love is OK.”), or desires (e.g., “In everyday life, how often do you have spontaneous fantasies about having sex with someone you have just met?”). Scores on these subscales can also be summed to create a global measure of sociosexual orientation (Penke & Asendorpf, 2008). Higher scores on each of the subscales or the global measure indicate greater willingness to engage in uncommitted sexual relationships. We used the five-point response scale version of the SOI-R (Penke & Asendorpf, 2008). See table 2.1 for descriptive statistics.

	Global	Attitude	Desire	Behavior
Men (N = 1244)	27.1 (7.91)	10.1 (3.82)	10.71 (3.16)	6.32 (3.15)
Women (N = 3209)	22.7 (7.72)	8.22 (3.61)	8.10 (3.17)	6.38 (3.03)

Table 2.1 Mean SOI-R scores (and standard deviation) grouped by participant sex.

2.2.3 State-level variables

For each state plus Washington DC, data for the human development index, gross domestic product per capita, infant mortality rate (per 1000 live births), percent of low-birth-weight infants (percent of all infants with birth weights below 2500g), teenage pregnancy rate (number of births per 1000 girls aged 15-19 years), life expectancy at birth, and percent of children (under 6 years of age) living in poverty were obtained from the 2013/2014 report of the US Social Science Research Council's Measure of America Project (http://www.measureofamerica.org/measure_of_america2013-2014/). Data provided in this report are for 2010. Data for women's median age at first marriage, fertility rate (number of women with births in the previous 12 months per 1000 women), and adult sex ratio (total number of men aged between 15 and 49 years of age divided by the total number of women aged between 15 and 49 years of age) were obtained from the 2010 US Census Bureau's American Community Survey (http://factfinder2.census.gov/).

2.3 Results

First, we subjected all state-level variables to Principal Component Analysis (PCA) using varimax rotation and Kaiser normalization. This analysis produced 3 orthogonal factors (see Table 2.2). The first factor explained 45.0% of the variance in scores and was highly correlated with life expectancy at birth and infant mortality rate. We labeled this factor the *environmental demand factor*. The second factor explained 24.9% of the variance in scores and was highly correlated with fertility rate, adult sex ratio, and women's median age at first marriage. We labeled this factor the *scarcity of female mates (SoFM) factor*. The third factor explained 15.1% of the variance in scores and was highly correlated with gross domestic product per capita. We labeled this factor the *wealth factor*. Repeating this factor analysis using direct oblimin rotation produced three non-orthogonal factors, each of which were highly correlated with the corresponding factor produced using varimax rotation (all $|r| > .98$). This suggests the results of our multilevel analyses using these factors are not an artifact of the factors being forced to be orthogonal.

State-level variables	Environmental demand factor	Scarcity of female mates (SoFM) factor	Wealth factor
Infant mortality rate	.853	-.175	-.007
% of low-birth-weight infants	.846	-.245	.167
Teenage pregnancy rate	.867	.371	-.003
Life expectancy at birth	-.935	-.043	.075
% of children living in poverty	.866	-.045	-.275
Adult sex ratio	-.342	.791	-.204
Fertility rate	.083	.901	.082
Women's median age at first marriage	-.140	-.822	.415
Gross domestic product per capita	-.030	-.147	.943
Human development index	-.735	-.347	.541

Table 2.2 Component matrix for principle component analysis of all state-level variables.

We first tested for between-state effects of the *environmental demand factor, scarcity of female mates* (*SoFM*) *factor*, and *wealth factor* on participants' global SOI-R scores (i.e., the sum of scores on the three SOI-R subscales) using multilevel modeling. All analyses were carried out using R (R Core Team, 2013), *lme4* (Bates et al., 2014), and *lmerTest* (Kuznetsova et al., 2013) packages. The full output for each model is included in Appendix 1.1.

Participants were grouped by state (each participant's Internet Protocol address was used to determine their location) and global SOI-R scores were entered as the dependent variable at the participant level. *Participant age* (centered at the mean age) and *participant sex* (dummy coded as 0 = female, 1 = male) were entered as predictors at the participant level and scores on the *environmental demand factor, SoFM factor,* and *wealth factor* were entered at the state level. The model included a random intercept term at the state level. Initial analyses with interactions between participant sex and the *environmental demand factor, SoFM factor,* and *wealth factor* at the participant level revealed no significant interactions (*participant sex*environmental demand*: $t = 1.24$, $p = .215$; *participant sex *SoFM*: $t = 0.59$, $p = .557$; *participant sex *wealth*: $t = 1.02$, *p* = .308). Consequently, these interactions were dropped from the model, in order to interpret the overall effects of the three socio-ecological factors.

This analysis revealed a significant negative effect of the *SoFM factor* (*t* = –4.02, *p* < .001), indicating that participants in states where female mates were more scarce reported being less willing to engage in uncommitted sexual relationships. In contrast, the *environmental demand factor* (*t* = –1.27, *p* = .211) and *wealth factor* (*t* = 1.20, *p* = .234) did not have significant effects. A significant effect of *participant sex* (*t* = 15.6, *p* < .001) indicated that men generally reported being more willing to engage in uncommitted sexual relationships than did women. A significant effect of *participant age* (*t* = 9.35, *p* < .001) indicated that older participants generally reported being more willing to engage in uncommitted sexual relationships than did younger participants.

Next, we repeated this analysis separately for scores on each of the three subscales of the SOI-R. We carried out these analyses in light of preliminary analyses that indicated differences in the relationships between the *SoFM factor* and scores on the three SOI-R subscales.

Analysis of the attitude subscale revealed no interactions between *participant sex* and any of the state-level factors (*participant sex***environmental demand*: *t* = 0.49, *p* = .623; *participant sex* **SoFM*: *t* = –0.06, *p* = .950; *participant sex* **wealth*: *t* = 1.06, *p* = .289), so these interactions were dropped from the model. This analysis showed a significant negative effect of the *SoFM factor* (*t* = –4.42, *p* < .001) and effects of both *participant sex* (*t* = 14.17, *p* < .001) and *participant age* (*t* = 7.19, *p* < .001). Men had higher scores on the attitude subscale than did women and older participants had higher scores on the attitude subscale than did younger participants. There were no effects of the *environmental demand factor* (*t* = –1.53, *p* = .134) or the *wealth factor* (*t* = 0.93, *p* = .354).

Analysis of the desire subscale revealed no interactions between *participant sex* and the *SoFM factor* (*t* = 0.01, *p* = .990) or *participant sex* and the *wealth factor* (*t* = 0.67, *p* = .506), so these interactions were dropped from the model. Here, the analysis revealed a significant negative effect of the *SoFM factor* (*t* = –3.24, *p* = .002), a significant effect of *participant sex* (*t* = 25.1, *p* < .001), and a significant negative effect of *participant age* (*t* = –2.41, *p* = .016). Men had higher scores on the desire subscale than did women and older participants had lower scores on the desire subscale than did younger participants. Additionally, this analysis of the desire subscale of the SOI-R showed a significant positive effect of the *wealth factor* (*t* = 2.10, *p* = .040) and a negative effect of the *environmental demand factor* (*t* = –2.14, *p* = .035), which was qualified by an interaction between *environmental demand* and *participant sex* (*t* = 2.14, *p* = .033). This interaction indicated that women, but not men, in states with more demanding environments reported lower scores on the desire subscale of the SOI-R.

Analysis of the behavior subscale revealed no interactions between *participant sex* and any of the state-level factors (*participant sex*environmental demand*: *t* = 0.25, *p* = .801; *participant sex*SoFM*: *z* = 1.58, *p* = .115; *participant sex*wealth*: *t* = 0.64, *p* = .524), so these interactions were dropped from the model. This analysis showed significant effects of *participant sex* (*t* = –3.71, *p* < .001) and *participant age* (*t* = 18.0, *p* < .001). Women had higher scores on the behavior subscale than did men and older participants had higher scores on the behavior subscale than did younger participants. There were no other effects of state-level variables (*environmental demand*: *t* = 0.12, *p* = .908; *SoFM*: *t* = –1.31, *p* = .196; *wealth*: *t* = –0.11, *p* = .910).

2.3.1 Additional analyses

Although our main analyses used a composite measure of environmental demand that was based on the measures used in Schmitt's (2005) analyses of regional variation in sociosexual orientation, other studies have used measures of parasite stress (i.e., measures of the incidence of infectious diseases, specifically) to investigate this issue (Fincher & Thornhill, 2012). Because parasite stress and our *environmental demand factor* could plausibly tap different aspects of environmental demand, we repeated our analyses replacing our *environmental demand factor* with Fincher and Thornhill's (2012) measure of US state-level variation in *parasite stress*. Fincher and Thornhill's (2012) measure of *parasite stress* was derived from US Center for Disease Control (CDC) statistics for the incidence of infectious diseases between 1993 and 2007. The results of these alternative analyses of our data are summarized below and are described in full in Appendix 1.2.

For the analyses of global SOI-R and the attitude subscale, the negative effects of *SoFM* remained significant and neither *wealth* nor *parasite stress* had any significant effects. For the analysis of the desire subscale, the negative effect of *SoFM* and positive effect of *wealth* remained significant and there were no significant effects of *parasite stress*. For the analysis of the behavior subscale, neither *SoFM, wealth*, nor *parasite stress* had any significant effects. These alternative analyses suggest that the absence of consistent effects of our environmental demand factor in our main analyses is not a consequence of this factor inadequately reflecting state-level variation in parasite stress.

2.4 Discussion

We tested for possible relationships between participants' sociosexual orientation and US state-level variation in socio-ecological variables previously found to predict country-level variation in sociosexual orientation (e.g., Schmitt, 2005). Principle component analysis of these socio-ecological variables produced three orthogonal factors reflecting state-level variation in scarcity of female mates, environmental demands, and wealth. Multilevel analyses showed that the scarcity of female mates factor, but not environmental demand or wealth factors, predicted variation in men's and women's global sociosexual orientation. Participants in states where female mates were particularly scarce reported being less willing to engage in uncommitted sexual relationships. The scarcity of female mates factor was comprised primarily of state-level variation in fertility rate, age at first marriage and adult sex ratio. All of these variables index, to a certain extent, the composition of mating markets, such that in states with high fertility, available female mates are more scarce, similarly in states where women tend to get married earlier, available female mates are more scarce and finally adult sex ratio is the ratio of men to women in a given state.

Our findings complement Schmitt (2005), who also suggested that measures of the scarcity of female mates in the local population were a particularly important socio-ecological factor for regional differences in sociosexual orientation. Importantly, we extend this previous work in several ways.

First, all previous research on this issue used the same dataset, which was collected by Schmitt (2005). We show that the conclusion that scarcity of female mates is a particularly important socio-ecological factor for regional differences in sociosexual orientation is also true of a new dataset. In addition, this new dataset was collected from participants in a single country, addressing concerns that translating Simpson and Gangestad's (1991) Sociosexual Orientation Inventory (SOI) into multiple languages may introduce systematic country-level differences in SOI scores (Schmitt, 2005).

Second, while previous work examined a global measure of sociosexual orientation only, our use of Penke and Asendorpf's (2008) Revised Sociosexual Orientation Inventory (SOI-R) meant that we could investigate regional variation in the different components of sociosexual orientation (attitude, desire, and behavior), in addition to global sociosexual orientation. Our analyses of these different subscales showed that scarcity of female mates predicted scores on the attitude and desire subscales, but not the behavior subscale. Because attitudes and desires are not constrained in the same way that behaviors are (Penke & Asendorpf, 2008), this pattern of results supports the proposal that regional differences in sociosexual orientation reflect psychological adaptations evoked by the local environmental conditions (Schaller & Murray, 2008; Thornhill et al., 2010, Schmitt, 2005). Additionally, while the environmental demand and wealth factors were not implicated in global SOI-R scores, analyses of individual subscales of the SOI-R showed that the desire subscale was also related to the environmental demand factor in female participants and wealth factor in both sexes. These latter results suggest that some aspects of sociosexual orientation may be influenced by environmental demands and wealth, independent of the effects of scarcity of female mates.

Third, we investigated the relationships between socio-ecological measures and sociosexual orientation using a method in which individual participants' data are grouped, but not aggregated, by region. This is important because aggregating data may give a misleading impression of the responses that are typical for individuals in each region (Pollet et al., 2014). Our analyses address this concern using multilevel analyses, following recent recommendations by Pollet et al. (2014).

Fourth, prior work either used simple correlations to demonstrate relationships or used multiple regression to simultaneously test for the possible effects of many intercorrelated variables. By contrast, we used factor analysis to generate three orthogonal factors, each reflecting a different aspect of socio-ecological condition: scarcity of female mates, environmental demands, and wealth. We then showed that state-level variation in global sociosexual orientation was predicted by the scarcity of female mates factor, but not the environmental demand or wealth factors. Similar results were obtained when we replaced our environmental demand factor with Fincher and Thornhill's (2012) parasite stress measure, suggesting that our largely null results for the environmental demand factor were not a consequence of this factor inadequately reflecting variation in parasite stress. Thus, our results raise the possibility that the effects of measures of environmental demand and wealth on sociosexual orientation reported in previous research (Barber, 2008; Schaller & Murray, 2008; Thornhill et al., 2010; Schmitt, 2005) may be due to intercorrelations with measures of the scarcity of female mates or, alternatively, do not generalize to this new dataset. Perhaps more importantly, our results suggest that the effect of scarcity of female mates emphasized by Schmitt (2005) is not an artifact of effects of environmental demands or wealth, at least in our sample.

Our study addresses key limitations of prior work (Barber, 2008; Schaller & Murray, 2008; Thornhill et al., 2010; Schmitt, 2005) to present strong evidence for a link between scarcity of female mates and regional differences in men's and women's mating strategies. Interestingly, our results also complement other recent work demonstrating that, across bird species, pair bonds are more stable when sex ratios are male-biased (Liker et al., 2014). Together, these results suggest that scarcity of female mates can have similar effects on mating strategies in diverse taxa. We suggest that further work is needed to investigate the causal links among regional differences in the scarcity of female mates, individuals' sociosexual orientations, and regional differences in cultural norms and values, such as anti-promiscuity morality (Price et al., 2014) or religiosity.

Chapter 3: Are physiological and behavioral immune responses negatively correlated? Evidence from hormone-linked differences in men's face preferences

Preface

This chapter is adapted from:

Kandrik, M., Hahn, A. C., Fisher, C. I., Wincenciak, J., DeBruine, L. M., Jones, B. C. (2017). Are physiological and behavioral immune responses negatively correlated? Evidence from hormone-linked differences in men's face preferences**.** *Horm. Behav. 87,* 57 – 61.

Abstract

Behaviors that minimize exposure to sources of pathogens can carry opportunity costs. Consequently, how individuals resolve the trade off between the benefits and costs of behavioral immune responses should be sensitive to the extent to which they are vulnerable to infectious diseases. However, although it is a strong prediction of this functional flexibility principle, there is little compelling evidence that individuals with stronger *physiological* immune responses show weaker *behavioral* immune responses. Here we show that men with the combination of high testosterone and low cortisol levels, a hormonal profile recently found to be associated with particularly strong physiological immune responses, show weaker preferences for color cues associated with carotenoid pigmentation. Since carotenoid cues are thought to index vulnerability to infectious illnesses, our results are consistent with the functional flexibility principle's prediction that individuals with stronger *physiological* immune responses show weaker *behavioral* immune responses.

3.1 Introduction

Pathogens have been a major selection pressure on all organisms, including humans (Schaller, 2011; Schaller et al., 2015; Schaller & Park, 2011; Tybur & Gangestad, 2011) The footprint of this selection pressure can be seen in the complex, effective mechanisms involved in the physiological immune system, such as antibody production (Czerkinksy et al., 1987). In addition to this physiological immune system, recent research has revealed the existence of a behavioral immune system that also functions to prevent and manage infectious diseases. These behavioral immune responses include behaviors, emotions, and cognitions that minimize contact with potential sources of pathogens (Tybur & Gangestad, 2011; Tybur et al., 2013).

Because behavioral immune responses can be costly (e.g., they can carry opportunity costs) the behavioral immune system would be expected to show functional flexibility. That is, the extent to which individuals are vulnerable to infectious diseases should affect how they resolve the trade off between the possible benefits (e.g., reduced risk of contracting infectious diseases) and costs (e.g., increased risk of incurring opportunity costs) of behavioral immune responses (Schaller et al., 2015; Tybur et al., 2013). A strong prediction of this functional flexibility principle is that individuals with stronger physiological immune responses will show weaker behavioral immune responses. However, although studies have tested for correlations between questionnaires that measure the strength of behavioral immune responses and self-reported infectious disease frequency and/or recency (deBarra et al., 2014, Stevenson et al., 2009), only one of these studies reported significant correlations (Stevenson et al., 2009). Moreover, significant correlations in this study were observed for only one of the two behavioral immune response questionnaires administered (Stevenson et al., 2009). Thus, there is little compelling evidence that individuals with stronger physiological immune responses show weaker behavioral immune responses.

Questionnaires for assessing vulnerability to infectious disease may be prone to reporting biases, which can obscure real relationships between variables and also cause spurious associations (Mortel, 2008). One method for avoiding such biases is to assess vulnerability to infectious disease by examining factors that are known to moderate physiological immune responses. Recent work suggests that stress and sex hormones are related to physiological immune responses. For example, Gettler et al. (2014) reported that men with higher salivary testosterone levels had stronger physiological immunity to infectious illnesses (as indexed by salivary secretory immunoglobulin A) and reported fewer cold/flu symptoms than did men with low testosterone levels. However, Rantala et al. (2012) demonstrated that, although men with higher testosterone levels showed stronger physiological immune responses to a hepatitis B vaccine, this relationship was significantly stronger among men who also had low cortisol levels. If the behavioral immune system does show functional flexibility, Rantala et al's (2012) results suggest that behavioral immune responses may be weakest among men with the combination of high testosterone and low cortisol.

Aversions to cues of poor health in conspecifics are thought to be a major component of the behavioral immune system (Park et al., 2012; Tybur et al., 2013). One such cue is low levels of carotenoid-related skin color. Carotenoids are pigments found in fruit and vegetables that play an important antioxidative role in disease resistance (Hughes, 1999; Sies, 1993). If not expended in this role, carotenoids are stored in skin tissue, giving skin a yellower, darker appearance (Alaluf et al., 2002). Consequently, yellower, darker facial skin may be a cue of good health and absence of disease (Jones et al., 2016; Lefevre et al., 2013; Lefevre & Perrett, 2014; Whitehead et al., 2012a, 2012b). People also show strong aversions to faces with low levels of carotenoid cues (Lefevre et al., 2013; Lefevre & Perrett, 2014) and perceive them to be unhealthy (Whitehead et al, 2012a; Stephen et al., 2011). Such aversions are thought to function, at least in part, to minimize contact with individuals who are currently ill (Lefevre et al., 2013; Lefevre & Perrett, 2014). The tendency to perceive faces in which carotenoid cues were increased to be particularly healthy has been reported when white participants in the UK judge the health of white faces and when black participants in South Africa judge the health of black faces, suggesting these perceptions are stable across different cultures and skin-color phenotypes (Stephen et al., 2011). Moreover, the human visual system is particularly sensitive to variation in facial skin coloration, relative to similar variation in non-face stimuli (Tan & Stephen, 2013).

In the current study, we investigated whether individual differences in men's preferences for faces manipulated along the three main color axes (yellow, lightness, red; Commission Internationale de L'Éclairage, 1976) were predicted by the interaction between their salivary testosterone and cortisol levels. Men's color preferences, testosterone levels, and cortisol levels were estimated by averaging their scores on these variables across five weekly test sessions in order to obtain reliable estimates of each man's typical hormone levels and preferences. If individuals who show stronger physiological immune responses do show weaker behavioral immune responses, as the functional flexibility principle suggests, men with higher testosterone levels would show weaker aversions to the absence of color cues associated with high susceptibility to infectious disease in faces and this relationship would be particularly strong among men who also had low cortisol levels.

The functional flexibility principle suggests that the combined effects of testosterone and cortisol may predict men's preferences for facial cues associated with infectious disease risk, such as the yellower and darker coloration associated with carotenoid pigmentation (Lefevre & Perrett, 2014, Whitehead et al., 2012b), but not facial cues that are associated with illnesses that are not contagious. Since facial redness is associated with oxygenated blood and, consequently, may be a cue of cardiovascular health (Stephen et al., 2009a), we also investigated the combined effects of testosterone and cortisol on men's preferences for facial redness. By contrast with our predictions for preferences for yellower, darker coloration, we did not expect these preferences to be related to men's testosterone and/or cortisol levels.

Because the behavioral immune responses are thought to function primarily to protect individuals from contracting infectious illnesses during social interactions with both women and men (e.g., Tybur et al., 2013), we would not expect it to be modulated by stimulus sex. By contrast, responses that were specific to opposite-sex faces would implicate responses relevant to mate choice, rather than behavioral immune responses.

3.2 Methods

3.2.1Participants

Forty-seven heterosexual men participated in the study (mean age = 21.99 years, *SD* = 3.19 years). All participants were students at the University of Glasgow (Scotland, UK). None of these men were currently taking any form of hormonal supplement and all indicated that they had not taken any form of hormonal supplement in the 90 days prior to participation. Participants were all of the heterosexual men tested in the first semester who met these criteria and completed the study. One additional man was tested but excluded from the dataset because his average cortisol level was more than five standard deviations above the mean for the rest of the sample.

3.2.2 Face stimuli

First, digital face photographs of 10 young adult white men and 10 young adult white women were taken against a constant background and under standardized diffuse lighting conditions. Participants were instructed to pose with a neutral expression and look directly at the camera. A GretagMacbeth 24-square miniColorChecker chart was included in each image for use in color calibration. The 20 face images were then color calibrated using a least-squares transform from an 11-expression polynomial expansion developed to standardize color information across images (Hong et al., 2001).

Next, we used methods described in Stephen et al. (2009b) to independently manipulate these face images’ yellowness, lightness, and redness in CIELab color space (Commission Internationale de L’Éclairage, 1976). CIELab color space is modeled on the human visual system and consists of three independent color axes: yellow (b*), lightness (L*), and red (a*). Two versions of each of the original faces were manufactured by manipulating yellow: one in which yellow was increased by 1.5 units and one in which yellow was decreased by 1.5 units. Two additional versions of each of the original faces were manufactured by manipulating lightness: one in which lightness was increased by 1.5 units and one in which lightness was decreased by 1.5 units. Two final versions of each of the original faces were manufactured by manipulating red: one in which red was increased by 1.5 units and one in which red was decreased by 1.5 units.

Importantly, these color manipulations only affect the manipulated color dimension (e.g., altering redness does not affect yellowness, and vice versa) and do not affect shape information or eye color (Stephen et al., 2012b). This technique for manipulating color information in faces has also been used in many other previous studies (e.g. Whitehead et al., 2012a; Stephen et al., 2011). These color manipulations, in which color values were increased or decreased by 1.5 units, are within the normal range of coloration for white adult faces (Whitehead et al., 2012b).

3.2.3 Procedure

All participants completed five weekly test sessions. All test sessions took place between 2pm and 5pm to minimize diurnal variation in hormone levels (Papacosta & Nassis, 2011). During each test session, participants provided a saliva sample via passive drool (Papacosta & Nassis, 2011). Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and avoid eating, smoking, drinking, chewing gum, or brushing their teeth in the 60 minutes prior to participation. Saliva samples were frozen immediately and stored at -32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis, where they were assayed using the Salivary Testosterone Enzyme Immunoassay Kit 1-2402 (*M* = 180.47 pg/mL, *SD* = 38.70 pg/mL) and the Salivary Cortisol Enzyme Immunoassay Kit 1-3002 (*M* = 0.19 µg/dL, *SD* = 0.08 µg/dL). All assays passed Salimetrics' quality control.

In each test session, participants also completed a facial color preference test that assessed their preference for facial yellowness, lightness, and redness. On this facial color preference test, the 30 pairs of male faces and 30 pairs of female faces (each pair consisting of two versions of a face; one version with increased color values and one version with decreased color values) were presented on a color-calibrated monitor. Participants were instructed to click on the face in each pair they thought was more attractive. Male and female faces were presented in separate blocks and both trial and block order were fully randomized. The side of the screen on which any given image was presented was also fully randomized. This type of facial color preference test has been used in previous studies to assess preferences for aspects of facial coloration (Lefevre & Perrett, 2014). The screen was calibrated using xRite i1 Display Pro colorimeter prior to testing. We also used principal component analysis to investigate possible intercorrelations among different aspects of men's color preferences. The local ethics committee approved all aspects of the procedure.

3.3 Results

First, we calculated the proportion of trials on which each participant chose the image with increased color values as the more attractive separately for each combination of test session and color axis (yellow, red, lightness). Preliminary analyses using linear mixed models in which test sessions were grouped by participant to test for within-subjects effects of testosterone and cortisol on color preferences showed no significant within-subject effects of men's testosterone or cortisol on any aspect of color preference (all $|t|$<1.20, all > .24). Because of this, and because color preferences were highly consistent across test sessions (*Cronbach's alphas*: yellow = .76, lightness = .76, red = .81), we averaged scores for each color axis across test sessions.

One sample t-tests comparing average color preferences with the chance value of 0.5 showed that men preferred faces with increased yellow over versions with decreased yellow (t = 4.94, p < .001, M=.59, SEM = .02), preferred faces with increased red over versions with decreased red (t = 6.08, p < .001, M = .62, SEM = .02), but did not prefer faces with increased lightness over versions with decreased lightness (t = 1.10, p = .28, M = .52, SEM = .02).

Men's hormone levels were also highly consistent across test sessions (*Cronbach's alphas*: testosterone =.91, cortisol = .76). Consequently, we also averaged these values across test sessions. Average testosterone and average cortisol levels were then centered on their means for analyses.

Next, we subjected the three color-preference scores to principal component analysis (with no rotation). The first component produced explained approximately 55% of the variance in scores and was strongly positively correlated with preferences for facial yellowness (r = .92), strongly negatively correlated with preferences for facial lightness (r = –.85), but only weakly positively correlated preferences for facial redness (r = .26). We labeled this component *dark yellow* component as it reflected preferences for yellower, darker skin. Men who scored high on this component showed stronger preferences for yellower and darker skinned faces. The second component explained approximately 35% of the variance in scores and was strongly positively correlated with preferences for facial redness ($r = .95$), positively correlated with preferences for facial lightness ($r = .38$), and weakly positively correlated with preferences for facial yellowness ($r = .09$). We labeled this component *light red* component as it reflected preferences for redder and lighter skin.

We then investigated individual differences in scores on the *dark yellow* component using a regression analysis in which average testosterone level (centered), average cortisol level (centered), and the interaction term were entered simultaneously as predictors. This analysis revealed a significant negative effect of average testosterone level ($t = -2.37$, *standardized beta* = –.44, $p = .022$) and a significant positive effect of the interaction term ($t = 2.83$, *standardized beta* = .46, $p = .007$). The effect of average cortisol level was not significant ($t = 1.01$, *standardized beta* = .17, $p = .32$). These results indicate that men with higher testosterone levels generally showed weaker preferences for yellower and darker skin coloration in faces and that this relationship was particularly strong among men with low cortisol (Figure 1). Repeating this analysis for scores on the *light red* component showed no significant effects (all absolute $t < 0.84$, all absolute *standardized beta* < .16, all $p > .40$).

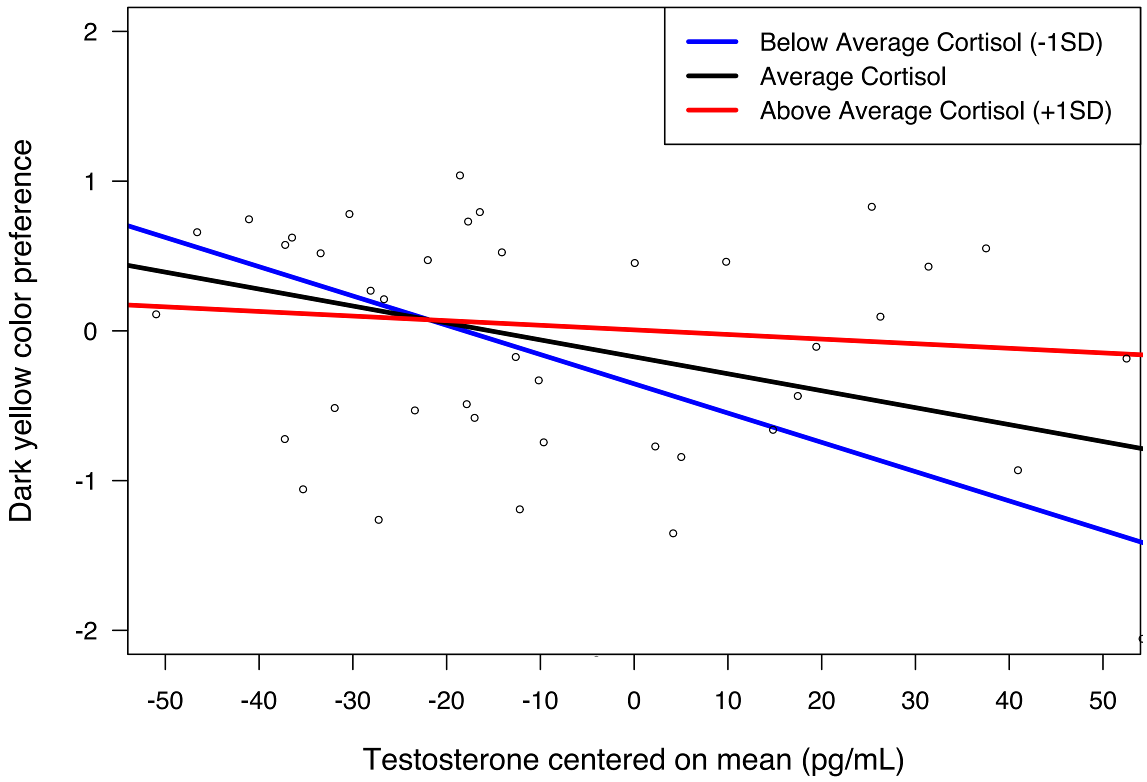

Figure 3.1 The interaction between average testosterone and average cortisol for scores on the *dark yellow* component. Men with higher testosterone levels generally showed weaker preferences for dark yellow facial coloration. However, this relationship was particularly strong among men with low cortisol.

Finally, we analyzed preferences for facial yellowness, lightness, and redness separately. For facial yellowness, the regression analysis revealed a significant negative effect of average testosterone level (*t* = –2.21, *standardized beta* = –.41, *p* = .033) and a significant positive effect of the interaction term (*t* = 2.65, *standardized beta* = .43, *p* = .011). The effect of average cortisol level was not significant (*t* = 0.77, *standardized beta* = .13, *p* = .45). An additional analysis, in which sex of face was included as a within-subject factor, showed that none of these effects were qualified by significant interactions with sex of face (all *p* > .32). For facial lightness, the regression analysis revealed a positive effect of average testosterone level that was not significant (*t* = 1.71, *standardized beta* = .33, *p* = .094) and a significant negative effect of the interaction term (*t* = –2.36, *standardized beta* = –.39, *p* = .023). An additional analysis showed that none of these effects were qualified by significant interactions with sex of face (all *p* > .52). The effect of average cortisol level was not significant (*t* = –0.70, *standardized beta* = –.12, *p* = .49). These analyses confirmed that men with high testosterone levels generally showed weaker preferences for carotenoid cues in faces and that this relationship was particularly strong among men with low cortisol. The corresponding analysis of preferences for facial redness showed no significant effects (all absolute $t < 1.14$, all absolute *standardized beta* < .23, all $p > .26$). An additional analysis showed no significant interactions with sex of face (all $p > .46$).

Repeating all of the analyses described above excluding three participants who reported non-white ethnicity did not alter the patterns of significant results. Including participant age as an additional predictor also did not alter any of these patterns of significant results.

3.4 Discussion

Our analyses of preferences for color cues in faces revealed that men with higher testosterone levels generally showed weaker preferences for yellower and darker skin coloration, which are characteristic of increased carotenoid pigmentation (Lefevre et al., 2013, Lefevre & Perrett, 2014; Whitehead et al., 2012a, 2012b). Importantly, this relationship was particularly strong among men who had low cortisol. Previous research has demonstrated that men with the combination of high testosterone and low cortisol show the strongest physiological immune responses (Rantala et al., 2012), while other research has implicated carotenoids in immune function (Hughes, 1999; Sies, 1993). Consequently, our results suggest that men with a hormonal profile associated with a stronger physiological immune response may show a weaker behavioral immune response (i.e., show weaker aversions to individuals displaying color cues associated with high vulnerability to infectious disease). Thus, our results are consistent with the functional flexibility principle’s prediction that individuals who are likely to show stronger physiological immune responses will show weaker behavioral immune responses (Schaller, 2011; Schaller et al., 2015; Schaller & Park, 2011; Tybur & Gangestad, 2011).

By contrast with our results for preferences for yellower and darker skin coloration, our analyses of preferences for facial redness found that these were not related to men’s testosterone or cortisol levels. Since previous research (Stephen et al., 2009a) suggests that facial redness is a cue of blood oxygenation and, consequently, may be a cue of cardiovascular health (i.e., aspects of physical condition that carry no direct infectious disease risk), this pattern of results is also consistent with the functional flexibility principle.

That the relationships between men's hormone levels and color preferences were not affected by the sex of faces judged also suggests that our findings reflect a behavioral immune response to the threat of contagious disease, rather than reflecting preferences that are specific to mating contexts or contexts implicated in intrasexual competition only. In other words, because our findings are unaffected by stimulus sex, it is unlikely that they are driven by mechanisms employed in either mate choice specifically or in assessments of the quality of potential competitors for mates only.

While our study employed measures of men's hormone levels and color preferences taken on multiple occasions, our sample size is relatively small (N=47) and we used an indirect measure of men's immunocompetence. Investigating the links between face preferences and physiological immune responses using larger samples and more direct measures of immune responses is needed to clarify the potential link between physiological immune responses and face preferences. Additionally, although increasing carotenoid consumption causes darker, yellower skin (Whitehead et al., 2012b), and carotenoids are implicated in physiological immune function (Hughes, 1999; Sies, 1993), further work is needed to demonstrate more direct links between these components of facial coloration and immune function.

In summary, we show that men with higher testosterone levels have weaker preferences for yellower and darker coloration cues in faces and that this relationship is particularly strong among men who have low cortisol. In combination with recent work reporting that men with the combination of high testosterone and low cortisol show particularly strong physiological immune responses (Rantala et al., 2012), our results provide preliminary support for functional flexibility in the behavioral immune system by suggesting that men with stronger physiological immune responses show relatively weaker behavioral immune responses. More generally, while studies have reported that between-individual differences in women's hormone levels predict differences in their judgments of others' attractiveness (Bobst et al., 2014, Roney & Simmons, 2008), the current study is one of the first to report associations between measured hormone levels and differences in men’s judgments of others’ attractiveness.

Chapter 4: Are men’s perceptions of sexually dimorphic vocal characteristics related to their testosterone levels?

Preface

The following chapter is reproduced from:

Kandrik, M., Hahn, A. C., Wincenciak, J., Fisher, C. I., Pisanski, K., Feinberg, D. R., DeBruine, L. M., Jones, B. C. *(*2016). Are men’s perceptions of sexually dimorphic vocal characteristics related to their testosterone levels? *PLOS ONE*, *11.* doi: 10.1371/journal.pone.0166855 .

All data and analyses scripts are available online from the journal at: http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0166855

Abstract

Feminine physical characteristics in women are positively correlated with markers of their mate quality. Previous research on men’s judgments of women’s facial attractiveness suggests that men show stronger preferences for feminine characteristics in women’s faces when their own testosterone levels are relatively high. Such results could reflect stronger preferences for high quality mates when mating motivation is strong and/or following success in male-male competition. Given these findings, the current study investigated whether a similar effect of testosterone occurs for men’s preferences for feminine characteristics in women’s voices. Men’s preferences for feminized versus masculinized versions of women’s and men’s voices were assessed in five weekly test sessions and saliva samples were collected in each test session. Analyses showed no relationship between men’s voice preferences and their testosterone levels. Men’s tendency to perceive masculinized men’s and women’s voices as more dominant was also unrelated to their testosterone levels. Together, the results of the current study suggest that testosterone-linked changes in responses to sexually dimorphic characteristics previously reported for men's perceptions of faces do not occur for men's perceptions of voices.

4.1 Introduction

Feminine physical characteristics are positively correlated with measures of women's reproductive health (e.g., Jasienska et al., 2004; Law Smith et al., 2006), general medical health (Gray & Boothroyd, 2012; Thornhill & Gangestad, 2006), and maternal tendencies (Law Smith et al., 2012). Given that these traits are highly valued in mates, women displaying feminine physical characteristics tend to be judged as more attractive than relatively masculine women (reviewed in Pisanski et al., 2014b, and Puts et al., 2012).

Several lines of evidence suggest that men's preferences for feminine characteristics in women's faces are stronger when their own testosterone levels are relatively high. For example, Welling et al. (Welling et al., 2008) reported that men showed stronger preferences for feminine shape characteristics in women's, but not men's, faces when their own testosterone levels were higher. Relatedly, Welling et al. (Welling et al., 2013) found that men who had been randomly allocated to the winning condition in a male-male contest (playing against another man in a video game with a fixed outcome) subsequently showed stronger preferences for feminine shape characteristics in women's faces than did men randomly allocated to the losing condition. Welling et al. (2013) did not measure men's testosterone levels. However, given that testosterone levels tend to be higher in winners of male-male contests than in losers (reviewed in Archer, 2006), Welling et al's (2013) results are consistent with men showing stronger preferences for feminine women when their own testosterone levels are relatively high.

Increased preferences for feminine women when men's own testosterone levels are high could occur because success in male-male competition increases access to high quality mates (Welling et al., 2013). Given that testosterone levels are associated with mating motivation in men (see Puts et al., 2015 for a recent review], increased preferences for feminine women when men's own testosterone levels are high could also reflect stronger preferences for high quality mates when men's mating motivation is strong (Welling et al., 2008).

To date, evidence that men show stronger preferences for feminine women when their own testosterone levels are high has come exclusively from studies investigating men’s preferences for feminine characteristics in women’s faces. However, sexually dimorphic characteristics are also present in the human voice (reviewed in Pisanski et al., 2014b, and Puts et al., 2012). Women’s voices tend to have both higher fundamental frequencies (i.e., higher pitch) and higher formant frequencies than do men’s voices (reviewed in Pisanski et al., 2014b, and Puts et al., 2012). These feminine acoustic characteristics are associated with attractiveness in women’s voices (Puts et al., 2012; Feinberg et al., 2008a; Jones et al., 2010; Pisanski & Rendal, 2011) and men tend to respond to femininity in women’s faces and voices in similar ways (Puts et al., 2012). Because previous research suggests that men’s preferences for femininity in women’s faces are stronger when their own testosterone levels are high (Welling et al., 2008, Welling et al., 2013), the current study used a longitudinal design to investigate whether men’s preferences for higher voice pitch and higher formant frequencies in women’s voices are stronger when their own salivary testosterone levels are high. Additionally, because previous research has reported that men show stronger preferences for feminine characteristics in women’s, but not men’s, faces when their own testosterone levels are high (Welling et al., 2008), we also assessed men’s preferences for manipulated pitch and formant frequencies in men’s voices. Men’s voice preferences were tested in five weekly test sessions, with each participant also providing a saliva sample in each test session.

While men tend to ascribe high attractiveness to women’s voices with feminine acoustic properties (reviewed in Puts et al., 2012), men tend to ascribe high dominance to men’s and women’s voices with masculine characteristics (e.g., low pitch and formants, reviewed in Puts, 2010). Moreover, previous research has shown that voices contain cues to men’s and women’s physical dominance (Puts et al., 2011; Sell et al., 2010). Research on men’s dominance judgments of men’s faces suggests that winners of male-male contests are less likely to ascribe high dominance to masculine men than are losers (Watkins & Jones, 2012). Welling et al. (2016) recently proposed that this effect of contest outcome on men’s perceptions of other men’s dominance could be due to the effects of testosterone on men’s dominance perceptions. Consequently, the current study also tested whether men were more likely to ascribe high dominance to men’s voices with masculine characteristics when their own testosterone levels were relatively low. We also examined men's dominance judgments of women's voices.

4.2 Methods

4.2.1 Participants

Forty-six heterosexual men participated in the study (mean age = 22.1 years, *SD* = 3.20 years). All participants were students at the University of Glasgow (Scotland, UK). None of these men were currently taking any form of hormonal supplement and all indicated that they had not taken any form of hormonal supplement in the 90 days prior to participation. One additional man was tested but excluded from the dataset because of an average hormone level that was more than five standard deviations above the sample mean. All participants provided written consent and all aspects of the study were approved by the School of Psychology (University of Glasgow) ethics committee.

4.2.2 Voice stimuli

Recordings of 6 men and 6 women between the ages of 18 and 25 speaking the English monopthong vowels, "ah"/ɑ/, "ee"/i/, "e"/ɛ/, "oh"/o/, and "oo"/u/, were made in an anechoic sound-controlled booth using a Sennheiser MKH 800 cardioid condenser microphone, at an approximate distance of 5-10 cm. Voice recordings were digitally encoded using an M-Audio Fast Track Ultra interface at a sampling rate of 96 kHz and 32-bit amplitude quantization, and transferred to a computer as PCM WAV files using Adobe Soundbooth CS5 version 3.0.

Following other recent work on perceptions of sexually dimorphic vocal characteristics (e.g., Pisanski et al., 2014a), we created two feminized and two masculinized versions of each original voice recording by independently manipulating voice pitch or formants using the Pitch-Synchronous Overlap Add (PSOLA) algorithm in Praat version 5.2.15 (Boersma & Weenink, 2013). Pitch was raised (feminized) or lowered (masculinized) by 10% from baseline while holding formants constant. Likewise formants were raised (feminized) or lowered (masculinized) by 10% from baseline while holding pitch constant. This process created 12 pairs of voices (6 male and 6 female) that differed in pitch and 12 pairs of voices that differed in formants (6 male and 6 female). Following these manipulations, we amplitude normalized the sound pressure level of all voices to 70 decibels using the root mean squared method. The male voice stimuli used in the current study have previously been used to investigate hormonal correlates of women's preferences for masculine characteristics in men's voices (Pisanski et al., 2014b). Voice pitch and formant measures for the feminized and masculinized voice stimuli are given in Appendix 2.1 (Table 7.2.1 and Table 7.2.2).

4.2.3 Procedure

All participants completed five weekly test sessions which took place between 2pm and 5pm to minimize diurnal variation in hormone levels (Papacosta & Nassis, 2011). During each test session, participants provided a saliva sample via the passive drool method (Papacosta & Nassis, 2011). Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and to avoid eating, smoking, drinking, chewing gum, or brushing their teeth in the 60 minutes prior to participation. Saliva samples were immediately frozen and stored at -32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis, where they were assayed using the Salivary Testosterone Enzyme Immunoassay Kit 1-2402 (*M* = 177.69 pg/mL, *SD* = 40.22 pg/mL). Although previous research examining links between men's hormone levels and responses to sexually dimorphic characteristics has focused on possible effects of testosterone levels (Welling et al., 2008; Welling et al., 2013; Welling et al., 2016), research on mating motivation (Pflüger et al., 2014; Roney et al., 2010) and male-male competition (Jiménez et al., 2012; Mehta & Josephs, 2010) more generally has also implicated cortisol. Consequently, men's saliva samples were also assayed using the Salivary Cortisol Enzyme Immunoassay Kit 1-3002 (*M* = 0.19 µg/dL, *SD* = 0.08 µg/dL). All assays passed Salimetrics' quality control.

In each of five test sessions, participants listened to 24 pairs of voices (each pair consisting of a masculinized and a feminized version of the same voice) through headphones and, on separate trials, reported which voice in each pair sounded either more attractive or more dominant. Male and female voice stimuli were presented in separate blocks of trials and attractiveness and dominance judgments were also made in separate blocks of trials. Block order, trial order, and the order in which participants listened to the masculinized and feminized versions in each pair were fully randomized. This type of test has been used to assess perceptions of masculinized versus feminized versions of voices in previous work (e.g., Jones et al., 2010; Pisanski et al., 2014a).

4.3 Results

First, we calculated the proportion of trials on which feminized versions of women's voices or masculinized versions of men's voices were chosen. This score was calculated separately for each combination of participant, test session, judgment (attractiveness, dominance), manipulation type (pitch manipulation, formant manipulation), and sex of voice (male, female). These scores were centered on 0.5 (i.e., chance).

Next, we investigated how these scores were related to men's current hormone levels. Attractiveness judgments of women's voices, attractiveness judgments of men's voices, dominance judgments of women's voices, and dominance judgments of men's voices were all analyzed separately.

In each analysis, we tested for effects of hormone levels on voice perceptions using multilevel modeling with test sessions grouped by participant (five test sessions per participant). Analyses were conducted using R (R Core team, 2013), *lme4* (Bates et al., 2014), and *lmerTest* (Kuznetsova et al., 2013). For analyses of responses to women's voices, the proportion of feminized voices chosen (centered on chance) was entered as the dependent variable at the test session level. For analyses of responses to men's voices, the proportion of masculinized voices chosen (centered on chance) was entered as the dependent variable, again at the test session level. Testosterone and cortisol levels were entered as predictors at the test session level, each centered on their subject-specific means. Manipulation type (effect-coded so that the pitch manipulation was assigned a value 0.5 and the formant manipulation was assigned a value -0.5) was also entered as a predictor at the test session level. Each model also included two-way interactions between current testosterone level and manipulation type and between current cortisol level and manipulation type. The analyses and results are specified in full in Appendix 2.2.

4.3.1 Attractiveness judgments of women’s voices

In our analysis of women’s vocal attractiveness, the intercept approached significance (*t* = 1.86, *p* =.070), indicating that men generally preferred feminized versions of women’s voices to masculinized versions. There were no other significant effects or interactions (all |*t*| < 1.10, all *p* >.274). Repeating this analysis with testosterone retained as a predictor, but excluding cortisol, or with cortisol retained as a predictor, but excluding testosterone, did not reveal any effects involving hormone levels (all |*t*| < 0.970, all *p* > .333).

4.3.2 Attractiveness judgments of men’s voices

In our analysis of men’s vocal attractiveness, the intercept was significant (*t* = 7.01, *p* < .001), indicating that men generally preferred masculinized versions of men’s voices to feminized versions. The effect of manipulation type was also significant (*t* = 5.40, *p* < .001), indicating that men showed stronger preferences for masculinized male voices manipulated in pitch (*M* = 0.18, *SD*= 0.23) than manipulated in formants (*M* = 0.09, *SD* = 0.23). There were no other significant effects or interactions (all |*t*| < 1.40, all *p* > .161). Repeating this analysis with testosterone retained as a predictor, but excluding cortisol, or with cortisol retained as a predictor, but excluding testosterone, did not reveal any effects involving hormone levels (all |*t*| < 1.69, all *p* > .093).

4.3.3 Dominance judgments of women’s voices

In our analysis of women’s vocal dominance, the intercept was significant (*t* = – 9.73, *p* < .001), indicating that men generally judged masculinized versions of women’s voices to be more dominant than feminized versions. The effect of manipulation type was also significant (*t* = – 4.23, *p* < .001), indicating that men chose masculinized female voices as the more dominant more often when voices were manipulated in pitch (*M* = – 0.24, *SD*= 0.22) than when they were manipulated in formants (*M* = – 0.16, *SD* = 0.26). There were no other significant effects or interactions (all |*t*| < 0.52, all *p* > .610). Repeating this analysis with testosterone retained as a predictor, but excluding cortisol, or with cortisol retained as a predictor, but excluding testosterone, did not reveal any effects involving hormone levels (all |*t*| < 0.54, all *p* > .590).

4.3.4 Dominance judgments of men's voices

In our analysis of men's vocal dominance, the intercept was significant (t = 14.36, p < .001), indicating that men generally judged masculinized versions of men's voices to be more dominant than feminized versions. There were no other significant effects or interactions (all $|t|$ < 1.25, all p > .241). Repeating this analysis with testosterone retained as a predictor, but excluding cortisol, or with cortisol retained as a predictor, but excluding testosterone, did not reveal any effects involving hormone levels (all $|t|$ < 1.06, all p > .290).

4.4 Discussion

The current study tested for possible relationships between within-subject changes in men's salivary testosterone and cortisol levels and their preferences for, and dominance perceptions of, voices manipulated in sexually dimorphic acoustic properties. Consistent with previous research, men generally judged masculinized male and female voices as more dominant than feminized versions (Puts, 2010) and judged masculinized male voices as more attractive than feminized versions (Jones et al., 2010). Also consistent with previous research (Feinberg et al., 2008a; Fraccaro et al., 2010), men tended to judge feminized female voices as more attractive than masculinized versions, although this effect of femininity only approached significance in the current study (p=.070). The weak preference for feminized versions of women's voices in the current study is likely a consequence of our manipulation of acoustic characteristics of voices (20% difference between feminized and masculinized versions) being very similar to the just-noticeable difference for men's judgments of women's vocal attractiveness (18% difference) reported by Re et al. (2012). This was done to avoid men's preferences for feminized versions of women's voices being at ceiling and masking potential relationships with hormone levels.

In contrast to our findings, a recent study found that within-subject changes in estradiol predicted women's preferences for vocal masculinity in men's voices (Pisanski et al., 2014a). This apparent sex difference in hormonal modulation of voice preferences may potentially reflect overall differences in mating strategies, as women may use more and finer-grained information about potential mates, or may be more sensitive to cues of quality, in order to offset potentially greater costs to their fitness associated with poor partner choice

(Trivers, 1972). The extent to which hormone-linked changes in social judgments of voices could be driven by effects of hormones on hearing is not known.

Previous research has suggested that men’s preferences for feminine characteristics in women’s, but not men’s, faces become stronger when their testosterone levels are high (Welling et al., 2008; Welling et al., 2013). By contrast with these results for men’s face preferences, the current study observed no significant effect of testosterone on men’s preferences for sexually dimorphic characteristics in either women’s or men’s voices. Previous research has also suggested that the tendency to ascribe dominance to men displaying masculine facial characteristics might also be greater when men’s own testosterone levels are low (Watkins & Jones, 2012; Welling et al., 2016). However, the current study observed no significant effect of testosterone on men’s dominance perceptions of either women’s or men’s voices. We also observed no effects of cortisol on men’s responses to sexually dimorphic vocal characteristics when judging the attractiveness or dominance of voices. Although previous research suggested that social perceptions of sexually dimorphic characteristics in voices are very similar to those reported in the face perception literature (Fraccaro et al., 2010; Feinberg et al., 2008b), it is possible that using more socially relevant stimuli (e.g., sentences) could produce effects of hormones on voice perception that were not apparent in the current study. The results of the current study suggest that hormone-linked changes in responses to sexually dimorphic characteristics that have previously been reported for men's perceptions of faces (Welling et al., 2008; 2013) do not occur for men's perceptions of voices.

Chapter 5 : Do salivary testosterone and cortisol levels predict men’s facial appearance?

Preface

The following chapter is reproduced from:

Kandrik, M., Hahn, A. C., Han, CH., Wincenciak, J., DeBruine, L. M., Jones, B. C. (*under revision*). Do salivary testosterone and cortisol levels predict men’s facial appearance? *Adapt. Hum. Behav. Physiol.* Invited revision.

Abstract

Many researchers have proposed that aspects of men’s facial appearance, such as their perceived attractiveness, health, and dominance, are associated with testosterone, cortisol, or their interaction. However, evidence for such associations is inconsistent across studies, potentially due to the use of suboptimal methods for estimating men’s hormone levels in which saliva samples were collected on only one or two separate occasions. In the current studies, we tested for associations between men’s rated facial attractiveness, health, and dominance and estimates of their testosterone and cortisol levels derived from samples collected on five separate occasions. Men’s facial dominance was associated with the interaction between their testosterone and cortisol levels; the faces of men with the combination of low testosterone and high cortisol were judged as less dominant. By contrast, men’s hormones were not related to their facial attractiveness or health. The inconsistent results from past research, together with the null results for attractiveness and health in the current study, suggest that adult hormone levels are less important for men’s facial appearance than many researchers have claimed.

5.1 Introduction

Male secondary sexual characteristics are dependent on testosterone levels in multiple species (Andersson, 1994). Since testosterone has immunosuppressive effects on males (see Foo et al., 2016, for a recent meta-analytic review), only males in good physical condition may be able to bear the immunosuppressive effects of testosterone (Folstad & Karter, 1992). Consequently, many researchers have suggested that exaggerated secondary sexual characteristics may be honest signals of male physical condition (Boothroyd et al., 2013; Rhodes et al., 2003; Thornhill & Gangestad. 2006). In humans, this reasoning leads to the predictions that men with high testosterone levels will appear to be attractive, healthy, and dominant. Given the importance of facial cues for human social interactions (see Little et al., 2011a, for a review), much of the work testing these predictions has focused on possible links between testosterone and aspects of men’s facial appearance.

Early research investigating possible links between testosterone and perceptions of men’s facial appearance reported that the faces of men with higher basal testosterone levels were perceived to be more masculine (Penton-Voak & Chen, 2004; Roney et al., 2006) and more attractive as short-term partners (Roney et al., 2006). However, other studies did not observe significant associations between men’s basal testosterone and their facial attractiveness, dominance or masculinity (Hönekopp et al., 2007; Neave et al., 2003; Pound et al., 2009; Whitehouse et al., 2015). Thus, evidence that basal testosterone levels are correlated with these aspects of men’s facial appearance is mixed.

More recently, researchers investigated the possible moderating role of stress hormones (e.g., cortisol) on the association between testosterone and men’s facial appearance (Rantala et al., 2012; Moore et al., 2011a, 2011b). Although short-term increases in cortisol levels stimulate immune responses, chronically elevated cortisol levels are associated with immunosuppression (Sapolsky et al., 2000; Martin et al., 2009). Research investigating the possible moderating role of cortisol on the relationship between men’s facial appearance and testosterone levels has also produced mixed results, however. Rantala et al. (2012) found that the faces of men with high testosterone levels were perceived to be more attractive and that this relationship was strongest among men who also had low cortisol levels. Moore et al (2011b) did not replicate these findings. Moreover, Moore et al. (2011a) reported a negative relationship between men's cortisol and facial attractiveness, but no relationship between testosterone and men's facial attractiveness, or the interaction between cortisol and testosterone and men's facial attractiveness. Moore et al. (2011a) also found that neither ratings of men's facial health nor ratings of their facial masculinity were related to men's testosterone, cortisol, or their interaction[1].

One of the possible explanations for the inconsistent results across studies of the possible links between men's hormone levels and facial appearance is the use of relatively unreliable (i.e., noisy) hormone measures. Testosterone and cortisol are highly reactive hormones that respond rapidly to environmental cues (e.g., Roney et al., 2003; Roney et al., 2007). However, the majority of previous studies of the possible links between men's hormone levels and facial appearance have estimated basal hormone levels from only a single measurement (Hönekopp et al., 2007; Neave et al., 2003, Penton-Voak & Chen, 2004; Roney et al., 2006, Whitehouse et al., 2015) or two measurements (Moore et al., 2011a, 2011b; Pound et al., 2009; Rantala et al., 2012). Consequently, research using more reliable estimates of men's hormone levels is required.

In light of the above, the current study investigated whether perceptions of men's facial appearance (rated attractiveness, health, and dominance) are predicted by men's testosterone, cortisol, or their interaction. By contrast with previous research, basal hormone levels were estimated from five saliva samples collected at weekly intervals.

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[1] The two studies by Moore et al. (2011a, 2011b) each tested for associations between hormone levels and facial appearance using both ratings of individual faces and ratings of prototypes manufactured to possess the average shape, color, and texture information of samples of men with different combinations of salivary cortisol and testosterone levels. Because their results for ratings of individual faces speak directly to the question of whether individual faces contain cues to hormone levels, we only discuss Moore et al's results for analyses of individual faces here.

5.2 Methods

5.2.1 Participants

Forty-five heterosexual men participated in the study (mean age = 22.0 years, *SD* = 3.31 years). All participants were students at the University of Glasgow (Scotland, UK). None of these men were currently taking any form of hormonal supplement and all indicated that they had not taken any form of hormonal supplement in the 90 days prior to participation. Participants were not instructed to clean shave. One additional man was tested but excluded from the dataset because his average cortisol level was more than five standard deviations above the mean for the rest of the sample.

5.2.2 Procedure

All participants completed five weekly test sessions. All test sessions took place between 2pm and 5pm to minimize diurnal variation in hormone levels (Papacosta & Nassis, 2011). During each test session, participants provided a saliva sample via passive drool (Papacosta & Nassis, 2011). Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and avoid eating, smoking, drinking, chewing gum, or brushing their teeth in the 60 minutes prior to participation. Saliva samples were frozen immediately and stored at -32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis, where they were assayed using the Salivary Testosterone Enzyme Immunoassay Kit 1-2402 (*M* = 182.10 pg/mL, *SD* = 43.15 pg/mL) and the Salivary Cortisol Enzyme Immunoassay Kit 1-3002 (*M* = 0.19 µg/dL, *SD* = 0.07 µg/dL). All assays passed Salimetrics' quality control.

In each of the five test sessions, each participant first cleaned his face with hypoallergenic face wipes. A full-face digital photograph was taken a minimum of 10 minutes later. Photographs were taken in a small windowless room against a constant background, under standardized diffuse lighting conditions, and participants were instructed to pose with a neutral expression. Camera-to-head distance and camera settings were held constant. Participants wore a white smock covering their clothing when photographed. Photographs were taken using a Nikon D300S digital camera and a GretagMacbeth 24-square ColorChecker chart was included in each image for use in color calibration. Following other recent work on social judgments of faces (e.g., Jones et al., 2015), face images were color calibrated using a least-squares transform from an 11-expression polynomial expansion developed to standardize color information across images (Hong et al., 2001). Images were masked so that hairstyle and clothing were not visible and standardized on pupil positions.

Next, the face photographs of the 45 men (225 face photographs in total) were rated for attractiveness, health, and dominance using 1 (low) to 7 (high) scales. Attractiveness, health and dominance were each rated in separate blocks of trials. Trial order was fully randomized within each block of trials. Thirty men and 43 women (mean age = 23.2 years, *SD* = 4.27 years) rated the faces with each individual rater randomly allocated to rate between 2 and 4 blocks of trials (mean number of raters per block of trials=32.3, *SD*=2.89). One rater chose not to report their age. Inter-rater agreement was high for each trait (all *Cronbach's alphas* > .94). Men's and women's ratings were also strongly positively correlated for all traits (all *r* > .89). Consequently, we calculated the mean dominance (*M* = 3.59, *SD* = 0.75), attractiveness (*M* = 2.89, *SD* = 0.59), and health (*M* = 3.97, *SD* = 0.60) rating for each man's face.

5.3 Results

We investigated the variation in dominance ratings of men's faces using a regression analysis, in which average testosterone level (centered on the group mean), average cortisol level (centered on the group mean), and the interaction term were entered simultaneously as predictors. This analysis revealed a significant positive effect of the interaction term (*t* = 2.09, standardized beta = 0.37, *p* = .043). Men's average testosterone or cortisol did not have any significant effects (all absolute *t* < 0.96, all absolute standardized beta < 0.20, all *p* > .344). The positive effect of the interaction term suggests that testosterone has a more positive relationship with dominance perceptions at higher levels of cortisol (Figure 1). In other words, men with high cortisol and low testosterone were perceived as less dominant than men with high cortisol and high testosterone, or than men with low cortisol (regardless of testosterone).

We repeated the same analysis to investigate the variation in attractiveness ratings and health ratings of men's faces. These analyses revealed no significant effects (all absolute *t* < 0.91, all absolute *standardized beta* < 0.20, all *p* > .366, and all absolute *t* < 0.78, all absolute *standardized beta* < 0.17, all *p* > .444, respectively). Including men's age as an additional predictor did not alter any of these patterns of results.

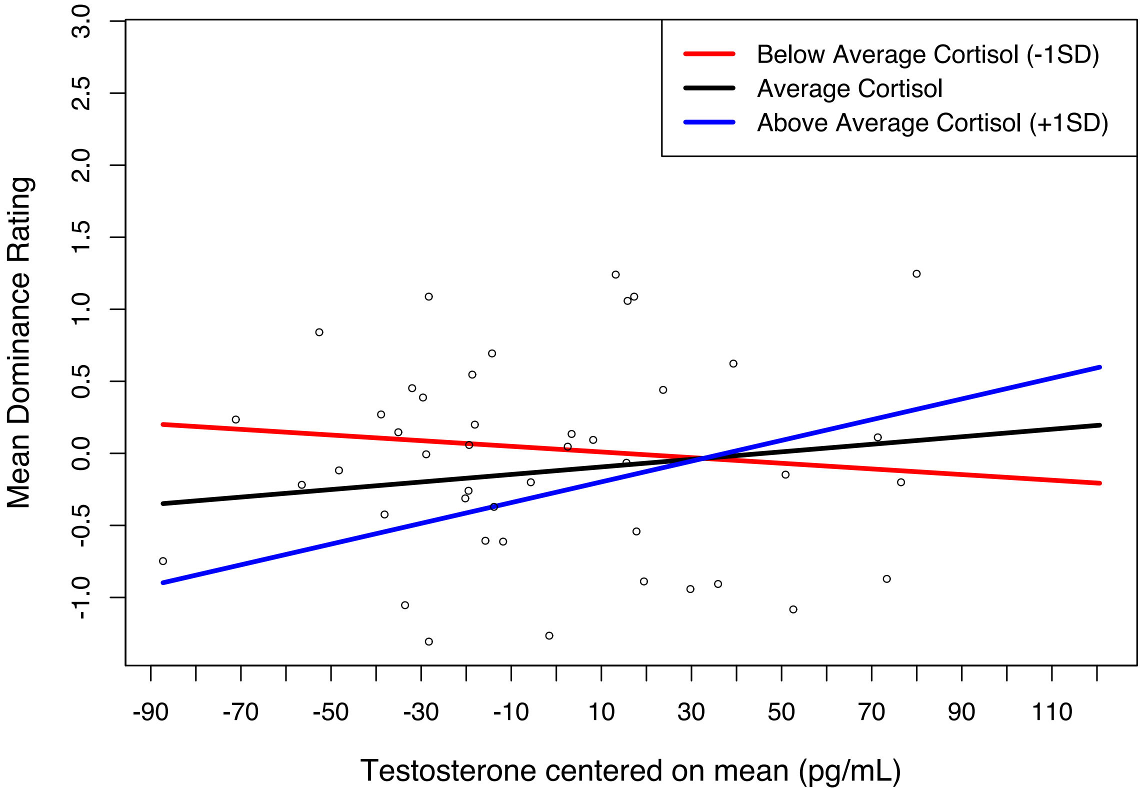


Figure 5.1 The interaction between average testosterone and average cortisol on men's dominance. Men with high cortisol and low testosterone were perceived as less dominant than men with high cortisol and high testosterone, or than men with low cortisol (regardless of testosterone).

5.4 Discussion

Here we tested for associations between perceptions of men's facial appearance (rated attractiveness, health and dominance) and their testosterone and cortisol levels, using estimates of men's trait hormone levels derived from saliva samples collected on five separate occasions. Men's facial attractiveness and perceived health were unrelated to their salivary testosterone and cortisol levels, or to the interactions between these two hormones, contrasting with previous research reporting that men with the combination of high testosterone and low cortisol tended to have the most attractive faces (Rantala et al., 2012). These null results are consistent with previous studies that also observed no significant relationships between men's testosterone levels and their facial attractiveness or health (e.g., Hönekopp et al., 2007; Neave et al., 2003; Moore et al., 2011a, 2011b). They are also consistent with previous work on attractiveness and perceived health in which the interaction between testosterone and cortisol was not significant (Moore et al., 2011a, 2011b).

By contrast with our null results for men's facial attractiveness and perceived health, the interaction between testosterone and cortisol was significant in our analysis of men's facial dominance. Specifically, men with the combination of high cortisol and low testosterone tended to have the least dominant-looking faces. Only one other study has tested whether cortisol moderates the relationship between testosterone and facial dominance in men. Consistent with our results, Moore et al. (2011b) found that a prototype face with the average shape, color and texture information of men with high cortisol and low testosterone levels was judged to be less dominant than prototype faces representing men with low cortisol and low testosterone, high cortisol and high testosterone, or low cortisol and high testosterone levels. Moore et al. (2011b) did not examine dominance ratings of individual faces, however. That men with the combination of high testosterone and low cortisol look particularly dominant would be consistent with research suggesting that such men actually are particularly dominant (Mehta & Josephs, 2010). Nonetheless, we note here that the effect would not be significant if we corrected for multiple comparisons, raising the possibility that it is a false positive.

One possible explanation for the inconsistent findings for facial appearance and men's hormone levels that have been reported in the face perception literature is the use of sub-optimal estimates of trait hormone levels. Estimating men's hormone levels from measures taken on only one or two occasions (as was the case in previous studies) may produce unreliable estimates. The current study used more robust hormone estimates that were calculated from measurements taken on five separate occasions. With these measures, we found no evidence for an association between circulating testosterone or cortisol levels and ratings of either men's facial attractiveness or health. Although we observed a significant interaction between testosterone and cortisol for facial dominance, further study is needed to establish whether this association is reliable. Whitehouse et al. (2015) recently reported a positive association between men’s facial masculinity and their prenatal exposure to testosterone (measured from blood samples taken from the umbilical cord), but not their current testosterone levels. These results, together with the null results of the current study, suggest that adult hormone levels may be relatively unimportant for men’s facial appearance.

Chapter 6: General discussion

6.1 Summary of main findings

While majority of research on mate preferences and mating strategies investigated variation in women's mate preferences and mating strategies, there are strong theoretical reasons based on Trade-off theory (Gangestad & Simpson, 2000) to expect variation in men's mating strategies and mate preferences. In this thesis I presented four empirical studies investigating variation in men's mating strategies and mate preferences at various levels ranging from regional variation in mating strategies to within-subject variation in men's preferences for sexually dimorphic acoustic characteristics.

The first study I presented, investigated possible relationships between women's and men's sociosexual orientation and US state-level variation in socio-ecological variables previously found to predict country-level variation in sociosexual orientation (e.g., Schmitt, 2005). Using multilevel analyses I showed that the scarcity of female mates factor, but not environmental demand or wealth factors, predicted variation in men's and women's global sociosexual orientation. In other words, participants in states where female mates were particularly scarce reported being less willing to engage in uncommitted sexual relationships, suggesting that members of the sex that is more scarce are better placed to pursue their preferred mating strategy, while members of the sex that is more abundant may need to adapt their preferred mating strategies in order to secure a mate.

The second empirical study I presented investigated the relationships between men's average hormone levels and their preferences for healthy color cues in faces. I showed that men with a hormonal profile of high testosterone and low cortisol levels showed the weakest preferences for yellower and darker skin coloration, which are characteristic of increased carotenoid pigmentation (Lefevre et al., 2013, Lefevre & Perrett, 2014; Whitehead et al., 2012a, 2012b). In combination with recent work reporting that men with the combination of high testosterone and low cortisol show particularly strong physiological immune responses (Rantala et al., 2012), and work implicating carotenoids in immune function (Huges, 1999; Sies, 1993), these results provide preliminary support for functional flexibility in the behavioral immune system by suggesting that men with stronger physiological immune responses show relatively weaker behavioral immune responses. More generally, this study is one of the first to report associations between measured hormone levels and differences in men's judgments of others' attractiveness.

The third empirical study tested for possible relationships between within-subject changes in men's salivary testosterone and cortisol levels and their preferences for, and dominance perceptions of, women's and men's voices manipulated in sexually dimorphic acoustic properties. Men's preferences for sexually dimorphic acoustic characteristics were not related to their testosterone levels, cortisol levels or their interaction. Similarly, men's dominance perceptions of sexually dimorphic acoustic characteristics were not related to their testosterone levels, cortisol levels or their interaction. The results of this study suggest that current hormone levels do not mediate men's perceptions of sexually dimorphic vocal characteristics.

In the final empirical chapter I presented a study that tested for associations between perceptions of men's facial appearance (rated attractiveness, health and dominance) and their testosterone and cortisol levels, using estimates of men's trait hormone levels derived from saliva samples collected on five separate occasions. Men's facial attractiveness and perceived health were unrelated to their salivary testosterone and cortisol levels, or to the interaction between these two hormones. However, men with the combination of high cortisol and low testosterone tended to have the least dominant-looking faces. Nonetheless, the effect would not be significant if corrected for multiple comparisons, raising the possibility that it is a false positive. The null results from the current study, together with previous findings reporting no associations between men's circulating hormone levels and their attractiveness, dominance and health (Hönekopp et al., 2007; Moore et al., 2011a, 2011b; Neave et al., 2003; Pound et al., 2009; Whitehouse et al., 2015), suggest that adult hormone levels may be relatively unimportant for men's facial appearance.

6.2 Theoretical contributions

Here I tested several predictions from Trade-off theory, which states that both men and women have a repertoire of mating strategies which can be adaptively chosen in response to one's condition and environment, resulting in a systematic variation (Gangestad & Simpson, 2000). My first empirical study tested whether women's and men's mating strategies adaptively change with socio-biological factors like health risks and wealth, and found no evidence for systematic variation at a cross-regional level. Women's and men's mating strategies only varied with the proportion of the two sexes in a region, highlighting the importance of mating market forces and intersexual competition on mating strategies. As women's optimal mating strategies are not optimal for men (i.e., they do not maximize men's reproductive potential and vice-versa), this intersexual conflict is resolved by mating market forces, benefiting the sex that is more scarce to be better placed to pursue their preferred mating strategy.

A second general prediction from the Trade-off theory is that mate preferences should vary adaptively according to one's own condition (Gangestad & Simpson, 2000), as the pursuit of high quality mates can be costly, but the choice of mates of relatively poor/low quality can have deleterious effects on an individual's reproductive potential as well. I showed that these effects may extend to choice of potential social partners, as men's preferences for healthy color cues in faces did not differ between women's and men's faces, and men with a hormonal profile associated with particularly strong immune function could reap the benefits of interactions with mates or social partners who might be immunocompromised, while men whose immune function may be weaker are more sensitive to cues of poor health in others.

Thirdly, I tested whether hormone-mediated changes previously reported to affect men's preferences for putative cues of quality in female faces (Welling et al., 2008, Bird et al., 2016) also exist in men's preferences for putative cues of quality in female voices. Previous research suggested that testosterone-mediated shifts in men's preferences for facial femininity could happen via increased mating motivation (discussed in Welling et al., 2008). The null finding I presented in this thesis shows that this is not the case for women's voices. There may be multiple explanations for this; for example, men may not be using sexually dimorphic acoustic properties as cues of quality to the extent previously reported, or may not be as sensitive to sexually dimorphic vocal properties as they are to sexually dimorphic face shape. This also suggests that there might be a sex difference in androgen-mediated sensitivity to putative cues of quality in potential mates, as Pisanski et al., (2014a) reported that estradiol positively predicted within-subject changes in women's preferences for masculine men's voices.

Lastly, I also tested the trade-off of costly signaling of one's condition. Testosterone is immunosuppressive (Foo et al., 2016) and necessary for development of masculine face shape (e.g., DeBruine, 2014; Little et al., 2011a; Penton-Voak & Chen, 2004). Therefore, only men in particularly good condition should be able to bear costs of immunosuppression, and still be able to invest energetic resources into development of these traits. However, I found no association between men's circulating levels of testosterone or cortisol and men's facial attractiveness or health, suggesting that adult hormone levels may not be important for these aspects of men's facial appearance. My finding that men with the combination of high cortisol and low testosterone were perceived as least dominant is consistent with other research showing that testosterone and cortisol jointly modulate dominance (Mehta & Josephs, 2010). However, this effect would not be significant if corrected for multiple comparisons, raising the possibility that it is a false positive.

6.3 Methodological contributions

My work presented here improves on previous studies investigating cross-cultural variation in sociosexual orientation by utilizing multilevel linear mixed effects models. Previous literature analyzed aggregated data at the highest (e.g., region, country, state) level. This is problematic, as these aggregate scores do not necessarily reflect scores typical of individuals within regions, and hide potentially meaningful between-subject variation within countries, and at the extreme can lead to Simpson's Paradox, such that the effects at individual and aggregated levels may be in opposite direction (Pollet et al., 2014). Linear mixed effects models allow testing for effects at higher levels using scores of individuals and thus getting around problems of aggregation. Furthermore, in two of my chapters I used Principal Component Analysis to investigate latent relationships among my predictor variables. I then used resultant factors as predictors in my analyses, reducing the potential for variance inflation, which is a consequence of using multiple highly correlated predictors in analyses.

Data in three of my chapters are from a data collection that used a longitudinal design, where participants were tested 5 times in weekly intervals. This approach offers multiple benefits. Previous research studying between subject differences in men's hormone's levels and their effects on men's behavior or appearance tended to use one or two hormone samples as a measure of trait hormone levels which may be suboptimal given high reactivity of these hormones. By contrast I present studies with very robust and precise estimates of men's trait hormone levels based on five samples. Furthermore this design also allows me to test for effects of natural within-subject variation in hormones on men's behavior and preferences as I did in Chapter 4.

6.4 Limitations and future directions

While my findings from chapter 2 show that scarcity of female mates but not health risks or wealth predict people's sociosexual orientation, they do so on a relatively homogeneous western sample of people living in the USA. It is still necessary to investigate whether this pattern of results generalizes to other more heterogeneous samples, by including non-western, less developed populations. Furthermore, it is reasonable to expect that both socio-biological factors and mating-market factors should have stronger effects when measured at a smaller scale (e.g., community, village, town, etc.) as individuals are more likely to be aware of these and personally experience these factors, therefore studies at a finer scale of regional variation are necessary to fully interpret findings from large region level variation. Such studies can then also inform currently unknown cross-level patterns (Pollet et al., 2014), by showing whether effects of socio-biological factors on variation in mating strategies at a large scale (nation, state) parallel effects of variation at the smaller scale. Secondly they also may inform at what geographical level are measurements of socio-biological level no longer sensitive to variation in individual's mating strategies.

As mentioned earlier, while the study in chapter 3 employed measures of men's hormone levels and color preferences taken on multiple occasions, the sample size is relatively small (N=47) and the combination of hormone levels used is an indirect measure of men's immunocompetence. Investigating the links between face preferences and physiological immune responses using larger samples and more direct measures of immune responses is needed to clarify the potential link between physiological immune responses and face preferences. Additionally, although increasing carotenoid consumption causes darker, yellower skin (Whitehead et al., 2012b), and carotenoids are implicated in physiological immune function (Hughes, 1999; Sies, 1993), further work is needed to demonstrate more direct links between these components of facial coloration and immune function. The nature of these functionally flexible behavioral immune responses complimenting physiological immunity could further be tested experimentally. By utilizing paradigms with vaccine administration, previously used in studying immunocompetence (Rantala et al., 2012, 2013), participants physiological immunity could be safely challenged to test for state effects of physiological immunity on behavioral immune responses. Additionally the effects of carotenoids on skin lightness are inconsistent across previous studies with some studies showing increases in skin lightness following beta-carotene supplementation while others showed no changes in skin lightness in the face, but overall decreases in skin lightness across the body (Whitehead et al., 2012a, 2012b) and studies using experimental manipulations of carotenoid skin coloration decreased facial lightness (Lefevre et al., 2013; Lefevre & Perrett, 2014). More recently Henderson et al. (2017) reported changes in decreases in skin lightness and redness following an infection. Taken together these results warrant further investigation into both color cues of health appearance as well as underlying mechanisms facilitating skin color changes associated with acute illness, and more general poor health.

In chapter 4 I report no associations between men’s perceptions of sexually dimorphic acoustic properties and within-subject variation in their hormone levels, while other studies showed that within-subject changes in hormones modulate men’s perceptions of sexually dimorphic facial characteristics (Welling et al., 2008, Bird et al., 2016). Although previous research suggested that social perceptions of sexually dimorphic characteristics in voices are very similar to those reported in the face perception literature (Fraccaro et al., 2010; Feinberg et al., 2008b), it is possible that using more socially relevant stimuli (e.g., sentences, non-verbal vocalizations) could produce effects of hormones on voice perception that were not apparent in the current study. I also report no significant preference for feminine female voices. This may be due to a floor effect, as the size of manipulation for feminine voices is only 2% above previously reported just-noticable differences, which could mean that participants did not accurately detect the manipulation. This is however unlikely, as I show that masculinized female voices were perceived as more dominant. Alternatively it is also possible that men may not be using sexually dimorphic acoustic properties as cues to quality to the extent previously reported, or may not be as sensitive to sexually dimorphic vocal properties as they are to sexually dimorphic face shape when their testosterone levels are high. These alternative explanations should be investigated by comparing testosterone related within-subject changes in preferences for both facial and vocal femininity within the same sample of men.

6.5 Conclusion

The evidence presented in the current thesis is a starting point for further work of systematic investigation of regional, between-individual, and within-individual variation in men's mate preferences and mating strategies, using more robust methods. Further work should focus on how patterns of results reported here generalize to new more heterogeneous samples, use more direct measurements of immune function, wider range of more social relevant stimuli, and consider hormone levels throughout development as potential mechanisms for development of sexually dimorphic traits in men.

7. Appendices

7.1 Appendix 1: Scarcity of female mates predicts regional variation in men’s and women’s sociosexual orientation across US states

7.1.1 Full outputs for analyses

Dependent Variables
soi_global = Global SOI score
soi_attitude = Attitude subscale of the SOI
soi_desire = Desire subscale of the SOI
soi_behavior = Behavior subscale of the SOI

Participant-level Independent Variables
age.c = Participant age (centered)
sex = Participant sex (0 = female, 1 = male)
state = In which of 50 US states (+DC) is the participant

State-level Independent Variables
sofm = Scarcity of Female Mates factor
demand = Environmental Demand factor
wealth = Wealth factor
parasite = Parasite stress (from Fincher & Thornhill, 2012)

The following analyses show the equations and fixed effects produced by the summary() function of lmerTest for all analyses reported in the Results section. Full models explore potential interactions between participant sex and the state-level factors, while reduced models remove non-significant interactions with sex in order to interpret the overall effects of factors that do not interact with sex (e.g., the effect of ‘sofm’ in a full model is the effect of sofm on female participants, while the effect of sofm:sex is how different this effect for male participants).

Global SOI – Full Model

```
Formula: soi_global ~ 1 + age.c + sofm * sex + demand * sex + wealth * sex + (1 |
state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)   22.46986    0.16864   53.00000 133.242  < 2e-16 ***
age.c          0.16719    0.01786 4431.00000   9.360  < 2e-16 ***
sex            4.17672    0.27541 4452.00000  15.166  < 2e-16 ***
sofm          -0.77061    0.20117   64.00000  -3.831 0.000295 ***
demand        -0.31136    0.18818   81.00000  -1.655 0.101890    
wealth         0.14680    0.22691  156.00000   0.647 0.518614    
sofm:sex       0.19451    0.33094 4449.00000   0.588 0.556733    
sex:demand     0.40445    0.32642 4453.00000   1.239 0.215389    
sex:wealth     0.45216    0.44305 4441.00000   1.021 0.307519    
```

Global SOI – Reduced Model

```
Formula: soi_global ~ 1 + age.c + sex + sofm + demand + wealth + (1 | state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)   22.50896    0.16533   50.00000 136.146  < 2e-16 ***
age.c          0.16692    0.01786 4428.00000   9.345  < 2e-16 ***
sex            4.04577    0.26006 4451.00000  15.557  < 2e-16 ***
sofm          -0.70938    0.17629   38.00000  -4.024 0.000259 ***
demand        -0.21194    0.16708   49.00000  -1.269 0.210549    
wealth         0.24533    0.20463   93.00000   1.199 0.233612    
```

SOI Attitude Subscale – Full Model

```
Formula: soi_attitude ~ 1 + age.c + sofm * sex + demand * sex + wealth * sex + (1
| state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)  8.095e+00  9.110e-02  3.700e+01  88.852  < 2e-16 ***
age.c        6.062e-02  8.443e-03  4.452e+03   7.181 8.08e-13 ***
sex          1.759e+00  1.300e-01  4.445e+03  13.528  < 2e-16 ***
sofm        -4.287e-01  1.072e-01  4.700e+01  -3.997 0.000224 ***
demand      -1.556e-01  9.924e-02  5.300e+01  -1.568 0.122731    
wealth       5.326e-02  1.161e-01  9.700e+01   0.459 0.647448    
sofm:sex    -9.866e-03  1.562e-01  4.439e+03  -0.063 0.949651    
sex:demand   7.588e-02  1.541e-01  4.445e+03   0.492 0.622516    
sex:wealth   2.220e-01  2.094e-01  4.452e+03   1.060 0.289125    
```

SOI Attitude Subscale – Reduced Model

```
Formula: soi_attitude ~ 1 + age.c + sex + sofm + demand + wealth + (1 | state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)  8.099e+00  8.999e-02  3.500e+01  89.989  < 2e-16 ***
age.c        6.070e-02  8.441e-03  4.451e+03   7.191 7.53e-13 ***
sex          1.740e+00  1.228e-01  4.440e+03  14.173  < 2e-16 ***
sofm        -4.294e-01  9.724e-02  3.200e+01  -4.416 0.000107 ***
demand      -1.392e-01  9.075e-02  3.700e+01  -1.534 0.133542    
wealth       9.996e-02  1.071e-01  6.600e+01   0.933 0.354252    
```

SOI Desire Subscale – Full Model

```
Formula: soi_desire ~ 1 + age.c + sofm * sex + demand * sex + wealth * sex + (1 |
state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)  7.979e+00  6.236e-02  7.300e+01 127.951  < 2e-16 ***
age.c       -1.769e-02  7.334e-03  4.400e+03  -2.412  0.01591 *  
sex          2.736e+00  1.132e-01  4.453e+03  24.163  < 2e-16 ***
sofm        -2.087e-01  7.505e-02  8.800e+01  -2.781  0.00663 ** 
demand      -1.540e-01  7.097e-02  1.050e+02  -2.170  0.03230 *  
wealth       1.346e-01  8.791e-02  2.440e+02   1.531  0.12701    
sofm:sex     1.656e-03  1.361e-01  4.452e+03   0.012  0.99029    
sex:demand   2.929e-01  1.342e-01  4.448e+03   2.183  0.02909 *  
sex:wealth   1.211e-01  1.820e-01  4.425e+03   0.665  0.50587    
```

SOI Desire Subscale – Reduced Model

```
Formula: soi_desire ~ 1 + age.c + sofm + demand * sex + wealth + (1 | state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)  7.981e+00  6.132e-02  6.800e+01 130.146   <2e-16 ***
age.c       -1.764e-02  7.333e-03  4.398e+03  -2.405   0.0162 *  
sex          2.727e+00  1.087e-01  4.453e+03  25.073   <2e-16 ***
sofm        -2.072e-01  6.399e-02  4.800e+01  -3.237   0.0022 ** 
demand      -1.503e-01  7.029e-02  1.000e+02  -2.139   0.0349 *  
wealth       1.617e-01  7.784e-02  1.270e+02   2.077   0.0398 *  
demand:sex   2.723e-01  1.276e-01  4.453e+03   2.135   0.0328 *  
```

SOI Behavior Subscale – Full Model

```
Formula: soi_behavior ~ 1 + age.c + sofm * sex + demand * sex + wealth * sex + (1
| state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)  6.417e+00  5.982e-02  6.300e+01 107.266  < 2e-16 ***
age.c        1.241e-01  6.887e-03  4.402e+03  18.020  < 2e-16 ***
sex         -3.134e-01  1.063e-01  4.453e+03  -2.949  0.00321 ** 
sofm        -1.399e-01  7.186e-02  7.600e+01  -1.947  0.05524 .  
demand      -5.674e-04  6.782e-02  9.400e+01  -0.008  0.99334    
wealth      -3.519e-02  8.350e-02  2.040e+02  -0.421  0.67387    
sofm:sex     2.016e-01  1.277e-01  4.452e+03   1.578  0.11465    
sex:demand   3.181e-02  1.260e-01  4.450e+03   0.253  0.80066    
sex:wealth   1.088e-01  1.709e-01  4.427e+03   0.637  0.52420    
```

SOI Behavior Subscale – Reduced Model

```
Formula: soi_behavior ~ 1 + age.c + sex + sofm + demand + wealth + (1 | state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)  6.437e+00  5.861e-02  5.800e+01 109.822  < 2e-16 ***
age.c        1.239e-01  6.887e-03  4.399e+03  17.994  < 2e-16 ***
sex         -3.724e-01  1.004e-01  4.453e+03  -3.710  0.00021 ***
sofm        -8.095e-02  6.164e-02  4.200e+01  -1.313  0.19629    
demand       6.832e-03  5.908e-02  5.100e+01   0.116  0.90839    
wealth      -8.419e-03  7.424e-02  1.090e+02  -0.113  0.90993    
```

Global SOI – Full Model with Parasite Stress

```
Formula: soi_global ~ 1 + age.c + sofm * sex + parasite * sex + wealth * sex + (1
| state)

Fixed effects:
               Estimate Std. Error         df t value Pr(>|t|)
(Intercept)    22.50225    0.17273   58.00000 130.272  < 2e-16 ***
age.c           0.16687    0.01786 4441.00000   9.341  < 2e-16 ***
sex             4.10201    0.27311 4451.00000  15.020  < 2e-16 ***
sofm           -0.85382    0.20471   64.00000  -4.171 9.34e-05 ***
parasite       -0.37547    0.27629   97.00000  -1.359    0.177
wealth          0.37111    0.25862   89.00000   1.435    0.155
sofm:sex        0.33546    0.32622 4446.00000   1.028    0.304
sex:parasite    0.74395    0.48947 4449.00000   1.520    0.129
sex:wealth      0.07856    0.45968 4452.00000   0.171    0.864
```

Global SOI – Reduced Model with Parasite Stress

```
Formula: soi_global ~ 1 + age.c + sex + sofm + parasite + wealth + (1 | state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)
(Intercept)   22.52076    0.17004   55.00000 132.444  < 2e-16 ***
age.c          0.16642    0.01786 4440.00000   9.316  < 2e-16 ***
sex            4.04686    0.26005 4450.00000  15.562  < 2e-16 ***
sofm          -0.76175    0.18163   40.00000  -4.194 0.000148 ***
parasite      -0.19641    0.24613   62.00000  -0.798 0.427899
wealth         0.37300    0.23227   57.00000   1.606 0.113805
```

SOI Attitude Subscale – Full Model with Parasite Stress

```
Formula: soi_attitude ~ 1 + age.c + sofm * sex + parasite * sex + wealth * sex +
(1 | state)

Fixed effects:
               Estimate Std. Error         df t value Pr(>|t|)
(Intercept)   8.110e+00  9.402e-02  4.300e+01  86.262  < 2e-16 ***
age.c         6.049e-02  8.441e-03  4.453e+03   7.166 8.98e-13 ***
sex           1.741e+00  1.289e-01  4.444e+03  13.506  < 2e-16 ***
sofm         -4.736e-01  1.105e-01  5.000e+01  -4.286 8.33e-05 ***
parasite     -2.302e-01  1.465e-01  6.000e+01  -1.572    0.121
wealth        1.869e-01  1.374e-01  5.900e+01   1.360    0.179
sofm:sex      2.545e-02  1.540e-01  4.435e+03   0.165    0.869
sex:parasite  2.635e-01  2.311e-01  4.442e+03   1.140    0.254
sex:wealth    1.105e-01  2.170e-01  4.446e+03   0.509    0.611
```

SOI Attitude Subscale – Reduced Model with Parasite Stress

```
Formula: soi_attitude ~ 1 + age.c + sex + sofm + parasite + wealth + (1 | state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)
(Intercept)    8.10878    0.09309   41.00000  87.107  < 2e-16 ***
age.c          0.06047    0.00844 4453.00000   7.165 9.08e-13 ***
sex            1.74103    0.12274 4440.00000  14.185  < 2e-16 ***
sofm          -0.46761    0.10133   35.00000  -4.615 5.08e-05 ***
parasite      -0.16826    0.13412   42.00000  -1.255    0.217
wealth         0.20387    0.12690   42.00000   1.607    0.116
```

SOI Desire Subscale – Full Model with Parasite Stress

```
Formula: soi_desire ~ 1 + age.c + sofm * sex + parasite * sex + wealth * sex + (1 | state)

Fixed effects:
               Estimate Std. Error         df t value Pr(>|t|)
(Intercept)   7.994e+00  6.396e-02  8.300e+01 124.981   <2e-16 ***
age.c        -1.784e-02  7.338e-03  4.425e+03  -2.432   0.0151 *
sex           2.687e+00  1.123e-01  4.453e+03  23.928   <2e-16 ***
sofm         -2.477e-01  7.616e-02  9.300e+01  -3.252   0.0016 **
parasite     -1.331e-01  1.053e-01  1.870e+02  -1.264   0.2080
wealth        2.239e-01  9.808e-02  1.550e+02   2.282   0.0238 *
sofm:sex      8.977e-02  1.342e-01  4.452e+03   0.669   0.5035
sex:parasite  3.559e-01  2.013e-01  4.452e+03   1.768   0.0771 .
sex:wealth   -8.701e-02  1.890e-01  4.453e+03  -0.460   0.6453
```

SOI Desire Subscale – Reduced Model with Parasite Stress

```
Formula: soi_desire ~ 1 + age.c + sofm + parasite + wealth * sex + (1 | state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)
(Intercept)  7.996e+00  6.272e-02  7.800e+01 127.493  < 2e-16 ***
age.c       -1.805e-02  7.338e-03  4.424e+03  -2.460  0.01393 *
sex          2.684e+00  1.069e-01  4.453e+03  25.097  < 2e-16 ***
sofm        -2.241e-01  6.550e-02  5.200e+01  -3.421  0.00122 **
parasite    -4.408e-02  9.186e-02  1.130e+02  -0.480  0.63227
wealth       1.955e-01  8.604e-02  9.100e+01   2.273  0.02540 *
```

SOI Behavior Subscale – Full Model with Parasite Stress

```
Formula: soi_behavior ~ 1 + age.c + sofm * sex + parasite * sex + wealth * sex + (1 | state)

Fixed effects:
               Estimate Std. Error         df t value Pr(>|t|)
(Intercept)   6.418e+00  5.943e-02  5.900e+01 107.985  < 2e-16 ***
age.c         1.241e-01  6.886e-03  4.409e+03  18.027  < 2e-16 ***
sex          -3.213e-01  1.054e-01  4.453e+03  -3.048  0.00232 **
sofm         -1.401e-01  7.081e-02  6.700e+01  -1.978  0.05205 .
parasite     -1.819e-03  9.821e-02  1.390e+02  -0.019  0.98525
wealth       -3.433e-02  9.139e-02  1.140e+02  -0.376  0.70788
sofm:sex      2.180e-01  1.259e-01  4.451e+03   1.731  0.08353 .
sex:parasite  1.198e-01  1.889e-01  4.452e+03   0.634  0.52618
sex:wealth    6.098e-02  1.774e-01  4.453e+03   0.344  0.73105
```

SOI Behavior Subscale – Reduced Model with Parasite Stress

```
Formula: soi_behavior ~ 1 + age.c + sex + sofm + parasite + wealth + (1 | state)

Fixed effects:
              Estimate Std. Error         df t value Pr(>|t|)
(Intercept)  6.435e+00  5.829e-02  5.400e+01 110.401  < 2e-16 ***
age.c        1.239e-01  6.886e-03  4.408e+03  17.994  < 2e-16 ***
sex         -3.723e-01  1.004e-01  4.453e+03  -3.710  0.00021 ***
sofm        -7.776e-02  6.075e-02  3.600e+01  -1.280  0.20862
parasite     2.508e-02  8.553e-02  8.200e+01   0.293  0.77004
wealth      -1.979e-02  8.004e-02  6.500e+01  -0.247  0.80551
```

7.1.2 Additional analyses (parasite stress)

Our main analyses used a composite measure of environmental demands that was based on the measures used in Schmitt's (2005) analyses of regional variation in sociosexual orientation. However, other studies have used measures of parasite stress to investigate this issue (Fincher & Thornhill, 2012). Consequently, we repeated our analyses replacing our *environmental demand factor* with Fincher and Thornhill's (2012) measure of US state-level variation in *parasite stress*.

We first tested for between-state effects of *parasite stress, scarcity of female mates* (*SoFM*) *factor*, and *wealth factor* on participants' global SOI-R scores As in our main analyses, participants were grouped by state and global SOI-R scores were entered as the dependent variable at the participant level. Also as in our main analyses, *participant age* (centered at the mean age) and *participant sex* (dummy coded as 0 = female, 1 = male) were entered as predictors at the participant level. Scores for *parasite stress,* the *SoFM factor,* and the *wealth factor* were entered at the state level. The model included a random intercept term at the state level. Initial analyses with interactions between participant sex and *parasite stress,* the *SoFM factor,* and the *wealth factor* at the participant level revealed no significant interactions (*participant sex*parasite stress*: t = 1.52, p = .129; *participant sex*SoFM*: t = 1.03, p = .304; *participant sex*wealth*: t = 0.17, p = .864). These results indicate that there were no significant sex differences in the effects of *parasite stress,* the *SoFM factor,* or the *wealth factor.* Consequently, these interactions were dropped from the model.

This analysis revealed a significant negative effect of the *SoFM factor* (t = –4.19, p < .001), indicating the participants in states where female mates were more scarce reported being less willing to engage in uncommitted sexual relationships. In contrast, *parasite stress* (t = –0.80, p = .428) and the *wealth factor* (t = 1.61, p = .114) did not have significant effects. A significant effect of *participant sex* (t = 15.56, p < .001) indicated that men generally reported being more willing to engage in uncommitted sexual relationships than did women. A significant effect of *participant age* (t = 9.32, p < .001) indicated that older participants generally reported being more willing to engage in uncommitted sexual relationships than did younger participants.

Next, we repeated this analysis separately for scores on each of the three subscales of the SOI-R. Analysis of the attitude subscale revealed no interactions between *participant sex* and any of the state-level variables (*participant sex*parasite stress*: t = 1.14, p = .254; *participant sex *SoFM*: t = 0.165, p = .869; *participant sex *wealth*: t = 0.51, p = .611), so these interactions were dropped from the model. Analysis showed a significant negative effect of the *SoFM factor* (t = –4.62, p < .001) and effects of both *participant sex* (t = 14.19, p < .001) and *participant age* (t = 7.17, p < .001). There were no effects of *parasite stress* (t = –1.26, p = .217) or the *wealth factor* (t = 1.61, p = .116).

Analysis of the desire subscale revealed no interactions between *participant sex* and any of the state-level variables (*participant sex*parasite stress*: t = 1.77, p = .077; *participant sex *SoFM*: t = 0.67, p = .504; *participant sex *wealth*: t = –

0.46, *p* = .645), so these interactions were dropped from the model. Here, the analysis revealed a significant negative effect of the *SoFM factor* (*t* = –3.42, *p* = .001), a significant effect of *participant sex* (*t* = 25.10, *p* < .001), and a significant negative effect of *participant age* (*t* = –2.46, *p* = .014). There was no effect of *parasite stress* (*t* = –0.48, *p* = .632). There was a significant positive effect of the *wealth factor* (*t* = 2.27, *p* = .025).

Analysis of the behavior subscale revealed no interactions between *participant sex* and any of the state-level variables (*participant sex*parasite stress*: *t* = 0.63, *p* = .526; *participant sex*SoFM*: *t* = 1.73, *p* = .083; *participant sex*wealth*: *t* = 0.34, *p* = .731), so these interactions were dropped from the model. Analysis showed significant effects of *participant age* (*t* = 18.00, *p* < .001) and *participant sex* (*t* = –3.71, *p* < .001). There were no other effects of state-level variables (*parasite stress*: *t* = 0.29, *p* = .770; *SoFM*: *t* = –1.28, *p* = .208; *wealth*: *t* = –0.25, *p* = .805).

7.2 Appendix 2: Are physiological and behavioral immune responses negatively correlated? Evidence from hormone-linked differences in men's face preferences

7.2.1 Distributions of hormone levels

Figure 7.2.1 Distribution of cortisol levels

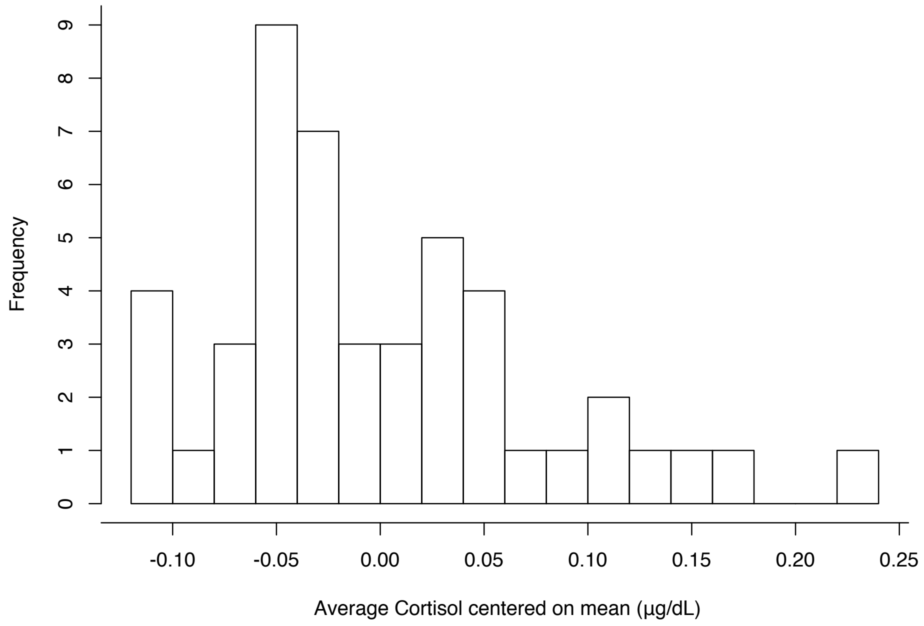
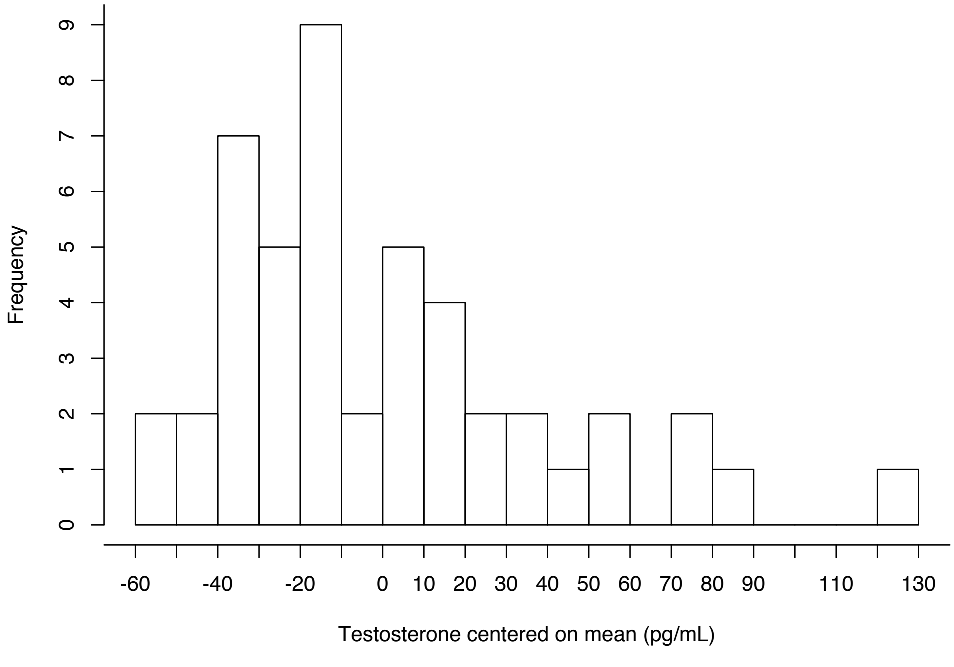


Figure 7.2.2 Distribution of testosterone levels



7.3 Appendix 3: Are men’s perceptions of sexually dimorphic vocal characteristics related to their testosterone levels?

7.3.1 Descriptive statistics of acoustic properties

Table 7.3.1 Mean (SEM) of voice pitch and formant measures from feminized and masculinized male voice stimuli (given in Hz).

Manipulation	*F*0	*F*1	*F*2	*F*3	*F*4	*F*n
Masculinized Pitch	111 (5)	457 (12)	1525 (44)	2567 (57)	3440 (104)	1997 (49)
Feminized Pitch	135 (6)	460 (11)	1525 (42)	2571 (58)	3437 (104)	1998 (48)
Masculinized Formants	123 (5)	421 (8)	1375 (43)	2351 (57)	3145 (103)	1823 (48)
Feminized Formants	123 (5)	513 (11)	1682 (47)	2817 (59)	3756 (109)	2192 (49)

Acronyms: *F*0 = fundamental frequency (pitch); *F*1-*F*4 = first to fourth formant; *F*n = mean formant frequency (an average of *F*1-*F*4). Mean *F*0 was measured using Praat’s autocorrelation algorithm with a search range set to 65-300 Hz. Formants *F*1-*F*4 were measured using the Burg Linear Predictive Coding algorithm. Formants were first overlaid on a spectrogram and manually adjusted until the best visual fit of predicted onto observed formants was obtained. All acoustic measurements were taken from the central, steady-state portion of each vowel, averaged across vowels for each voice, and then averaged across voices. This was done separately for each type of masculinity manipulation.

Table 7.3.2 Mean (SEM) of voice pitch and formant measures from feminized and masculinized female voice stimuli (given in Hz).

Manipulation	*F*0	*F*1	*F*2	*F*3	*F*4	*F*n
Masculinized Pitch	194 (6)	862 (31)	2029 (35)	3154 (47)	4203 (35)	2562 (27)
Feminized Pitch	237 (8)	867 (39)	2035 (33)	3160 (48)	4214 (32)	2596 (28)
Masculinized Formants	216 (7)	849 (39)	1999 (47)	3083 (58)	4123 (41)	2513 (41)
Feminized Formants	216 (7)	892 (31)	2027 (46)	3168 (41)	4220 (35)	2577 (28)

Acronyms: *F*0 = fundamental frequency (pitch); *F*1-*F*4 = first to fourth formant; *F*n = mean formant frequency (an average of *F*1-*F*4). Mean *F*0 was measured using Praat's autocorrelation algorithm with a search range set to 100-600 Hz. Formants *F*1-*F*4 were measured using the Burg Linear Predictive Coding algorithm. Formants were first overlaid on a spectrogram and manually adjusted until the best visual fit of predicted onto observed formants was obtained. All acoustic measurements were taken from the central, steady-state portion of each vowel, averaged across vowels for each voice, and then averaged across voices. This was done separately for each type of masculinity manipulation.

7.3.2 Distributions of hormone levels

Figure 7.3.2 Distributions of cortisol levels within-participants

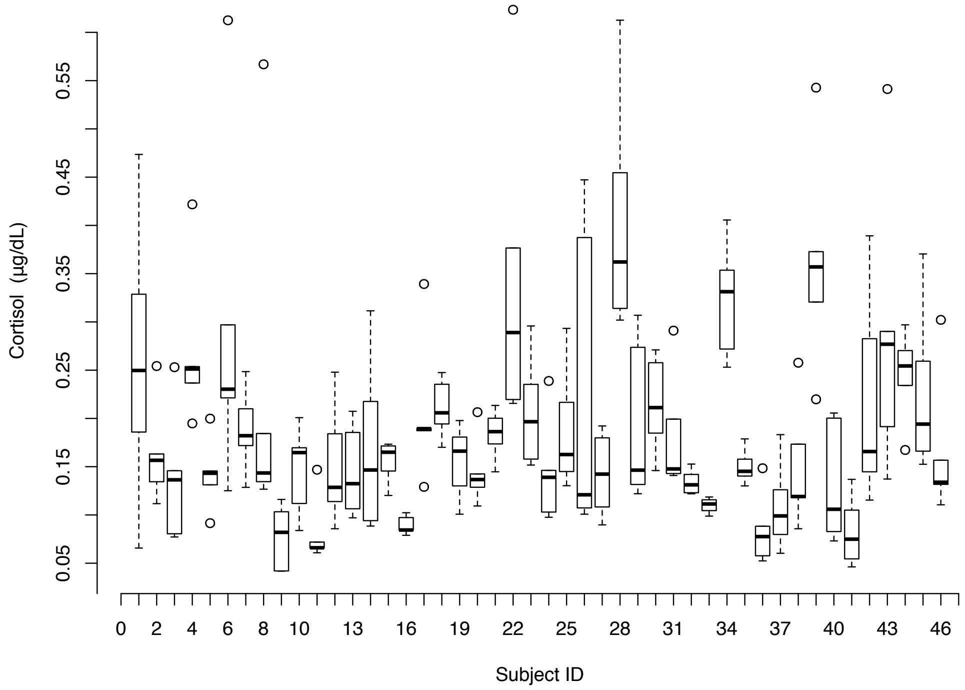
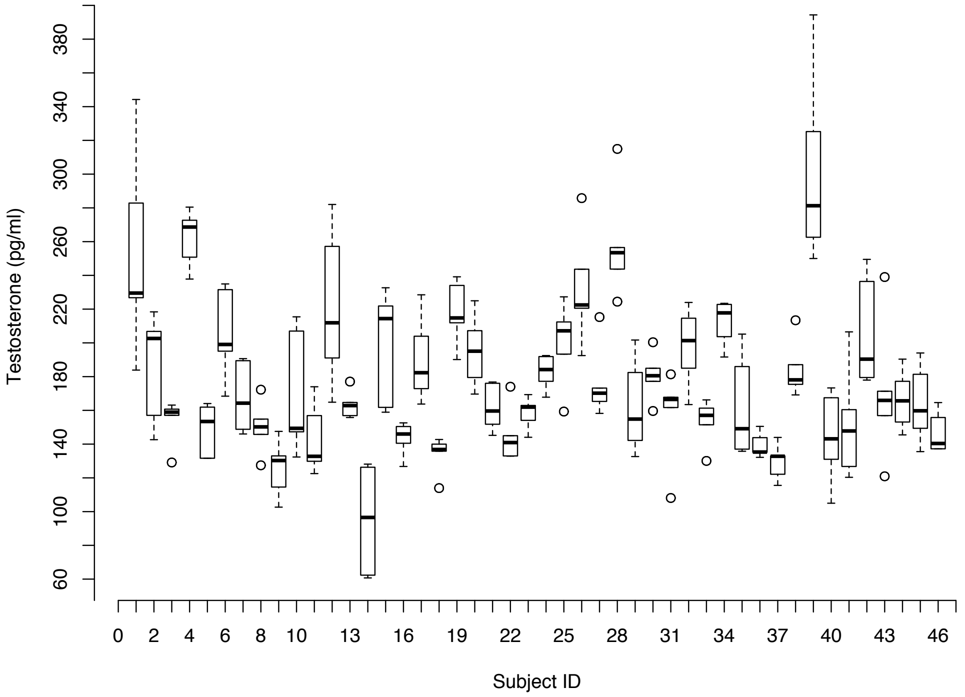


Figure 7.3.3 Distributions of Testosterone levels within-participants



7.3.3 Full outputs for analyses

Variable legend

fc_c = The forced-choice preference score (proportion of masculine male or feminine female voices chosen, centered on chance=0.5)
test.c = subject-mean centered testosterone (pg/mL)
cort.c = subject-mean centered cortisol (μg/mL)
manip.e = voice manipulation (effect-coded so pitch = +0.5, formant = -0.5)

Model predicting preferences for women’s voices (testosterone only)

```
Formula: fc_c ~ test.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid
   -52.5    -23.6     33.2    -66.5      453

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.38096 -0.61498  0.06103  0.67577  2.20396

Random effects:
 Groups          Name        Variance  Std.Dev.
 session:id_code (Intercept) 2.608e-18 1.615e-09
 id_code         (Intercept) 1.345e-02 1.160e-01
 Residual                    4.405e-02 2.099e-01
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                Estimate  Std. Error         df  t value  Pr(>|t|)
(Intercept)     3.659e-02  1.970e-02  4.600e+01   1.857   0.0697 .
test.c          3.466e-04  4.042e-04  4.140e+02   0.858   0.3916
manip.e        -6.521e-03  1.957e-02  4.140e+02  -0.333   0.7392
test.c:manip.e  6.944e-04  8.083e-04  4.140e+02   0.859   0.3908
---
```

Model predicting preferences for women’s voices (cortisol only)

```
Formula: fc_c ~ cort.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid
   -52.6    -23.7     33.3    -66.6      453

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.33887 -0.65613  0.07894  0.65009  2.17349

Random effects:
 Groups          Name        Variance Std.Dev.
 session:id_code (Intercept) 0.00000  0.0000
 id_code         (Intercept) 0.01345  0.1160
 Residual                    0.04404  0.2099
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                 Estimate   Std. Error       df  t value  Pr(>|t|)
(Intercept)      0.036593   0.019703  46.000000   1.857   0.0697 .
cort.c           0.124806   0.128882 414.000000   0.968   0.3334
manip.e         -0.006519   0.019570 414.000000  -0.333   0.7392
cort.c:manip.e  -0.206042   0.257765 414.000000  -0.799   0.4246
---
```

Full model predicting preferences for men’s voices

```
Formula: fc_c ~ test.c * manip.e + cort.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid 
  -108.3    -71.1     63.1   -126.3      451 

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
-2.46190 -0.67824  0.01972  0.67716  2.50080 

Random effects:
 Groups          Name        Variance  Std.Dev. 
 session:id_code (Intercept) 3.203e-16 1.790e-08
 id_code         (Intercept) 1.316e-02 1.147e-01
 Residual                    3.834e-02 1.958e-01
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                 Estimate   Std. Error        df  t value  Pr(>|t|)    
(Intercept)      1.348e-01  1.922e-02  4.600e+01   7.013 8.71e-09 ***
test.c           5.465e-04  3.894e-04  4.140e+02   1.403    0.161    
manip.e          9.855e-02  1.826e-02  4.140e+02   5.397 1.14e-07 ***
cort.c           1.142e-01  1.242e-01  4.140e+02   0.920    0.358    
test.c:manip.e   6.826e-04  7.789e-04  4.140e+02   0.876    0.381    
manip.e:cort.c -8.094e-02  2.484e-01  4.140e+02  -0.326    0.745    
---
```

Model predicting preferences for men’s voices (testosterone only)

```
Formula: fc_c ~ test.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid 
  -111.3    -82.4     62.7   -125.3      453 

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
-2.47535 -0.68325  0.01075  0.66603  2.48639 

Random effects:
 Groups          Name        Variance  Std.Dev. 
 session:id_code (Intercept) 2.724e-16 1.651e-08
 id_code         (Intercept) 1.315e-02 1.147e-01
 Residual                    3.843e-02 1.960e-01
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                Estimate   Std. Error       df  t value  Pr(>|t|)    
(Intercept)    1.348e-01  1.922e-02 4.600e+01   7.013 8.71e-09 ***
test.c         6.362e-04  3.775e-04 4.140e+02   1.685   0.0927 .  
manip.e        9.855e-02  1.828e-02 4.140e+02   5.391 1.18e-07 ***
test.c:manip.e 6.191e-04  7.549e-04 4.140e+02   0.820   0.4126    
---
```

Model predicting preferences for men’s voices (cortisol only)

```
Formula: fc_c ~ cort.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid 
  -109.6    -80.6     61.8   -123.6      453 

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
-2.46184 -0.66800  0.03588  0.65166  2.50976 

Random effects:
 Groups          Name        Variance  Std.Dev. 
 session:id_code (Intercept) 1.518e-16 1.232e-08
 id_code         (Intercept) 1.313e-02 1.146e-01
 Residual                    3.859e-02 1.965e-01
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                Estimate   Std. Error      df  t value  Pr(>|t|)    
(Intercept)      0.13478    0.01922  46.00000   7.013 8.71e-09 ***
cort.c           0.15787    0.12064 414.00000   1.309    0.191    
manip.e          0.09855    0.01832 414.00000   5.380 1.25e-07 ***
cort.c:manip.e  -0.02643    0.24129 414.00000  -0.110    0.913    
---
```

Full model predicting dominance perceptions of women’s voices

```
Formula: fc_c ~ test.c * manip.e + cort.c * manip.e + (1 | id_code/session)
   Data: data.dom.f

     AIC      BIC   logLik deviance df.resid 
   -53.1    -15.9     35.5    -71.1      451 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-2.5408 -0.6616 -0.1513  0.5771  2.8569 

Random effects:
 Groups          Name        Variance  Std.Dev. 
 session:id_code (Intercept) 1.667e-17 4.082e-09
 id_code         (Intercept) 1.506e-02 1.227e-01
 Residual                    4.317e-02 2.078e-01
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
               Estimate   Std. Error         df  t value  Pr(>|t|)    
(Intercept)    -1.996e-01  2.052e-02  4.600e+01  -9.727 9.75e-13 ***
test.c          2.007e-04  4.133e-04  4.140e+02   0.486    0.628    
manip.e        -8.188e-02  1.938e-02  4.140e+02  -4.226 2.93e-05 ***
cort.c         -4.000e-02  1.318e-01  4.140e+02  -0.304    0.762    
test.c:manip.e  4.266e-04  8.265e-04  4.140e+02   0.516    0.606    
manip.e:cort.c  5.974e-03  2.636e-01  4.140e+02   0.023    0.982    
---
```

Model predicting dominance perceptions of women’s voices (testosterone only)

```
Formula: fc_c ~ test.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid
   -57.0    -28.1     35.5    -71.0      453

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.5289 -0.6596 -0.1509  0.5761  2.8565

Random effects:
 Groups          Name        Variance Std.Dev.
 session:id_code (Intercept) 0.00000  0.0000
 id_code         (Intercept) 0.01506  0.1227
 Residual                    0.04318  0.2078
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
               Estimate    Std. Error        df  t value  Pr(>|t|)
(Intercept)    -1.996e-01  2.052e-02  4.600e+01  -9.727 9.75e-13 ***
test.c          1.693e-04  4.001e-04  4.140e+02   0.423    0.672
manip.e        -8.188e-02  1.938e-02  4.140e+02  -4.226 2.93e-05 ***
test.c:manip.e  4.313e-04  8.003e-04  4.140e+02   0.539    0.590
---
```

Model predicting dominance perceptions of women’s voices (cortisol only)

```
Formula: fc_c ~ cort.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid
   -56.6    -27.7     35.3    -70.6      453

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.5558 -0.6564 -0.1418  0.5883  2.8560

Random effects:
 Groups          Name        Variance Std.Dev.
 session:id_code (Intercept) 0.00000  0.0000
 id_code         (Intercept) 0.01505  0.1227
 Residual                    0.04322  0.2079
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                Estimate   Std. Error      df  t value  Pr(>|t|)
(Intercept)     -0.19963    0.02052  46.00000  -9.727 9.75e-13 ***
cort.c          -0.02398    0.12768 414.00000  -0.188    0.851
manip.e         -0.08188    0.01939 414.00000  -4.223 2.96e-05 ***
cort.c:manip.e   0.04003    0.25536 414.00000   0.157    0.876
---
```

Full model predicting dominance perceptions of men’s voices

```
Formula: fc_c ~ test.c * manip.e + cort.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid 
  -157.8   -120.6     87.9   -175.8      451 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-3.4863 -0.5036  0.1761  0.6273  2.2254 

Random effects:
 Groups          Name        Variance Std.Dev.
 session:id_code (Intercept) 0.004358 0.06601 
 id_code         (Intercept) 0.011438 0.10695 
 Residual                    0.030787 0.17546 
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                 Estimate Std. Error         df  t value  Pr(>|t|)    
(Intercept)     2.627e-01  1.829e-02  4.600e+01  14.362   <2e-16 ***
test.c         -1.718e-04  3.953e-04  1.840e+02  -0.435    0.664    
manip.e         1.087e-02  1.636e-02  2.300e+02   0.664    0.507    
cort.c          3.882e-02  1.261e-01  1.840e+02   0.308    0.758    
test.c:manip.e  6.040e-04  6.980e-04  2.300e+02   0.865    0.388    
manip.e:cort.c -2.773e-01  2.226e-01  2.300e+02  -1.246    0.214    
---
```

Model predicting dominance perceptions of men’s voices (testosterone only)

```
Formula: fc_c ~ test.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid 
  -160.2   -131.2     87.1   -174.2      453 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-3.4335 -0.5064  0.1547  0.6281  2.1625 

Random effects:
 Groups          Name        Variance Std.Dev.
 session:id_code (Intercept) 0.004264 0.0653  
 id_code         (Intercept) 0.011436 0.1069  
 Residual                    0.030994 0.1761  
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                 Estimate Std. Error         df  t value  Pr(>|t|)    
(Intercept)     2.627e-01  1.829e-02  4.600e+01  14.362   <2e-16 ***
test.c         -1.413e-04  3.828e-04  1.840e+02  -0.369    0.712    
manip.e         1.087e-02  1.642e-02  2.300e+02   0.662    0.509    
test.c:manip.e  3.863e-04  6.780e-04  2.300e+02   0.570    0.569    
---
```

Model predicting dominance perceptions of men’s voices (cortisol only)

```
Formula: fc_c ~ cort.c * manip.e + (1 | id_code/session)

     AIC      BIC   logLik deviance df.resid 
  -160.9   -131.9     87.4   -174.9      453 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-3.4627 -0.5105  0.1774  0.6216  2.1988 

Random effects:
 Groups          Name        Variance Std.Dev.
 session:id_code (Intercept) 0.004328 0.06579 
 id_code         (Intercept) 0.011434 0.10693 
 Residual                    0.030887 0.17575 
Number of obs: 460, groups:  session:id_code, 230; id_code, 46

Fixed effects:
                Estimate Std. Error        df  t value  Pr(>|t|)    
(Intercept)      0.26268    0.01829  46.00000  14.362   <2e-16 ***
cort.c           0.02511    0.12212 184.00000   0.206    0.837    
manip.e          0.01087    0.01639 230.00000   0.663    0.508    
cort.c:manip.e  -0.22909    0.21586 230.00000  -1.061    0.290    
---
```

7.4 Appendix 4: Do salivary testosterone and cortisol levels predict men's facial appearance?

7.4.1 Distributions of hormone levels

Figure 7.4.1 Distribution of cortisol levels

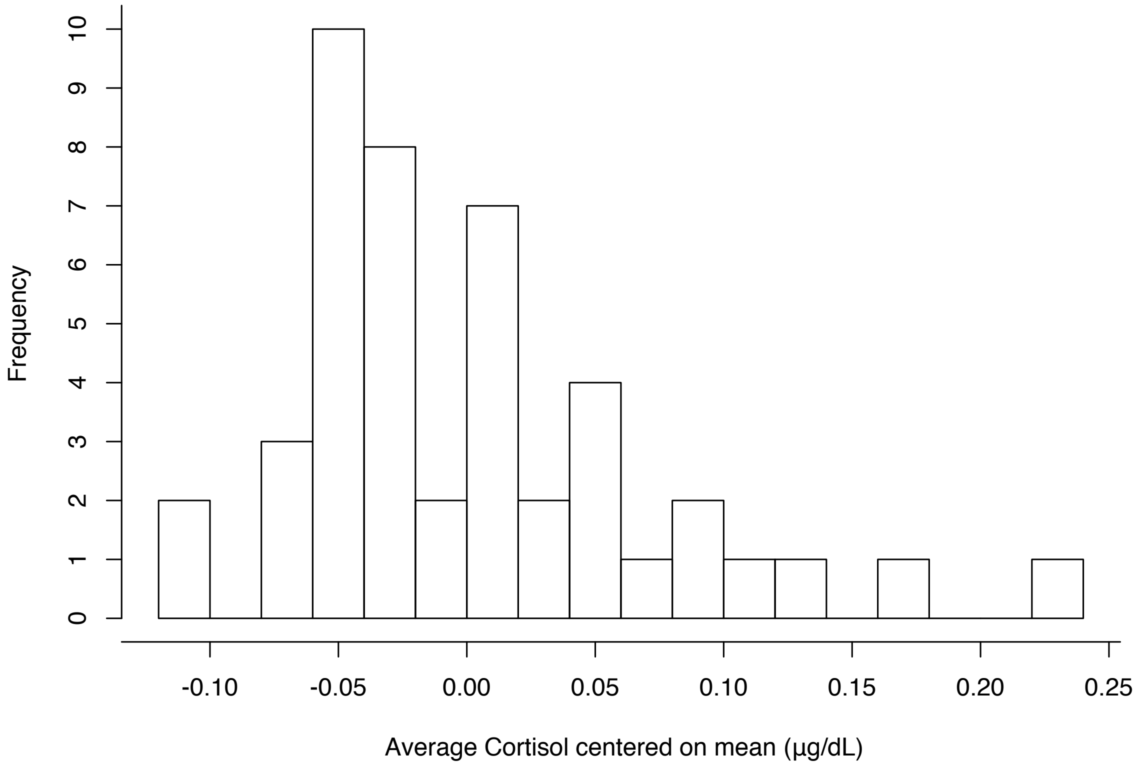
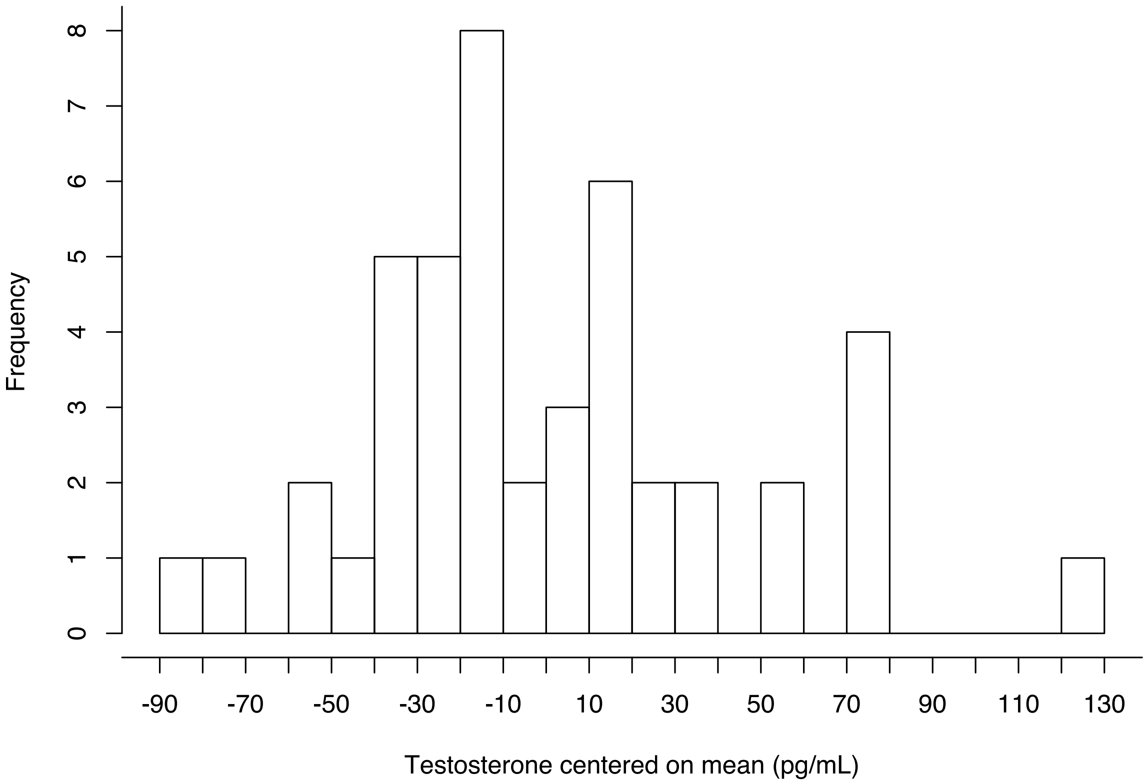


Figure 7.4.2 Distribution of testosterone levels



7.4.3 Full analyses results

Table 7.4.3 Inferential statistics for the 3 analyses reported in chapter 5

Attractiveness	Standardized ß	*t*	*p*
Testosterone (T)	0.03	0.16	.975
Cortisol (C)	-0.20	-0.91	.366
TxC	0.06	0.03	.976
Health			
Testosterone (T)	-0.09	-0.28	.641
Cortisol (C)	-0.17	-0.77	.444
TxC	1.11	0.59	.556
Dominance			
Testosterone (T)	0.15	0.79	.434
Cortisol (C)	-0.20	-0.96	.344
TxC	3.75	2.09	.043

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