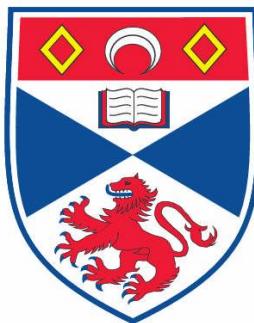


Investigating Facial Correlates of Dominance and Trustworthiness: Their Biological Underpinnings and Perceptual Properties

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This thesis is submitted in partial fulfilment for the degree of Doctor of Philosophy
at the
University of St Andrews

28/02/2013

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I, Carmen Lefevre, hereby certify that this thesis, which is approximately 38,000 words in length (excluding references), has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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Collaboration Statement

Throughout the experimental chapters (Chapters 2-7) in this thesis, I have used the pronoun ‘we’ instead of ‘I’. This work is my own in terms of hypotheses, analyses and conclusions; however, the Perception Lab is an inherently collaborative environment with other members frequently assisting in the running of participants and the development of software. Such collaborative effort must be acknowledged. The plural pronoun reflects the fact that, in publication the following experiments carry multiple authorships and is used in keeping with intellectual honesty.

The current thesis is partly based on works submitted to and accepted for publication in peer-reviewed academic journals. These articles, along with the list of contributing authors, are identified at the beginning of each relevant chapter. In the following the contribution of each author, in order of appearance, is briefly outlined: Dr. Gary Lewis contributed to the theoretical conception and writing of article versions of chapters 2-4. Prof. Timothy Bates contributed intellectual guidance on chapter 2 and provided data for chapters 3 and 5. Dr. Milena Dzhelyova provided data and helped with analysis of 3D data in chapter 3; she also contributed to the theoretical conception and analyses in chapter 6. Dr. Vinet Coetzee and Prof. Ian Deary contributed data used in chapter 3. Finally, Dr. Lars Penke provided data used in chapters 4 and 7.

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Abstract

Information conveyed by the face can be used in social encounters to make fast decisions about another person. Recently, a new model of face perception has been postulated (Oosterhof & Todorov, 2009) suggesting that there are two basic judgements that underlie person evaluations from faces: dominance and trustworthiness. But on the basis of which cues are these judgements made, and do these cues have biological validity? In this thesis I investigate two putative facial cues to dominance and trustworthiness; namely, facial width-to-height ratio (fWHR) and skin yellowness.

In men, fWHR has previously been linked to aggressive and dominant behaviour as well as the perception of these traits. Here I show that a more positive dominance related trait (achievement striving) is also related to this metric, indicating a general association of fWHR to dominance rather than simple aggression. Furthermore, I explore the biological underpinnings of this metric by showing 1) that contrary to initial findings and predictions fWHR is not sexually dimorphic, and 2) that fWHR is associated with testosterone, indicating a physiological link between appearance and behaviour. Additionally, I extend current work on fWHR by showing that it acts as a cue to dominance not only in humans but also in non-human primates.

The second part of the current thesis firstly identifies skin yellowness as a novel cue used in trustworthiness judgement. It shows that this putatively carotenoid induced cue to current health is not only employed in mate choice context but may also play an important role in other social context and in judgements of who poses an adequate partner for social interactions. Secondly, I show that skin yellowness is inversely related to testosterone levels in men, showing for the first time an association between this carotenoid induced signal and testosterone in humans thereby extending previous work in birds.

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Chapter 1. Facial signalling and social perception

1.1 Faces are special

Human faces are perhaps the most informative and complex social stimuli (Bruce & Young, 1998). Humans rely on information available from the face in almost all encounters with other people, not least because faces are the primary source of recognition and identification (Bruce & Young, 1986). Adults are experts at recognising faces, being able to recognise thousands of individuals at a glance, even over long periods of aging and from a novel viewpoint. Aside from information concerning a person's identity (Grill-Spector & Kanwisher, 2005; Yip & Sinha, 2002) that can allow for correct identification of familiar individuals even after 50 years (Bahrick, Bahrick, & Wittlinger, 1975), information about social categories (e.g. sex, race, and approximate age; Cloutier, Mason, & Macrae, 2005; Martin & Macrae, 2007; Ito & Urland, 2003, 2005), health state (e.g. Kalick, Zebrowitz, Langlois, & Johnson, 1998; Coetzee; Perrett & Stephen, 2009), sexual attractiveness (e.g. Locher, Unger, Sociedade, & Wahl, 1993; Perrett et al., 1998), emotional states (e.g. happy, angry; Oosterhof & Todorov, 2008), intentions (e.g. aggression; Carré, McCormick, & Mondloch, 2009) and even some aspects of personality (e.g. Little & Perrett, 2007; Penton-Voak et al., 2006) is readily, perhaps automatically, extrapolated from faces (Bruce & Young, 2012).

Information gathered from the face can subsequently be utilised by the perceiver in decision-making processes concerning further behaviour towards, and interactions with, the encountered individual. Indeed, inferences drawn from the face alone are utilised in economic decisions (Scharlemann et al., 2001; Van't Wout & Sanfey, 2008), political electoral decisions (Antonakis & Delgas, 2009; Ballew & Todorov, 2007; Little et al., 2007; Olivola & Todorov, 2010a; Todorov et al., 2005), criminal sentencing (Blair et al., 2004; Eberhardt et al., 2006; Porter et al., 2010; Zebrowitz & McDonald, 1991), as well as in occupational contexts (Hamermesh & Biddle, 1994; Langlois et al., 2000; Mazur et al., 1984; Montepare

& Zebrowitz, 1998; Mueller & Mazur, 1996; Rule & Ambady, 2008). Compared to other sources of information available from a person, such as the voice, smell, or behaviour, the face is immediately and permanently observable, and static facial features tend to be fairly stable over time yielding perhaps particularly informative cues. It follows that understanding exactly what information is conveyed by the face, and how accurately and readily this information is perceived by others, forms the basis for understanding social interaction.

1.1.1 Some evidence that faces are special

Much research indicates a special status of faces in comparison to most other objects. Faces are likely processed differently than other objects (Farah et al., 1998; McKone et al., 2007; Sinha et al., 2006; Yue et al., 2006) with several notable experimental results illustrating this discrepancy; namely, the inversion effect, the part-whole effect, and the composite face effect. The inversion effect demonstrates that face recognition, in contrast to object recognition, is highly dependent on orientation; inverting faces drastically reduces recognition performance (poorer accuracy and longer reaction times; McKone et al., 2007; Yin, 1969). The part-whole effect refers to a higher recognition accuracy of facial features (e.g. nose, mouth) when these are presented as part of a face rather than in isolation (Tanaka & Farah, 1993; Tanaka & Sengco, 1997). There is no such effect for houses or scrambled faces and the effect is lost in inverted faces. Finally, the composite face effect (Young et al., 1987) occurs when a top-half of one face is aligned with the bottom half of another face. This composition renders recognition of either face half extremely difficult. The effect holds even for simple category recognition such as gender (Baudoin & Humphreys, 2006), race (Michel et al., 2007), and emotional expression (Calder et al., 2000). Importantly, the composite face effect is reduced or even eliminated when the two face halves are laterally offset or the

combined face is inverted (Hole, 1994; Young et al., 1987), indicating specific processing ability for intact and upright, in other words natural, faces.

These findings are in line with faces being processed holistically (configural processing), with less part decomposition taking place than for other objects. In holistic processing, instead of individual features (nose, mouth etc.) being processed independently, both the features themselves as well as the relative spatial arrangement of these features are processed as a perceptual whole, a gestalt (Farah, et al., 1998; Maurer et al., 2002). It is likely that holistic processing enables us to distinguish between faces even when they only differ in small details, a task that has to be fulfilled during many daily interactions. While holistic processing and the inversion effect are not entirely unique to faces, they seem to only be present when a viewer has developed expertise in distinguishing objects or individuals from a group. For example, dog breeders and judges showed less accurate recognition for inverted dogs, while novices did not (Diamond & Carey, 1986). Similarly, studies using ‘greebles’, novel objects that share common traits with faces: a small number of parts in a common configuration that exhibit small differences between objects, found that after extensive training, participants show evidence of configural processing (Gauthier et al., 1998; Gauthier & Tarr, 2002). These findings may indicate that while humans have great expertise in face processing, they do not possess an ability that is unique to faces.

In support of these behavioural findings, there is extensive neuroscientific evidence for specialised processing of faces in the brain. For instance, single cell recording studies in macaques have demonstrated neurons that selectively respond to faces (Desimone, 1991; Perrett et al., 1991; Tsao et al., 2006) and early neuroimaging work using fMRI has shown similarly specialised brain areas in humans (Kanwisher et al., 1997; although see Gauthier et al., 2000). These results led some to propose that automatic processing of faces is evident (Farah, 1995), and several studies indeed provide evidence that at least basic features such as

sex, approximate age and race of a face are rapidly and seemingly automatically encoded (Cloutier et al., 2005). To this end, exposure of as little as 38ms has been found sufficient to form trait judgements from a face (Bar et al., 2006); although similarly rapid processing of objects has also been reported (e.g. Keysers et al., 2001; Potter et al., 2010), thus questioning whether rapid processing is specific to faces.

In addition to the behavioural findings in adults, there is also support for the special status of faces from work on neonate perception. Only minutes after birth, infants show a preferential tracking behaviour towards face-like stimuli over non-face stimuli of equivalent complexity. These results hold both for attention tracking methods (Goren et al., 1975; Johnson et al., 1991) and for paired preference methods (Mondloch et al., 1999), and are perhaps particularly intriguing when taking into account that new-borns have very limited visual resolution: the visual system is fairly immature at birth and especially fine detail cannot yet be processed (Bruce & Young, 2012). Moreover, infants are able to discriminate between human and non-human primate faces and preferentially attend to human faces (but not bodies) providing further evidence for a mechanism specific to face discrimination (Heron-Delaney et al., 2011). On the other hand, infants' ability to distinguish individual faces seems more general than that of adults: six month old infants can discriminate between individual primate faces just as well as between individual human faces, with this ability being lost around nine months of age (Pascalis et al., 2002), supporting a general 'perceptual narrowing' of neural networks following selective exposure.

Furthermore, infants also show preferential looking at faces that are found more attractive by adult observers (Kramer et al., 1995; Langlois et al., 1987), an effect present even hours after birth (Slater et al., 1998) and that generalises across races and ages (Langlois et al., 1991; van Duuren et al., 2003), potentially indicating an innate preference for signals of mate quality. However, more recent research suggests that a bias towards average (or

prototypical) faces may account for this observation (Ramsey et al., 2004) since prototypical faces are found to be attractive (Langlois & Roggman, 1990).

In summary, there is considerable evidence for some preferential treatment of faces by human minds. But why are faces so important? One approach to the study and understanding of social signalling through faces arises from evolutionary theory. It posits that facial cues and expressions (as well as their perception) have evolved over time because they serve to resolve an evolutionary problem. Being able to discern accurate and relevant basic information concerning for instance age, sex, group membership, and status from the faces, in a split second should be advantageous as it enables the perceiver to react in a differentiated and appropriate manner. Accurate perception can yield a meaningful reaction, supporting claims that ‘perceiving is for doing’ (Zebrowitz & Montepare, 2006).

With this in mind, the following sections of this introductory chapter will explore a range of mechanisms that might explain the evolution of specific facial characteristics. In particular, the influences of sexual dimorphism and testosterone on facial appearance as well as behaviour will be reviewed and research concerning links between personality and appearance as well as behaviour and appearance will be discussed.

1.2 Facial Cues and Signals

1.2.1 Distinction between a ‘cue’ and a ‘signal’

In this thesis the terms ‘cue’ and ‘signal’ will be used frequently. A brief introduction and definition of each term is thus required. Any trait that is used to gather information about the individual to which it belongs can be referred to as a ‘cue’. Cues can be phenotypical (e.g. morphology, colouration) but also environmental, such as for example

resources or territory, which can provide information about the individual's ability and status (Candolin, 2003). Importantly, no assumption is made about why a given cue has evolved: typically the selection pressure for a cue is thought to be different from its use as a cue. For example, physical strength may be used as a cue to assess mate quality or dominance of an individual; however, the selection pressure for building muscle mass may have been the ability to fight-off or outrun predators.

The term 'signal' on the other hand refers to a specific type of cue that, at least in part, evolved for the purpose of cueing or communicating a certain quality of the individual to the observer. Crucially, signals are beneficial for both the sender of the signal and the receiver. They can consist of a single cue or a group of cues (components) that are evaluated in conjunction with each other. Good examples of signals are the brightly coloured plumages of many bird species (e.g. Hill & Montgomerie, 1994). Signals are under a somewhat different selection pressure compared to other traits, since the evolution of a signal relies upon co-evolution of the signaller and the observer. Signals that are retained through evolution must be chosen/understood by the perceiver. Simultaneously, those individuals that are able to understand the meaning of a given signal will have higher chances of (offspring) survival since they can utilise the information gathered from the signal when assessing another individual (Johnstone, 1997).

1.2.2 Honest Signals

An immediately evident problem of signalling is that signals may be copied. Since, by definition, signals evolve solely for the purpose of communication, they are not necessarily tied to any other fitness benefit. Fisher (1930) thus argued that a trait that at some point during evolution signals mate quality will be selected for; this selection will in turn

induce a positive feedback ‘runaway’ mechanism which then ultimately renders the specific trait originally selected for irrelevant for the survival fitness of the individual. It follows that in order for a signal to remain meaningful over time, some cost (fitness reduction) that prevents extensive copying is attached to the signal (Zahavi, 1975; 1987), such that the bearer of a given signal can demonstrate their quality by their ability to survive the ‘handicapping’ effects of the signal. Possible costs include health implications, higher risk from predators, or increased risk through intra-male competition. Honest signals are those signals then whose magnitude accurately represents the intrinsic quality being advertised by the signaller (Maynard Smith & Harper 2003).

1.3 Sexual Dimorphism

Sexual dimorphism refers to phenotypic characteristics that differ between males and females of the same species (Barber, 1995). Many dimorphic features are thought to develop during puberty in response to increased levels of androgens and oestrogens (sex hormones; Andersson, 1994). In *Homo sapiens* a number of sexually dimorphic traits have been identified, including gross morphological traits such as body mass (e.g. Smith & Jungers, 1997), body height (Eveleth, 1975; Alexander et al., 1979; Gray & Wolfe, 1980; Wolfe & Gray, 1982) and brain size (Sowell et al., 2006; Peters et al., 1998), as well as behavioural (e.g. dominance; Grammer & Thornhill, 1994; Thornhill & Gangestad, 1996) and cognitive traits (e.g. mental rotation; Collins & Kimura, 1997).

Additionally and of particular interest here, sexual dimorphism has been reported for several components of facial structure (Perrett et al., 1998). Following testosterone exposure in utero and particularly during puberty when sex differences get exaggerated, men develop larger jaws and more prominent brow ridges compared to women (Enlow, 1982; Verdonck et

al., 1999), in whom oestrogens inhibits the growth of these features but encourages the development of fat deposits in lips and cheeks leading to a neotonous (child-like) appearance (Enlow, 1982). Aside from shape differences, a number of studies also report consistent differences in skin colour (e.g. Frost, 1994; Jablonski & Chaplin, 2000; Van den Berghe & Frost, 1986; but see Wagner et al., 2002) with females being lighter than males, probably owing to higher skin melanin content and a quicker tanning response in men (Harvey, 1985; Hulse, 1967). These differences in colour are only evident after puberty, indicating links to androgens (e.g. Mesa, 1983).

1.3.1 Causes of sexual dimorphism – Sexual Selection

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

Charles Darwin, 1859, p.88

Evolutionary theory posits two major strands of selection: natural selection and sexual selection. Natural selection refers to the notion of the ‘survival of the fittest’ (Darwin, 1859): Those individuals who, due to natural variation, possess a characteristic that has some advantage in the given environment that the individual finds itself in, will be more likely to survive and reproduce. This enhanced reproductive success then causes the genes associated with the advantageous trait to be passed on to the next generation, while genes associated with less advantageous variations of the same trait will not be passed on, or will be passed on to a lesser degree, causing the population mean of that trait to slowly shift towards the optimum for a given environment. In essence, evolution occurs through differential

reproductive success: reproduction and survival of the offspring is more important than the survival of the parent generation, since only reproduction allows for an individual's genes to 'survive'. It follows also that the best measure of an individual's quality is the reproductive success of that individual (i.e. number of offspring that survive to reproductive age).

The second force that is postulated in evolutionary theory is sexual selection. Since in most species, males and females are under similar natural selection pressures, sexual selection was first postulated by Darwin (1859; 1871) as an explanation for the evolution of exaggerated, highly noticeable characteristics (e.g. ornaments, calls, mating behaviours) present only in one sex and not obviously advantageous to survival. Sexual selection refers to the differential processes of mate-choice by the opposite sex (inter-sexual selection) and competition for mates within the same sex (intra-sexual competition). Sexual selection occurs when certain traits cause members of one sex to predominantly mate with members of the opposite sex who possess these traits, thus enhancing reproductive success (Andersson, 1994; Barrett et al., 2002). Sexual selection and natural selection do not have to be exclusive; traits favoured by sexual selection may also be naturally selected for, however this is not a necessity (Andersson, 1994; see also Fisher 1930).

Both strands of sexual selection are thought to be owed to a simple, almost universal principle first postulated by Bateman (1948). Bateman's principle states that 1) variance in number of offspring of males exceeds that of females; 2) males have higher variance in number of mates compared to females; and 3) in males there is a significant correlation between number of mates and number of offspring, whereas in females there is not. These conditions, in particular the last one, are thought to be necessary for the evolution of sexual dimorphism. The principle is based on the observation that in most animal species females invest more energy and time in their offspring (pregnancy, birth, feeding etc.) compared to males. As a consequence the maximal reproductive potential of females is lower than that of

males and there tend to be fewer fertilizable females than sexually active males at any given time (operational sex ratio; Emlen, 1976) rendering females a limited resource. Males must therefore compete among themselves for mating opportunities (intra-male competition): males are interested to engage in as many copulations as possible and accordingly develop displays to advertise their quality (Daly & Wilson, 1983). Females on the other hand must be selective whose offspring they should invest their valuable time and energy in and are thus the choosing sex (Clutton-Brock & Vincent, 1991). Notably, there are some exceptions to this rule, where males have a greater role in care of offspring and the females are the displaying sex, for example seahorses (Clutton-Brock & Vincent, 1991). Furthermore, some recent work has pointed out that while the Bateman principle remains valid, several environmental factors may limit the potential for sexual selection (Byers & Dunn, 2012; Jennisons et al., 2012).

1.3.1.1 Inter-sexual selection – Mate Choice

Sexual dimorphism may arise as a result of inter-sexual selection (Andersson, 1992), whereby certain characteristics are retained or even amplified because they are favoured by members of the opposite sex or in other words, are found attractive. As noted above, preference for a given trait by members of the opposite sex do not necessarily reflect natural selection benefits associated with this trait. Indeed, Fisher (1915, 1930) argued that female preferences could evolve as a consequence of a self-reinforcing runaway process. He posited that if in a given population a female preference for a certain trait developed initially (e.g. as a by-product of biased information processing in the brain; e.g. Endler & Basolo, 1998; Ryan & Rand, 1993) then in subsequent generations both the trait and the preference for this trait would be reinforced. It follows that those traits that evolved by this sexual selection process may not be linked to any inherent quality of the bearer; at least once the selection pressure has been operational for many generations. Attempts to model Fisher's concept

mathematically have indicated that while this selection process is in principle possible, it can only manifest itself under very specific circumstances in which the costs of the bearing the signal are weak (Bulmer, 1989; Kirkpatrick, 1982; Pomiankowski, 1987; Weissing, 2012).

It has therefore often been argued that traits are attractive as a function of acting as a signal (see section 1.2 for clarification of terminology) of mate quality, both in terms of direct and indirect benefits to the chooser (e.g. Hamilton & Zuk, 1982; Zahavi, 1975). Direct benefits arising from mating with an attractive mate might include resources, parental care, and health (reduced risk of contagion and death) and are thought to increase fecundity and survival of the chooser; while indirect benefits refer to genetic qualities such as heritable immune function that increase the survival and reproductive success of offspring and thus the reproductive success of the chooser, usually the female (Bateman, 1948).

1.3.1.1.1 Inter-sexual selection and faces

Male preference for femininity in female faces is universally accepted, with numerous studies reporting this effect across cultures (e.g. Cunningham et al., 1986, 1995; Dunkle & Francis, 1990; Johnston et al., 2001; Jones & Hill, 1993; Perrett et al., 1998; Rhodes et al., 2000, 2003). Both natural faces that possess more feminine features (e.g. Cunningham et al., 1986, 1995; Koehler et al., 2004) as well as faces with artificially exaggerated feminine traits (e.g. Perrett et al., 1998; Rhodes et al., 2000) are consistently rated as more attractive. In line with these findings, femininity is linked with youth (Perrett et al., 1998), fertility (Johnston, 2000; Johnston & Franklin, 1993; Law Smith et al., 2006; Symons, 1979), and maternal tendencies (e.g. Law Smith et al., 2011). High oestrogen/androgen ratios have been linked with both feminine appearance and fertility and are thus thought to be the underlying physiological link between femininity (i.e. sexual dimorphism) and fertility (Law Smith et al., 2011; Rhodes, 2006). Indeed O'Toole and colleagues (1998) suggest that female femininity and attractiveness are virtually identical,

because sex classification efficiency is explained as well by attractiveness as it is by femininity. Although, this position has more recently been questioned by work employing mathematical models of facial attractiveness. This work identified an additional dimension that runs orthogonally to sexual dimorphism and equally and independently contributed to female facial attractiveness (Said & Todorov, 2011). While the exact nature of this dimension is currently unclear, skin colouration may be an important contributor.

Preferences for masculine traits in male faces are less clear. Several studies have noted that females prefer males who possess masculine facial features such as wide jaws and thick brow ridges (e.g. Cunningham et al., 1990; Grammer & Thornhill, 1994; Keating, 1985; Johnston et al., 2001; Scheib et al., 1999), with this preference perhaps most evident during the ovulatory phase of the female menstrual cycle (see Gangestad & Thornhill, 2008 for review; but also see Penton-Voak et al., 1999, Penton-Voak & Perrett, 2000) and when assessing preferences for short-term relationships (e.g. Penton-Voak et al., 1999). This pattern of attraction suggests that male facial masculinity may reflect inherent mate quality important for offspring fitness. However, it is noteworthy that many other studies have failed to confirm a preference for masculine male faces by females (e.g. Boothroyd, et al. 2005; Perrett et al. 1998; Scott et al., 2010). One possible explanation for these ambiguous findings may be a condition dependent preferences for masculinity. For example Little and colleagues (2001) show that women's self-rated attractiveness positively influences masculinity preferences and argue that only these women can withstand the negative personality attributes (low investment) of high quality men.

These conflicting findings may, at least in part, be driven by methodological differences: while most studies assessing preferences for masculinity using ratings (both of masculinity and attractiveness) of natural faces find such a preference (Cunningham et al., 1990; Gillen, 1981; Koehler et al., 2004; Neave et al., 2003; O'Toole et al., 1998; Rhodes et

al., 2003; Scheib et al., 1999), studies using faces manipulated along a masculinity-femininity continuum find a preference for feminine facial characteristics (Penton-Voak et al., 1999, 2001; Perrett et al., 1998; Rhodes et al., 2000; Swaddle & Reiersen, 2002). Recent work employing an objective measure of sexual dimorphism in face shape (Principal component analysis of shape vectors) rather than ratings as source for masculinity scores found no association between attractiveness and masculinity (Scott et al., 2010; Stephen et al., 2012).

It follows from the equivocal results outlined above that male facial appearance may have been shaped by mechanisms other than female mate choice, in particular intra-male competition. The following section will discuss the theoretical implications and evidence supporting a role of competition in the evolution of male (facial) appearance.

1.3.1.2 Intra-sexual competition

An alternative, albeit not mutually exclusive, perspective on the development of human sexual dimorphism, in particular through influences on male appearance, is intra-sexual competition. As outlined above, in most species due to an uneven operational sex ratio (Emlen, 1976; Emlen & Oring, 1977), males must compete to win the favour of females. Besides displaying their genetic quality to the opposite sex, males may also compete amongst each other for females, by forcefully excluding competitors from access to females. Such intra-sex competition for access to mates encourages the development and retention of weaponry and strong, large bodies for use in physical fights (Puts, 2010).

Indeed in most mammal and bird species males are larger than females (Alexander et al., 1979; Clutton-Brock et al., 1977; Wiley, 1974) with this difference generally more pronounced in polygynous as compared to monogamous species (Harvey et al., 1978; Clutton-Brock et al., 1980). However, selection pressures arising from intra-sex competition

are highly complex depending on a number of contributors. For instance the type of competition typical for a species influences the development of specific sexually dimorphic features: pushing contests (e.g. in ungulates), for example, lead to selection for larger body size while biting contests (e.g. in many primate species) encourage enlarged canines and bite strength but body size dimorphism is typically small (Clutton-Brock, 1983).

The trade-off between exclusive access to females and the dangers of physical fights (namely injury and death) has likely contributed to the great variation in mating systems observable across species, ranging from males controlling harems of females by fierce intra-sex competition (e.g. Gorilla) to relatively low-conflict multi-male multi-female living groups with shared mate access (e.g. Capuchin; for review see Kappeler & van Schaik, 2002). In addition, female group distribution and size is thought to be determined by resource availability and predator threat and in turn determines distribution of males (Leutenegger & Kelly, 1977; Lindenfors et al., 2004). In species living in groups with similar numbers of males and females and in species with monogamous mating systems, contests among males are less necessary and males therefore show reduced signs of competition such as canine size and overall body size dimorphism compared to males of species with single-male polygyny (Clutton-Brock & Harvey, 1984; Leutenegger & Kelly, 1977).

Although perhaps less evident in humans, intra-male competition is necessarily the gateway to sexual selection: if competition between males of a species is decisive in terms of mate access such that only ‘winners’ are able to gain access, then mate choice by the female only takes place within this pre-selected group of ‘winners’ (Puts, 2010). It is remarkable then that intra-sexual competition as a selection pressure has had relatively little attention with regards to human appearance: of articles published on topics concerning sexual selection less than 25% published in the journals *Evolution and Human Behavior* and *Human Nature*

between 1997 and 2007 had ‘dominance and status competition’ as their topic (while 75% were concerned with mate choice; Puts, 2010).

In humans there are several markers of sexual dimorphism that may be indicative of selection pressures arising from intra-male competition: Men are typically taller (Eveleth, 1975; Alexander et al., 1979; Gray & Wolfe, 1980; Wolfe & Gray, 1982) and bigger (e.g. Smith & Jungers, 1997) than women. The modest sex difference in total body mass of approximately 15-20% (Mayhew & Salm, 1990) is misleading: the copious fat stores in human females are unique amongst primates (Pond & Mattacks, 1987) and hide sex differences in lean body mass. Men have 40% more fat free mass (Lassek & Gaulin, 2009; Mayhew & Salm, 1990). Moreover, and important with regards to fighting ability, men have on average 61% more total muscle mass than women (Illner et al., 2000; Kim et al., 2004; Phillips, 1995; Shen et al., 2004; Wetter & Economos, 2004). While lower body strength (leg strength) is around 65% higher in men than women (Bishop et al., 1987; Falkel et al., 1985; Wilmore, 1978), the difference is even greater when only assessing upper body strength: men show 75% more arm muscle mass (Abe et al., 2003; Fuller et al., 1992; Gallagher et al., 1997; Nindl et al., 2002) leading to around 90% higher upper body strength (Bohannon, 1997; Murray et al., 1985; Stoll, 2000) as compared to women. This difference is analogous to the sexual dimorphism in Gorillas (Zihlman & MacFarland, 2000), the most dimorphic of all living primates. Upper body strength is thought to be of particular benefit in physical fighting encounters (Sell et al., 2009) thus high selection pressures may have shaped this body area to be strong in men.

Men also show a greater propensity to aggressive and dominant behaviour compared to woman (Archer, 2004; 2006; 2009), with such behaviours likely being linked to contests amongst men. Even young boys engage in more play-fight than girls and the number of play-fights a boy engages in is positively linked to the perception of his dominance by peers

(Pellegrini, 1995; Pellegrini & Smith, 1998). The difference in male and female self-reported physical aggression has been reported to be one standard deviation while there were only small differences for verbal aggression, hostility and anger (Buss & Perry, 1992). Furthermore, war killings are almost entirely committed by men (Adams, 1983) and so are 95% of same sex non-war related homicides (Daly & Wilson, 1988; Wilson & Daly, 1985). In several small-scale societies a third of adult males are reported to die of violent causes (Keeley 1996), with one report even suggesting a rate as high as 59% (Bennett Ross 1984). Finally, reports of ancestral skeletal analyses indicate that throughout human history interpersonal violence was ubiquitous, particularly amongst men (Walker, 2001).

1.3.1.2.1 Intra-sexual competition and faces

The incidence of mandibular fractures is around five times higher in men than in women with the primary cause being violent assault, indicating blows to the skull to be common in men (Adi et al., 1990; Haug et al., 1990; Scherer et al., 1989; Sojat et al., 2001). It is then perhaps not surprising that men have evolved to have more robust skulls than women, if robustness is designed to resist fracture from blows typically encountered during fights. In particular, the brow ridges and mandibles are typically used to sex skulls because they are larger in males than females (Buikstra, & Ubelaker, 1994).

In addition to protection, it is conceivable that masculine (i.e. sexually dimorphic) facial features may act as a signal associated with male competitive ability and increased access to resources through successful outcomes in dominance contests. There is considerable evidence from comparative work that visible signs of competitiveness or status (e.g. physical size) are advantageous in intra-sex conflicts since they may obviate the need for physical fighting with its associated costs by signalling fighting ability or rank to opponents (Preuschoft & van Schaik, 2000). Immediately and permanently visible cues should be particularly useful because they allow for accurate and fast judgment by observers. Facial

features associated with masculinity (i.e. sexual dimorphism) may be ideal for this purpose (see also section 1.5.2 on Dominance). For instance the striking sex difference in facial hair has often been explained by intra-male competition: bearded faces appear more aggressive and of higher social status than the same faces clean-shaven (Dixson & Vasey, 2012).

If facial masculinity indeed honestly signals increased capability, masculine individuals may be perceived as more physically dominant by rivals and mates (Mueller & Mazur, 1996; Swaddle & Reierson, 2002). In support of this model, facial masculinity has been reported to correlate with physical strength (Fink et al., 2007; Windhager et al., 2011) and allows may mediate the accurate perception of the relative strength of an individual from faces (Sell et al., 2009). Accordingly, individuals displaying greater facial masculinity may have been preferred by females on account of their superior capacity to accrue fitness-enhancing resources (Puts, 2010). While research assessing links between masculinity and attractiveness yields inconclusive results, studies of masculinity and perceived dominance have generally found positive associations and large effect sizes (e.g. DeBruine et al., 2006; Puts, 2010).

In sum, intra-sexual competition, although often neglected in recent evolutionary psychology literature, is of great importance when attempting to explain the development of sexually dimorphic traits in humans. Moreover, this alternative explanation to human (male) appearance seems to be supported largely by findings indicating that sexually dimorphic male traits are linked to dominant behaviour and act as cues to dominance. Implications of dominance signalling and perception will be explored further in section 1.5.2.

1.3.2 The problem of Individual Differences

A problem arising from the population level approach taken by many evolutionary accounts is the seeming assumption that all members of a species are identical. Hypotheses are made only in the general context of an adaptive preference or behaviour but individual differences are mostly neglected. However, it is without question that there is large variation between individuals in terms of their behaviours and preferences thus necessitating research both at general population level and at the individual level to capture and understand these present differences. While individual differences in areas such as personality and intelligence are widely studied and acknowledged, individual differences can also be observed in other areas perhaps more relevant to evolutionary theory, for example differences have been observed in mate preferences (e.g. Little et al., 2001; Penton-Voak et al., 1999) and aggressive behaviour (for review see Archer, 2009).

However, this problem has been acknowledged and addressed: Tooby and Cosmides (1990) and Buss (1991) have put forward theories of how individual differences can be explained within an evolutionary framework. Four contexts are postulated in which individual differences can be sustained:

- 1) When alternative genetically determined or learned life strategies exist that have different underlying predispositions (e.g. restricted and unrestricted types of sociosexuality; Gangestad & Simpson, 1990).
- 2) When early environmental effects cause individuals to adopt different developmental strategies or calibrate psychological mechanisms differently (e.g. effects of early father absence; Belsky et al., 1991; Boothroyd & Perrett, 2008).
- 3) When there are situation dependent alternative strategies or when behavioural frequencies can reliably be evoked by individuals occupying different niches (e.g.

the prevalence of cheaters in the environment may affect the development of a cheater detection mechanism; Cosmides, 1989).

- 4) When the effectiveness with which alternative strategies can be adopted in turn depends on individual differences in ability or morphology (e.g. men with strong, large bodies can adopt a more aggressive, intimidating strategy compared to small, weak men).

1.4 The role of Testosterone

Testosterone is one of the major sex hormones produced by the body, occurring in both men and women. While present in females, where it is produced by the adrenal cortex and ovaries, its concentration is far greater in males (up to five fold that of females; Mazur et al., 1997), where the Leydig cells of the testis and the adrenal cortex produce the hormone. In men testosterone is secreted in spurts and its concentration in the bloodstream can change within minutes, thus complicating reliable measurement (Mazur & Booth, 1998). In addition, testosterone concentrations follow a circadian rhythm with levels being highest and most variable in the morning post waking, but dropping and stabilising in the afternoon, or after around 5-7 hours of waking (Dabbs, 1990).

Testosterone has an influence on male behaviour and appearance throughout their lifetime, with effects differing at different crucial life stages, namely prenatally, during puberty and in adulthood. Prenatally (during pregnancy and shortly after birth) testosterone, produced by the testes that in turn are produced under developmental control of a gene on the Y chromosome, masculinises the foetus. Under high testosterone exposure during early pregnancy, even genetically female foetuses will develop male forms, as has been demonstrated both in animal studies and in humans with developmental abnormalities

(Breedlove, 1992; Naftolin, 1981; Wilson et al., 1981). In addition, in utero testosterone prepares male configurations of brain and body structures that are activated by increased testosterone later in life, in particular during puberty (Mazur & Booth, 1998). During puberty testosterone is thought to affect further physical and mental masculinisation, likely contributing to the typical increase in muscle mass, bone mass and body hair in men (Mooradian et al., 1987). Finally, during adulthood testosterone influences behaviour (see 1.4.2).

1.4.1 Testosterone and Facial Appearance

It is generally assumed that sexual dimorphism is, at least in part, caused by the influence of sex hormones during development, both in utero and at puberty (e.g. Kirkpatrick & Ryan, 1991; Perrett et al., 1998). Testosterone levels have been linked to the development of many sexually dimorphic traits in humans (Bardin & Catterall, 1981; Bulygina et al., 2006; Tanner, 1990). Facial masculinity, defined as sexual dimorphism, should then closely map onto developmental and potentially adult testosterone levels. However, albeit widely assumed, only few studies have assessed links between facial appearance and hormone levels and effects are currently not well understood. Verdonck et al. (1999) treated delayed puberty in boys with low doses of testosterone over a six-month period. The team compared body and face structures changes during the treatment period with age and height matched controls and reports significantly greater growth in several cranio-facial components for the testosterone treated group: upper and total face height, mandible (jawbone) and ramus (upper part of the jawbone) length. Although these are interesting results, there are several problems with this study: firstly the sample size is extremely small; only seven boys with delayed puberty were treated and assessed. Additionally, there are no delayed puberty controls in this study, making

it impossible to assess whether the changes recorded are actually caused by the testosterone treatment as opposed to the natural onset of puberty.

Whether adult circulating testosterone is linked to formal measures of facial morphology has only been assessed in a single study. Pound and colleagues (2009) computed a global facial masculinity index using five facial metrics previously shown to be reliably sexually dimorphic (Penton-Voak et al., 2001), and measured both baseline and reactive levels of testosterone in a sample of 57 men. Reactive testosterone measures were taken after participants won in an artificially controlled, competitive betting task, a scenario previously shown to significantly elevate testosterone levels (e.g. Archer, 2006)¹. While failing to replicate associations between circulating testosterone levels and perceived facial masculinity (Penton-Voak & Chen, 2004), Pound et al. (2009) observed that reactive, but not baseline, testosterone was positively associated with the global facial masculinity index of participants. Additionally, the association between baseline testosterone and facial masculinity also showed a positive trend but did not reach statistical significance.

In addition, several studies have investigated links between testosterone and perceived masculinity in males. While several studies report this association (e.g. Penton-Voak & Chen, 2004, N=50; Roney et al., 2006, N=51), the body of literature in this field is equivocal: several studies report no association between perceived facial masculinity and measured baseline testosterone levels (Pound et al., 2009, N=57; Neave et al., 2003, N=48; Peters et al. 2008, N=119; see also Johnston, 2006). At least Peters et al. (2008) controlled for age in their analyses, a variable possibly confounding the relationship between testosterone and perceived

¹ The betting task employed in this study involved predicting the outcome of sumo wrestling bouts based on fictive information about the wrestlers. Participants were made believe that they were in direct competition with other participants about making the most successful bet. They were also exposed to vicarious competition through seeing a chosen wrestler compete and win.

masculinity: testosterone is negatively associated with age, while perceived masculinity is often positively linked to age.

Another line of research into links between appearance and hormones has assessed a putative measure of in-utero developmental testosterone to oestrogen ratio: the second-to-fourth digit ratio (2D:4D; Manning et al., 1998, 2000; Williams et al., 2003). 2D:4D is found to be sexually dimorphic (Baker, 1888; George, 1930) with males on average showing lower ratios than females. This sex difference is already present in two-year-old children (Manning et al., 1998) and may be established prenatally between week 13 and 14 post conception (Phelps, 1952; Garn et al., 1975; Manning et al., 1998). The early emergence of 2D:4D is thought to be influenced by and thus reflect hormone exposure during pregnancy. High androgen to oestrogen ratio is thought to cause masculinisation of 2D:4D (Manning et al., 1998) and studies assessing congenital adrenal hyperplasia (CAH), a condition characterized by the overproduction of prenatal androgens, offer limited support for this assumption (Brown et al., 2002; Ökten et al., 2002 but see Buck et al., 2003). Finally, research assessing androgen receptor genes found that number of CAG repeats (androgen sensitivity is positively associated with this measure) showed a positive correlation with right (but not left) 2D:4D (Manning et al., 2003). Adult levels of testosterone might be linked to in utero levels of testosterone and thus to 2D:4D and one study reports this link (Manning et al., 1998) but another study failed to show an association (e.g. Neave et al., 2003) leaving the case currently unresolved.

Despite the unclear links between 2D:4D and testosterone, several studies have used it as a proxy measure of testosterone and assessed associations with facial appearance. For instance, Fink et al. (2005) incorporated a formal measure of global facial shape, calculating the average face-shape associated with high and low 2D:4D ratio (N=106). This study found that men with a low digit ratio (associated with higher prenatal testosterone) exhibited a

wider jaw and zygomatic arch (i.e. face width) as compared to those with a higher digit ratio. Other studies assessed associations between both circulating testosterone measures and 2D:4D with perceived masculinity. Neave et al. (2003) reported links of perceived facial masculinity with 2D:4D ratio, but not with measured baseline testosterone levels; and Ferdenzi et al. (2011) found no association between perceived facial masculinity and 2D:4D ratio.

In summary, the evidence for a link between perceived as well as morphological masculinity and testosterone is tentative. Testosterone having some effect on face shape seems plausible and with reasonable, albeit limited, support. If then testosterone is associated with facial appearance the obvious question that follows is whether testosterone-linked appearance is considered as attractive by women. Roney et al. (2006) report that testosterone levels positively predicted attractiveness as a short-term, but not long-term, mate. Peters and colleagues (2008) on the other hand, show a link between testosterone levels and cumulative mating success (a measure combining number of sexual partners, age at first intercourse, number of relationships, and cheating and poaching behaviour) but not facial attractiveness or masculinity, but their effect sizes are small ($r = .1$) thus results should be treated with caution. Moreover, Swaddle and Reierson (2002) report a negative correlation between facial attractiveness and putatively testosterone-linked facial shape in men. Taken together these studies do not allow for conclusive evidence of an association between testosterone and facial attractiveness in men.

1.4.2 Testosterone and behaviour

Testosterone has traditionally been associated with mating and status seeking behaviour (e.g. Mazur & Booth, 1998) and has been suggested to reflect personality (Sellers

et al., 2007), with recent work advancing understanding of more intricate effects of testosterone on social and economic interactions (see Eisenerger et al., 2011). As such, testosterone may provide one important physiological underpinning of morphology-behaviour associations in men. Individual differences in testosterone levels correlate with dominance in adult and adolescent men (Carré et al., 2009; Grant & France, 2001; Rowe et al., 2004; Vermeersch et al., 2010) and have been associated with power motivation (Stanton & Schultheiss, 2009) and increased vigilance to status-threats (van Honk et al., 1999; Wirth & Schultheiss, 2007). Additionally, intra-individual rapid fluctuations in testosterone levels occur in response to and in anticipation of successful outcome of competition and aggressive interactions (Salvador, 2005; Wingfield et al., 1990; Mazur & Booth, 1998; Archer, 2006; Oliveira, 2009; see also section 1.4.3).

Moreover, testosterone has been associated to mating strategy and relationship status (Gray et al., 2002; McIntyre et al., 2006; van Anders & Watson, 2007; van Anders et al., 2007) such that testosterone levels of men in monogamous relationships are lower than compared those of single men (McIntyre et al., 2006; van Anders & Watson, 2007) and men with multiple partners (van Anders et al., 2007). Furthermore, fathers show lower levels of testosterone compared to single men and non-fathers (Berg & Wynne-Edwards, 2001, Burnham et al., 2003, Fleming et al., 2002, Gettler et al., 2011; Gray et al., 2002) and several studies have indicated a causal relationship such that testosterone levels drop following fatherhood (Berg & Wynne-Edwards, 2001, Gettler et al., 2011; Storey et al., 2000). These findings suggest an adaptive mechanism whereby reduced testosterone levels may lead to behavioural changes advantageous to pair bonding and child rearing (Wynne-Edwards & Reburn, 2000). These changes possibly dampen male status seeking behaviour to ensure safety for children and mother.

In addition to own behaviour, the perception of others may also be affected by the testosterone levels of an observer. Work on individual differences in testosterone has indicated that individuals with higher baseline testosterone levels react more vigilantly to angry faces, likely interpreting them as a challenge (van Honk & Schutter, 2007). Additionally, work administering testosterone to women has shown a subsequent decrease in empathy (van Honk et al., 2011) and trustworthiness (Bos et al., 2010). Recent behavioural work further indicates that own dominance, a putatively testosterone linked trait, decreases sensitivity to cues to dominance in faces of others (Watkins et al., 2010). Taken together, these findings indicate a role of testosterone in social perception relevant to competition.

1.4.3 The Challenge Hypothesis

The ‘challenge hypothesis’ (Archer, 2006; Wingfield et al, 1990) states that testosterone rises as a consequence of challenging situations, such as intra-sex competition and sexual arousal; importantly, only these increases in testosterone, rather than baseline testosterone, are suggested to associate with aggression and other status related traits. The hypothesis further states that individual differences in testosterone reactivity are contingent on dominance as a result of the cumulative effect of successful outcomes of challenges.

Following this model, situations in which men compete for the interest of women or over status should lead to rises in testosterone. Several studies have found this effect, whereby exposure to a single attractive woman was sufficient to raise testosterone levels in men (Ronay et al., 2010; Roney et al., 2003; 2007). Interestingly testosterone increased also in such situations in which there were no other males present; indicating that the rise in testosterone may occur in preparation for mating rather than as a reaction to intra-sex competition. Similarly, the outcome of competition between men has been shown to affect testosterone levels: testosterone increased in winners relative to losers in both physical

(Mazur & Lamb, 1980) and non-physical (Gladue et al., 1989; Mazur et al., 1992; McCaul et al., 1992; Pound et al., 2009) contests. Testosterone levels can also increase in mere anticipation of a contest (e.g. Booth et al., 1989; Mazur et al., 1992) and watching members of the own group or a supported sports team win or lose causes rises and drops of testosterone respectively (Bernhardt et al., 1998). While these overall effects appear to be fairly robust, there are individual differences in the magnitude of testosterone change (Cohen et al. 1996; Edwards et al. 2005; Pound et al., 2009).

It is these individual differences that are of interest with respect to appearance. That is, if facial masculinisation is affected by testosterone levels during puberty, it is possible that not baseline levels but rather total tissue exposure to the hormone is closest aligned with appearance outcomes. Two consequences follow: firstly, men who exhibit a stronger hormonal reaction to competitive or sexual situations will be exposed to more testosterone compared to those men who have a lesser reaction. Secondly, irrespective of individual differences in hormone reactivity, those men that experience more competitive situations will have higher total exposure.

1.4.4 Immunocompetence Handicap Hypothesis

One model for the development of secondary sexual traits such as facial masculinity is the immunocompetence handicap hypothesis (ICHH; Folstad & Karter, 1992). This model is based on two core assumptions. First it posits, that secondary sexual traits (e.g. facial masculinity in males) emerge as a function of testosterone exposure during development (Verdonck et al., 1999); and second it posits, that testosterone acts as an immunosuppressant (Grossman, 1985). Under this model, then, the successful expression of elaborate secondary sexual traits requires exposure to high levels of testosterone, and only males of high genetic

quality will be able to sustain this exposure without deleterious consequences (Zahavi & Zahavi, 1997).

The immunocompetence handicap hypothesis (ICHH) was first proposed by Folstad and Karter (1992) and has since been hugely influential in evolutionary theories and empirical studies. Two models underlie the assumptions of the ICHH: Zahavi's (1975) handicap hypothesis and Hamilton & Zuk's (1982) parasite model. The handicap hypothesis states that while males need to express certain characteristics that advertise their mate quality these characteristics will simultaneously pose a handicap and are thus costly for the bearer. If a signal for instance ultimately lowers an individual's quality then only such an individual that is of high genetic quality can afford to express this signal without being affected by the costs. The handicap is attached to a fitness signal to prevent 'cheaters' from expressing the signal in absence of good quality. The parasite model that states that only males with high quality genes can fully express secondary sexual characteristics without suffering reduced fitness from pathogen or parasite load. In their study Hamilton & Zuk (1982) report that across bird species, individuals with lower parasite load show brighter plumages and more sexual display. Although several theoretical arguments have been put forward against a link between signalling and parasites (Getty, 2002; Kotiaho, 2001).

The ICHH predicts an intricate interplay between a number of mechanisms (see Figure 1) with the endocrine system, the immune system and the parasite load of an individual all influencing the expression and maintenance of secondary sexual characteristics and behaviours (dominance).

Under these models cheaters would not come about since they could not withstand the deleterious effects of testosterone and thus their reproductive fitness would be reduced (Folstad & Karter, 1992). Importantly, it follows that each male has an optimum level of testosterone, on the balance between maximal expression of secondary sexual characteristics and bearable immunosuppression.

Although numerous studies have attempted to test this hypothesis, the literature remains equivocal to the validity of ICHH. In a comprehensive meta-analysis Roberts et al. (2004) assessed evidence for the ICHH from studies in which testosterone levels had been experimentally manipulated in a variety of species. While they report an overall negative link between testosterone and immune function, this link disappeared when they controlled for

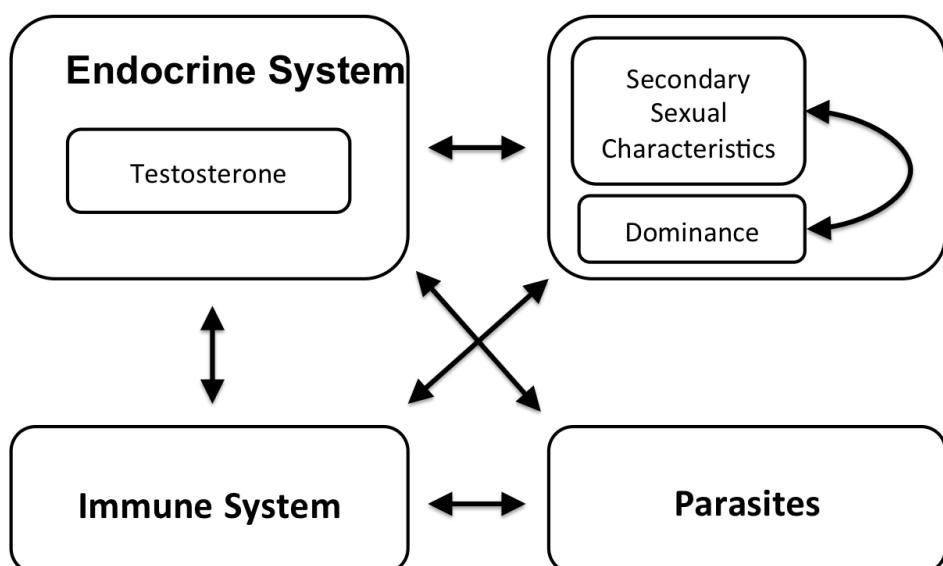


Figure 1: Graphic representation of the interactions predicted by the immunocompetence handicap hypothesis. Adapted from Folstad & Karter, 1992.

non-independence of studies and the overrepresentation of certain species indicating that current evidence for the ICHH should be treated with caution.

With regards to the face literature, support for the immunocompetence perspective has come from work linking sexually dimorphic facial features to circulating (Penton-Voak, & Chen, 2004) and reactive levels of testosterone (Pound et al., 2009) suggesting that facial masculinity may indeed signal genetic fitness (Folstad & Karter, 1992; Penton-Voak & Chen, 2004; Thornhill & Gangestad, 2006). However, it is noteworthy that several other studies have failed to confirm core predictions from the theory, such as a preference for masculine male faces by females (e.g. Boothroyd et al., 2005; Perrett et al., 1998; Scott et al., 2010).

1.5 Personality

“We Wheelwrights do not scoff at the appearance of things. Things often are as they appear. First impressions matter.”

A Prayer for Owen Meany, John Irving, 1989

Personality describes basic individual differences in behavioural, emotional and attitudinal patterns. The personality of an individual is thought to be relatively stable over time (e.g. Terracciano et al., 2006; Lucas & Donnellan, 2011) and is often described by a range of personality traits. There have been a number of approaches of categorising personality and creating a universal taxonomy, but recent interest in personality and individual differences research largely emerged when a broad consensus was reached concerning the validity of a five factor model of personality (namely: neuroticism, extraversion, openness to experience, agreeableness and conscientiousness; Norman, 1963;

Costa & McCrae, 1992). This model has become the most widely accepted in the last decade (John et al., 2008).

1.5.1 Personality attribution from faces

The question whether people can determine other's personality solely from assessing their faces has been of great interest throughout the last century (Hollingworth, 1922; Secord, 1958; Shepherd, 1989). Studies have focused on accuracy of assessment (e.g. Hollingworth 1922; Penton-Voak et al., 2006) and the cognitive processes underlying personality attribution to faces (e.g. Cloutier et al., 2005; Secord, 1958). To this end, social cognition research has investigated the formation of social categories (e.g. sex, race) and their implication on social interaction (e.g. Eberhardt et al., 2006; Macrae et al., 2005; Quinn & Macrae 2005); while evolutionary psychology has produced a literature highlighting the importance of facial attractiveness and maturity in personality perception (e.g. McArthur & Apatow, 1983; Penton-Voak et al., 2006; Rhodes, 2006; Montepare & Zebrowitz, 1998). Recently, a new addition of work in this field has been made by social cognitive neuroscience with several studies assessing the neural correlates of personality perception from faces (e.g., Adolphs et al., 1998; Aharon et al., 2001; Engell et al., 2007; O'Doherty et al., 2003; Said et al., 2009; Winston et al., 2002).

One important result arising from this research is that observers readily attribute personality judgements to faces of individuals they have never encountered before and show high inter-rater agreement, indicating a similar utilisation of available cues between individuals (e.g. Hollingworth, 1922; Penton-Voak et al., 2006). However, consensus of judgement does not necessarily suggest accuracy or validity and work in this area is inconclusive. Studies assessing accuracy of judgement indicate that some personality traits

might indeed be accurately perceptible from the face while others are not. For the traits extraversion, power, approachability and warmth there are at least moderate positive correlations between self-report measures and face ratings (Berry, 1991; Berry & Brownlow, 1989; Penton-Voak et al., 2006; Pound et al., 2007). On the other hand, suggestibility (Bachmann & Nurmoja, 2006), agreeableness and conscientiousness (Pound et al., 2007) are not accurately perceived. Naumann and colleagues (2009) additionally demonstrated that accuracy of personality judgements is enhanced when full body photographs depict a spontaneous posture and expression.

While currently not fully understood, one reason for people's fast personality judgements from faces and their high agreement when doing so may be category activation. That is, facial cues may trigger categorisation of an individual, which then in turn leads to stereotype activation (Cloutier et al., 2005). It is currently not clear whether such category activation occurs spontaneously or only when people are specifically required to make a categorical judgement (e.g. sex) for a presented stimulus (Macrae & Bodenhausen, 2000; Quinn & Macrae, 2005). Category activation has typically been reported to occur with very basic categories such as age, sex and race (Macrae & Bodenhausen, 2000), but it is not unconceivable that a specific facial trait may activate a (sub)category that triggers stereotypes of specific personality traits. Although such stereotypes will almost inevitably be an overgeneralisation, they may account for the large agreement in personality perception from faces.

In attempt to capture systematic differences in faces of people scoring high or low on a given personality trait, several studies have assessed ratings of composite faces (Little & Perrett, 2007; Penton-Voak et al., 2006). Penton-Voak and colleagues (2006) and Little and Perrett (2007) created composites faces of men and women scoring both very high and very low on each of the respective 'big five' personality dimensions (Costa & McCrae, 1992).

These composit faces were then rated for all five personality dimensions by a group of naïve raters. Penton-Voak's (2006) results indicated that in particular extraversion and agreeableness could be discerned accurately from both male and female composite faces. Little and Perrett (2007) found the same high accuracy and additionally showed accuracy for contentiousness attributions. Moreover, both studies highlight a possible confound: those composites that represented socially desirable personality traits (namely agreeableness, extraversion and emotional stability) were rated as significantly more attractive than their low scoring counterparts. This result is largely in line with earlier research showing a tendency for assigning more desirable personality characteristics to attractive faces (e.g. Dion et al., 1972; Eagly et al., 1991). This association is often referred to as the 'halo effect' (Nisbett & Wilson 1977) and has been found repeatedly.

Not only the big five personality traits but also more nuanced attitudes and behaviours can be detected from faces with some accuracy. Self-reported sociosexuality (i.e. promiscuous tendencies) and interest in infants could also be perceived at above chance rates from facial photographs (Boothroyd et al., 2008; Roney et al., 2006). In similar fashion, "cheaters", in prisoner's dilemma games (Verplaetse et al., 2007) as well as sexual relationships (Rhodes et al., 2013) are identified above chance level from facial photographs. Even religiosity is accurately perceived from standardised full body shots (Naumann et al., 2009), although group differences in grooming and style of clothing may confound these results. While these findings are of great interest, care should be taken not to over-interpret them, since above chance performance does not imply perfect accuracy. Furthermore, in many cases confounding variables may influence results (e.g. clothing and hair style in both the sociosexuality and religiosity study).

Nonetheless, the research outlined above provides reasonable evidence for a link between facial appearance and at least some personality traits; but what are the facial

components that lend themselves to personality judgements? As Hassin and Trope (2000) point out, these components need not be specific features but may instead be configural or holistic in nature or consist of multiple features. In an early study, Squier and Mew (1981) compared self-reported personality data for twenty subjects with short and square faces with that of twenty subjects with long, angular faces. Results indicated that those individuals with long, angular faces were more responsive, assertive and genuine; whereas the subjects with short, square faces were more restrained, comforting and shrewd. Another early piece of research reports a positive link between ratings of male baby-facedness and self-report measures of warmth and approachability as well as a negative link with aggression (Berry & Brownlow, 1989). Whether these personality traits would also be accurately perceived by others was not assessed in these studies.

More recently, several studies employing more elaborate designs also found links between facial appearance and personality traits: Kramer and Ward (2010) replicated findings of Little and Perrett (2007) discussed above and demonstrate that, at least in female faces, internal facial features alone (eyes, nose, and mouth), presented configurally (i.e. in their natural configuration) but in absence of the outer shape of the face, were sufficient for above chance level discrimination of several personality traits (Agreeableness, Extraversion, and Neuroticism, accuracy: ~ 65-87%). In a more recent study the same group (Jones et al., 2012) demonstrated accuracy in personality judgements from 3D face stimuli. These findings largely refute criticism associated with posture cues often found in 2D photographs; controlling posture Agreeableness and Neuroticism were still correctly attributed above chance level. Finally, personality traits consistent with predictions derived from the good genes and mating trade-off hypotheses (e.g. risk taking, high mating effort) have been linked to facial masculinity (Kruger, 2006), providing some support for a self-fulfilling prophecy theory (Zebrowitz, 1999).

Moreover, a number of studies have assessed the role of facial symmetry in personality perception from faces. Symmetry is consistently linked with attractiveness (Grammer & Thornhill, 1994; Jones et al., 2001; 2004; Penton-Voak et al., 2001; Scheib et al., 1999) and is thought to signal genetic quality (Møller & Swaddle, 1997). Two studies report less symmetrical faces to be perceived as more neurotic, less agreeable, and less conscientious (Noor & Evans, 2003; Shackelford & Larsen, 1997). Moreover, Shackelford and Larsen (1997) showed that not only self-report but also behavioural measures of personality were somewhat matched to perception. Fink and colleagues (2005) elaborated on this work by directly assessing the big five personality traits and measuring facial symmetry. Their results align with results obtained in perceptual studies (see above) on some traits: facial symmetry was negatively linked to neuroticism and positively associated with extraversion, but not on others: agreeableness was negatively correlated with facial symmetry. Attempting to replicate Fink's study in a larger sample, Pound and colleagues (2007) only found an association between self-reported extraversion and symmetrical facial features. Moreover, a recent study by Hope et al. (2011) failed to replicate any symmetry associations with the big five in two studies, indicating that current evidence for an association is equivocal at best.

In an attempt to capture the basic axes along which faces are evaluated, Oosterhof and Todorov (2008) identified commonly used face descriptors (e.g. attractive, mean, weird, caring) and had neutral faces rated on these dimensions. Subsequently, these ratings were subjected to Principal Component analysis yielding 2 principal components that accounted for 63% and 18% of the variance respectively. Due to the loading structure the authors interpret their PCs as ‘valence/trustworthiness’ and ‘dominance’. When exaggerating differences between faces at either end of the two components, it is evident that trustworthiness perceptions were driven by facial expression resembling approachability

(angry – happy) while dominance perceptions were driven by features indicating physical threat (strength – weakness). These findings indicate a relatively simple, highly effective, face categorisation mechanism based on an overgeneralisation of an adaptive harm-detection ability. Although this mechanism allows for rapid judgements, these are not necessarily accurate.

1.5.2 Dominance – bridging evolutionary theory and personality science

If dominance is indeed one of the two axes underlying social judgements as Oosterhof and Todorov (2008) suggest, then dominance is likely of pivotal importance in social interactions. Following theories of intra-sexual competition, dominance refers to the ability to exert power over other individuals within the group and to acquire and hold on to resources and mates (e.g. Drews, 1993). Competition among men is a central driving force of human evolution (Keeley, 1996; Manson & Wrangham, 1991): Those individuals who achieve higher status are afforded greater access to mates and resources (Andersson, 1994). Direct physical competition can, however, be extremely costly (through risk of injury or death), indicating that adaptations to reduce the costs of competition should have emerged (Puts, 2010; Sell et al., 2009). In particular, costs associated with incorrectly assessing the competitive abilities of other men are likely very high. It follows that being able to discern who poses a potential threat is advantageous and may have shaped mechanisms that allow for accurate signalling and perception of these abilities.

Many non-human primate species have strict, linear dominance hierarchies with sometimes fierce physical competition between males to assert power and status and in various species sexually dimorphic traits are linked to male fighting ability (Bergeron et al., 2010), physical strength (Fink et al., 2007; Malo et al., 2009), and reproductive success

(Preston et al., 2003), indicating the importance of masculine traits in competition (Santos et al., 2011). Moreover, in social species access to resources may be critically influenced by social status and dominance (Sell et al., 2009).

Theory posits that animals learn to distinguish others on such signals relative to the population mean and are then able to calculate their chance of winning a fight based upon previous experience. Only in cases where both individuals (the challenger and the challenged) gage a good chance of winning a physical fight, fighting will occur. If the dominance hierarchy is clear (e.g. through evident difference in size or rank) both individuals usually concur to their position without fight, in order to avoid potential costs through injury.

1.5.2.1 Dominance and Facial Appearance

Dominance is of pivotal importance in interpersonal perception (Wiggins, 1979) and in other animals, honest signalling of dominance is commonly observed (Johnstone, 1995). Judgements of another's dominance from their face are made consistently and rapidly (Carré et al., 2009) and even children as young as four years of age are able to discern a dominant from a submissive face (Keating & Bai, 1986). Moreover, dominance judgements appear to be fairly accurate: ratings of men's dominance were positively associated with their physical strength in Caucasians (Fink et al., 2007) and Tsimane forager-farmers from the Bolivian Amazonas (Undurraga et al., 2010) perhaps suggesting a universal ability for accurate dominance perception. Furthermore, final military rank was predicted by ratings of dominance from year book photographs of first year cadets (Mueller & Mazur, 1996; 1997).

Being able to assess the dominance of others is likely an adaptive trait since it provides information about who poses a possible threat but also who might be a suitable ally in the fight over resources and mating opportunities (Sell et al., 2009; 2010). In support of

this theory, recent differential work points towards an effect of perceiver dominance on the ability to accurately perceive dominance cues. In line with the argument that men lower in dominance are more likely to incur costs when misjudging an opponent's capabilities, less dominant men were more sensitive to cues of other men's dominance levels (Watkins et al., 2010). Moreover, in several nonhuman species, winners of recent confrontations are more likely to engage in future aggressive conflict compared to losers (Hsu, Earley, & Wolf, 2006) with similar, albeit testosterone mediated, results found in humans (Mehta & Josephs, 2006). In line with this work, Watkins and Jones (2012) report that men primed to imagine losing (versus winning) confrontations with other men consequently demonstrated greater sensitivity to dominance cues in other men's faces.

The cues of male dominance seem fairly well established. Robust body build, low voice, beards, and masculine facial appearance all have been linked to increased dominance perception (DeBruine et al., 2006; Frederick & Haselton, 2007; Neave & Shields, 2008; Perrett et al., 1998; Puts et al., 2006). In fact, while it has been argued that male facial (and bodily) appearance has emerged through mate-choice (e.g. Weston et al., 2004) there is little support for this theory. Instead, most male-typical characteristics have larger effects on dominance compared to attractiveness perception (Puts, 2010).

1.5.3 Trustworthiness

The other basic axis of face evaluation according to Oosterhof and Todorov (2008) is trustworthiness (or valence). Similar to dominance, assessment of trustworthiness may be of particularly great importance to social interaction. Much research has assessed the perception of trustworthiness and a number of clear results have emerged. These include findings indicating how consensual judgements of trustworthiness are formed (e.g. Krumhuber et al.,

2007; Rule et al., 2009; Todorov et al., 2009; Zebrowitz et al., 1996) and how trustworthiness perceptions predict individual life outcomes (Rule et al., 2010; Zebrowitz et al., 1996). The ability to discern trustworthiness following first impressions is likely of great importance for social interactions. For example, a recent study found lowered accuracy in trustworthiness perception, paired with a diminished anterior insula response to untrustworthy faces in older adults (Castle et al., 2012). These findings are of interest in light of findings indicating that older adults are disproportionately vulnerable to fraud (Langenderfer & Shimp, 2001), perhaps because they find it more difficult to distinguish between trustworthy and untrustworthy individuals.

1.5.3.1 Trustworthiness and Facial Appearance

Peoples show relatively high agreement when judging trustworthiness of others (e.g., Krumhuber et al., 2007; Rule et al., 2009; Todorov et al., 2009; Zebrowitz et al., 1996). Furthermore, these judgements are readily provided, even after short exposure times to face stimuli; ratings following an exposure of 100ms did not statistically differ from judgements made without time constraints (Willis & Todorov, 2006). Even more rapid judgements, made at 33ms lead to judgements with an above chance accuracy, although the level of accuracy was significantly lower compared to unconstrained judgements (Todorov et al., 2009). In line with these results, several studies suggest automaticity in trustworthiness perception. When performing face memory (Engell et al., 2007) or age judgement (Winston et al., 2002) tasks on faces with varying degrees of trustworthiness (as assessed from ratings), amygdala activation was inversely correlated to trustworthiness levels of each face. This indicates automatic and implicit trustworthiness perception even in situations in which trust assessment is not relevant.

Perhaps the most compelling exploration of trustworthiness perception encompasses a number of neuroimaging studies that highlight the importance of the amygdala for judgements of trustworthiness from faces. This is consistent with a more general amygdala involvement in threat detection and fear response (e.g. Adolphs et al., 1994; Morris et al., 1996; Whalen et al., 2001). Patients with bilateral amygdala damage showed deficiency in accurate detection of trustworthy from faces, whereby the criterion for ‘correct’ responses was the consensual assessment by healthy individuals (Adolphs et al., 1998; 2001; 2002). Moreover, amygdala response to faces increased with increased untrustworthiness appearance both in explicit (Winston et al., 2002) and implicit (Engel et al., 2007) trustworthiness assessment tasks. Interestingly, in Engel and colleagues’ study, amygdala response was more strongly associated with average ratings of trustworthiness derived from a group of independent raters, compared to the participant’s own trustworthiness assessment. This result indicates that it is generalizable, likely structural, facial properties of trustworthiness that elicit an amygdala response rather than idiosyncratic trustworthiness perceptions by the individual judge (see also Honekopp, 2006).

Interpreting the amygdala-trustworthiness relationship has been complicated however, by several studies indicating a more general association of the amygdala with social judgements (e.g. Oosterhof & Todorov, 2008; Todorov et al., 2008a,b), assessment of motivational cues (Cunningham et al., 2008), as well as general arousal (Rule et al., 2011). Additionally, two studies have reported a quadratic, rather than linear, amygdala response to trustworthy faces; responses were strongest to both very untrustworthy and very trustworthy faces (Said et al., 2009; Todorov et al., 2008a). These results may reflect the emotional valence of faces both high and low on trustworthiness, as the amygdala responds somewhat more to emotionally expressive compared to neutral faces. Even though not fully understood

then, it is evident that the amygdala plays a pivotal part in the social brain (e.g. Amodio & Frith, 2006) with particular emphasis on the evaluation of other people (Schiller et al., 2009).

If people agree on which faces appear more or less trustworthy, then they should be employing a common strategy to determine whom to trust and this strategy must rely on cues available from static facial images. Research into this question has identified a number of potential cues seemingly influencing trustworthiness decisions, which can broadly be divided into cues of emotional expression (e.g. Krumhuber et al., 2007; Todorov et al., 2008; Zebrowitz et al., 2010) and cues of permanent facial structure (e.g. Stirrat & Perrett, 2010; Todorov et al., 2008a). Todorov and colleagues (2008a) modelled faces differing in trustworthiness by systematically manipulating shape components in computer-generated faces. They established a number of structural facial features relevant to trustworthiness appearance: low inner eyebrows, shallow cheekbones, thin chins and deep nose sellions (nose bridge) were the strongest predictors of un-trustworthiness (Todorov et al., 2008a). Adding to this literature, Stirrat and Perrett (2010) report that manipulation of facial width-to-height ratio (fWHR) in men (see also section 1.6.2) influenced trustworthiness perception, even when facial identity was held constant. Those faces with higher fWHR (i.e. wider faces) were perceived as less trustworthy. Furthermore, facial masculinity (sexual dimorphism) decreased perceived trustworthiness in several studies (Buckingham et al., 2006; Oosterhof & Todorov, 2008; Perrett et al., 1998), indicating an association between sex and trustworthiness.

Oosterhof and Todorov (2009) exaggerated faces along the axis created from faces perceived as high and low in trustworthiness respectively. The resulting facial images were emotionally expressive: trustworthy faces appeared happy and were characterised by Λ-shaped brows and U-shaped mouths. Untrustworthy faces on the other hand, appeared angry and were characterized by V-shaped eyebrows and ∩-shaped mouths. It follows that trustworthiness ratings may be linked to perceptions of emotional expressions rather than

facial structures, perhaps indicating an overgeneralization (see Zebrowitz et al., 2010; Zebrowitz & Motepare, 2008).

As noted earlier, agreement does not necessarily align with accuracy. A growing body of literature has accordingly assessed the question whether trustworthiness perceptions from faces capture actual behaviour and have yielded mixed results. In an early study, Bond and colleagues (1994) found that people, whose faces were perceived as less trustworthy, were more willing to participate in experiments involving deception, indicating some validity of judgments. Similarly, using trust games (experimental games designed to mimic economic exchanges based on social interaction) two studies found that those participants, whose faces were rated as more trustworthy, behaved in a cooperative manner (Stirrat & Perrett, 2010; 2012; Verplaetse et al., 2007). In two perhaps more ecologically valid studies, participants reliably rated the faces of violent criminals as less trustworthy than those of criminals who had committed non-violent crimes (Stillman et al., 2010) and the faces of America's Most Wanted criminals were rated as less trustworthy than the faces of winners of great honors such as Nobel laureates (Porter et al., 2008). A recent study by Rule et al. (in press) does, however, not replicate these results under more controlled testing conditions. In fact in this extensive and well-controlled study, across five experiments, the authors find no evidence for accuracy of trustworthiness judgments from faces, although high agreement was present. These findings, question whether trustworthiness can be accurately perceived from faces, but indicate that some underlying trait (or traits) in the face leads people to trust judgments. One possibility may be that people use cues to a related trait, e.g. aggressiveness, friendliness or health, and subsequently extrapolate their trustworthiness perception from this cue.

1.6 Facial structure links to behaviour

1.6.1 Facial structure and politics

Political attitudes are a permanent topic of hot debate and some people may be less open about their political alliance than others. According to recent research however, hiding ones convictions might be harder than expected. In the US students were able to accurately determine the political orientation (Republican or Democrat) of both elected party officials and college students (Rule & Ambady, 2010). This study identifies two facial characteristics as informative: faces perceived as democratic were also seen as warmer, while faces perceived as republican appeared higher in power. Whether these personality attributions are accurate was not assessed in this study but other studies have found links between political attitudes and personality that support the associations reported here: conservatism correlates positively with social dominance (Sidanius & Pratto, 1999), perhaps a measure similar to power, and openness to experience has been associated with a more liberal political attitude (Carney et al., 2008). Similarly results were demonstrated by showing that unknown politicians from other countries are assigned to the correct political ideology (Bull & Hawkes, 1982; Samochowiec et al., 2010). Samochowiec, Wänke, and Fiedler (2010) show that the use of mute video clips did not improve performance over photographs indicating that static cues are sufficient for the inference of cues relevant to the detection of political attitudes.

Aside from people's ability to detect political affiliation, research has also demonstrated an effect of facial cues on electoral outcomes. Testing pairs of unknown election contestants, adults and even children reliably chose the actual winner as their preferred leader in an imaginary journey (Antonakis & Dalgas, 2009). Similarly, ratings of competence of facial photographs account for 70% of the variance in U.S. election results (Atkinson et al., 2009; Ballew & Todorov, 2007; Todorov et al., 2005); with similar results

across cultures including Finland, Mexico, Brazil and Japan (Berggren et al., 2011; Lawson et al., 2010; Rule et al., 2010; but see Poutvaara et al., 2009). Competence judgements predicted election outcomes even when they were made after just a 100ms exposure to the facial photographs of the candidates (Ballew & Todorov, 2007). This work does however not assess whether face shape itself or some other intrinsic property of the candidate that is visible from the face (e.g. their age or gender) is predictive of voting decisions.

Little and colleagues (2007) addressed this question by calculating the nominal shape difference of winning and losing candidates in elections from five different countries and applying this difference to a neutral facial identity. This procedure ensures that all other facial characteristics (e.g. age) are controlled. Not only did results show an above-chance in-lab voting preference for the face shape of the winner in each pair but also did the amount of in-lab preference predict the margin of the popular vote. In order to better understand facial correlates of party membership Carpinella and Johnson (2013) assessed facial sex typicality in members of the U.S. House of Representatives and found that female republicans have more feminine facial features compared to democrats but there was no effect for males. These results however, while statistically significant are based on both a small sample of women (republican women: N=17) and small effect sizes, making them hard to interpret. Taken together, the studies discussed indicate cross-culturally consistent effects: appearance-based judgments inform political perceptions although the facial cues used for such judgments remain poorly understood (Olivola & Todorov, 2010b; Wänke et al., 2012).

1.6.2 Facial width-to-height ratio: links to behaviour

One facial metric that has recently been of interest to research is the facial width-to-height ratio (fWHR). This metric is defined as the bizygomatic width divided by upper face height (see Figure 2). Originally identified as sexually dimorphic in several monkey and ape species (Weston et al., 2004), the facial width-to-height ratio was postulated as a tool for sexing human skulls, as it showed sexual dimorphism independently of body size dimorphism (Weston et al., 2007). Weston and colleagues argued that males and females have different growth trajectories, diverging at puberty, for bizygomatic width but not upper face height leading to males exhibiting greater fWHR than females. Divergence at puberty might indicate an involvement of sex hormones, likely testosterone, since these have previously been shown to be linked with general masculinisation of facial bone structure (Verdonck et al., 1999).

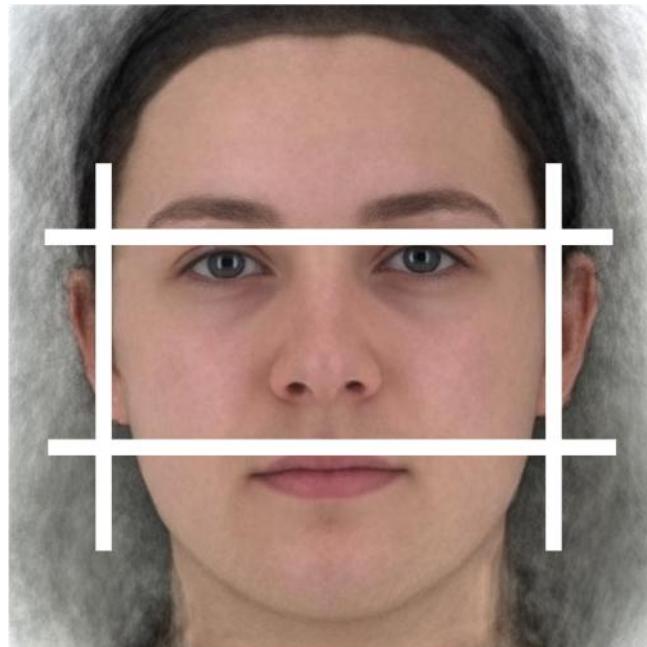


Figure 2: Illustration of the facial width-to-height ratio (fWHR) measure: Horizontal lines represent the distance between the upper-lip and the highest point of the eyelids (upper-face height); vertical lines represent the maximum distance between the left and right facial boundary (bizygomatic width). fWHR was calculated as bizygomatic width divided by upper-face height.

The sexual dimorphism found in fWHR led to research assessing possible behavioural correlates with this metric. Carré and McCormick (2008) argued that the sexual dimorphism of fWHR may be indicative of a selection pressure that is independent of body size, leading them to postulate possible links to masculine personality (dominance) and behaviour (aggression). Both dominance and aggression have previously been shown to be reliably sexually dimorphic in humans (Archer, 2006; see also section 1.5.2). Using an in-lab aggression paradigm (point subtraction aggression paradigm²; Cherek, 1981) Carré and McCormick report for higher fWHR to be associated with more aggressive behaviour ($R^2=15\%$). Trait dominance, as assessed using the International Personality Item Pool scales (Goldberg et al. 2006), did not mediate the relationship between fWHR and aggressive behaviour. There was no effect for women. Following these in-lab results Carré and McCormick (2008) also report a link between fWHR and a more ecologically valid measure of aggression: penalty points in hockey players.

Several follow-up studies report additional links between fWHR and behaviours that might all be interpreted to be dominant or status seeking. Employing a laboratory based trust game, Stirrat and Perrett (2010) show that men with higher fWHR were more likely to exploit their opponents, lending themselves as untrustworthy. Similarly unethical behaviour, measured as the probability to cheat and deceive, was positively associated with fWHR (Haselhuhn & Wong, 2012), although the association with cheating was mediated by self-reported sense of power. Finally, fWHR of CEOs has been linked to the economic performance of their companies (Wong et al., 2011) and in a study of in-group and out-group

² The point-subtraction-aggression paradigm: Participants are led to believe they are paired with a same-sex partner and their task is to earn points that can later be exchanged for money. There are three response option to earn points: 1) hitting response key 1 a hundred times increases the point-count by one; 2) hitting response key 2 ten times steals one point from the opponent but does NOT add this point to the participant's count although when the simulated opponent chooses this option points ARE added to their count (only possible after the simulated opponent has first stolen from the participant); and 3) hitting response key 3 ten times protects the points of the participant from being stolen. The use of option 2 (stealing points) is used as a measure of aggressive behaviour.

behaviour, men with higher fWHR were found to act more self-sacrificing for their in-group (Stirratt & Perrett, 2012). Facial width has also been linked to cause of death in a large forensic skull sample of men who died as a consequence of homicide: narrower faced men were more likely to have been killed by direct contact violence compared to wider faced men (Stirrat et al., 2012). These results may provide support for a link between fWHR and dominance, since more dominant men are likely stronger and thus may be more costly to kill in direct fight.

These behavioural results are of particular interest in light of findings looking at the influence of fWHR on the perception of personality traits and behaviours. As described above (section 1.5) several traits can be attributed to faces, sometimes accurately so. With regards to fWHR, studies have convincingly demonstrated that it facilitates the accurate perception of aggressiveness, dominance (Carré et al., 2009), and untrustworthiness (Stirrat & Perrett, 2010). It has further been shown that fWHR is indeed the informative facial metric: when assessed in relation to other facial features and metrics, fWHR was the only significant predictor of perceived aggression (Carré et al., 2010) and when artificially altering the same face to be high or low on fWHR, Stirratt & Perrett (2010) found that the high fWHR versions were reliably chosen as appearing less trustworthy. Even children (age 8) and observers from a race different than the face rated, could successfully use fWHR as a cue to perceived aggression (Short et al., 2012).

However, there have also been several recent studies questioning the validity of some of the behavioural associations of fWHR that have been reported. Deaner et al. (2012) failed to replicate the association between hockey penalties and fWHR and instead suggest body weight as a better predictor of aggressive behaviour, at least in this highly specialised group. In line with this suggestion, Coetzee et al. (2010) find a positive correlation between body mass index (Weight (kg) / Height² (m); BMI) and fWHR, which suggests that BMI

should be controlled when assessing links to behaviour. Moreover, the status of fWHR as sexually dimorphic has recently been questioned, a study using a large Turkish sample found no difference in this measure (Özener, 2012).

1.7 The current thesis

Faces play an important role in social interaction since they can provide differentiated information about a person. In this chapter, I have discussed several ways in which faces differ, including facial shape and in particular shape dimorphism as well as facial skin colour. I explored how differences in appearance are linked to a variety of behavioural traits such as dominance and trustworthiness and that in many cases the perception of behavioural traits from neutral faces is surprisingly accurate. Hormones are likely one physiological link between appearance and behaviour and to this end; I discussed how testosterone influences male facial appearance and its close relationship to status seeking and mating behaviour of men. As far as perceptual qualities from faces are concerned, recent research has suggested that dominance and trustworthiness function as basic traits perceptual from faces that then in turn inform more elaborate judgements (Oosterhof & Todorov, 2008). But which facial cues are diagnostic and what physiological mechanisms underpin these traits?

In line with the assumption that dominance and trustworthiness are the two basic dimensions accurately perceivable from faces and underlying other inferences (Oosterhof & Todorov, 2008), the current thesis will assess facial attributes in relation to these perceptual traits with two main aims: 1) to investigate the status of facial width-to-height ratio as a valid cue to dominance and 2) to investigate healthy skin colour, as a cue to current condition, with respect to trustworthiness assessments and biological underpinnings.

Chapters 2- 5 will examine properties of the facial-width-to-height ratio a metric closely associated with dominance and dominance linked behaviours as well as their perception. Currently, several studies have linked fWHR to aggression and dominance as well as untrustworthiness. Whether more positive personality attributes are also linked to fWHR is currently not clear. Accordingly, I investigate whether achievement striving, a positive attribute that is conceptually closely related to dominance, is linked to fWHR in a group of highly achieving individuals: US presidents (Chapter 2).

In chapter 3 and 4 I investigate physiological assumptions previously made about fWHR: firstly I test in four large samples whether this metric is sexually dimorphic. Since fWHR is thought to be sexually dimorphic and links to behaviours such as aggression, it has often been argued to be influenced by testosterone. However, to date this relationship has not been formally established. In chapter 4 I thus investigate this putative association in two samples. One sample contains measures of both baseline and reactive testosterone (see section 1.5.2.1 for more details on reactive testosterone).

Chapter 5 investigates whether links between fWHR and dominance are restricted to humans. If fWHR is indeed a signal of dominance that has been selected, it is likely that similar associations exist in species closely related to humans. Such associations would indicate a phylogenetically old trait that is of evolutionary advantage across species. To this end, I measure fWHR in a sample of Capuchin monkeys and test links with keeper rated dominance as well as alpha status in both males and females.

The final two chapters assess the importance of healthy skin colouration on social judgements and possible links between skin colour and testosterone. In chapter 6 possible associations between healthy skin colour and perceived trustworthiness are explored. Results

indicate an effect of healthy skin colouration on perceived trustworthiness. Finally, chapter 7 investigates possible links between testosterone and healthy skin colour.

Chapter 2. Facial width-to-height ratio predicts achievement striving in US presidents

This chapter is based on work that has been published in a peer-reviewed journal:

Lewis, G. J., Lefevre, C. E., & Bates, T. C. (2012). Facial width-height ratio predicts achievement drive in US presidents. *Personality and Individual Differences*, 52, 855-857.

Contribution to this chapter: My contribution to this chapter was equal with that of Gary Lewis, we conceived and designed the study together. I collected and measured face images of presidents. Gary Lewis collated personality measures. We jointly conducted statistical analyses and contributed equally to the write-up.

Abstract

Facial width-to-height ratio (fWHR) has been associated with aggression, unethical behaviour, company profit, and dominance; however, it is currently unclear whether this facial trait relates to politically relevant character traits. Here we examine fWHR in an elite sample of political leaders, former US presidents ($n = 29$), who were rated for forcefulness, pacifism, inflexibility, and achievement drive; traits potentially linked to fWHR. The first three of these traits were unrelated to fWHR, but we found a positive association between fWHR and achievement drive ($r = .58$, $p < .01$), and a negative association to the trait “poise and polish” ($r = -.38$, $p < .05$). These results extend associations of behaviour with facial structure to individuals in the highest echelons of power, suggest connections from biology to politically relevant character traits, and indicate that fWHR may also be associated with achievement-striving alongside associations with dominance and aggression.

2.1 Introduction

While recent research has expanded our knowledge concerning biological influences on politically relevant attitudes and behaviour (e.g. Alford et al., 2005; also see Eaves & Eysenck, 1974, and Martin et al., 1986), the identification of specific biological markers linked to behaviour among those acting in a political capacity is still in its infancy. Here we examine the association of facial width-to-height ratio (fWHR; the bizygomatic width divided by upper-face height: see Figure 3), a putatively sexually-dimorphic trait [wording in keeping with published manuscript, but see chapter 3] previously associated with measures of aggression (Carré & McCormick, 2008), cheating, sense of power, and deception (Haselhuhn & Wong, 2012), and corporate success (Wong et al., 2011), to a set of conceptually related character traits with relevance to political decision-making among a set of elite political leaders: former US presidents.

The sexually dimorphic nature of fWHR in the human skull was first highlighted by Weston, Friday, and Lio (2007; but see Özener, 2012, chapter 3), indicating that adult men had higher fWHR than women, independent of body size and age. Speculating that the sexual dimorphism of fWHR may represent an honest signal of physical dominance, perhaps as a function of developmental testosterone exposure (e.g. Verdonck et al., 1999), Carré and McCormick (2008) found that fWHR was associated with aggressive behaviour in men, (although not in women). Haselhuhn and Wong (2012) reported broadly similar results, finding that men with higher fWHR self-reported a greater sense of power, and were more likely to deceive or cheat when this would increase their personal financial gain. Furthermore, Stirrat and Perrett (2010) observed that males with greater fWHR were more prone to exploit the trust of others and were less trusted than counterparts with lower fWHR.

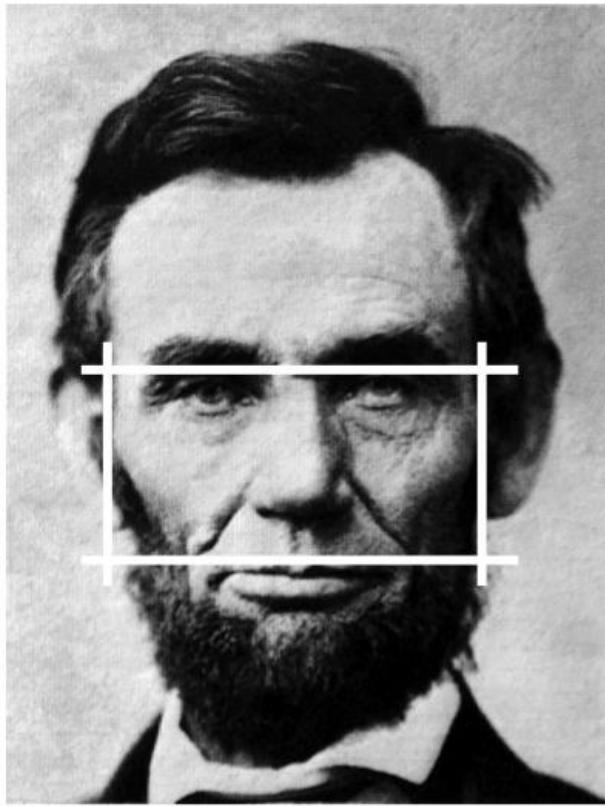


Figure 3: Illustration of the facial width-to-height ratio (fWHR) measure: Horizontal lines represent the distance between the upper-lip and the highest point of the eyelids (upper-face height); vertical lines represent the maximum distance between the left and right facial boundary (bizygomatic width). fWHR was calculated as bizygomatic width divided by upper-face height

While a range of character traits likely influence political attitudes (Lewis & Bates, 2011), those linked to fWHR – dominance, aggression, and a greater sense of power – are perhaps of special importance for political decision making (along with conceptually related traits such as forcefulness, (low) pacifism, and inflexibility; Simonton, 1986; see also Winter, 2003). It is currently unclear, however, which of these politically relevant character traits might be associated with fWHR. For instance, if fWHR, as a possible proxy measure of testosterone exposure (see chapter 4), is a direct marker of increased aggression (Finkelstein et al., 1997), then pacifism should be associated with lower fWHR. Alternatively, if fWHR

represents status concerns rather than aggression per se, it may be linked to achievement striving, with connections to factors such as military decisions being contingent on circumstance (e.g. van Honk et al., 2011).

To better understand the association of fWHR with politically relevant personality traits, we investigated fWHR in all former US presidents for whom adequate photographs and character information were available. This group presented a set of key advantages for the study: Firstly, reliable measures on a range of politically relevant character traits have been reported for these presidents (Simonton, 1986). Secondly, using this sample of elite individuals allowed us to investigate correlates of political behaviour at the very highest level of politics, serving to inform whether biological traits associate with actualised politically relevant behaviour.

In line with previous work, showing links from fWHR to aggression and dominance, we hypothesised that fWHR would positively predict the character traits of achievement drive, inflexibility, and forcefulness, and negatively predict pacifism.

2.2 Methods

2.2.1 Face Stimuli

29 frontal photographs of former US presidents were analysed (see Table 1). 14 Presidents could not be analysed because either no adequate frontal photograph was available (ruling out several early presidents) or had not been rated by Simonton (1986), whose data extended only as far as the presidency of Ronald Reagan.

Prior to fWHR measurement, all images were horizontally aligned and scaled according to inter-pupillary distance. Following the methodology of Carré and McCormick

(2008), bizygomatic width was measured as the maximum horizontal distance between the right and left facial boundary; upper-face height was measured as the vertical distance between the highest point of the upper-lip and the highest point of the eyelids. The fWHR was calculated as width divided by height (see Table 1 for individual fWHR measures).

2.2.2 Character Traits

We utilised Simonton's (1986) psychometric analysis of all former US presidents until Reagan. Personality descriptions were collected for each of the presidents from numerous historical texts that were anonymised and transcribed onto index cards for subsequent rating. These text descriptions were then rated on the Gough Adjective Scale (Gough & Heilbrun, 1965), consisting of 300 adjectives. Several judges performed ratings of each trait utilising a 7-point likert scale (1=definitely not applicable; 7=definitively applicable; 4=not distinctive on this trait). Subsequently, ratings were subjected to reliability analysis, which 110 adjectives survived. Aggregated rating scores of these 110 adjectives were then subjected to factor analysis which yielded 19 factors with Eigenvalue greater than 1, 14 of which were retained and 5 rejected on grounds of being trivial in explanatory power. The 14 retained factors were: Moderation, friendliness, intellectual brilliance, Machiavellianism, poise and polish, achievement-drive, forcefulness, wit, physical attractiveness, pettiness, tidiness, conservatism, inflexibility, and pacifism.

Of these 14 factors, 4 were of specific interest here: Achievement drive (highest factor loadings: persistent = .76; quitting = -.88), forcefulness (highest factor loadings: energetic = .64; active = .63), inflexibility (highest factor loadings: stubborn = .47; rigid = .41) and pacifism (highest factor loadings: peaceable = .61; courageous = -.48), on account of their conceptual overlap with both dominance and aggression.

2.3 Results

For achievement drive, one data point (Grant) was more than 4 standard deviations from the mean and so was removed from subsequent analyses (no other data point was more than ± 1.8 SDs from the mean). fWHR (mean = 1.99, SD = .11) significantly predicted achievement drive ($r = .58$, $df = 26$, $p = .001$; see Figure 4), but not forcefulness ($r = .13$, $df = 27$, $p = .50$), inflexibility ($r = .17$, $df = 27$, $p = .38$), and pacifism ($r = -.08$, $df = 27$, $p = .70$), although these associations were all in the predicted direction. Linear regression was next used to examine the relationship of achievement drive to fWHR, controlling for potential confounds of age at incumbency and rated intellectual brilliance and interactions with age. The overall model was significant ($r^2 = .41$, $F(4, 23) = 5.50$, $p = .005$, with a highly significant independent effect of fWHR ($\beta = .60$, $p = .001$).

Table 1: Names and facial width-to-height ratio of the US presidents used in the study.

President	fWHR	President	fWHR
John Quincy Adams	1.99	William H Taft	2.01
Zachary Taylor	1.86	Woodrow Wilson	1.78
Millard Fillmore	2.04	Warren G Harding	1.91
Franklin Pierce	1.89	Calvin Coolidge	2.04
James Buchanan	1.88	Herbert Hoover	2.30
Abraham Lincoln	1.93	Franklin D Roosevelt	1.88
Andrew Johnson	2.18	Harry S Truman	2.01
Ulysses S Grant	2.07	Dwight D Eisenhower	2.04
Rutherford B Hayes	1.93	John F Kennedy	2.13
James Garfield	2.06	Lyndon B Johnson	2.04
Chester A Arthur	1.80	Richard Nixon	1.91
Grover Cleveland	2.05	Gerald Ford	1.96
Benjamin Harrison	1.88	Jimmy Carter	2.15
William McKinley	1.90	Ronald Reagan	1.98
Theodore Roosevelt	2.03		

The additional 10 factors from Simonton (1986) were analysed in a purely exploratory capacity to investigate further associations with fWHR. Of these, only poise and polish ($r = -.38, p <.05$) showed a significant negative association with fWHR.

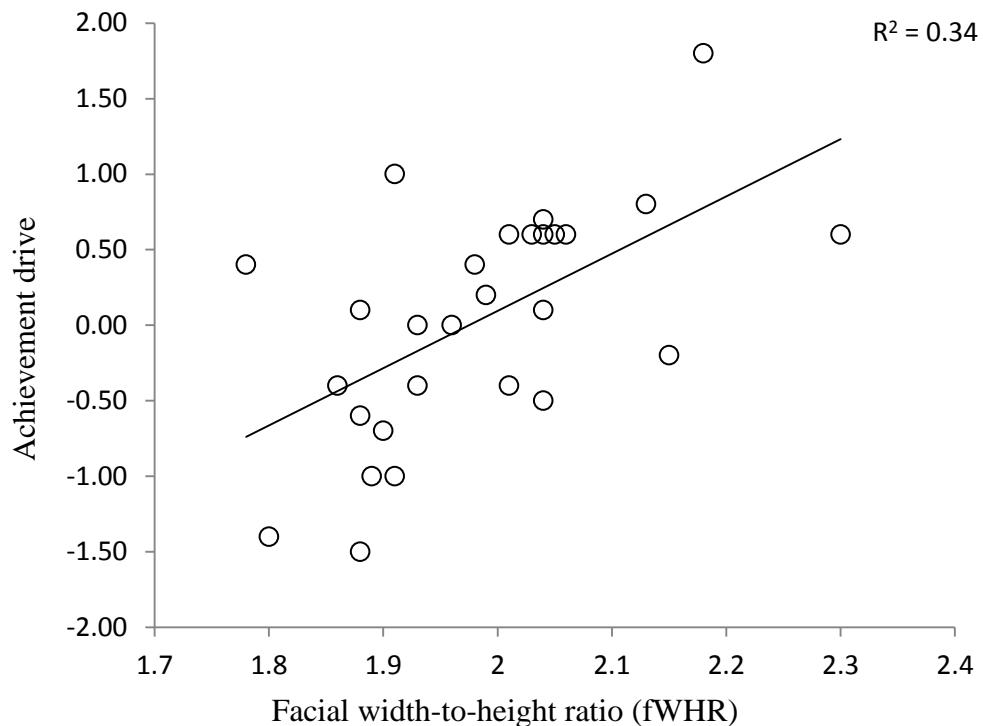


Figure 4. Association between facial width-to-height ratio and achievement drive in former US presidents.

2.4 Discussion

The current findings relate facial width-to-height ratio (fWHR) to achievement drive in a sample of exceptional political figures: former US presidents. The findings refine and extend recent work indicating fWHR is a morphological marker of dominance-seeking (Carré & McCormick, 2008; Haselhuhn & Wong, 2012). Contrary to prediction, we did not observe an association from fWHR to forcefulness, inflexibility, or pacifism. One possibility for this null finding is that fWHR does not serve as a marker of aggression per se, but is related

instead to biological factors influencing striving or capacity for status-achievement. This may reflect the significant association with achievement drive and not with the aggression-linked traits of forcefulness and (low) pacifism. A role in status-seeking would reflect more closely current thinking in endocrinology concerning the behavioural effects of testosterone, a hormone linked to sexually dimorphic traits (e.g. Finkelstein et al., 1997): while testosterone has been linked to aggression (Finkelstein et al., 1997), this link is now argued to be a situationally-contingent manifestation of a broader motivation to achieve status (Eisenegger et al., 2011; van Honk et al., 2011). For presidents, signs of aggression are likely to be counterproductive – interpreted as a sign of low, rather than high, capacity for status (cf. Furlow et al., 1998). In contrast, in the sporting arena, aggression may be a more clearly sanctioned method of status achievement (at least in some sports), perhaps reflecting the association of fWHR with aggression in ice-hockey players (Carré & McCormick, 2008).

The natural constraint on the sample size imposes a limitation to this study in that we were unable to detect small effects. Furthermore, it is not clear whether the conclusions of this study generalize to the wider population. Future work utilising larger and more representative samples, as well as extending this work to broader political figures, will be valuable. In addition, we were constrained in the measures of pacifism and forcefulness used. These may not directly assess aggression or dominance but rather be personality concepts linked to sociability and activity. For example, forcefulness had its highest loadings on the items “energetic” and “active”, which perhaps reflect trait extraversion (Costa & McCrae, 1992) more so than aggressive forcefulness per se.

In summary, we report an association between the facial width-height ratio and individual differences in achievement drive in a sample of former US presidents. These findings extend recent work associating this facial structure to elite political figures and suggest that biology may influence character traits with subsequent political implications.

Chapter 3. No evidence for sexual dimorphism of facial width-to-height ratio in four large adult samples

This chapter is largely based on work that has been published in a peer-reviewed journal:

Lefevre, C. E., Lewis, G. J., Bates, T. C., Dzhelyova, M., Coetzee, V., Deary, I. J., & Perrett, D. I. (2012). No evidence for sexual dimorphism of facial width-to-height ratio in four large adult samples. *Evolution and Human Behavior*, 33, 623-627.

Abstract

Sexual dimorphism in physical appearance may be an important cue in both intra- and inter-sex competition. Recently, the facial width-to-height ratio (fWHR) has been proposed as a novel sexually dimorphic morphologic measure, with men suggested to have a higher fWHR than women. Currently, however, the status of fWHR as a sexually dimorphic trait is unclear. Here we tested for sexual dimorphism in fWHR, as well as in three additional, previously reported, facial measures, in four (three Caucasian and one African) independent samples. In three of the four samples, no significant sex differences in fWHR were observed. In one sample males showed a significantly *lower* (rather than higher) fWHR than females (this effect was no longer significant after controlling for Body Mass Index). By contrast, significant and large sex differences were observed in all four samples for each of the three previously validated facial metrics; namely: (i) lower face/face height, (ii) cheekbone prominence, and (iii) face width/lower face height. These results provide strong evidence against the claim that fWHR, at least as measured from the surface of the face, is sexually dimorphic.

3.1 Introduction

Sexual dimorphism refers to phenotypic characteristics that differ between males and females of the same species (Barber, 1995). In *Homo sapiens* a number of sexually dimorphic traits have been identified, including gross morphology (e.g. body mass, brain size; Peters et al., 1998; Sowell et al., 2006), behaviour (e.g. dominance; Grammer & Thornhill, 1994; Thornhill & Gangestad, 1996), and cognition (e.g. mental rotation; Collins & Kimura, 1997). Recently, attention has focused on sexual dimorphism in facial structure (e.g. Penton-Voak et al, 2001; Perrett et al., 1998): men tend to have larger jaws and more prominent brow ridges compared to women (Enlow, 1982). Of specific interest in the current study, recent work has suggested that the facial width-to-height ratio (fWHR: the ratio of bizygomatic width to upper face height; see Figure 5a) is a sexually dimorphic facial dimension, independent of body size (Weston, et al., 2007). However, not all studies have observed this dimorphism (Özener, 2012). Here we test the hypothesis of sexual dimorphism in fWHR utilising four homogenous samples, across two ethnicities (White European and Black African). Additionally we test the validity of several other putatively sexually dimorphic facial features.

Sexual dimorphism may arise as a result of inter-sexual selection (Andersson, 1992), whereby certain characteristics are retained or even amplified because they are favoured by members of the opposite sex. In the case of facial structures, several studies have noted that females prefer males who possess masculine facial features such as wide jaws and thick brow ridges (e.g. Johnston et al., 2001), with this preference perhaps most evident during the ovulatory phase of the female menstrual cycle (see Gangestad & Thornhill, 2008 for review; but also see Penton-Voak et al., 1999, Penton-Voak & Perrett, 2000). This pattern of attraction suggests that male facial masculinity may reflect inherent mate quality important

for offspring fitness. In line with this theory, fWHR may then also have become sexually dimorphic through a preference in females for men with high fWHR.

One model for the development of secondary sexual traits such as facial masculinity is the immunocompetence handicap hypothesis (Folstad & Karter, 1992). This model is based on two core assumptions. Firstly, secondary sexual traits (e.g. facial masculinity) emerge as a function of testosterone exposure during development (Verdonck et al., 1999); secondly, testosterone acts as an immunosuppressant (Grossman, 1985). Under this model, then, the successful expression of elaborate secondary sexual traits requires exposure to high levels of testosterone, and only males of high genetic quality will be able to sustain this exposure without deleterious consequences (Zahavi & Zahavi, 1997).

Support for the immunocompetence perspective has come from work linking sexually dimorphic facial features to circulating (Penton-Voak, & Chen, 2004) and reactive levels of testosterone (Pound et al., 2009) suggesting that facial masculinity may indeed signal genetic fitness (Folstad & Karter, 1992; Penton-Voak & Chen, 2004; Thornhill & Gangestad, 2006). However, it is noteworthy that several other studies have failed to confirm core predictions from the theory, such as a preference for masculine male faces by females (e.g. Boothroyd et al. 2005; Perrett et al., 1998; Scott et al., 2010).

An alternative perspective posits that masculine facial features may be a signal associated with increased access to resources through successful outcomes in dominance contests, perhaps via testosterone's association with enhanced muscle mass and physical strength (Griggs et al., 1989). If facial masculinity honestly signals increased capability, such individuals may be perceived as more physically dominant by rivals and mates (Mueller & Mazur, 1996; Swaddle & Reierson, 2002). In support of this model, facial masculinity has been reported to correlate with physical strength (Fink et al., 2007; Windhager et al., 2011),

as well as allowing others to estimate the relative strength of an individual (Sell et al., 2009). Accordingly, individuals displaying greater facial masculinity may have been preferred by females on account of their superior capacity to accrue fitness-enhancing resources (Puts, 2010).

In either model, then, establishing those dimensions on which sex differences in facial morphology exist is of considerable importance as these may reflect processes that shape intra-sex competition and /or inter-sex mating dynamics. As noted above, the fWHR has been proposed as one such sexually dimorphic facial feature. Support for sexual dimorphism in the fWHR of human faces was based on direct skull measures in a sample of 121 modern black African skulls (68 male) from the Raymond Dart collection, University of Witwatersrand, South Africa (Weston et al., 2007). The sample varied in age at death from less than 1 year to 30 years, with only about half the sample being fully grown at time of death. These findings were replicated in a mixed-ethnicity photographic sample of 88 North American undergraduates (37 male: Carré & McCormick, 2008). Subsequent studies identified a range of sexually-dimorphic behavioural traits linking to fWHR amongst males: these include aggression (Carré & McCormick, 2008; although see Deaner et al, 2012), self-reported power (Haselhuhn & Wong, 2012), and dishonesty (Stirrat & Perrett, 2010). It has also been shown to signal aggression and untrustworthiness to others (Carré & McCormick, 2009; Stirrat & Perrett, 2010).

Despite the considerable attention centred on hypotheses derived from models assuming that fWHR is sexually dimorphic, this dimorphism itself has not yet been well established. The two studies reporting a sex difference in human samples (Carré & McCormick, 2008; Weston et al., 2007) possessed small sample sizes and, in the case of Carré and McCormick (2008), contained mixed ethnicities. With regard to the latter issue, African populations may differ from Caucasians in their face shape (Enlow, 1982) suggesting

potential bias in mixed ethnicity samples. Importantly, a recent attempt to replicate the sexual dimorphism of fWHR (Özener, 2012) reported no significant sex difference of fWHR in a Turkish sample larger than those of the initial positive studies ($n = 470$).

3.1.1 The Current Study

Sexual dimorphism in facial structure has broad reaching implications both for theory and applications and so confirming this putative sex difference is important for several lines of enquiry in evolutionary biology and psychology. Accordingly, here we examined sex differences in facial width-to-height ratio in three adult European samples and one adult African sample. Additionally, we measured three other previously documented sexually dimorphic facial dimensions: (i) lower face/face height, (ii) cheekbone prominence, and (iii) face width/lower face height (see Penton-Voak et al., 2001 and Figure 5b) which have previously been linked to reactive testosterone (Pound et al., 2009). These additional measures allowed us to establish that the samples used in this study could produce known sexually dimorphic characteristics and also to establish whether these metrics are associated with fWHR.

One Caucasian sample was photographed using 3D imaging which yields methodological advantages for this type of study: specifically, 3D photographs provide to-scale representations of a participant's head, removing potential measurement errors that may arise from artefacts of head posture, i.e. faces rotated with respect to the camera in the horizontal or vertical planes.

3.2 Method

3.2.1 Participants

Four samples of human facial photographs were analysed. In all samples, participants were photographed with standardised distance to the camera and lighting and were instructed to keep a neutral facial expression.

Sample 1: 99 female (mean age = 20.21, age range = 18-25) and 46 male (mean age = 20.24, age range = 18-27) Caucasian undergraduate students. Participants were photographed using a Fujifilm Finepix S5Pro digital camera.

Sample 2: 306 Scottish adults (169 female) from the Lothian Birth Cohort 1921 (Deary et al., 2004; Penke et al., 2009) who were all born in 1921 and approximately 83 years old – with a narrow range of ages – at the time of picture collection. Photographs were taken using a Nikon E5700 digital camera.

Sample 3: 124 male (mean age = 20.44; age range = 18-30) and 131 female (mean age = 20.25; age range = 18-28) Caucasian undergraduate students. Participants had 3D head model photographs taken using a 3dMD camera (for technical details see <http://www.3dmd.com/3dmdface.html>). Hair and clothing were occluded in all images before processing.

Sample 4: 110 female (mean age = 19.80; age range 18-26) and 108 male (mean age = 20.65; age range 18-29) black South African undergraduate students. They were photographed using a Sony Cybershot DSC P72 or a Fujifilm Finepix S5Pro digital camera.

3.2.2 Facial Measures

Prior to measurement (using the Psychomorph software package; Tiddeman et al., 2001, <http://users.aber.ac.uk/bpt/jpsychomorph/>), faces in all 2D samples were horizontally aligned and scaled to the same interpupillary distance. fWHR was measured by calculating the bizygomatic width (maximum horizontal distance from the left facial boundary to the right facial boundary) to upper-face height (vertical distance from the mid-point of the upper-lip to the highest point of the eyelids) ratio from photographs (see Figure 5a, and Stirrat & Perrett, 2010). For the 3D sample, measurements were made using Morphanalyser (Coetzee et al., 2011; <http://cherry.dcs.aber.ac.uk:8080/wiki/MorphAnalyser>). We also calculated facial metrics as described by Penton-Voak et al. (2001; see Figure 5b); namely, (i) lower face/face height (vertical distance from mean eye height to gnathion/vertical distance from

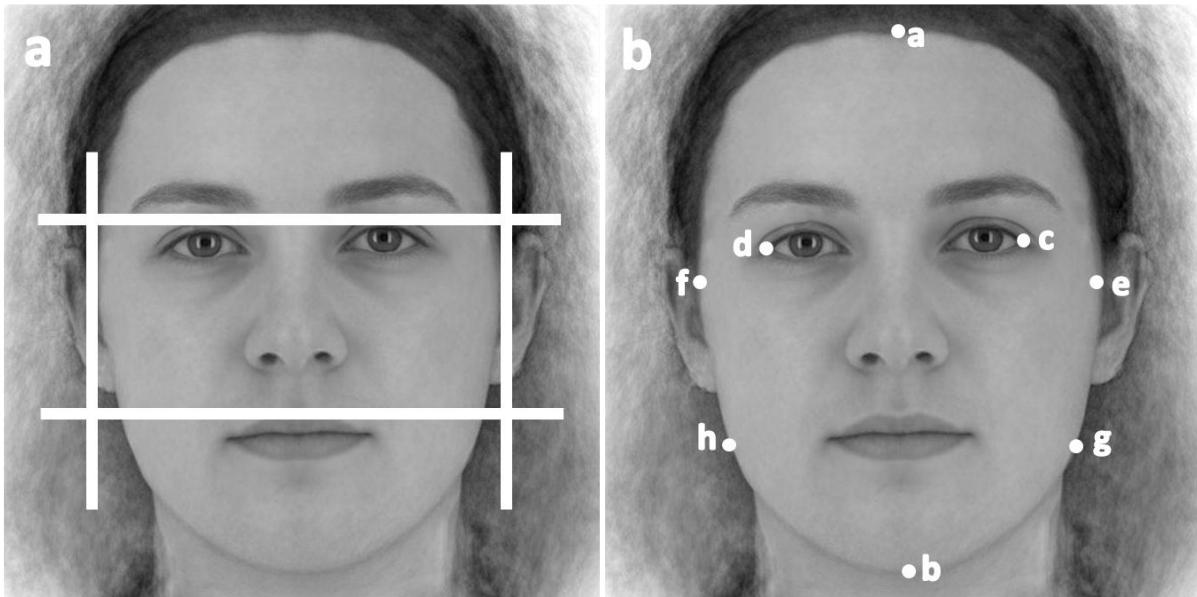


Figure 5: Examples of measures and measuring points used for morphometric calculations.

Measure for fWHR (a): horizontal lines represent the distance between the upper lip and highest point of the eyelids (upper face height), vertical lines represent the maximum distance between the left and right facial boundary (bizygomatic width). fWHR was calculated as width divided by height. Morphometric calculations (b): (i) Lower face/face height: c-b/a-b, (ii) cheekbone prominence: e-f/g-h, and (iii) face width/lower face height: e-f/c-b.

trichion to gnathion), (ii) cheekbone prominence (bzygomatic width/vertical distance between left and right gonion approximation), and (iii) face width/lower face height (bzygomatic width/vertical distance from mean eye height to gnathion).

3.3 Results

Descriptive statistics for facial metrics in all four samples are shown in Table 2. The hypothesis that fWHR would be greater in males than in females was tested in each sample using independent t-tests, with fWHR as the dependent variable, and sex as the independent variable. Analysis revealed no significant sex differences for fWHR in Samples 1, 2, or 4, (all $p > .10$); moreover, in all cases the difference between mean fWHR of women compared to men was in the opposite direction to that predicted (i.e., female fWHR was higher than that of males (see Table 2). In Sample 3, this female advantage in fWHR reached significance.

Slightly different nasion approximations have been used in the literature (Carré & McCormick, 2008; Stirrat & Perrett, 2010): We therefore re-analysed all faces following Carré & McCormick's methods. These measures yielded slightly lower mean fWHR values but also showed no sex differences (all $p > .10$).

Coetzee et al. (2010) report a positive association between fWHR and BMI. We therefore tested for effects of BMI on fWHR in Sample 1, 2, a subset of Sample 3 (91 males, 98 females) for whom BMI data were available, and in Sample 4 using ANCOVA (see Table 3). BMI was moderately correlated with fWHR in all samples (Sample 1: $r = .27$, $p = .001$; Sample 2: $r = .23$, $p < .001$; Sample 3: $r = .40$, $p < .001$; Sample 4: $r = .23$, $p = .001$). Sex differences remained non-significant for samples 1, 2, and 4 and became non-significant in sample 3.

Table 2: Sexual dimorphism in morphologic measurements. Sample 1: Caucasian undergraduate students; Sample 2: Scottish adults; Sample 3: Caucasian undergraduate students, with 3D photographs; Sample 4: South African black students.

		N	mean	SD	t	p
Sample 1 (Caucasian young adults)	fWHR					
	<i>Male</i>	46	2.12	.182	1.59	.114
	<i>Female</i>	99	2.17	.157		
	Lower face/face height					
	<i>Male</i>	46	.629	.037	4.07	<.001
	<i>Female</i>	99	.607	.027		
	Cheekbone prominence					
	<i>Male</i>	46	1.14	.045	4.56	<.001
	<i>Female</i>	99	1.17	.036		
	Face width / lower face height					
	<i>Male</i>	46	1.21	.073	3.07	.003
	<i>Female</i>	99	1.25	.066		
Sample 2 (Caucasian adults age 83)	fWHR					
	<i>Male</i>	137	2.06	.170	1.47	.142
	<i>Female</i>	169	2.09	.164		
	Lower face/face height					
	<i>Male</i>	N/A	-	-	-	-
	<i>Female</i>					
	Cheekbone prominence					
	<i>Male</i>	137	1.15	.048	4.20	<.001
	<i>Female</i>	169	1.18	.055		
	Face width / lower face height					
	<i>Male</i>	137	1.25	.067	2.37	.019
	<i>Female</i>	169	1.27	.069		
Sample 3 (Caucasian young adults, 3D)	fWHR					
	<i>Male</i>	124	1.84	.127	2.69	.008
	<i>Female</i>	131	1.88	.114		
	Lower face/face height					
	<i>Male</i>	124	.662	.041	5.18	<.001
	<i>Female</i>	131	.640	.025		
	Cheekbone prominence					
	<i>Male</i>	124	1.14	.074	14.72	<.001
	<i>Female</i>	131	1.29	.086		
	Face width / lower face height					
	<i>Male</i>	124	1.15	.072	9.43	<.001
	<i>Female</i>	131	1.23	.080		
Sample 4 (African young adults)	fWHR					
	<i>Male</i>	108	2.20	.237	1.36	.175
	<i>Female</i>	110	2.24	.204		
	Lower face/face height					
	<i>Male</i>	108	.595	.029	5.37	<.001
	<i>Female</i>	110	.576	.022		
	Cheekbone prominence					
	<i>Male</i>	108	1.12	.037	4.62	<.001
	<i>Female</i>	110	1.15	.044		
	Face width / lower face height					
	<i>Male</i>	108	1.18	.060	5.50	<.001
	<i>Female</i>	110	1.22	.057		

Note. Sample 1 df = 143; Sample 2 df = 304; Sample 3 df = 253; Sample 4 df = 216.

Table 3: The effects of sex on fWHR, controlling for BMI and the interaction of sex*BMI, separately for each of the four samples.

Sample	Overall model	Sex	BMI	Sex*BMI
	F	F	F	F
1	4.79*	0.10	7.72*	<0.01
2	6.45**	0.15	16.99**	0.02
3	20.10**	1.80	38.46**	0.50
4	4.17*	0.07	7.85*	0.03

Note. All results are from ANCOVA models with BMI as a continuous covariate. Sample 1 df=141; Sample 2 df = 302; Sample 3 df = 186; Sample 4 df = 212. *p<.01, **p<.001.

The other three face measures – lower face/face height, cheekbone prominence, and face width/lower face height – were highly sexually dimorphic in all samples (all ps < .019; see Table 2). Note that lower face/face height could not be calculated for the second sample (older adults) because the upper facial boundary could not be reliably determined in some of the men due to receding hairlines.

The correlations between fWHR and width/lower face height were consistently positive (all rs > .399, all ps < .001). Lower face/face height was negatively associated with fWHR in Sample 1 (Caucasian young adults, r = -.233, p < .001) and sample 3 (3D Caucasian young adults, r = -.170, p =.007), but positively in Sample 4 (African faces, r = .149, p < .05). Cheekbone prominence was only associated with fWHR in Sample 3 (r = -.138, p < .05).

3.4 Discussion

In the present study we tested whether facial width-to-height ratio (fWHR) and three other morphologic face measures are sexually dimorphic. In three of four tested samples of both Caucasian and African individuals we found no evidence for a greater fWHR in men than women. Moreover, and in contrast to recent work, in a 3D-head-model sample (Sample 3), men had a significantly *lower* fWHR than women, with all other samples showing the same directional trend; however, the effect in the 3D faces disappeared when controlling for BMI. In the other samples, controlling for BMI did not affect the results, although BMI itself was significantly (positively) associated with fWHR in each sample tested.

We assessed three other previously reported sexually dimorphic face measures: lower face/face height, cheekbone prominence and face width/lower face height. These measures yielded reliable sex differences in the direction expected from prior research (Penton-Voak et al., 2001; Pound et al. 2009), for each of our four samples. The correlations between fWHR and these three metrics were not straightforward. Face width/lower face height was positively associated with fWHR in all samples in contrast to the negative association expected if fWHR relates to facial masculinity. Furthermore, while lower face/face height was positively (as expected) associated in the African sample the association was negative in Caucasian samples 1 and 3. Finally, cheekbone prominence was negatively associated with fWHR (as predicted) in only one of our samples (Caucasian 3D), with no association in the other samples. Hence facial width-to-height ratio is not consistently associated with other measures of morphological masculinity in facial structure.

The size and homogeneity of the four assessed samples in the current study may, at least in part, explain why results presented here differ from some earlier work. Previous studies reporting sexual dimorphism of fWHR (Carré & McCormick, 2008; Weston et al.,

2007) were conducted in relatively small samples vulnerable to influences from sampling bias and sample specific results. Several factors could cause spurious sex differences in facial measures, including BMI and ethnicity. BMI is positively associated with fWHR (Coetzee et al., 2010) and an unequal distribution of BMI between sexes may potentially cause apparent sex differences in this measure. Ethnic effects for fWHR may also exist in line with work demonstrating differences in facial bone structures between ethnic groups (Enlow, 1982). Accordingly, mixed ethnicity samples (as with Carré & McCormick, 2008) could also affect results.

The present results give rise to the question why fWHR apparently associates with a range of sexually dimorphic behaviours (e.g. aggression and dominance in men: Carré & McCormick, 2008; Stirrat & Perrett, 2010) yet itself is not sexually dimorphic. One possible answer comes from research into facial soft tissue distribution. This work highlights that women, even when controlling for BMI, have greater facial adiposity, especially around the cheeks, than men (Enlow, 1982). This difference in facial adiposity may potentially conceal a sex difference in bone structure: men may have higher bizygomatic width than women, but this difference may not be apparent in 2D or 3D face measures because sex differences in facial adiposity obscure or reverse differences in fWHR when measured from the skin surface. As such, facial metrics measured on the surface may reflect the underlying bone structure more accurately in males than females due to men's lower facial adiposity. This, then, might explain why fWHR is related to behavioural traits in men (e.g. Carré & McCormick, 2008; Haselhuhn & Wong, 2012; Lewis et al., 2012 / chapter 2; Carré et al., 2009; Stirrat & Perrett, 2010; Stirrat & Perrett, 2012) but apparently not in women (Haselhuhn & Wong, 2012). It should be noted, however, that recent work by Stirrat, Stulp and Pollet (2012), assessing fWHR directly from skulls, also found no mean sex difference in a large sample ($n = 862$) suggesting alternative explanations may be required.

In summary, the present study strongly suggests that there are no sex differences between males and females in fWHR as measured on the surface of the face in either Caucasian or African populations. We did, however, successfully replicate previous work reporting sexual dimorphism in several other facial structures. These findings have implications for claims about sexual selection and behaviours believed to be associated with factors underlying facial structures and in particular the facial width-to-height ratio.

Chapter 4. Telling facial metrics: Facial width is associated with testosterone levels in men

This chapter is largely based on work that has been submitted to a peer-reviewed journal:

Lefevre, C. E., Lewis, G. J., Perrett, D.I. & Penke, L. (2013). Telling facial metrics: facial width-to-height ratio is associated with testosterone levels in men. *Evolution and Human Behavior.*

Abstract

High facial width-to-height ratio (fWHR) has been associated with a cluster of behavioural traits in men, including aggression and status-striving. This association between face structure and behaviour may be caused by testosterone. Here we investigate the relationship of both baseline and reactive testosterone levels to fWHR. In addition, we assess the link between testosterone and three well-characterised sexually dimorphic facial metrics. Testosterone was measured in one sample of males ($n = 185$) before and after a speed-dating event. An additional sample provided only baseline testosterone measures ($n = 92$). fWHR was positively associated with testosterone reactions to potential mate exposure and marginally associated with baseline testosterone in Sample 1. We found a positive association with baseline testosterone and fWHR in Sample 2. In addition, face-width-to-lower-height ratio was positively associated with testosterone in both samples, suggesting that, in particular, facial width (scaled by two measures of facial height) is associated with testosterone. Importantly, our results also indicate that there is no association between adult testosterone levels and the sexual dimorphism of face shape. Thus, while our findings question the status of sexual dimorphism as a proxy measure of testosterone, they do indicate that testosterone is linked to fWHR and might underlie the relationship between fWHR and behaviour.

4.1 Introduction

As described in previous chapters, the facial width-to-height ratio (fWHR; see Figure 6) has been identified as a facial metric with links to a range of behavioural traits in men. fWHR has been shown to predict aggression (Carré & McCormick, 2008; but see Deaner et al., 2012; Özener, 2012), deception (Haselhuhn & Wong, 2012), and untrustworthiness (Stirrat & Perrett, 2010), but also more positive behaviours such as achievement striving (Lewis et al., 2012/chapter 2) and self-sacrifice towards the in-group (Stirrat & Perrett, 2012). Moreover, several studies have demonstrated that individuals are able to discern other individuals' tendency to aggression (Carré et al., 2009) and trustworthiness (Stirrat & Perrett, 2010) from fWHR. While this research indicates that the face, and in particular fWHR, acts as a cue to behaviour, it is currently unclear what constitutes the physiological mechanisms underlying this anatomy–behaviour association. Here, in two samples, we examine whether levels of baseline and reactive testosterone are associated with fWHR. We also investigate the association of testosterone with three well-characterised sexually dimorphic facial metrics; namely, 1) lower-face to whole-face-height, 2) cheekbone prominence, and 3) face-width to lower-face-height (see Figure 6 and chapter 3; Penton-Voak et al., 2001), alongside a global morphometric measure of facial masculinity (Pound et al., 2009).

4.1.1 Face Structure and Testosterone Levels

Recent work reported sexual dimorphism in fWHR, with males showing higher fWHR than females (Carré & McCormick, 2008; Weston et al., 2007). While this claim of sexual dimorphism in fWHR has since been challenged (Lefevre et al., 2012 / chapter 3; Özener, 2012; Stirratt et al., 2012), several of the behaviours linked to fWHR (e.g. aggression, dominance) are also known to be sexually dimorphic. For example, males show

consistently higher levels of direct physical aggression than females (Archer, 2006). Testosterone levels, which themselves show large sex differences (e.g. Mazur et al., 1997), have been proposed as a common underlying factor linking fWHR to behaviour (e.g. Carré & McCormick, 2008).

Consistent with the suggestion that testosterone mediates the association between fWHR and behaviour, a number of behavioural characteristics similar to those associated with fWHR have been linked both to direct and indirect measures of testosterone. For example, basal circulating testosterone levels are associated with levels of dominance in men (e.g. Josephs et al., 2003; Mazur & Booth, 1998). Additionally, second-to-forth digit ratio (2D:4D) – a putative proxy measure of in-utero testosterone exposure (Manning et al., 1998, 2000; Williams et al., 2003) – has been linked both to levels of self-reported (Bailey & Hurd, 2005) and lab-induced aggression (Millet & Dewitte, 2007).

Work seeking to associate testosterone with facial shape has also provided some support for a potential link with fWHR. In an early study, Verdonck et al. (1999) observed that testosterone administration enhanced craniofacial growth in delayed puberty male adolescents. In particular, these authors report enhanced growth of upper and total face height, and the mandible (jawbone) and ramus (upper part of the jawbone) length. However, these results should be treated with some caution as the sample size was small ($N=7$) and the boys assessed were all showing delayed puberty, making their development likely not fully comparable to healthy controls.

In addition, several studies have linked testosterone levels to perceived facial masculinity in men. Roney and colleagues (2006) report a moderate correlation ($r = .34$) between ratings of masculinity in natural, unmodified faces and baseline testosterone levels. Similarly, using a forced-choice paradigm, Penton-Voak and Chen (2004) report a weak, but

significant, association between testosterone levels and masculine appearance. In pairs of either natural or composite faces the face higher in testosterone was chosen as more masculine 53% and 57% of the time respectively. The authors argue that only men with very high or very low levels of testosterone may be visually distinguishable in terms of their masculinity.

However, other studies find no links between testosterone and masculinity. A study using almost identical methods to Roney et al. (2006), but with a much larger set of men, found no association between perceived facial masculinity and testosterone levels (Peters et al., 2008). Similarly, Neave et al. (2003) reported links of perceived facial masculinity with second-to-forth digit ratio (2D:4D), but not with measured baseline testosterone levels; and Ferdenzi et al. (2011) found no association between perceived facial masculinity and 2D:4D ratio.

Fink et al. (2005) incorporated a formal measure of global facial shape, calculating the difference between the average face-shape of men with high and low 2D:4D ratio. This study found that men with a low digit ratio (associated with higher prenatal testosterone) exhibited a wider jaw and zygomatic arch (i.e. face width) as compared to those with a higher digit ratio. However, direct reports of an association between circulating testosterone levels and facial metrics are (to our knowledge) limited to a single study (Pound et al., 2009). In this study, the authors computed a global facial masculinity index using five empirically derived, sexually dimorphic facial metrics (see Penton-Voak et al., 2001), and measured both baseline and reactive levels of testosterone. Reactive testosterone measures were taken after participants won in a manipulated competitive betting task, a scenario previously shown to significantly elevate testosterone levels (e.g. Archer, 2006). While failing to replicate associations between testosterone measures and perceived facial masculinity, Pound et al. (2009) observed that reactive, but not baseline, testosterone was positively associated with a

global facial masculinity measure. It is noteworthy that the association between baseline testosterone and facial masculinity also showed a positive trend towards statistical significance in this study, suggesting that the relationship between face shape and baseline testosterone might not be completely absent, but instead may reflect a weaker link than the association with reactive testosterone.

The above findings reported by Pound et al. (2009) are in line with the “challenge hypothesis” (Archer, 2006; Wingfield et al., 1990), which states that testosterone rises in challenging situations within the mating context, serving as a sexually selected physiological mechanism that calibrates the optimal effort put into intra-sexual competition. Moreover, only the increase in testosterone, rather than baseline testosterone per se, is suggested to associate with aggression and other status-related traits. Accordingly, reactive testosterone may serve as a better predictor of behaviour as compared to baseline levels of testosterone.

4.1.2 The current study

Determining whether an association exists between facial structure and testosterone is important in order to advance understanding of the underlying basis for links between behaviour and facial characteristics. Particularly, associations between testosterone and fWHR should be examined in light of recent work indicating that fWHR is not sexually dimorphic (Lefevre et al., 2012 / chapter 3; Özener, 2012; Stirrat et al., 2012). Moreover, in line with the challenge hypothesis and the work described above, facial metrics associated with aggression and status (e.g. fWHR) may be more closely linked to testosterone reactivity in response to competitive mating opportunities compared to baseline testosterone measures (Ronay & Von Hippel, 2010; Roney et al., 2003; Roney et al., 2007). Accordingly, here we sought to establish whether fWHR, alongside three sexually dimorphic facial metrics

(Lefevre et al., 2012 / chapter 3; Penton-Voak et al., 2001) and a global measure of facial masculinity (Pound et al., 2009), predict baseline testosterone (samples 1 and 2) and testosterone reactivity in response to competitive exposure to potential mates in a speed-dating context in (sample 1).

4.2 Method

4.2.1 Participants

Sample 1: Facial metrics and testosterone measures from 188 Caucasian men (mean age = 33.6 years, SD = 7.5, range: 20 to 54 years) who participated in the Berlin Speed Dating Study (Asendorpf et al., 2011) were analysed. All participants were singles drawn from the general population whose motivation to participate was the chance to find a real-life romantic or sexual partner.

Sample 2: This sample consisted of 79 Caucasian male undergraduate students (mean age: 20.50 years, age range: 18-25 years).

4.2.2 Speed-dating procedure in Sample 1

Participants took part in one of 17 speed-dating events during which each man met between 8 and 14 women (Mean \pm SE = 11.4 ± 1.7) of an age similar to their own (within-session age range = ± 4.8 years) for 3 minutes each. The ‘dates’ took place in booths equipped with two opposing chairs, cameras, and microphones. Men and women were led to these booths independently to minimise prior contact between the sexes. Women stayed in their allocated booth, while men rotated until each woman had interacted with each man (for details see Asendorpf et al., 2011, and Back et al., 2011b). Body height (m) and weight (kg):

dressed, but without jackets or shoes) were measured directly before speed-dating began, from which the body mass index (BMI; kg/m²) was calculated.

4.2.3 Facial measures

Sample 1: Participants were recorded with a camcorder on a tripod while standing upright in front of a white background under standardised lighting in order to allow the extraction of various standardised facial photographs. The frame with the most frontal and neutral recording of each participant's face was converted into a picture. Prior to measurement, all pictures were horizontally aligned and scaled to the same inter-pupillary distance (using the Psychomorph software package; Tiddeman et al., 2001; <http://users.aber.ac.uk/bpt/jpsychomorph>). fWHR was measured by calculating the bizygomatic width (maximum horizontal distance from the left facial boundary to the right facial boundary) to upper-face height (vertical distance from the mid-point of the upper-lip to the highest point of the eyelids) ratio from pictures (see Figure 6a, and Stirrat & Perrett, 2010). We also calculated facial metrics as described by Penton-Voak et al. (2001; see Figure 6b); namely, (i) lower-face/whole-face-height (vertical distance from mean eye height to gnathion/vertical distance from trichion to gnathion), (ii) cheekbone prominence (bizygomatic width/horizontal distance between left and right gonion approximation), and (iii) face-width/lower-face-height (bizygomatic width/vertical distance from mean eye height to gnathion). Intercorrelations between facial metrics are reported in Table 4.

Table 4: Intercorrelations of facial metrics in Sample 1 (above diagonal) and 2 (below diagonal).

	fWHR	Ch. P.	fW/IFH	IFH/wFH	GM
fWHR	/	-.06	.76**	-.16*	-.32**
Cheekbone prominence (ChP)	-.04	/	.10	-.03	-.52**
Face-width/lower-face-height (fW/IFH)	.65**	.18	/	-.24**	-.61**
Lower-face/whole-face-height (IFH/wFH)	-.14	-.07	-.43**	/	.45**
Global masculinity (GM)	-.25*	-.45**	-.57**	.60**	/

† p ≤ .10; * p < .05; ** p < .01. fWHR = facial width-to-height ratio, T = testosterone.

Additionally a global facial masculinity index, as previously calculated by Pound et al. (2009), was computed following their exact methodology: Five facial metrics were measured (see Figure 6), z-transformed and aligned such that a positive value referred to a more masculine score. These measures were then summed.

Sample 2: Photographs were taken under standardised lighting conditions during one of the testing sessions. Photographs in this study were taken specifically for morphometric analyses and were thus highly controlled for posture, expression and camera angle. All face metrics, as well as the global facial masculinity, were computed as described for sample 1.

4.2.4 Testosterone measures

Sample 1: Saliva samples were collected both directly (within 5 minutes) before and after the speed-dating. The speed-dating events lasted approximately 2 hours. The samples

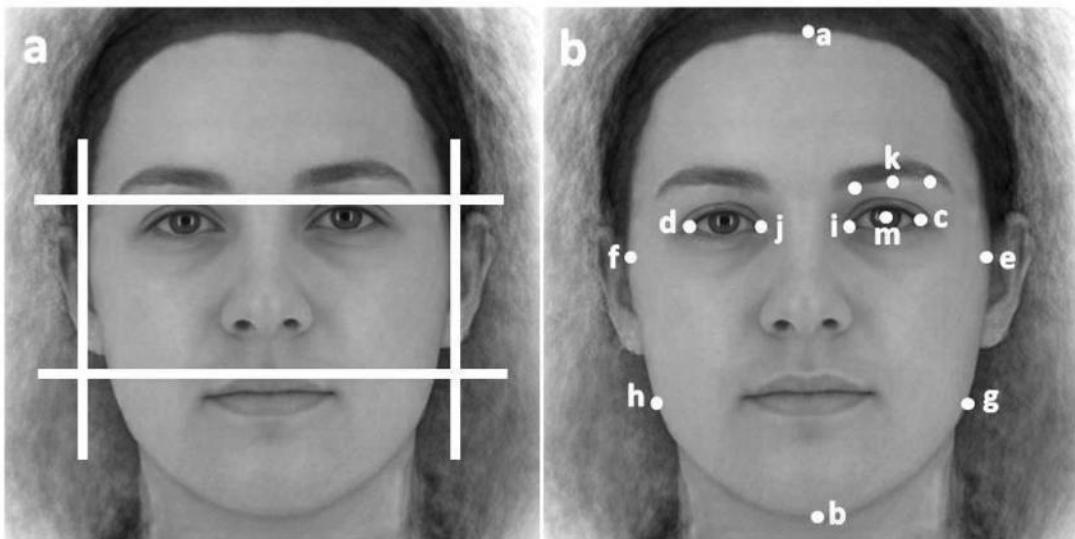


Figure 6: Examples of measures and measuring points used for morphometric calculations. Note: Panel (a) Measure of fWHR: horizontal lines represent the distance between the upper lip and highest point of the eyelids (upper face height), vertical lines represent the maximum distance between the left and right facial boundary (bzygomatic width). fWHR was calculated as width divided by height; Panel (b) Morphometric calculations: (i) Lower-face/whole-face-height: c-b/a-b, (ii) cheekbone prominence: e-f/g-h, and (iii) face-width/lower-face-height: e-f/c-b. Additional measures used to calculate the masculinity index: (i) eyewidth: c-d/i-j and (ii) mean eyebrow height: mean k-m/a-b.

were taken by a male research assistant in a waiting room with all male participants of the event present. Male and female participants had been guided to entrances on different sides of a large university building and to separate waiting rooms, so there had been no interaction between sexes at time of the baseline saliva collection. Samples were collected by passive drool using a Salicap tube (www.ibl-international.com) and a straw. In order to control for potential diurnal effects samples were always collected between 3:30 pm and 4:30 pm (baseline) and 5 pm and 7 pm (post-exposure). All samples were visually inspected for blood contamination at time of collection; contaminated samples were excluded from further analysis. To avoid food contamination, participants were asked not to eat and to only drink water during the event.

Immediately following the end of the speed-dating event, specimens were frozen and stored at -20°C until analysis was performed by the Biopsychological Lab of the Technical

University Dresden using IBL luminescence immunoassays (sensitivity 5 pg/ml). After defrosting samples were centrifuged for 10 min and 50 μ l of samples were introduced into the respective wells of a microtiter plate. Next 50 μ l of enzyme conjugate followed by 50 μ l of testosterone antiserum were added to each well. Plates were then incubated for 4 h at room temperature. After discarding incubation solution and washing plates four times using 250 μ l of diluted wash buffer, 50 μ l Chemiluminescence Reagent AP was added to each well. After 10mins relative luminescence units were measured using a luminometer. Inter- and intra-assay variability was below 12%. For each participant, testosterone levels were analysed in duplicates.

Sample 2: During two testing session salivary testosterone was assessed. As in Sample 1, all samples were visually inspected for discolouration indicating blood contamination. Discoloured samples were excluded from analysis. Testosterone levels were calculated as the average of these two samples (for full details see Moore et al., 2011a,b) yielding high reliability for baseline measures.

4.2.5 Individual Differences measures used in Sample 1

In order to test for possible moderation of testosterone-fWHR relationships comparable to ‘winning’ in Pound et al. (2009), three potential moderators were assessed: 1) Self-perceived competitiveness of the speed-dating event was assessed immediately after the event by aggregating two items: “I saw the conversations as competitions to win the women’s favour” and “I have experienced the other men as competitors”, both on 5-point Likert scales from “strongly disagree” to “strongly agree”. The two items were substantially correlated ($r = .43$, $p < .001$); 2) Self-perceived mating success during the speed dating, measured as number of times each man predicted that he was chosen by a woman directly after each

speed-date (perceived mating success). We used predicted female choice instead of actual female choices because the two variables were not correlated ($r = .12$, $p = .12$; see Back et al., 2011a for details) and thus only perceived mating success should be expected to have an effect on testosterone levels; 3) Average flirting behaviour of all female dating partners a man encountered, which was reliably rated for every 30 second interval of the 3-minute speed-dates from video recordings showing the woman only by two independent raters and then aggregated to a single flirting score per interaction and averaged across all female dates (see Back et al., 2011b for details). The average overall-flirting rating for all women each man encountered can be interpreted as a measure of exposure to female courtship behaviour.

4.3 Results

4.3.1 Sample 1

4.3.1.1 *Facial metrics and testosterone*

Testosterone levels more than three standard deviations from the mean were removed prior to analyses, since outliers of such magnitude are likely caused by imperfect testosterone sampling (e.g. contamination). This reduced the dataset by 3, and 4 participants for baseline and post-exposure testosterone levels, respectively. Furthermore, all testosterone variables were positively skewed and were therefore transformed to normal distribution using square-root transforms³. Untransformed means for baseline and post-exposure testosterone were 88.9 (SD=44.3) and 88.6 (SD = 45.2) pg/ml, respectively.

³ Results including outliers showed significant links between facial metrics and post-exposure testosterone (post T); however, when including outliers associations between fWHR and baseline testosterone with age and BMI as covariates showed non-significant results, albeit in the same direction as reported in the text ($rs .11 - .12$, $ps .11 - .14$).

Consistent with previous work (e.g. Harman et al., 2001), age was negatively associated with baseline ($r = -.31$, $p < .001$) and post-exposure ($r = -.25$, $p < .001$) testosterone levels. Thus, all associations between testosterone and facial measures were age-controlled. Baseline- and post-exposure testosterone levels were significantly correlated ($r = .57$, $p < .001$). Associations between facial metrics and baseline testosterone are displayed in Table 5. fWHR was associated with testosterone as predicted. Results for lower-face/whole-face-height and face-width/lower-face-height were unexpected because they suggest that more female-typical scores on these metrics were associated with greater testosterone levels.

Although there were no mean differences between baseline- and post-exposure testosterone ($t_{182} = 0.55$, $p = .59$, $d = 0.08$), we further assessed whether facial structure was

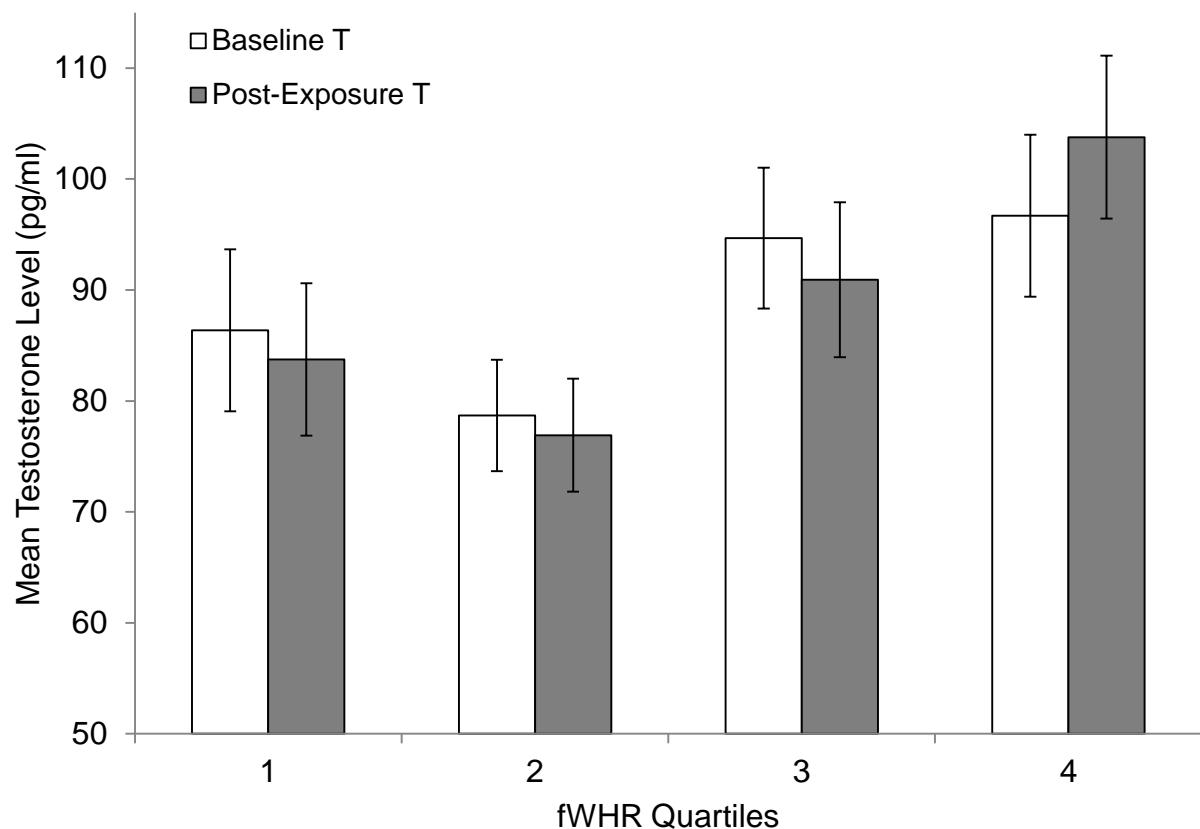


Figure 7: Mean baseline and post-exposure testosterone levels across fWHR quartiles (1 = lowest quartile, 4 = highest quartile).

linked to testosterone change during the speed-dating event. To this end, we examined whether post-exposure testosterone correlated with the assessed facial metrics, controlling for baseline testosterone levels using partial correlations. There was a positive association of testosterone change with fWHR and face-width/lower-face-height as well as a negative association with lower-face/whole-face-height (see Table 5). As an additional illustration, Figure 7 details mean baseline and post-exposure testosterone across quartiles for fWHR. Only men with high fWHR show an overall tendency to increase in testosterone during the speed-dating event, although this group difference was non-significant ($p = .66$).

Because BMI has been shown to associate both with face metrics (Coetzee et al., 2010; Lefevre et al., 2012 / chapter 3) and testosterone levels (Osuna et al., 2006), we next examined whether testosterone showed independent effects on facial structure controlling for BMI (in addition to age and baseline testosterone). Links between post-exposure testosterone and both fWHR and lower-face/whole-face-height were robust to this additional control (see Table 5). Facial appearance associated with high and low levels of testosterone, respectively, is shown in Figure 8. As an illustration we created composite faces of 20 individuals with high and low testosterone levels in each sample. In order to visualise shape associations with testosterone over and above those associated with BMI, the two groups of individuals included in the composite faces were matched for average BMI. These images indicate, in line with results, that high testosterone is associated with wider and shorter faces.

We next assessed possible moderation of the relationship between reactive testosterone and fWHR by self-reported competitiveness, self-perceived success (the expected number of follow-up dates) during the speed dating, as well as average rated flirting behaviour of all female dates men encountered. Regression models with post-exposure testosterone as the dependent variable and fWHR, baseline testosterone, one of the

moderators, and the moderator*fWHR interaction as predictors were run. None of these moderations showed a significant effect (all $p > .28$).

Table 5: Partial correlations between both baseline testosterone (Pre-T) and post-exposure testosterone (Post-T) with facial structure and rated masculinity controlling 1) only age and 2) both age and BMI. Partial correlations between post-exposure testosterone and facial structure controlling for 1) pre-exposure testosterone and 2) pre-exposure testosterone, age, and BMI in Sample 1.

	pre-T (c. Age) df = 178	pre-T (c. Age, BMI) df = 177	post-T (c. Age) df = 178	post-T (c. Age, BMI) df = 177	post-T (c. pre-T & age) df = 177	post-T (c. Pre-T, age, BMI) df = 176
fWHR	.13†	.11	.21**	.19*	.18*	.16*
Cheekbone prominence	.08	.12	.01	.05	-.10	-.03
Face-width/lower- face-height	.14†	.12	.19*	.17*	.18*	.13†
Lower-face/whole- face-height	-.04	.04	-.14†	-.14†	-.21**	-.20**
Global masculinity	-.02	-.03	-.11	-.12†	-.12	-.13†

† $p \leq .10$; * $p < .05$; ** $p < .01$. fWHR = facial width-to-height ratio, T = testosterone, c. = control variables.

4.3.1.2 Global facial masculinity and testosterone

There was no association between the global facial masculinity index and either baseline ($r = .02$, $p = .77$) or post-exposure testosterone ($r = -.08$, $p = .26$). Furthermore, there was no significant association between global facial masculinity and testosterone change ($r = -.11$, $p = .13$), or testosterone change controlling age and BMI ($r = -.13$, $p = .08$). Additionally, global facial masculinity showed a negative association with age ($r = -.15$, $p = .04$).

Finally, associations between global facial masculinity and facial metrics were assessed: there was a negative correlation with fWHR ($r = -.32$, $p < .001$), face-width/lower-face-height ($r = -.61$, $p < .001$) and cheekbone prominence ($r = -.52$, $p < .001$) and positive correlation with lower-face/whole-face-height ($r = .45$, $p < .001$). Apart from fWHR these metrics form part of the basis for the masculinity index, thus there is an intrinsic interdependence between these metrics and the index.

4.3.2 Sample 2

Two fWHR data points more than two standard deviations from the mean were removed, leaving 90 cases. All other facial measures were normally distributed with no outliers. There was no association of testosterone with either age ($r = -.06$, $p = .60$) or BMI ($r = -.05$, $p = .63$). However, since BMI was highly correlated with fWHR ($r = .31$, $p = .005$) and cheekbone prominence ($r = -.26$, $p = .02$), BMI was controlled in subsequent analyses.

Partial correlations revealed positive associations between testosterone and fWHR ($r = .26$, $p = .03$), as well as face-width/lower-face-height ($r = .28$, $p = .02$). In addition, cheekbone prominence was (marginally) negatively correlated with testosterone ($r = -.21$, $p = .07$). There was no association with lower-face/whole-face-height ($r = -.08$, $p = .59$). Finally, there was again no association between testosterone and global facial masculinity ($r = .08$, $p = .49$).



Figure 8: High and low testosterone averages of each sample. Averages of the twenty men with lowest (left) and highest (right) testosterone levels in Sample 1 (top) and Sample 2 (bottom).

4.4 Discussion

Evidence from two samples supports a link between circulating testosterone levels and behaviourally-relevant facial structures in adult men; namely, facial width. Of particular interest, facial width-to-height ratio (fWHR) showed positive marginal associations with

baseline testosterone in sample 1 and positive significant associations baseline testosterone in sample 2. Moreover, in sample 1 fWHR was positively associated with testosterone reactivity following exposure to potential mates. These latter findings are consistent with predictions arising from the “challenge hypothesis” (Archer, 2006; Wingfield et al., 1990).

Additionally, our results showed a positive association of reactive (Sample1) and baseline (Sample 1 and 2) testosterone with face-width/lower-face-height, and a negative association of reactive testosterone with lower-face/whole-face-height (Sample 1). These results run contrary to previous assumptions in the literature: More “feminine” scores on these two facial measures were associated with *higher* (rather than lower) levels of testosterone. These results indicate that faces of men with high testosterone levels were relatively shorter and wider than faces of men with lower levels of testosterone. While a limited number of studies have previously associated testosterone with facial elongation (Verdonck et al., 1999) and both measured and perceived masculinity (Penton-Voak & Chen, 2004; Pound et al., 2009), other studies have failed to do so (e.g. Neave et al., 2003). As noted above, we confirmed this association for face-width/lower-face-height across both samples suggesting this finding is robust.

It should be borne in mind that while we found associations between testosterone and face-width/lower-face-height as well as lower-face/whole-face-height (albeit in the “feminine” direction); globally measured facial masculinity was not associated with testosterone in either of our samples. This discrepancy might, in part, be explained by the difference in context between Pound et al.’s (2009) study and the current study. While in Pound’s study men’s testosterone rose in response to winning in an experimental competitive betting task, the best indicators of competition (self-reported perceived competitiveness of the event after the speed dating) or ‘winning’ (self-perceived mating success and video-rated exposure to female flirting during the speed dating) available to us in this natural speed

dating design did not predict testosterone reactivity or moderate the association between fWHR and testosterone reactivity. These findings are somewhat surprising in light of the challenge hypothesis, but might partly be due to an insufficiently strong operationalization of ‘challenge’ and ‘winning’. However, very strong effects of ‘challenge’ and ‘winning’ should probably have shown up. Therefore it is more plausible that testosterone levels changed here directly in response to meeting potential mates (Ronay & van Hippel, 2010; Roney et al., 2003, 2007). However, even if being able to discriminate ‘winners’ and ‘losers’ better might have yielded stronger associations with post-exposure testosterone than those reported here, it is unlikely that these responses would have changed in direction. Taken together, these results suggest that rather than facial sexual dimorphism (i.e. masculinity or femininity) showing links to testosterone, instead only more specific facial metrics are associated with testosterone.

The finding that fWHR, which itself does not appear to be sexually dimorphic (Lefevre et al., 2012 / chapter 3; Özener, 2012), is linked to testosterone, is somewhat counterintuitive and thus merits discussion. Moreover, the observation that face-width/lower-face-height is associated with testosterone in the more “feminine” direction also requires further consideration. There are a number of possible explanations for these results. Firstly, while recent findings show no sex difference in fWHR (Lefevre et al., 2012 / chapter 3; Özener, 2012), there are known sex differences in facial adiposity: women have larger fat deposits than men, particularly around the cheek-area, even when controlling for BMI (Enlow, 1982). As such, sexual dimorphism in facial bone structure may be “masked” (e.g. fWHR), or even reversed (e.g. face-width/lower-face-height), by this additional facial adiposity in women. However, this explanation does not account for the lack of sexual dimorphism found in fWHR as measured on skulls that was recently reported by Stirrat et al.

(2012). Further work, then, establishing the status concerning the sexual dimorphism of these facial metrics, particularly from skull measures, will be valuable.

An alternative, and perhaps more compelling, explanation stems from possible sex differences in the underlying mechanisms influencing facial bone growth. While there is some direct evidence for testosterone affecting facial bone growth in men (Verdonck et al., 1999), other research has highlighted the importance of oestrogen and growth hormone on bone growth in both sexes (Juul, 2001; Ohlsson et al., 1998). Importantly, women, compared to men, have higher average levels of both oestrogen and growth hormone (e.g. Mazur et al., 1997; Frantz et al., 1965), indicating a stronger influence of these hormones on bone growth in females. In short, because women have more subcutaneous facial fat and higher levels of oestrogen and growth hormone, facial morphology in men and women likely reflects different growth and endocrine mechanisms and is thus not easily comparable.

Furthermore, considering men typically exhibit around five times higher baseline testosterone concentrations compared to women (Mazur et al., 1997), identical effects of testosterone on bone growth in both sexes would likely yield far more striking structural differences between men and women than those that are observed. Following this, differences in testosterone may be directly related to facial bone size (and particularly facial width) within men, while distinct factors may influence these facial metrics in women; that is, factors underlying inter-sex differences in facial metrics may not reflect intra-sex differences. In turn, labelling the poles of facial metrics measured *within-sex* on the basis of *between-sex* differences (i.e. “more masculine” vs. “more feminine”) may be erroneous. This interpretation may account for why more “feminine” face-width/lower-face-height scores associate with higher testosterone: Simply put, influences underpinning intra-sex differences may not be isomorphic with the influences driving inter-sex differences.

As suggested above, differential effects of testosterone on bone growth may be unique to men. Individual differences in facial physiognomy linked to testosterone within males may then reflect variance in total testosterone exposure during (pubertal) development. In line with this argument, our results indicate stronger links between facial structure and reactive testosterone compared to baseline testosterone measures. That is, if facial bone structure is affected by testosterone levels during puberty (see also Verdonck, 1999) it is possible that total tissue exposure to the hormone is more closely aligned with appearance outcomes than baseline measures (see Pound et al., 2009 for a similar argument). There is convincing literature indicating a rise in testosterone levels following perceived success in a competitive situation ('winning'; e.g. Booth et al., 1989; Mazur et al., 1997) and in exposure to potential mates (Ronay & van Hippel, 2010; Roney et al., 2003, 2007). Two consequences follow: firstly, men who exhibit a stronger hormonal reaction to positive outcomes of competitive or mating situations will be exposed to more testosterone compared to those men who have a lesser reaction. Secondly, irrespective of individual differences in hormone reactivity, those men that experience winning more competitive situations will have higher total exposure.

Finally, fWHR may pose a better proxy measure of testosterone levels compared to other facial metrics or assessments derived from sexual dimorphism: fWHR has been repeatedly associated with dominant behaviours in males and as such reflects individual differences in male behaviour. Measures that are based on sexual dimorphism, such as other measures assessed here and elsewhere, may not capture intra-male variation in testosterone, if indeed testosterone's influence on growth is male specific.

In summary, the current studies provide the first empirical evidence for an association between facial width and testosterone levels. Moreover, the results show that global facial masculinity does not associate with testosterone thus contradicting previous work. These findings provide support for testosterone's role as a physiological link between face structure

and behavioural traits that are linked to testosterone and further add to the understanding of mechanisms underlying facial cues to behaviour.

Chapter 5. Facial width-to-height ratio is linked to dominance and status in the primate face

This chapter is largely based on work that has been submitted to a peer-reviewed journal:

Lefevre, C. E., Wilson, V.A.D., Morton, F.B., Brosnan, S., Paukner, A. & Bates, T. C. (under review). Facial width-to-height ratio predicts dominance in capuchin monkeys.

Abstract

Visible signs of dominance can be advantageous in intra-sexual competition because they may obviate the need for physical fighting. Immediately and permanently visible cues should therefore be particularly useful since they can allow observers to make accurate and fast judgments about the rank and/or fighting abilities of others. In this context, facial width-to-height ratio (fWHR), a putatively sexually dimorphic metric, has been linked to dominant behaviour in humans. Here we assess whether fWHR is linked to dominance and status in capuchin monkeys (*Sapajus apella*) as well as whether it is sexually dimorphic. Results indicate a robust positive association of fWHR and continuously assessed dominance ('Assertiveness') as well as alpha-status in both males and females. Furthermore, fWHR showed significant sexual dimorphism, emerging during puberty. This is the first report of an association between face-shape and behaviour in non-human primates, and indicates that selection for facial width may be linked to intra-sex competition in both sexes.

5.1 Introduction

Visible signs of dominance can be advantageous in intra-sexual competition by obviating the need for physical fighting (e.g. Sell et al., 2009). For instance, species differences in canine size are associated with the frequency and costs of contest competition (e.g. Plavcan et al., 1995). Additionally, physical size has been linked to social rank in various species, including, for instance, primates (e.g. Plavcan, 2012; Plavcan & vanSchaik, 1997), elephant seals (Michael et al., 1994), and even fish (e.g. *Centropyge bicolor*, Ang & Manica, 2010). However, several traits that are commonly associated with dominance are not always readily visible to observers. For example, in many species, canine size is only visible when the mouth is open. As such, immediately and permanently visible cues to dominance should be particularly useful because they can enable observers to make fast and accurate judgments about the rank and/or fighting ability of others. Indeed, such cues may be especially vital when encountering individuals for the first time.

Facial width-to-height ratio (fWHR) has been identified as one of several permanently visible traits associated with dominance in humans. For example, in human males, fWHR is associated with aggression (Carré & McCormick, 2008 but see Deaner et al., 2012; Özener, 2012), deception (Haselhuhn & Wong, 2012), achievement striving (Lewis et al., 2012 / chapter 2), and self-sacrifice for the in-group (Stirrat & Perrett, 2012). Importantly, several studies of humans have also shown that an individual's fWHR is linked to others' perception of their dominant behaviour (Carré et al., 2009; Stirrat & Perrett, 2010; Carré et al., 2010; Stirrat & Perrett, 2010). In humans, fWHR is independent of body size (Weston et al., 2007) as well as facial sexual dimorphism (e.g. Lefevre et al., 2012 / chapter 3; Özener, 2012), indicating that individual differences in fWHR are not simply a by-product of scaling. Thus, fWHR appears to signal dominance in humans, and may therefore play an important role in shaping decision-making during social interactions.

It is currently unclear, however, whether fWHR is linked to dominant behaviour in other animals. If fWHR is a cue to dominance, and is advantageous to the bearer (e.g. by obviating the need for unmatched fights), then this cue may also exist in other species with dominance hierarchies, particularly those species that are phylogenetically closely related to humans (i.e. other primates). By specifically examining the link between fWHR and dominance in nonhuman primates, a greater understanding of the biological and evolutionary bases of this relationship in humans may be achieved.

To this end, here we investigate the association between fWHR and dominant behaviour in a nonhuman primate, the brown capuchin monkey (*Sapajus apella*) hereafter referred to as *Sapajus* (see Alfaro et al., 2012 for recent taxonomy change). *Sapajus* have a relatively weak, linear dominance hierarchy and live in female-bonded groups (Izawa, 1980; Janson, 1985) that typically include multiple male members (Boinski, 1996) as well as one dominant alpha-male and alpha-female (Di Bitetti, 1997). In studies of humans, the absence of a significant sex difference in fWHR (Kramer et al., 2012; Lefevre et al., 2012 / chapter 3; Özener, 2012) and minimal dimorphism in canine size (Kapila et al., 2011) suggests that canine size – previously argued to account for lower fWHR dimorphism in species such as *Gorilla* (Weston et al., 2004) – cannot fully account for species differences in fWHR-dimorphism. In other words, fWHR is not an obligate substitute for canine dimorphism. Weston et al. (2004) show low sexual dimorphism for canine size but high dimorphism for fWHR in *Sapajus*. Thus, *Sapajus* is an ideal species to test predictions about the relationship between fWHR and dominance in the relative absence of interactions with canine size. In line with previous findings from human studies, we hypothesized that *Sapajus* fWHR would be significantly associated with individual differences in dominant behaviour in males, but not females (Hypothesis 1).

Research in humans has largely refuted the presence of sexual dimorphism in fWHR, suggesting a more intricate association between fWHR and dominance than previously assumed (e.g. Kramer et al., 2012; Lefevre et al., 2012 / chapter 3; Özener, 2012). In contrast, Weston et al. (2004) report that fWHR is a sexually dimorphic trait in some, but not all, primate species. For instance, across species (including *Sapajus*), an inverse association exists between levels of fWHR dimorphism and canine dimorphism such that dimorphism in fWHR emerges only when dimorphism for canine size is reduced (Weston et al., 2004). While Weston and colleagues argue that this association indicates a selection trade-off between intra-sexual competition (favouring canine size) and inter-sexual mate choice (favouring facial width), it may also indicate a trade-off between visible cues to dominance (fWHR) and weaponry (larger canines). In either case then, it is important to determine whether the visibility of fWHR is sexually dimorphic. Because Weston et al. (2004) used skulls to measure fWHR, here we attempt to replicate their findings for *Sapajus* fWHR by taking measurements directly from subjects' faces. In line with Weston et al.'s predictions, we hypothesized that fWHR is a sexually dimorphic trait in *Sapajus* (Hypothesis 2).

Finally, theory concerning dominance cues in humans suggests a link between dominant behaviour and testosterone (e.g. Mazur & Booth, 1998), which in turn has been associated with fWHR (chapter 4). In *Sapajus*, males reach sexual maturity at around six years of age, and like in humans, this developmental transition is associated with testosterone (Bercu et al., 1983; Rey et al., 1995). Thus, we hypothesized that sex differences in fWHR would exist among sexually mature subjects, but not sexually immature subjects (Hypothesis 3).

5.2 Method

5.2.1 Sample

The sample consisted of 64 individuals (29 female, mean age 12.9 ± 10.1 years; 35 male, mean age 9.1 ± 8.6 years) from three sites: The ‘Living Links to Human Evolution’ Research Centre (Macdonald & Whiten, 2011) of the University of St Andrews, in Edinburgh Zoo (6 female, mean age 8.2 ± 4.0 years; 10 male, mean age 11.4 ± 13.4 years), the Language Research Center, Georgia State University (13 female, mean age 15.3 ± 11.8 years; 9 male, mean age 10.9 ± 5.80 years), and the Laboratory of Comparative Ethology at the National Institutes of Health (10 female, mean age 12.8 ± 9.20 years; 16 male, mean age 6.6 ± 4.50 years). Following Izawa (1980), animals were categorised as either adult (age ≥ 6 ; N = 43) or juvenile (N = 21). Infants less than one year old were excluded. For a subset of individuals, body weight information was available (N = 46, 34 adult, data taken at US sites). Therefore, we tested for interactions between weight and fWHR among these individuals.

5.2.2 fWHR Measures

Measures were based on frontal facial photographs. Prior to measurement, photographs were aligned and scaled according to interpupillary distance. fWHR was then computed as the ratio of bizygomatic-width (maximum horizontal distance from the left to the right facial boundary) to upper face height (vertical distance from the mid-point of the upper lip to the highest point of the eyelids; see Figure 9) using Psychomorph (Tiddeman et al., 2001). Measurement reliability was good (ICC = .86) based on a subset of photographs (N = 18) measured twice. In addition, measures from several photographs per individual (mean = 4.69, SD = 2.44) were averaged in order to maximise the signal to noise ratio. All images were taken within 1 calendar year, thus controlling for longitudinal changes.

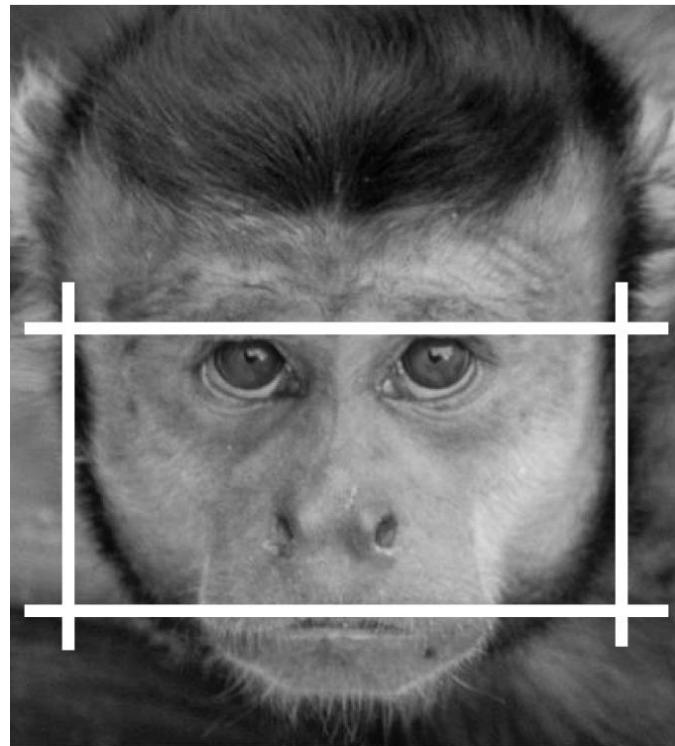


Figure 9: Illustration of the facial width-to-height ratio measure in the capuchin face: facial width (distance between vertical lines) divided by upper face height (distance between horizontal lines).

5.2.3 Dominance and alpha-status measures

5.2.3.1 *Alpha status*

Alpha-status was assessed by observation of behaviours including wariness of other group members, being sought out for mating, number of offspring, frequent grooming, and ability to take food from humans and other monkeys (see Fragaszy et al., 2004). In each subgroup, one male and one female were accorded alpha-status, yielding a total of 18 (7 female) alpha individuals. Animals were housed in a total of seven breeding groups, accounting for the seven female and seven of the male alpha individuals; the additional four male alpha individuals in our data set are comprised of one alpha male who died and has since been replaced by a new alpha individual and three males who are the dominant male in male-only living groups. There was complete inter-rater agreement for alpha-status assignment.

5.2.3.2 Individual Differences in Dominant Behaviour

Dominance was assessed using the Hominoid Personality Questionnaire (Weiss et al., 2009). Details of this analysis can be found in Morton et al. (in press). Briefly, 127 study subjects (64 of which were also used in the present study) were rated on 54 items by researchers and handlers familiar with the individuals being rated ($M = 3.24$ raters, $SD = 1.61$). Subjects were rated on each adjective, using a 7-point scale ranging from 1 (no expression) to 7 (high expression). Each item consisted of an adjective paired with 1-3 sentences defining it within the context of primate behaviour. For instance, *fearful* was defined as “Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away or other signs of anxiety or distress”. Reliability of ratings within and across raters was good ($ICC = .63$, $SD = 0.14$), therefore all raw ratings were entered into a Principle Components Analysis. Five components were identified from these ratings: Assertiveness, Openness, Neuroticism, Sociability, and Attentiveness. Individual t-scores were calculated for each monkey on each of the five personality dimensions, and these scores predicted relevant behaviour up to one year later (e.g. scores on Sociability positively correlated with time each monkey spent in close proximity to others; Morton et al., in press). Thus, ratings were considered to be valid measures of real-world behaviour among the study subjects.

Here we use individual scores on Assertiveness as a measure of dominant behaviour in our 64 subjects. The highest loadings for this dimension were bullying (.93), aggressive (.92), and dominant (.91) (Morton et al., in press). Assertiveness was positively correlated with behaviours typical of dominance in *Sapajus* (e.g. time spent grooming and aggressing others; Morton et al., in press; Fraga et al. 2004). Assertiveness was also positively associated with alpha-status, in both males ($t(33) = 6.69$, $p < .001$, 95% CI [1.04, 1.96]) and females ($t(25.6) = 5.35$, $p < .001$, 95% CI [0.90, 2.02]) indicating that this factor captured

behaviour relevant to the dominance hierarchy. There was no difference between sexes for Assertiveness scores ($t(41) = 1.03$, $p = .31$), suggesting similar levels of dominance in both sexes, and reflecting findings from studies of dominance in this species (i.e. adult males are no more/less dominant than adult females; Fraga et al., 2004).

5.3 Results

There were no significant differences between sites for either age ($F(2,61) = 1.4$, $p = .25$, $\eta_p^2 = .04$), sex ($F(2,61) = 1.27$, $p = .29$, $\eta_p^2 = .04$), fWHR ($F(2,61) = 0.28$, $p = .76$, $\eta_p^2 = .01$) or rated dominance ('Assertiveness'; $F(2,61) = 0.23$, $p = .79$, $\eta_p^2 = .01$). Data were therefore collapsed across sites.

We first tested the hypothesis that fWHR undergoes age-related changes focussed around puberty, using regression with fWHR as the dependent variable and age as independent predictor. Because we also hypothesised sexually dimorphism, sex and the interaction of sex \times age were included as covariates. Analysis revealed significant effects of sex ($\beta = .38$, $p < .05$) and sex \times age ($\beta = -.77$, $p < .001$) but not age ($\beta = .08$, $p = .47$) on fWHR (overall model: $F(3,60) = 8.18$, $p < .001$), suggesting both sex differences and different developmental trajectories of fWHR for males and females (Figure 10). To ensure that these effects were not driven by aging related changes or life-history differences among the oldest animals (as opposed to maturational changes during puberty), the analysis was replicated excluding 9 animals older than 20 years. Results showed independent effects of age ($\beta = .50$, $p < .001$) and sex \times age ($\beta = -.70$, $p < .01$) as well as a marginal effect of sex ($\beta = .46$, $p = .06$).

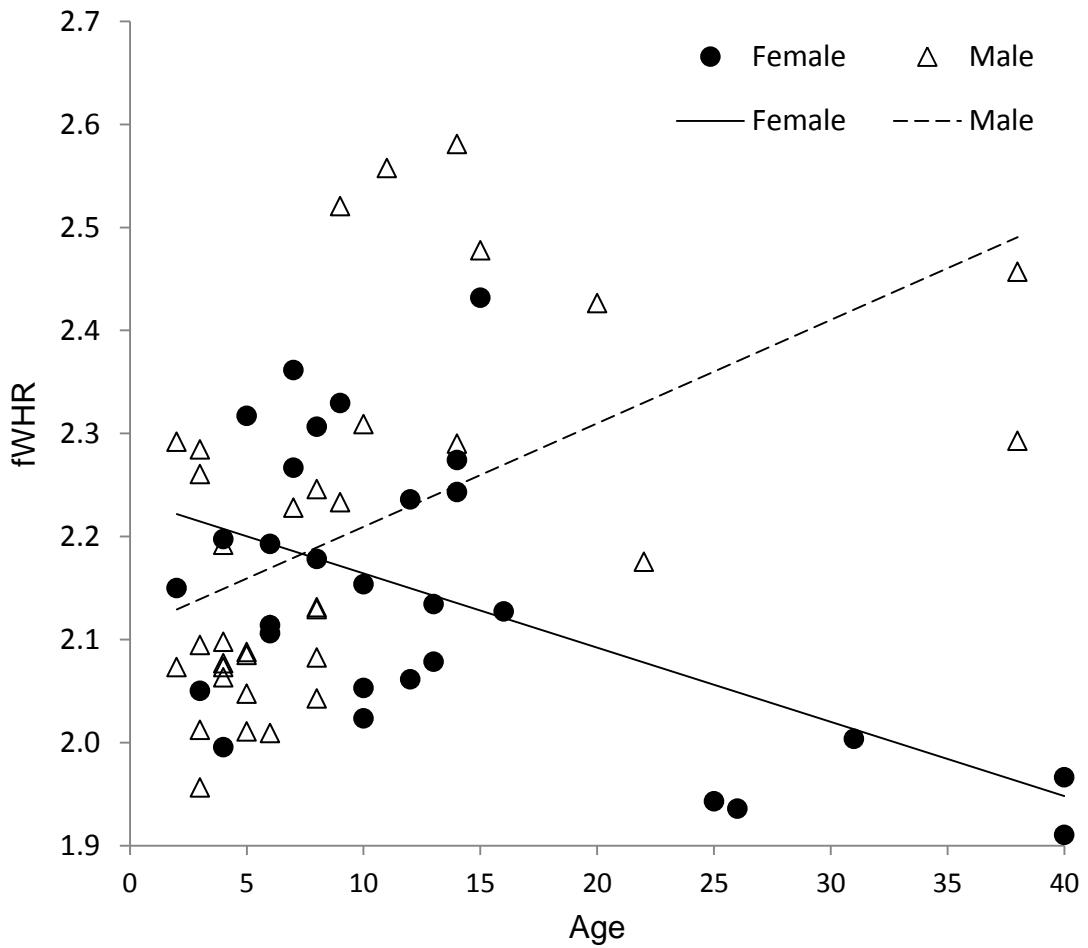


Figure 10: Linear effects of age and sex on fWHR.

As predicted, among adults, males showed higher fWHR than females ($t(41) = 2.78$, $p < .01$) but there was no significant sex differences among juveniles ($t(19) = 0.65$, $p = .52$).

We next assessed whether fWHR was predictive of alpha-status and rated Assertiveness in adults. In a logistic regression, fWHR ($\beta = 7.86$, $p < .01$) significantly predicted alpha-status (overall model: $X^2(3) = 15.89$, $p = .001$, $R^2 = .42$), controlling for sex ($\beta = 0.72$, $p = .37$, $SE = .81$) and age ($\beta = 0.09$, $p < .05$, $SE = .05$). In order to assess whether these differences could be accounted for by a response to gaining alpha-status, we further assessed whether rated Assertiveness among all adult animals was predicted by fWHR (Figure 11). There was no difference between sexes for Assertiveness scores ($t(41) = 1.03$, p

$= .31$). Rated Assertiveness (overall model: $F(3,42) = 5.49$, $p = .003$, $R^2 = .28$) was significantly predicted by fWHR ($\beta = .55$, $p = .001$) but not by either sex ($\beta = .07$, $p = .66$) or age ($\beta = -.07$, $p = .62$). This association was further robust, when assessing non-alpha animals only (fWHR: $\beta = .43$, $p = .050$).

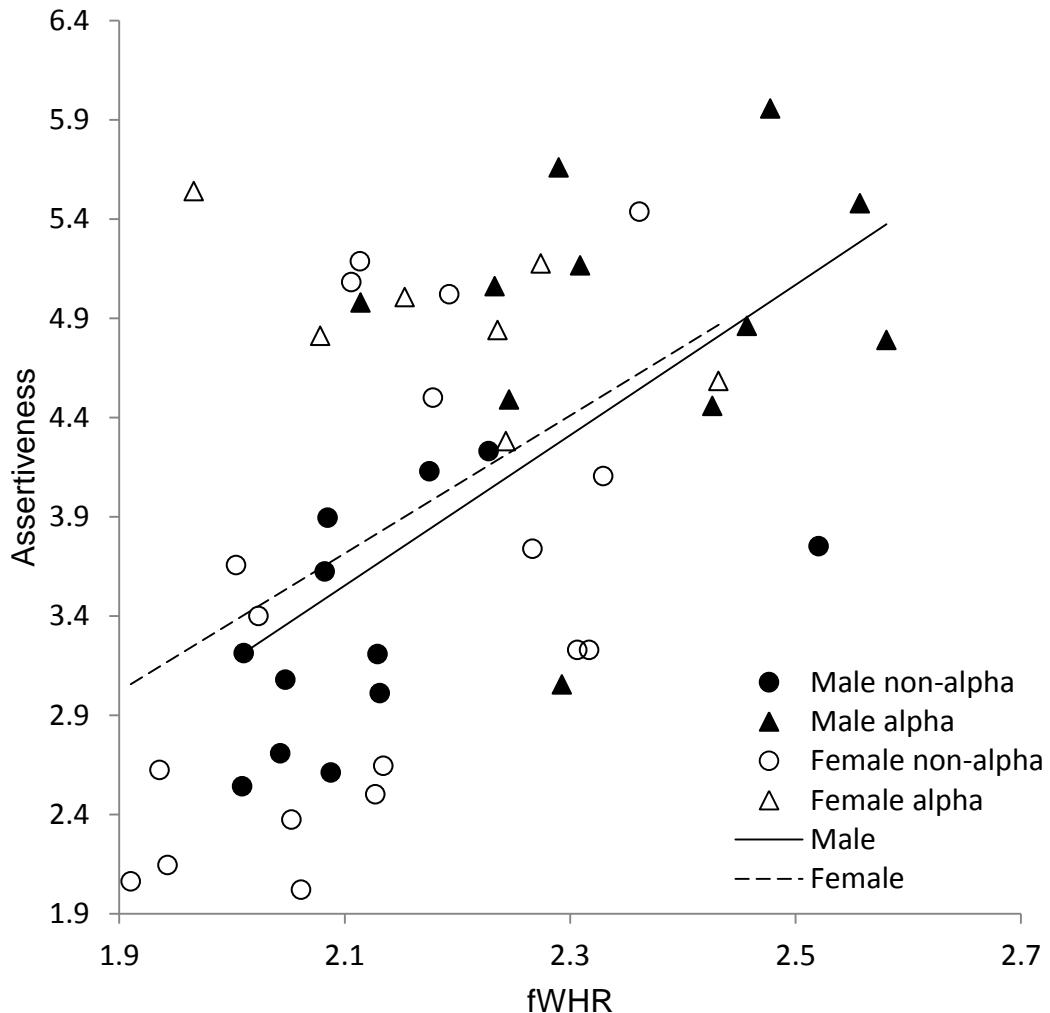


Figure 11: Association of Assertiveness and fWHR in adult males and females.

For a subset of individuals body weight information was available ($N = 46$, 34 adult, data taken at US sites). In line with findings in human fWHR (Lefevre et al., 2012 / chapter 3), weight and fWHR were correlated in all individuals ($r = .56$, $p < .001$), and adults only ($r = .64$, $p < .001$). In order to test whether weight mediated sex differences in adults, an

ANCOVA was conducted with weight ($F(1,30) = 9.70$, $p < .01$), sex ($F(1,30) = .42$, $p = .52$) and sex \times weight ($F(1,30) = .26$, $p = .61$) as predictors of fWHR. This analysis revealed that sex differences in fWHR were fully mediated by weight (full model: $F(3,30) = 7.08$, $p = .001$, $\eta_p^2 = .42$) in this subset.

We next tested whether weight affected the relationship between fWHR and rated Assertiveness in adult individuals. Weight correlated non-significantly with rated Assertiveness ($r = .28$, $p = .10$), but controlling for weight did not alter the relationship between Assertiveness and fWHR: in a regression model controlling for sex ($\beta = -.03$, $p = .88$), age ($\beta = .01$, $p = .98$), and weight ($\beta = -.11$, $p = .65$), rated dominance was still significantly predicted by fWHR ($\beta = .58$, $p < .01$).

5.4 Discussion

Our findings show that fWHR is a distinct, sexually dimorphic trait in *Sapajus* that is closely associated with two different measures of dominant behaviour (alpha status and assertive personality) in both males and females. Similar relationships were found in both sexes after controlling for the body weight and age of each subject.

We also found a relationship between dominance and fWHR in both sexes, which is contrary to previous findings in humans where the link between dominant behaviour and fWHR has been reported exclusively in males (e.g. Carré & McCormick, 2008; Haselhuhn & Wong, 2012; Stirrat & Perrett, 2010). One explanation for this discrepancy might be that human and *Sapajus* females express dominant behaviour in different ways. For example, while numerous studies in humans indicate that men exhibit dominant behaviour and aggression to a much larger extent than women (e.g. Archer, 2004; 2009), in *Sapajus* no such difference is observed between the sexes (Fragaszy et al., 2004). Thus, unlike humans, both

male and female *Sapajus* may be exposed to similar selection pressures associated with dominant behaviour. Although the current study did not directly assess whether *Sapajus* employ fWHR as a cue of dominance, a similar mechanism to that found in humans is likely. Future research should clarify whether fWHR functions as a cue to dominance in *Sapajus*.

There was no relationship between fWHR and age among female *Sapajus*, suggesting that fWHR remains relatively stable throughout a female's life span. In contrast, male fWHR was positively associated with age, suggesting an increase during sexual maturation. Accordingly, sex differences were only observed in adult individuals, with males having a significantly larger fWHR than females. These findings may indicate that male sex hormones (testosterone) are involved in the development of fWHR, as has previously been reported in humans (chapter 4). Weston et al. (2004) previously detected sex differences in *Sapajus* fWHR using measurements taken from skulls. Here, we confirm that sex differences exist in *Sapajus* fWHR using measurements taken directly from subjects' faces. It should be noted however, that these sex differences were mediated by sex differences in body weight in the sub-sample that had weight measurements available.

The lack of a significant sex difference in fWHR (Lefevre et al., 2012 / chapter 3; Özener, 2012) and minimal dimorphism in canine size (Kapila et al., 2011) in humans suggests that canine size – previously argued to account for lower fWHR dimorphism in species such as *Gorilla* (Weston et al., 2004) – cannot fully account for species differences in fWHR-dimorphism. In other words, fWHR is not an obligate substitute for canine dimorphism. To examine the evolution of fWHR and canine size as dominance cues, it will be necessary to measure the association between these traits and dominance in other primate species.

5.4.1 Conclusions and future directions

Humans and *Sapajus* last shared a common ancestor some 43 million years ago (Steiper & Young, 2006). Thus, the existence of an association between fWHR and dominance in both species suggests that the relationship is phylogenetically old, perhaps derived through common selective pressures associated with dominance (e.g. a robust skull structure to successfully withstand blows to the head). However, further data are needed on species that vary in their display of dominance (e.g. egalitarian versus despotic species) and sexual dimorphism. Moreover, as in human studies, we found a relationship between fWHR and dominance in adult *Sapajus* males; however, further work is necessary to test whether this means that both species experience similar underlying hormonal interactions with fWHR during development (chapter 4). Finally, to better understand the underlying mechanism(s) that link fWHR to dominant behaviour in *Sapajus* and other species, it would be of particular value to examine the sex-specificity of the behavioural correlates of fWHR (e.g. aggression), and associated endocrinological make-ups.

In summary, this study is the first to demonstrate a link between facial shape and dominant behaviour in a nonhuman species. Our findings indicate that fWHR has the potential for being a permanently visible signal to dominance in *Sapajus*. However, further research will be needed to determine whether, like in humans, fWHR is indeed used by *Sapajus* as a cue for dominance, and whether this trait is associated with advantages to the bearer (e.g. frequency and level of aggression given/received).

Chapter 6. Trusted and attractive? Cues to health impact perceived trustworthiness and attractiveness.

This chapter is largely based on work that has been submitted to a peer-reviewed journal:

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Contribution to this chapter: My contribution to this chapter was equal with that of Milena Dzhelyova, we conceived and designed the study together. I prepared stimuli for the study and prepared the online experiment. Milena conducted raw data cleaning and basic analyses. We conducted inferential statistics jointly and contributed equally to the write-up.

Abstract

In line with evolutionary theory and the ‘behavioural immune system’, cues to health are crucial for mate choice and for judgments of who to trust in social interactions. Skin colour may cue current health, while masculinity may cue long-term health, but is associated with negative personality traits (e.g. uncooperativeness). We therefore investigated the contributions of facial skin colour and masculine face shape to attractiveness and trustworthiness perception. Male faces were manipulated in both skin colour (healthy/unhealthy) and face shape (feminine/masculine). Healthy colour increased attractiveness and trustworthiness ratings. Feminine-shaped faces were perceived as more trustworthy while masculine shaped faces were perceived as more attractive. Attractive male faces either had a healthy colour or a masculine-shape, but possession of both characteristics did not elevate attractiveness further, suggesting non-additive effects of the two cues. The results support the notion of a behavioural immune system and indicate that the interplay between cues for mate choice is more complex than previously thought.

6.1 Introduction

Individual differences in facial appearance affect judgements of attractiveness, personality, and even behaviour. For example, previous research demonstrates high agreement in judgements of attractiveness (e.g. Langlois et al., 2000), as well as attributions of behavioural traits such as aggression (e.g. Carré et al., 2009) and trustworthiness (e.g. Stiratt & Perrett, 2010). While most work to date has examined the influence of face shape on these characteristics, more recently the impact of facial skin status on attractiveness and health has become apparent (e.g. Scott et al., 2010; Stephen et al., 2009) with some work indicating that skin colour affects attractiveness independently of face shape (Stephen et al., 2009). It is currently not known whether facial morphology and skin colour interact or have an additive effect in optimising the mate quality inferred from these physical cues. Skin colour, a putative measure of current health (e.g. Stephen et al., 2009), may not only influence attractiveness but also affect other social judgments influencing, for example, trustworthiness perception. People may be more willing to engage in social interactions, and thus show trust, when risk of infection is low (Schaller & Park, 2011). We therefore investigated the impact of healthy facial skin colour and masculine face shape on the perception of both attractiveness and trustworthiness in males.

Female mate preferences are thought to be based on direct (i.e. parental investment; resource availability; good health) or indirect (i.e. good genes) benefits accrued from the male (e.g. Trivers, 1972; Zahavi, 1975). Sexually dimorphic male facial shape may act as a cue to both these benefits. Firstly, facial masculinity has been linked to a better medical history (Rhodes et al., 2003), and shorter durations of past illnesses (Thornhill & Gangestad, 2006), indicating an association with general long-term health. Consistent with this is the putative role of testosterone in contributing both to facial masculinity (Pound et al., 2009; although see chapter 4) and a strengthened immune response (Rantala et al., 2012; although

see chapter 7). Secondly, prominent male-typical facial features (e.g. prominent brow ridges, broad chin) increase dominance perception (e.g. DeBruine et al., 2006; Perrett et al., 1998) and are often seen as a cue to physical strength and social status (Fink et al., 2007; Mueller & Mazur, 1997), linking masculinity to direct benefits through ability to acquire resources. Despite these observations, female attraction to masculine-shaped faces is equivocal to date with some studies finding this preference (e.g. DeBruine et al., 2006) but others finding preferences for feminine facial features (e.g. Perrett et al., 1998).

While effects of facial masculinity on social judgements and mate choice are well investigated, the impact of skin colouration has been largely neglected. This paucity in the literature is unfortunate because skin colouration has been linked to facial attractiveness, perhaps as a cue to current health (e.g. Scott et al., 2010; Stephen et al., 2012) thus indicating direct benefits (i.e. low pathogen load and an ability to acquire resources). In particular, skin yellowness, which is associated with levels of carotenoids (potent antioxidants), may indicate current health status: carotenoid levels can change in response to dietary changes (Stahl et al., 1998; Whitehead et al., 2012) and parasite infestation (Koutsos et al., 2003).

It follows that skin colour may also affect other social judgements. Social interactions offer great interpersonal benefits but at the same time pose a potential risk of infection, since many diseases are transmitted as a result of proximity to or contact with another person. In line with this trade-off, groups of people that may bear particularly high pathogen loads are associated with negative prejudice (e.g. Park et al., 2003). Further research suggests a positive association between levels of parasite stress in the environment and strength of in-group favouritism (Fincher & Thornhill, 2012) thus providing additional support for a pathogen-avoidance strategy in social life.

From this perspective, then, such facial cues that denote current pathogen load (i.e. skin colour) may be important when deciding who to engage with in social interactions. In addition, there may be material benefits to interactions with healthy people. Healthy individuals will tend to live longer and accumulate more resources during their lifespan. Thus, cooperation with healthy individuals may produce a higher pay-off than cooperation with unhealthy partners. Indeed, in an economic game people reciprocated with apparently healthy partners more than unhealthy partners, though initial trust decisions were unaffected by apparent health (Krupp, DeBruine & Jones, 2011).

6.1.1 The present study

In order to better understand the impact of face shape and colour on social judgements, in the current study we sought to establish the differential influence of healthy skin colouration and masculine shape on the perception of attractiveness and trustworthiness of male faces. The perception of trustworthiness as a social judgement is of particular interest because it has been proposed as a key predictor of a range of assessments about other people's personality, appearance and emotional state (Oosterhof & Todorov, 2008), and thus is crucial for social interactions and survival. Since skin colour is used as a cue to health (Stephen et al., 2009), which is beneficial for both mate choice and social interaction, we expected healthy skin colour to positively affect both attractiveness and trustworthiness ratings independent of face shape. Previous research has suggested that masculine-shaped faces are perceived as less emotional, honest and cooperative as compared to feminine-shaped faces (Perrett et al., 1998); importantly, they are also trusted less (Oosterhof & Todorov, 2008), thus we anticipated facial masculinity to decrease trustworthiness perception. We were further interested in establishing a possible interaction between face

shape and face colour in attractiveness judgements. Thus, we independently manipulated faces along two axes: skin colour (healthy – unhealthy) and face shape (masculine – feminine), creating four versions of each face. All versions of each face were rated for both attractiveness and trustworthiness.

6.2 Methods

6.2.1 Participants

One hundred and five (30 male) heterosexual participants, age range 18 – 39 years (mean = 26.17, SD = 4.93) completed an online experiment.

6.2.2 Stimuli

Stimuli consisted of 12 male identities that were each created by combining five images of Caucasian males ($M = 22.3$ years, $SD = 7.75$ years) and manipulated both in shape (masculine / feminine) and colour (healthy looking / unhealthy looking) resulting in four versions of each identity. Identities were shape transformed by applying $\pm 50\%$ of the linear difference between Caucasian male and female prototypes, creating a masculinised and a feminised version of each identity (for details see Tiddeman, Burt, & Perrett, 2001).

Shape-transformed stimuli were then colour transformed following previous work showing that added skin yellowness increases health perception (e.g. Stephen et al., 2009). We therefore manipulated all faces to be more or less yellow by adding and subtracting ± 8.7 units of yellowness (b^* in the CIELab colour space, see Stephen et al., 2009 for details) to all faces (Figure 12a). This value was derived from a pilot experiment which indicated that on

average this amount of yellowness was added to Caucasian faces to make them appear optimally healthy. Images were cropped so that only the face and neck were visible (see Figure 12b).



Figure 12: A) Endpoint masks representing skin colour differences associated with fruit and vegetables consumption (left: more fruit and vegetables; right: less fruit and vegetables). Note: Colour differences are applied to the whole face except for the eyes. 5 pixel Gaussian blur is applied for a smoother colour transition. B) Examples of stimuli (left to right: masculine shape/ healthy colour; feminine shape/ healthy colour; masculine shape/ unhealthy colour; feminine shape/ unhealthy colour).

6.2.3 Procedure

Stimuli were divided into four sets of 12. Each set comprised one version of each identity (e.g. feminine shaped and healthy coloured). Participants rated only one set of stimuli so that they would not see the same identity twice. Ratings were made on a 7-point Likert scale for attractiveness (1 - not very attractive; 7 - very attractive) and trustworthiness (1 - not very trustworthy; 7 - very trustworthy) in two independent blocks. Image presentation within

each block and block order was randomised. Images remained on the screen until participants responded.

6.3 Results

For each participant, the averaged attractiveness and trustworthiness ratings for each combination of skin colour and face shape transformations were calculated. A mixed ANOVA with rating type (attractiveness; trustworthiness), face shape (feminine; masculine) and face colour (healthy; unhealthy) as within-subject variables, and participants' gender (female; male) as a between-subject variable was performed on the mean ratings given by the participants. Effect sizes are provided by reporting partial η^2 and Pearson's correlation coefficients.

As expected, a main effect of face colour, $F(1,103) = 15.63, p < .001, \eta_p^2 = .13, r = .36$, suggested that stimuli with healthy face colour ($M = 3.68, SEM = .08$) were rated as more attractive and trustworthy than those with unhealthy face colour ($M = 3.36, SEM = .09$). This effect was greater in attractiveness as compared to trustworthiness ratings (although both $p \leq .011$) as indicated by a significant interaction between face colour and rating type, $F(1,103) = 8.28, p = .005, \eta_p^2 = .07, r = 0.27$ (see Figure 13a). An interaction between rating type and face shape, $F(1,103) = 9.74, p = .002, \eta_p^2 = .09, r = .29$ indicated that while shape-masculinised faces were rated as more attractive ($t(104) = 3.11, p = .002$), they tended to be judged as less trustworthy compared to a feminised face shape ($t(104) = 1.95, p = .05$; see Figure 13b).

There was an interaction between face shape and face colour, $F(1,103) = 7.12, p = .009, \eta_p^2 = .06, r = .25$ which was further qualified by a three-way interaction among rating type, face shape and face colour, $F(1,103) = 4.59, p = .034, \eta_p^2 = .04, r = .21$. Post-hoc

analysis indicated that the interaction between face shape and face colour was present in attractiveness ratings, $F(1,103) = 11.59$, $p = .001$, $\eta_p^2 = .10$, $r = .32$ but not in trustworthiness ratings, $F(1,103) = .11$, $p = .736$. For feminine-shaped faces, healthy looking colour was rated as more attractive than unhealthy looking colour, $t(104) = 7.67$, $p < .001$, $r = .60$ but healthy looking colour did not influence masculine-shaped faces ($p = .18$ see Figure 14). Alternatively, for healthy looking coloured faces, shape of the face had no effect ($p = .72$),

but for unhealthy looking coloured faces, masculine faces were rated as more attractive than feminine faces, $t(104) = 5.83, p < .001, r = .50$.

Finally, a main effect of rating type, $F(1,103) = 23.29, p < .001, \eta_p^2 = .18, r = .43$, indicated that on average trustworthiness ratings ($M = 3.74, SEM = .07$) were higher than attractiveness ratings ($M = 3.27, SEM = .10$). No other main effects or interactions reached

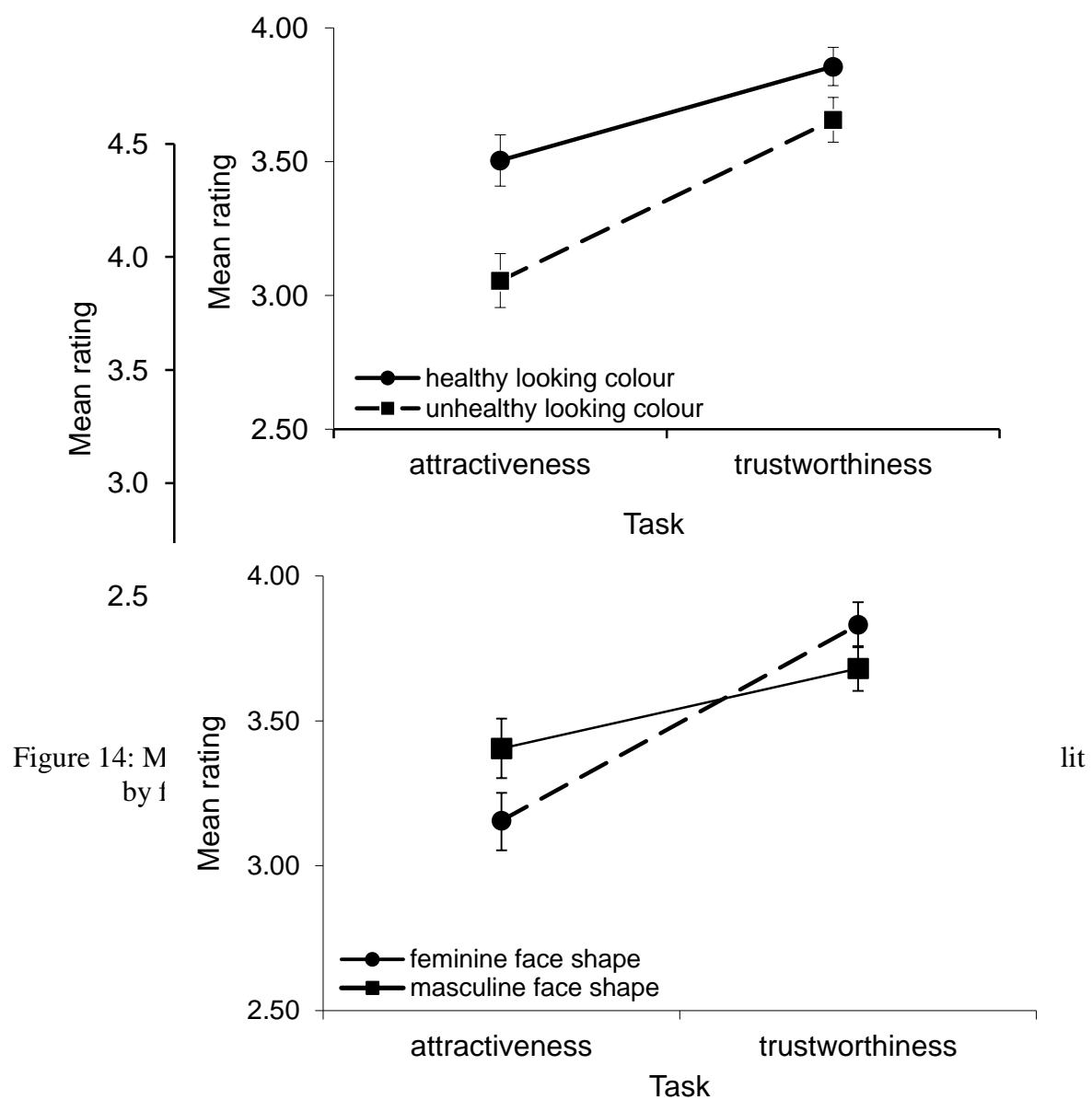


Figure 14: M
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Figure 13: Mean attractiveness and trustworthiness ratings (error bars represent SEM) dependent on stimuli skin colour (A) and face shape (B).

significance.

6.4 Discussion

Here we present evidence for context-dependent differences in the importance of shape and colour cues in male faces. We investigated the effects of health-linked skin colour and sexually dimorphic face shape on the perception of both attractiveness and trustworthiness. Our results indicate that healthy looking skin colour positively influences both trustworthiness and attractiveness. In line with previous work, we further found that masculine face shape is seen as more attractive, while feminine face shape is perceived as more trustworthy. Perhaps more notably, we present evidence suggesting that masculine face shape and healthy skin colour are independently sufficient cues to facial attractiveness. For a male face to be considered attractive either shape masculinity or healthy colouration need to be present; however, the presence of both these cues does not additionally elevate attractiveness. Hence, colour and shape interact in facial attractiveness judgments: healthy skin colour elevates attractiveness only in those faces with a feminine shape; conversely masculinity is more attractive only in faces with an unhealthy skin colour.

The perception of masculine-shaped and healthy coloured faces as attractive is in line with some previous work (e.g. Stephen et al., 2012; Scott et al., 2010), although there is equivocality with regards to masculine shape cues and perceived attractiveness (e.g. DeBruine et al., 2006; Perrett et al., 1998). Both masculine face shape and healthy skin colour are thought to signal health, with face shape acting as a cue to long-term and developmental health (e.g. Rhodes, et al., 2003; Thornhill & Gangestad, 2006) and skin colour indicating current health (e.g. Scott et al., 2010). Furthermore, our results indicate that current health status is particularly important in those males that do not exhibit cues of good genes or status (i.e. masculine facial structure). If facial masculinity is present as a possible cue to long-term

immunity and health (Rantala et al., 2012; Rhodes et al., 2003) the current health state of an individual may be less predictive of survival. Conversely, individuals with a relatively poor general predisposition, as potentially exhibited by feminine face shape, may also be valuable mates, but only if they are in good current health. Skin colour would then be a pivotal cue of quality in these individuals.

The influence of healthy face colour on trustworthiness judgments found here suggests that apparent current health influences trust decisions. Healthier individuals may pose a better investment both in a social and economic sense. They live longer and will likely acquire more resources throughout their lifespan as compared to less healthy individuals. In addition and perhaps more importantly, healthy people may be preferred as partners for social interactions *per se*, because they are less likely to carry and pass on illnesses (Schaller & Park, 2011). Contrary to Krupp et al. (2011), our data indicate that cues to current health increase perceived trustworthiness. This discrepancy could be due to differences in the measures of trust and health used. We asked our participants to rate trustworthiness while Krupp et al. (2011) measured trust by assessing investments made in a partner. It is worth noting that even though the measures are different, trustworthiness perception is concordant with behaviour in economic games (e.g. Stirrat & Perrett, 2010) and, as such, similar outcomes can be inferred. Additionally, manipulating skin colour as an approximation of current health, as opposed to utilising general health ratings, should be less confounded by uncontrolled cues to long-term health (weight; masculinity) and facial expression. It is also possible that the manipulation of the images led to unintended changes of the stimuli that might have an impact on the results (increased contrast between the lips and the eyes or lighter facial hair); however we think that this explanation is less likely to have led to our results. Future experiments should address this possibility.

Consistent with previous studies showing that facial masculinity increases the attribution of negative personality traits (e.g. Perrett et al, 1998); we found that masculine face shape appeared to be perceived as less trustworthy than feminine face shape. The converse effect of masculinity on attractiveness and trustworthiness perception may suggest a context-dependent utilisation of cues associated with more than one relevant trait. For example, in mate choice masculinity provides cues to good health and status (desirable traits in a mate), while in social attributions, it is mainly used as a cue of dominance (an undesirable trait in a trading partner given the risk of exploitation, Stirrat & Perrett, 2010). The dissociation in the perception of masculine males as more attractive but less trustworthy, reported here, challenges previous findings of an elevated positive perception or ‘halo effect’ of attractive individuals (for review see Langlois et al., 2000).

6.4.1 Conclusion

In summary, the results presented here indicate that facial cues to partner’s quality may be interdependent and that the importance of facial cues is contingent on the social judgement made. We demonstrate that skin colour, as a cue of current health, impacts trustworthiness perception. In line with recent work on the behavioural immune system (Schaller & Park, 2011), our work indicates that cues to current health are imperative for social judgements. Additionally, we show that, at least in mate choice, short- and long-term cues to partner’s quality interact, indicating that these attributes cannot be understood as independent. These results provide important advances in the understanding of social interactions and mate choice.

**Chapter 7. Testing predictions of the
immunocompetence handicap hypothesis:
Carotenoid-linked skin colouration is negatively
associated with testosterone levels.**

Abstract

The immunocompetence handicap hypothesis states that only men with good quality immune function can sustain the immunosuppressant effects arising from high levels of testosterone and can thus express testosterone-associated physical features. Recently, skin yellowness presumably induced by carotenoids, potent antioxidants contained in fruit and vegetables, has been demonstrated to be attractive and healthy looking in humans. Following similar findings in birds, we assessed whether testosterone levels affect signs of carotenoid deposition in the skin. In two samples of Caucasian men we measured skin yellowness and circulating testosterone levels, with one sample also containing reactive testosterone measures. Men with higher testosterone levels, both baseline and reactive, showed lower skin yellowness. These results indicate that skin yellowness, which might reflect carotenoid deposition in the skin, is a cue to low testosterone, and suggest that carotenoids are required to buffer suppressive effects of testosterone on the immune system. In high testosterone men carotenoids might be used-up rather than deposited in the skin.

7.1 Introduction

Being able to ascertain the genetic and conditional quality of a potential mate poses an evolutionary advantage (Andersson, 1994). Accordingly, appearance-based signalling of mate value (e.g. through ornamentation) has been repeatedly shown in non-human animals and has been argued to also exist in humans (e.g. Thornhill & Gangestad, 1999; Rhodes, 2006). Two important, distinct mechanisms through which such signals are thought to arise are 1) dietary carotenoids that are layered into the skin or feathers and 2) androgen induced melanisation (Peters, 2007). Similar colour or shape-based signalling systems have also been proposed in humans with male facial masculinity (sexual dimorphism) as an androgen linked signal of genetic quality (e.g. Folstad & Karter, 1992; Penton-Voak & Chen, 2004; Pound et al., 2009; Roney et al., 2006) and skin yellowness as a carotenoid based signal of current condition (e.g. Stephen et al., 2009). Indeed, slightly raised skin yellowness is perceived as attractive and healthy looking by observers (e.g. Stephen et al., 2009).

Parallel lines of research indicate that the evolutionary stability of each signalling system stems from costly trade-offs between signalling ability and immune function: androgens can be immunosuppressive (Folstad & Karter, 1992; but see Roberts et al., 2004) and promote oxidative stress (Alonso-Alvarez et al. 2007; Buchanan et al. 2001; Wikelski et al. 1999), while carotenoids stored in colourful ornaments can no longer function as antioxidants in aid of the immune response (Horak & Saks, 2003; Møller et al., 2000; von Schantz et al., 1999). Possible interactions between androgens and carotenoid-induced signals are currently not well understood, although a comprehensive model has been proposed suggesting that the trade-off between immunity and ornamentation is mediated by testosterone (Peters, 2007). Some initial work in birds indicates that testosterone treatment in male birds increases bioavailability of carotenoids (Blas et al., 2006; McGraw et al., 2006), but the evidence as to whether this enhances or diminishes carotenoid based ornament

colouration is equivocal (e.g. Casagrande et al., 2011; 2012; McGraw et al., 2006; Mougeot et al., 2007; Stoehr & Hill 2001). Moreover, whether similar effects are present in humans is currently not known. To this end, we investigate possible associations of testosterone levels with carotenoid induced skin colouration in human males.

Importantly, a system built on appearance-based cues to quality can only function if the expressed cues are honest, or in other words accurately reflect the individual's quality. Honesty can be enforced when building a given cue is costly (Zahavi, 1975; 1987). For appearance-based cues such costs are not immediately apparent, but theory posits that they are associated with disease resistance (e.g. Zahavi & Zahavi, 1997). Both androgen and carotenoid linked signals are argued to involve trade-offs with immune-function: 1) through testosterone induced immunosuppression (Folstad & Karter, 1992), and 2) by carotenoids being used for signalling instead of immune response (Horak & Saks, 2003; von Schantz et al., 1999). These perspectives are detailed below.

7.1.1 Testosterone linked quality signals

One model for the development of secondary sexual traits such as facial masculinity is the immunocompetence handicap hypothesis (ICHH; Folstad & Karter, 1992). This model is based on two core assumptions. First, it posits that secondary sexual traits (e.g. facial masculinity in males) emerge as a function of testosterone exposure during development (Verdonck et al., 1999); and second that testosterone acts as an immunosuppressant (Grossman, 1985; Angele et al., 2000; Messingham et al., 2001; cf. Roberts et al., 2004) and increases oxidative stress (Alonso-Alvarez et al., 2007). Under this model, then, the successful expression of elaborate secondary sexual traits requires exposure to high levels of

testosterone, and only males of high genetic quality will be able to sustain this exposure without deleterious consequences (Zahavi & Zahavi, 1997).

Accordingly, testosterone linked cues are assumed to signal health and in particular heritable immunocompetence (e.g. Gangestad & Buss 1993; Lie et al., 2008; Perrett et al., 1998; Rantala et al., 2012; Thornhill & Gangestad 1999) and considerable, albeit not entirely consistent evidence for a link between testosterone and expression of sexual ornaments has been found in birds. For instance, testosterone is positively related to badge size in house sparrows (Eens et al., 2000) and frontal shield thickness and colour in moorhens (Evans et al., 2000; Buchanan et al., 2001; Gonzalez et al., 2001). Furthermore, testosterone increases wattle size and male aggressiveness in pheasants (Briganti et al., 1999) and comb size in the junglefowl (Zuk et al., 1995). Similar relationships have also been observed in other taxa, including enhancement of nuptial skin coloration in lizards (Salvador et al., 1996) and increased antler size in white-tailed deer (Ditchkoff et al., 2001). Several other studies have however failed to find associations between testosterone and ornamentation (e.g. in red-winged blackbirds; Weatherhead et al., 1993), indicating that the association between testosterone and ornamentation is complex although, in sum, appears to be present (Owens & Short, 1995; Kimball & Ligon, 1999).

In humans, while several traits have been identified as putative testosterone signals including odour, voice pitch, body size, and various facial features (e.g. Brown et al., 2008; Feinberg et al., 2005; Fink & Penton-Voak, 2002; Grammer et al., 2005; Grammer & Thornhill, 1994; Penton-Voak et al., 1999; Perrett et al., 1998; Rhodes et al., 2003), most research has focused on male facial masculinity, i.e. sexual dimorphism (e.g., Barber, 1995; DeBruine et al., 2006; Johnston et al., 2001; Moore et al., 2009; Penton-Voak et al., 1999; Perrett et al., 1998; Rhodes et al., 2003; Scarbrough & Johnston, 2005; Smith et al., 2009; Swaddle & Reierson, 2002; Thornhill & Gangestad, 2006; Waynforth et al., 2005). To date,

the evidence for a direct link between facial masculinity and either testosterone (Verdonck et al., 1999; Penton-Voak & Chen, 2004; but see chapter 4; Neave et al., 2003) or health (Rhodes et al., 2003; Thornhill & Gangestad, 2006) is however limited.

7.1.2 Carotenoid based ornamentation as a signal of quality

Aside from androgen-based signals of quality, research in birds has also revealed honest signals of health based on carotenoids. These potent antioxidants are ingested with diet and have been shown to positively affect immune response (Alaluf et al., 2002; Chew & Park, 2004). Theory posits that the storage of carotenoids in ornamentation prevents a simultaneous use for immune response and oxidative stress reduction (Dowling & Simmons, 2009). Only individuals who both require fewer carotenoids to counteract oxidative stress arising from illness, in their immune defence and who possess superior foraging skills can allocate great amounts of the pigment to ornamentation while still maintaining a highly functioning immune response. Several studies in birds support this link: parasite infestation reduced carotenoid levels in guppies and chicken (Olson & Owens, 1998), while nematode infection led to dull supra-orbital combs, a carotenoid linked signal, in red grouse (Martinez-Padilla, et al., 2007). Carotenoid based ornamentation is, in line with this argument, found appealing by the opposite sex in several bird and fish species (e.g. Lozano, 1994), as well as in humans (Stephen et al., 2011; 2012).

Recently, carotenoids have also been associated with appearance in humans (Stephen et al., 2011; Whitehead et al., 2012) such that skin yellowness is affected by carotenoids via their incorporation in the epidermis (Alaluf et al., 2002; Stamatas et al., 2004). Plasma carotenoid levels can change within days in response to dietary changes (Stahl et al., 1998) and parasite infestation (Koutsos et al., 2003) and skin colour has been shown to respond to

dietary changes within a few weeks (Whitehead et al., 2012), indicating its signalling power. Furthermore, carotenoids have been linked to immunocompetence and disease resistance in humans: for example, carotenoid levels are reduced in individuals suffering from HIV or malaria and in individuals with elevated serum α 1-antichymotrypsin (an indicator of infection: Friis et al., 2001). Conversely, carotenoid supplementation has proven beneficial for thymus gland growth in children (Seifter, et al., 1981) and has been shown to increase T-lymphocyte number in healthy adults (Alexander et al., 1985). Accordingly, since carotenoids are potent antioxidants they are likely depleted by oxidative stress, reducing plasma levels and skin yellowness in times of high immune-stress.

7.1.3 Links between testosterone and carotenoid signalling

As outlined above, increased bioavailability of carotenoids may counteract the negative effects of testosterone on the immune system. This suggests a possible relationship between testosterone and carotenoid levels. Some initial work in birds indicates such an association between testosterone levels and levels of plasma carotenoids. In zebra finch, natural levels of circulating blood testosterone positively predicted blood carotenoid concentration and lipoprotein concentration (McGraw et al., 2006). Lipoproteins bind carotenoids taken in with diet and act as carriers in the blood stream. Thus lipoprotein concentrations have direct effects on carotenoid availability (McGraw & Parker, 2006). Blas and colleagues (2006) report an increase in plasma carotenoid levels after experimentally increasing testosterone levels in red-legged partridges. A similar study conducted in zebra finch (McGraw & Ardia, 2007) on the other hand, found a decrease in plasma carotenoids following testosterone treatment and a subsequent immune challenge, indicating that available carotenoid stores are used up to counteract immunosuppressant effects of high

levels of testosterone when necessary. It follows that, while the exact mechanism is currently not understood, an association between testosterone and carotenoids appears to be present (see also Vinkler & Albrecht, 2010).

Whether testosterone levels are associated with the size or colouration saturation of carotenoid based ornamentation is less clear. While several studies report a positive link in several bird species (Casagrande et al., 2011; 2012; McGraw et al., 2006; Mugeot et al., 2007), other studies in birds find no association (Blas et al., 2006; Peters et al., 2012) or a negative association (Stoehr & Hill 2001) and a study in stickleback fish provided similarly inconclusive results (Kurtz et al., 2007). Another study looking at house finches found that treatment with high levels of testosterone resulted in paler, rather than redder, carotenoid induced plumage colouration during moult (Stoehr & Hill, 2001), potentially indicating a negative effect of too high testosterone levels on ornamentation. Taken together, these studies provide some indication that testosterone has an effect on carotenoid-based integument colouration at least in birds (and fish); however, the direction of this association and the required level of change are currently not understood.

7.1.4 The Current Study

Following the ICHH, testosterone required to produce sexual ornamentation will have deleterious effects on the immune system (Folstad & Karter, 1992). However, it remains unclear whether high levels of circulating testosterone will cause the immune response of high quality males to plummet below that of low testosterone males or whether regardless of deleterious effects of testosterone immunity remains highly functioning. To this end, we investigated whether skin yellowness, as a proxy measure for carotenoid signalling, is linked to testosterone levels in human males. We use both baseline and reactive testosterone

measures following exposure to potential mates (Roney et al., 2003) in order to test both associations with habitual and maximal testosterone levels.

In line with research conducted in birds, an association between testosterone levels and carotenoid colouration should be present. However, (at least) two competing hypothesis are apparent: Firstly, if skin yellowness is a signal of immunocompetence, and males with higher testosterone levels are of higher quality and thus have higher immunocompetence, then we would expect a positive association between testosterone and skin yellowness. On the other hand, if testosterone indeed lowers immune function below average then we expect to see a negative association between testosterone and skin yellowness.

7.2 Methods

7.2.1 Samples

Sample 1: Skin colour and both baseline and reactive testosterone measures from 188 Caucasian men (mean age = 33.6 years, SD = 7.5, range: 21 to 54) who participated in the Berlin Speed Dating Study (Asendorpf et al., 2011) were analysed. Participants took part in a speed-dating event. Each man met between 8 and 14 women (Mean \pm SE = 11.4 \pm 1.7) of an age similar to their own (within-session age range = \pm 4.8 years) for 3 minutes each (for details see Asendorpf et al., 2011; Back et al., 2011). Body height (m) and weight (kg: dressed, but without jackets or shoes) were measured directly before speed dating began, from which the body mass index (BMI; kg/m²) was calculated.

Sample 2: Skin colour and two measures of baseline testosterone from 43 Caucasian male undergraduate students (mean age: 20.43 years, age range: 18-24 years) were measured. For 32 participants body height (m) and weight (kg: dressed, but without jackets or shoes)

were assessed during one of the testing sessions and were used to calculate the BMI in this subset.

7.2.2 Skin colour measures

Sample 1: Participants were recorded with a camcorder on a tripod while standing upright in front of a white background under standardised lighting in order to allow the extraction of various standardised facial photographs. The frame with the most frontal and neutral recording of each participant's face was converted into a picture (for full details see Asendorpf et al., 2011).

Sample 2: Photographs were taken under standardised lighting conditions in front of a white background during one of the testing sessions.

In both samples, skin colour was assessed from photographs. Images were aligned and scaled to the same interpupillary distance. Next, skin patches were cut from the right cheek above the beard line (using the Psychomorph software package; Tiddeman et al., 2001, <http://users.aber.ac.uk/bpt/jpsychomorph/>). All patches were visually inspected to ensure absence of beard hair or blemishes. For each skin patch the average colour was calculated in the CIELab colour space producing mean L*, a* and b* values for each individual. The CIELab colour space is commonly used in human perceptual work and is modelled on the human visual system and designed to be perceptually uniform, a one-unit change is approximately of the same magnitude regardless of the dimension of change (Martinkauki, 2002). The system is defined by three colour axes: L* (lightness), a* (green-red) and b* (blue-yellow).

7.2.3 Testosterone measures

Sample 1: Saliva samples were collected both directly (within 5 minutes) prior to (baseline testosterone) and after the speed-dating (reactive testosterone). The speed-dating events lasted approximately 2 hours. The samples were taken by a male research assistant in a waiting room with all male participants of the event present. Male and female participants had been guided to entrances on different sides of a large university building, so there had been no interaction between sexes at time of the baseline saliva collection. Samples were collected using a Salicap tube (www.ibl-international.com) and a straw. In order to control for potential diurnal effects samples were always collected between 3:30pm and 4:30pm (pre-exposure) and 5pm and 7pm (post-exposure). All samples were visually inspected for discolouration arising from blood contamination; suspicious samples were excluded from further analysis. To avoid food contamination, participants were asked not to eat and to only drink water during the event.

Immediately following the end of the speed-dating event, specimens were frozen and stored at -20°C until analysis was performed by the Biopsychological Lab of the Technical University Dresden using IBL luminescence immunoassays (sensitivity 5pg/ml). After defrosting samples were centrifuged for 10 min and 50 µl of samples were introduced into the respective wells of a microtiter plate. Next 50 µl of enzyme conjugate followed by 50 µl of testosterone antiserum were added to each well. Plates were then incubated for 4h at room temperature. After discarding incubation solution and washing plates four times using 250 µl of diluted wash buffer, 50 µl Chemiluminescence Reagent AP was added to each well. After 10mins relative luminescence units were measured using a luminometer. Inter- and intra-assay variability was below 12%. For each participant testosterone levels were analysed in duplicates.

Sample 2: During both a morning and an afternoon testing session (sessions were not separated by more than 24 h) salivary testosterone was assessed. Testosterone measures were calculated as the average of these two samples (for full details see Moore et al., 2011). All samples were visually inspected for blood contamination and discoloured samples were excluded from subsequent analysis. Following collection, samples were frozen at -20°C until analysis at Queen Margaret University Immunoassay Laboratories. Analysis was performed using an in-house enzyme-linked immunoabsorbant assay (Al-Dujaili, 2006). The assay procedure used the indirect, competitive binding technique. Assay sensitivity was 1.5 pg ml⁻¹; intra- and inter-assay coefficients, obtained over 50 assay runs, were 2.7 % and 6.8 %, respectively; cross reactivity with related compounds was minimal and the standard curve was highly reproducible ($r = 0.998$), for more details see Moore et al. (2011).

7.3 Results

7.3.1 Sample 1

Testosterone measures more than three standard deviations from the mean were removed prior to analyses. This reduced the dataset by 3 and 4 participants for baseline and reactive testosterone levels, respectively. Additionally, both testosterone variables were positively skewed and were therefore transformed to normal distribution using square-root transforms. For skin yellowness (b^*), in order to achieve normality, cases more than three standard deviations from the mean were removed ($N=3$). This left 182 cases for analysis (mean = 11.42, SD = 1.56).

Initial zero-order correlations between testosterone levels and b^* revealed a significant negative association of b^* with both baseline ($r = -.16$, $p < .05$) and reactive ($r = -.20$, $p < .01$) testosterone levels (Figure 15).

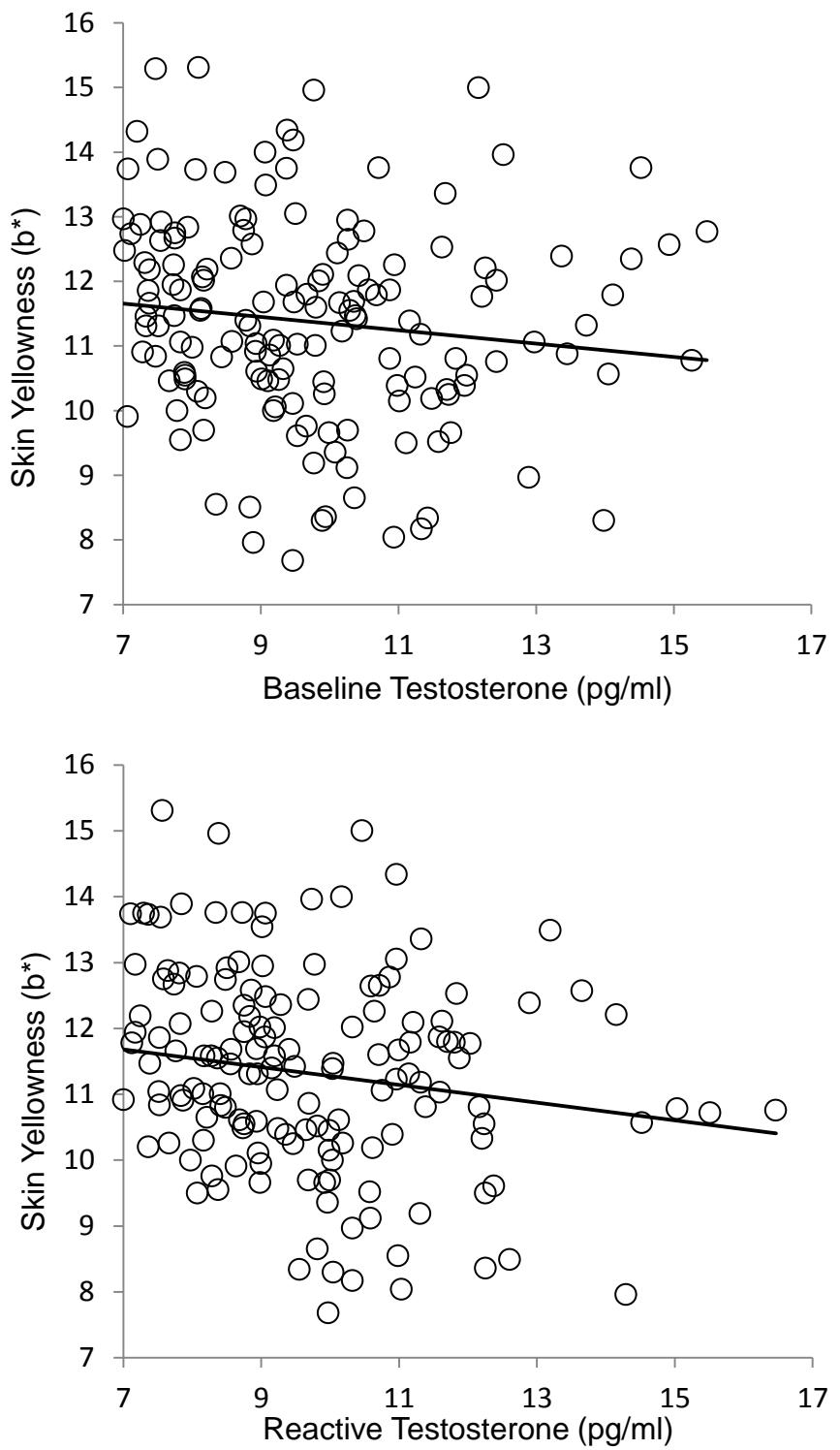


Figure 15: Zero-Order associations of skin yellowness with baseline (left) and reactive (right) testosterone in Sample 1.

Changes in skin yellowness (b^*) are typically caused either by carotenoids or by melanin (sun tan). Changes in melanin are additionally associated with large changes in skin lightness (L^* ; see Stephen et al., 2011). Although zero order correlations between testosterone and L^* were non-significant (baseline: $r = .12$, $p = .11$; reactive: $r = .09$, $p = .24$), L^* was controlled for in order to assess the association between b^* and testosterone independently of L^* . Additionally, testosterone has been negatively associated with age (e.g. Harman et al., 2001) and BMI (Osuna et al., 2006), which both may also be linked to skin tone, with age being linked to skin darkness (Green & Martin, 1990) and BMI having been associated with lower levels of plasma carotenoids (Andersen et al., 2006). We therefore added age and BMI as further control variables, resulting in a regression model with testosterone, L^* , age, and BMI as predictor variables for skin yellowness (b^*). For baseline testosterone, the overall model was significant ($F(4,178) = 2.45$, $p < .05$) with testosterone ($\beta = -.15$, $p = .05$) and skin lightness ($\beta = .15$, $p < .05$) being independent significant predictors. Neither age nor BMI were significant predictors (both $p > .20$).

The same model was repeated with reactive testosterone as measured following exposure to potential mates during speed dating as the predictor variable. Again, the overall model was significant ($F(4,178) = 3.29$, $p = .01$) and both testosterone ($\beta = -.19$, $p=.01$) and skin lightness ($\beta = .16$, $p < .05$) were again independent predictors. Neither age nor BMI were significant predictors (both $p > .26$).

7.3.2 Sample 2

Skin yellowness (b^* , mean = 9.54, SD = 1.91) values were positively skewed.

In order to achieve normality, the data was log transformed.

Initial zero-order correlations between b^* and testosterone revealed a negative

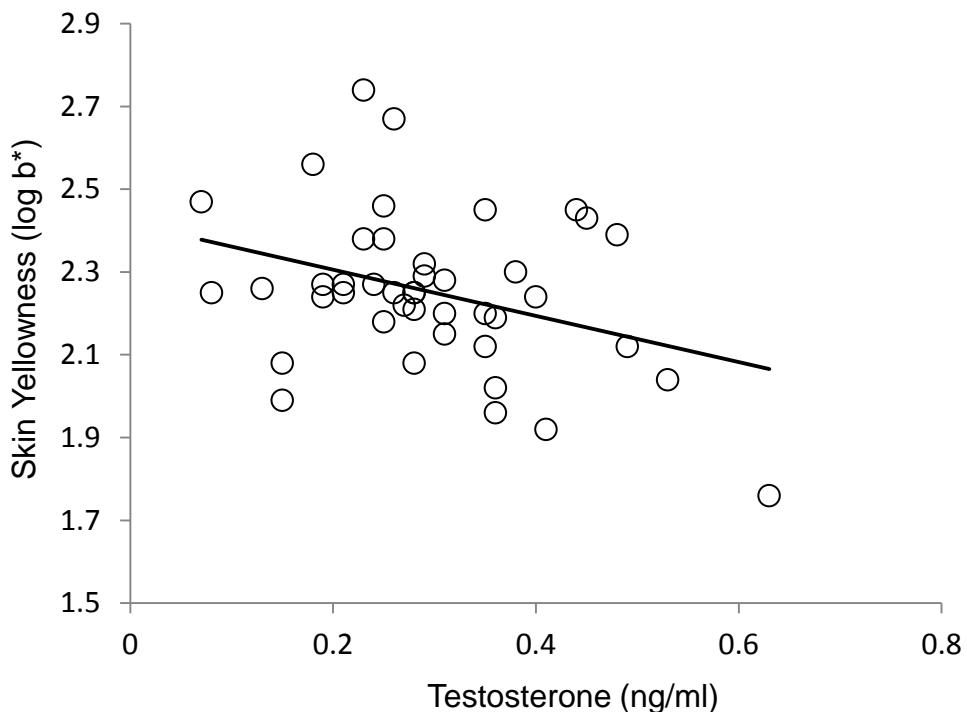


Figure 16: Zero-order association between Skin yellowness and testosterone in sample 2.

association ($r = -.35$, $p = .02$; Figure 16). Next a regression model was built to control for skin lightness (L^*), age and BMI, although again, L^* was not associated with testosterone ($r = -.03$, $p = .86$). The overall model was significant ($F(4,27) = 4.86$, $p = .004$) with testosterone independently predicting skin yellowness ($\beta = -.32$, $p = .04$). Skin lightness ($\beta = .32$, $p = .04$) and age ($\beta = .40$, $p = .01$) also contributing the model, while BMI ($\beta = .17$, $p = .25$) did not predict b^* .

7.4 Discussion

We tested possible links between testosterone and health linked skin colouration (yellowness) in men. We found, in two samples, a negative association between yellowness and testosterone levels (both baseline and reactive). These effects cannot be accounted for by differences in melanin content of the skin because melanin has large effects on skin lightness, and the effects reported here were independent of skin lightness effects. This indicates that carotenoids may cause the association of skin yellowness and testosterone found here. Our result support the hypothesis that testosterone acts as an immunosuppressant and raises oxidative stress; hence men with higher testosterone levels require higher levels of carotenoids as antioxidants to buffer these effects.

Skin yellowness is thought to be caused by carotenoids, anti-oxidants that have to be ingested from a healthy diet and layered onto the skin. There is evidence from both human and non-human animal research that carotenoids have antioxidant and immunoenhancing capacity and are used up by the immune system in times of poor health (Alonso-Alvarez et al., 2004; Blount et al., 2003; McGraw & Ardia, 2003, 2005; Surai, 2002). The trade-off theory of carotenoid function between health and ornamentation suggests that carotenoids used for immune response can no longer be utilised in ornamentation, resulting in duller, less colourful ornamentation following immune stressors (Alonso-Alvarez et al., 2004; Blount et al., 2003; Faivre et al., 2003; McGraw & Ardia, 2003; 2005). The current findings indicate that such processes may occur in humans: individuals with higher levels of testosterone may experience its immunosuppressive effects, which in turn may be buffered by the capacity of carotenoids to boost the immune system. It follows that fewer carotenoids are available for deposition in the skin to create healthy colouration (ornamentation).

While the mean difference between skin yellowness of high and low testosterone individuals was fairly small (sample 1 following median split: 0.65 units of b*, compared to a SD of 1.56 units), previous research indicates that differences of similar magnitude are perceptible (Whitehead et al., 2012). Thus, the possible negative consequences of high testosterone may be directly evident to observers, since skin yellowness has been linked to perceived current health and attractiveness (Stephen et al., 2011). These findings may be of additional importance for the on-going debate concerning male facial attractiveness: following the immunocompetence handicap hypothesis, theory suggests that men with high testosterone levels should be attractive and pose high quality mates (e.g. Andersson, 1994). However, if, as indicated by the current findings, there is a trade-off between current condition (as advertised by skin yellowness) and genetic quality (putatively advertised by facial masculinity) then this trade-off may pose an added dimension to women's mate choice behaviour.

Additionally, we find maximal levels of testosterone show a closer association with skin yellowness than habitual levels. This result may indicate that carotenoid depletion by immune function is dependent upon total tissue exposure to testosterone over time, rather than baseline levels. In other words, high reactive testosterone bouts may cause temporary or long-lasting immunosuppression that requires buffering through carotenoids.

The findings presented here have some limitations that warrant mentioning. We did not control for life-style factors that may systematically influence the relationship between testosterone and carotenoids. There are at least two possible life-style factors that may affect our findings: firstly, carotenoids are ingested when consuming fruit and vegetables (Alaluf et al., 2002), thus if higher testosterone levels are associated with lower fruit and vegetable consumption, a less yellow skin colouration would be expected (Whitehead et al., 2012).

Although it is unlikely that a systematic relationship exists between diet and testosterone future research should assess this possible confound. Secondly, exercise levels may differ between men with high and low testosterone levels. Recent work by Vierck and colleagues (2012) indicates that high levels of exercise may raise oxidative stress in the body and subsequently lower skin yellowness. However, this study did only assess immediate changes (within minutes after the exercise) and did not measure longer-term changes in skin colouration or oxidative stress.

In summary, this is the first study to assess links between testosterone and health-linked signalling in humans. It provides support for a trade-off model, whereby carotenoids, ingested through diet, function either as antioxidants or are layered in the skin for ornamentation and provides evidence for high testosterone men exhibiting higher immune-stressors.

Chapter 8. General Discussion

The aim of this thesis was to better understand links between physiological aspects of the face and behaviour as well as the perception of behaviour. In this chapter, I first briefly summarise the core findings of my thesis. I then discuss the theoretical implications of the work reported here. Finally, I outline work that might be conducted to extend the findings of the current thesis to shed further light on issues discussed here.

8.1 Summary of Findings

The work reported in this thesis employs a number of approaches, including facial morphology, endocrinology, comparative approaches, and laboratory experiments, to investigate 1) links between facial appearance and behaviour, as well as the perception of behaviour, and 2) possible underlying factors influencing these links. First, in two studies we show an association between facial width-to-height ratio (fWHR) and personality. Chapter 2 assessed links of fWHR with achievement striving in US presidents. The measure of achievement striving was generated from factor analysis and had high loadings on persistence and (negatively) on quitting. These findings add a further nuance to the picture of personality traits and behavioural attributes linked to facial appearance and support theoretical arguments for an intricate, rather than simple, mechanism of testosterone behaviour links. US presidents posed a particularly interesting opportunity sample, because every individual in this sample is achieving at the highest level and is highly competitive and skilled. That we still find an association of the remaining variance in achievement striving and appearance suggests for this link not to be driven by extremes of society, such as low SES or low education groups. One note of concern might be the depiction of famous figures in accordance with their personality, although more commonly known in painting, photographers also portrait their

subjects in accordance with what they believe to be the common perception of their personality to be. It is thus possible that findings in this study were to some extend inflated.

In chapter 5 we showed that fWHR is linked to personality in a non-human primate: the capuchin. In particular, we were able to show links with both alpha-status and assertiveness in both male and female capuchins. These results indicate that the same facial features link to competitive behaviour across species, supportive of a model positing a common selection pressure in humans and other animals for fWHR as a behavioural marker, and perhaps a signal. While it is currently not clear what anatomical advantage facial width provides, at least two candidates deserve mentioning. First, fWHR may be linked to bite strength or, in other words, superior weaponry. The masseter muscle, responsible for bite force, runs below the zygomatic arch. Thus, larger muscles that afford greater bite strength may require the zygomatic arch to be positioned more laterally, in turn leading to a greater facial width. In this case then, fWHR would signal bite strength, a marker related to dominance in several species (e.g. Clutton-Brock, 1983). Second, fWHR may indicate a robust skull structure. Males have stronger skulls than females, perhaps to resist fracture from blows typically encountered during fights (Buikstra, & Ubelaker, 1994). Within males, a wider zygomatic arch may relate to a stronger skull structure, thus indicating greater ability to withstand injury during fighting encounters.

Second, we assessed the underlying physiological architecture of fWHR. In Chapter 3 we falsified the claim that in humans men have wider faces than women. Interest in fWHR as a potential marker of behaviour originated in Weston et al.'s (2007) claim of reliable sex differences in this metric, as assessed from skulls and early work on photographs replicated these differences (e.g. Carré & McCormick, 2008). We assessed four large samples (total N>900) of different, well controlled, demographics, namely Caucasian undergraduate students (in 2D and 3D photographs), Caucasian elderly, and African students. While we

confirmed reliable sex differences in three previously validated facial metrics (Penton-Voak et al., 2001), none of the samples showed sex differences in fWHR, raising the question of whether findings linking fWHR to dominance-like behaviours in men have a specific physiological basis. We addressed this question in Chapter 4: in two samples we investigated testosterone as a possible underlying mechanism linking fWHR and behaviour. The behaviours that have been associated with fWHR are typically thought to be masculine (aggression, dominance), and some have been linked to testosterone. In two samples we demonstrated this link between fWHR and testosterone levels. In addition to baseline testosterone measures, in one sample we also assessed reactive testosterone levels as a consequence of a dating-scenario. In line with the ‘challenge hypothesis’, a theory positing that testosterone is raised in challenging situations, and that this raised level of testosterone is a more adequate measure of ‘competitiveness’, we show a stronger link between fWHR and reactive testosterone as opposed to baseline testosterone in this sample. Thus, while previous work stressed the importance of testosterone for sex differences, my work highlights its potential importance concerning variation *within* males, highlighting that within-sex variation can be meaningful.

In the second part of my thesis we assessed the importance of healthy skin colour (skin yellowness) in social interactions (Chapter 6) and possible endocrine associations with this putative signal of current condition. In more detail, we show in chapter 6 that higher skin yellowness is not only found attractive but also linked with increased perceived trustworthiness of individuals. We interpret these findings in light of the ‘behavioural immune system’ theory, which posits the existence of behavioural measures to avoid possible disease contraction. Deciding whom to have social interactions with (i.e. who to trust) may be influenced by an assessment of the likelihood for that person to be currently ill and contagious. To this end, skin yellowness is thought to arise as a function of ingested

carotenoids layering in the skin and thus reflects current health status. Low skin yellowness may then indicate current illness and may thus motivate observers to shun such individuals in favour of those with cues to good health so as to avoid contagion. In the following chapter (Chapter 7), we investigated whether testosterone levels are associated with skin yellowness in men. Skin yellowness is thought to arise as a function of ingested carotenoids layering in the skin and reflect current health status, as carotenoids can act as antioxidants and thus aid in the immune response (e.g. Dowling & Simmons, 2009). Additionally, testosterone is thought to suppress immune function (e.g. Grossman, 1985) potentially leading to a higher demand for bioavailability of carotenoids, preventing these from depositing in the skin. Our results are in line with this prediction, showing an inverse relationship between carotenoid-linked skin yellowness and testosterone levels in two samples. These results are important in light of the on-going debate concerning testosterone as a biomarker of genetic quality and health; testosterone effects may not always commensurate with an indication of a heritable improvement in health outcomes.

8.2 Implications for Theory

8.2.1 Testosterone reflects within sex rather than between sex variation

To date, theory has widely assumed that sexual dimorphism in humans (and other animals) is largely attributable to differences in sex hormones (e.g. Andersson, 1994), and furthermore, that within sex variation in hormone levels would be mapped onto the sexual dimorphism vector. However, results presented here (Chapter 3 and 4) largely question this theoretical position. We observed both a lack of association between testosterone and sexually dimorphic facial features, as well as a relationship with a non-sexually dimorphic metric: fWHR. While more research will be needed to confirm these results, they indicate a

dissociation of within sex and between sex variance of appearance based traits. This suggests the need for a broader theoretical framework of facial signalling incorporating both sexual dimorphism and within sex variation. In particular, intra-sexual selection in men will mostly be influenced by cues to competence and strength: these cues may have evolved independently of inter-sexual variation, if relevant selection pressures are distinct in men and women. To further illustrate this point, female breast size may be associated with fertility and parous status in women. Yet the dimorphism in chest measure is not indicative of quality in men: smaller chest circumference (the dimorphic opposite to breast size in women) is not linked to great, but instead lower masculinity.

8.2.2 Facial width associates with dominance-linked traits in non-human primates

The facial width-to-height ratio has to date been argued to reflect behavioural traits. Our findings indicate that these associations are not specific to humans, but also exist in phylogenetically closely related species. Considering capuchin and humans last shared a common ancestor around 43 million years ago, this association may be phylogenetically old and likely follows common selection pressures in both species. These selection pressures may arise from intra-sexual competition, which is thought to follow a similar strategy in humans and capuchin, both of whom live in multi-male, multi-female groups. Facial width may then signal bite strength (i.e. ability to injure) or skull robustness (i.e. ability to withstand injury) in both species as outlined above. These findings add to theory concerning the evolution of appearance based signals and cues to behaviour, since they indicate that facial signals are not human specific.

8.2.3 Healthy appearance is important for social interactions

Skin yellowness has recently been identified as an additional facial cue to current condition in humans (e.g. Stephen et al., 2011; Whitehead et al., 2012) and has been found to be attractive (Stephen et al., 2012). Findings in this thesis indicate that skin yellowness affects social interactions other than mate choice: while facial masculinity, thought to be a cue for genetic quality, has negative implications on trust decisions (probably because of several negative behavioural and personality traits associated with high masculinity); skin yellowness, as a signal for current health and condition, positively affects trust. A likely explanation for these findings arises from the ‘behavioural immune system’ theory: social interactions can be costly and thus pose a trade-off between cost (risk of infection) and benefits (e.g. resources, alliances). It follows that interactions with healthy individuals are more beneficial because risk factors are minimised. Skin yellowness may be of particular interest in this context, since it is thought to signal current health (as opposed to long-term health). These findings add to the growing body of literature investigating the functions of the behavioural immune system. In particular, current theory predicts group-level behavioural changes (e.g. elevated in-group favouritism; greater xenophobia; Fincher & Thornhill, 2012) as well as differences in mate preferences (DeBruine et al., 2010), as a result of high disease prevalence. The current work extends this theoretical framework to indicate behavioural implications at the individual level. In addition, our results provide important empirical evidence that the attribution of trust is not a simple halo-effect (‘what is attractive is good’), as masculinity was found attractive but not trustworthy, indicating a specific role of skin yellowness on trust, over and above its links with attractiveness.

8.3 Future Directions

8.3.1 How are appearance and behaviour linked?

While my work in this thesis has focused on one particular facial metric (fWHR), future research should expand this work to a more general approach of understanding facial and bodily signalling with specific links to competition. Intra-male competition is one of the major driving forces in human evolution (Keeley, 1996; Manson & Wrangham, 1991): those individuals who achieve higher status are afforded greater access to mates and resources (Andersson, 1994). Direct physical competition can, however, be extremely costly (through risk of injury), indicating that adaptations to reduce the costs of competition should have emerged (Puts, 2010; Sell et al., 2009). In particular, costs associated with incorrectly assessing the competitive abilities of other men may have shaped mechanisms that allow for accurate signalling and perception of these abilities. Several important research questions arise from this: Which particular facial and bodily structures are associated with actual competitive behaviours? Which facial structures reliably signal competitive behaviours? What are the underlying physiological bases of these associations between facial structure and behaviour?

To date, relatively little research has focused on this topic, although recent studies, including my own doctoral work, have indicated that facial and bodily features predict behaviours and physical ability linked to competition (e.g. aggression, achievement drive, upper-body strength: Carré et al., 2009; Lewis et al., 2012 / chapter 2; Sell et al., 2009). This work has provided initial support for the importance of male facial and bodily signalling in the context of intra-sex competition. With regards to physiological bases of morphology-behaviour associations, testosterone may provide one important link: it has been associated with facial appearance (Chapter 4), and has been suggested to reflect personality (Sellers et

al., 2007). Individual differences in testosterone levels correlate with dominance in adult and adolescent men (Carré et al., 2009b; Grant & France, 2001; Rowe et al., 2004; Vermeersch et al., 2010) and have been associated with power motivation (Stanton & Schultheiss, 2009) and increased vigilance to status-threats (vanHonk et al., 1999; Wirth & Schultheiss, 2009). Additionally, intra-individual changes in testosterone levels occur following anticipation and successful outcome of competition (for review see Salvador, 2005). In line with these findings, the ‘challenge hypothesis’ (Archer, 2006; Wingfield et al., 1990) suggests that men have relatively low levels of testosterone except when they are in a situation of either intra-sex competition or mating context when testosterone levels rise (Roney et al., 2003; 2006). Thus, behavioural patterns as well as facial and bodily features should be more closely linked to reactive rather than baseline levels of testosterone (Pound et al., 2009).

It follows that several questions are outstanding: 1) establishing those morphological features of faces and bodies linked to baseline and reactive testosterone; 2) assessing whether these baseline and reactive testosterone-linked features are associated with competitive personality traits; 3) testing whether competitive personality traits can be perceived from the face and whether these perceptions are mediated by the testosterone-linked facial traits identified; 4) testing how individual differences in observer dominance affect sensitivity to cues to competitiveness in faces; and 5) testing how intra- and inter-individual differences in baseline and reactive testosterone levels in the observer affect perceptions of others in the context of competition and status.

8.3.2 Comparative work in face perception

One line of enquiry arising from the findings concerning the behaviour appearance links in non-human primates presented here (chapter 5) concerns the question whether non-

human primates employ cues to behaviour present in the faces of their conspecifics. In an initial study Deaner et al. (2005) demonstrated that rhesus macaques would sacrifice fruit juice (a highly valued treat) for the opportunity to view faces of high-status monkeys while requesting juice ‘payment’ to look at low status individuals. In this work monkeys were, however, only presented with faces of familiar individuals thus rendering any extrapolation concerning the use of facial features other than for recognition impossible. In order to assess whether monkeys do use facial cues to behaviour, studies using facial photographs of individuals previously unknown to the participating monkey should be conducted. For instance, it would be informative to replicate Deaner et al.’s (2005) study using faces of unfamiliar individuals that are high and low in dominance respectively, as well as transforms of individual faces along the dominance axis to control for identity. A similar approach to the problem of face perception in monkeys would be to adapt a forced choice design whereby the participant is rewarded for looking at one of two possible screens, thus being able to freely choose which screen to attend to. Furthermore, research should assess the status of fWHR as a cue to dominance in a wider range of primate species and disentangle the relationship of canine size, fWHR and dominance (see Weston et al., 2004).

Outstanding questions discussed in this section are: 1) do primates use facial cues to dominance (e.g. fWHR) to judge another’s dominance; 2) is fWHR a cue to dominance across other primate species; and 3) if primates are able to discriminate along these lines, are there individual differences according to own dominance in accuracy of these discriminations?

8.3.3 Exploring skin colour as a cue to current condition

The results presented in the current thesis indicate for skin yellowness to play an important role in social interactions other than mate choice, likely as a cue to current condition. The behavioural immune system has been suggested to act as a first line of defence against contracting disease in the shape of behaviours that are designed to avoid pathogens. This system was originally documented in animals (e.g. Kavaliers et al., 2005; Kiesecker et al., 1999) and has since been suggested to exist in humans (e.g. Kurzban & Leary, 2001; Schaller & Park, 2011). One of the behavioural implications is the trade-off between disease avoidance and interpersonal benefits arising from social interaction. Thus, the result presented here, indicating that the skin colour of an individual may be important when assessing the risks (of contagion) from interaction fit well into the behavioural immune system framework and warrant further exploration.

In particular questions regarding individual differences both at individual level and population level are of interest. With respect to differences at the individual level, two mechanisms have been proposed to associate with behavioural immune responses: disgust sensitivity (Oaten et al., 2009) and prejudice (Navarrete et al., 2007). The effects of these measures on sensitivity to and preference for skin yellowness should be explored using behavioural and questionnaire measures of disgust and prejudice. Additionally, priming experiments similar to Little et al. (2011) would be valuable in order to identify state dependent differences in trust decisions. In this experiment, participants were primed with images either high or low in pathogen prevalence (e.g. open wound vs. healed scar) and were subsequently asked to rate faces for attractiveness. Results indicated an increase in preference for symmetry and sex typicality in the high pathogen primed group compared to the low pathogen primed group. A similar experiment concerning skin colour and trust decisions would be informative concerning skin yellowness as a cue used in disease avoidance

strategies, with pathogen primed individuals would show stronger preferences for trusting faces higher in skin yellowness compared to non-pathogen primed participants. Furthermore, at population level, differences in yellowness preference may be associated with disease prevalence (see e.g. DeBruine et al., 2010 for similar result in masculinity preference). This effect should be detectable using online studies assessing the association between skin yellowness and trust ratings in various countries, when controlling population level skin colour differences.

In addition, behavioural paradigms should be employed to test effects of skin yellowness on social interactions. For instance trust- and economic games may provide better measures of behaviours in social interactions than simple rating studies do. Participants may, for example, make fairer offers to others with healthy compared to unhealthy skin colour. Such experimental paradigms should in turn be paired with individual differences measures (e.g. disgust sensitivity) to disentangle perceptual and behavioural effects of skin yellowness.

Key questions in this area are: 1) do individual differences in disgust sensitivity and prejudice align with preferences for skin yellowness in social interactions; 2) does disease prevalence at the population level predict preferences for skin yellowness in social interactions; and 3) do such preferences influence actual interpersonal behaviour as assessed in experimental economic (trust) games?

8.4 Summary

In sum, this thesis examines a range of appearance-linked cues to dominance and trustworthiness and their biological underpinnings. Across six studies, several core results stand out. First, facial width-to-height ratio, a cue to dominance, is associated with more positive personality traits, namely achievement striving. Second, while we find that this

metric is not sexually dimorphic, we show it is associated with raised testosterone levels in men thus providing an explanation for the links to perceptions of high fWHR faces and behaviour previously reported to be associated with fWHR. Third, facial width-to-height ratio shows similar links to behaviour in a non-human primate, the capuchin. This finding is of great interest for the deeper understanding of evolutionary origins of behaviour – appearance associations. Finally, we demonstrate that skin yellowness, a putative marker of current condition, is inversely associated with testosterone in men and increases trust perceptions in male faces, indicating its importance for social interactions. In closing, the studies presented here contribute to the literature by extending previous work on facial appearance as well as leading it in new directions relevant for the understanding of non-verbal behaviour in social contexts.

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Appendix: Ethics Approval



11 September 2012

Ethics Reference No: <i>Please quote this ref on all correspondence</i>	PS9129
Project Title:	Individual differences in preference for health cues in the face
Researchers' Names:	Carmen Lefevre, Milena Dzhelyova and Amanda Hahn
Supervisor:	Professor David Perrett

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 15th August 2012. The following documents were reviewed:

- | | |
|----------------------------------|------------|
| 1. Ethical Application Form | 11/09/2012 |
| 2. Participant Information Sheet | 11/09/2012 |
| 3. Consent Form | 11/09/2012 |
| 4. Debriefing Form | 11/09/2012 |
| 5. Questionnaires | 11/09/2012 |

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (<http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf>) are adhered to.

Yours sincerely

 Convenor of the School Ethics Committee

Ccs Prof. D. Perrett (Supervisor)
 School Ethics Committee