Universidade de Aveiro Departamento de Educação e Psicologia
Ano 2017

MARIANA DE LURDES CARRITO

O EFEITO DO DIMORFISMO SEXUAL E DA CONFIABILIDADE PERCEBIDA NAS PREFERÊNCIAS DE ATRATIVIDADE: UMA PERSPETIVA EVOLUTIVA

THE EFFECT OF SEXUAL DIMORPHISM AND PERCEIVED TRUSTWORTHINESS ON ATTRACTIVENESS PREFERENCES: AN EVOLUTIONARY PERSPECTIVE

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Psicologia, realizada sob a orientação científica da Doutora Isabel Maria Barbas dos Santos, Professora Auxiliar do Departamento de Educação e Psicologia da Universidade de Aveiro, e do Doutor David Ian Perrett, Professor Catedrático da Escola de Psicologia e Neurociências da Universidade de St. Andrews, Reino Unido.

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Dedico este trabalho aos meus pais. Levo-vos comigo para o futuro.

o júri

presidente

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agradecimentos

Within the chaos, evolution shades some light over my atheistic, anxious being. Studying it, even as lightly and superficially as I did, gave me a great deal of pleasure and purpose. I would like to thank my mentors, professors Isabel and Dave, for guiding me through this discovery. With both your generosity and knowledge, I finished this journey with a deep sense of self-growing. I also would like to thank my colleagues that became true friends, Beatriz, Bem-Haja, Ana Teresa, Jacqueline, Diana, and Laura, for sharing with me their curiosity and dreams. I deeply feel appreciated for my family, my own tree of life. Thank you, father, for teaching me how to wonder and be mesmerised by life. Thank you, mother, for your warm lap when I almost lost myself of belonging. Thank you, brother, for your admiration and belief, I also do believe in your great existence and bright future. And I thank you João, for being my life partner and balancing my nature with nurture. Finally, I thank all the students that helped both collecting the data and participating in the experiments; these stories are about you.

I will do my best to continue my ongoing search through this marvellous and mysterious life. None was or will be possible without the thing we call love, which is still, and probably always will be, unexplained and unresolved by science. I love and thank you all.

palavras-chave

Atractividade, dimorfismo sexual, masculinidade, feminilidade, confiabilidade, percepção de faces, preferências em odores.

resumo

O trabalho apresentado nesta tese teve como principal objetivo investigar o impacto do dimorfismo sexual e da confiabilidade percebida na atratividade humana, considerando os pressupostos da Psicologia Evolutiva.

O Capitulo 1 apresenta uma revisão da literatura relevante na área, apresentando as principais teorias relativas ao que determina a atração humana, os fatores que contribuem para uma aparência atraente e os aspetos subjacentes às diferenças individuais na escolha de parceiro. O Capítulo 2 descreve um estudo de potenciais evocados, que pretendeu investigar os correlatos neurofisiológicos da perceção da forma sexualmente dimorfa das faces. Faces que variaram nas características de masculinidade / feminilidade induziram respostas diferenciadas nos componentes P2, EPN e LPP. Modulações específicas aquando da apresentação de faces do sexo oposto foram visíveis em P2 e EPN. Além disso, diferenças entre sexos, tanto nos componentes precoces como nos tardios, revelaram diferenças no processamento visual que não foram evidentes nos resultados comportamentais. O Capítulo 3 apresenta três experiências, nas quais investigamos a influência da cor da pele sexualmente dimorfa, para além da forma, na atratividade facial. Quando lhes foi permitido que manipulassem faces de homens com o objetivo de as tornar o mais atraentes possível, as participantes do sexo feminino aumentaram a masculinidade da cor da pele e diminuíram a masculinidade da forma. A cor da pele é, assim, proposta como uma característica sexualmente dimorfa que desempenha um papel importante nas perceções de atratividade ao comunicar o valor como parceiro. O Capítulo 4 investiga a possibilidade das mulheres preferirem odores de homens com uma cor de pele mais masculina. Participantes do sexo feminino cheiram e avaliaram os odores de vários dadores do sexo masculino, e os resultados mostraram que os odores dos dadores com uma cor de pele mais masculina foram considerados mais apelativos (“likeable”) e saudáveis, mas menos viris (“maleness”). Os resultados foram discutidos considerando o efeito das estratégias reprodutivas com a influência simultânea de estereótipos cognitivos. No Capitulo 5, explorou-se o papel da confiabilidade percebida na atratividade, simultaneamente com possíveis diferenças individuais com base nos níveis de ansiedade de interação social. Ao permitir que participantes de ambos os sexos manipulassem faces, tal como no Capitulo 3, tanto os participantes do sexo masculino como as participantes do sexo feminino escolheram aumentar a confiabilidade percebida para aumentar a atratividade, especialmente quando consideraram relações a longo-prazo. Além disso, a ansiedade de interação social correlacionou-se positivamente com a preferência por confiabilidade em faces, possivelmente indicando uma atração aumentada por parceiros seguros e confiáveis em indivíduos ansiosos.

Finalmente, o Capitulo 6 sumariza os principais resultados, discute as suas possíveis implicações teóricas e apresenta várias propostas de estudos futuros.

keywords

Attractiveness, sexual dimorphism, masculinity, femininity, trustworthiness, face perception, odour preferences.

abstract

The work presented in this thesis aimed to investigate the impact of both sexual dimorphism and perceived trustworthiness on human attractiveness, considering the perspective of Evolutionary Psychology.
Chapter 1 reviews the relevant literature in the field, acknowledging the main theories about what determines human attraction, the factors that contribute to an attractive appearance and the sources of individual differences in mate choice. Chapter 2 describes an ERP study that aimed to investigate the neurophysiological correlates of the perception of sexually dimorphic shape in faces. Faces that varied in masculinity/ femininity features elicited differentiated responses in P2, EPN, and LPP components. Faces of the opposite sex of participants elicited specific modulations on the P2 and EPN. Also, sex differences in both early, and later components revealed differences in visual processing that were not evident in behavioural results. Chapter 3 presents three experiments, in which we investigated the influence of sexually dimorphic skin colour, in addition to shape, on the perception of facial attractiveness. When allowed to manipulate male faces to make them as attractive as possible, female participants increased skin colour masculinity and decreased shape masculinity. Skin colour is proposed as a sexually dimorphic feature that plays a role in attractiveness perception by advertising mate value. Chapter 4 investigates the possibility of women preferring the odours of men with a more masculine skin colour. Female participants were asked to smell and rate the odours of several male donors, and results showed that the odours of donors with a more masculine skin colour were considered as more likeable and healthy, but scored lower in maleness. The results were discussed taking into account the effect of reproductive strategies with the simultaneous influence of cognitive stereotypes. In Chapter 5, the role of facial features of perceived trustworthiness on attractiveness was explored, along with the effect of individual differences in social interaction anxiety levels. By allowing participants of both sexes to manipulate faces as in Chapter 3, both males and females chose to increase perceived trustworthiness to rise facial attractiveness, especially when considering long-term relationships. Moreover, social interaction anxiety correlated positively with the preference for facial trustworthiness, possibly indicating an increased attraction for trustworthy secure mates in anxious individuals. Finally, Chapter 6 summarises the main findings, discusses their possible theoretical implications and presents some proposals for future studies.

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WHR	Waist-to-hip ratio
fWHR	Facial width-to-height ratio
EPC	Extra-pair copulations
2D:4D	Ratio of the lengths of the second to fourth manual digits
MHC	Major Histocompatibility Complex
FA	Fluctuating asymmetry
EEG	Electroencephalography
ERP	Event-related potentials
P1	Positive deflection around 100 ms after stimulus onset
N170	Negative deflection around 170 ms after stimulus onset
P2	Positive deflection around 200 ms after stimulus onset
EPN	Early posterior negativity
LPP	Late positive potentials

Chapter 1. Introduction and literature review

To me, Beauty is the wonder of wonders. It is only shallow people who do not judge by appearances. The true mystery of the world is the visible, not the invisible.

— *Oscar Wilde, The Picture of Dorian Gray*

1.1. EVOLUTIONARY PSYCHOLOGY

Charles Darwin (1809–1882) proposed the theory of evolution in his book “On the Origin of Species” (1859). His work would revolutionise biology and influence many other natural sciences including Psychology (Dewsbury, 2009). With his journey of 5 years around the world, in a ship named *Beagle,* he collected information about a variety of species namely from the Galápagos Islands in the Pacific Ocean. While doing so, he questioned the contemporary idea that species were immutable. He proposed that species change over time and descend from the same ascendant. He also addressed Thomas Malthus’s (1798) work which introduced the notion that organisms exist in numbers far greater than the ones that can survive and reproduce. Darwin explained such phenomenon by means of Natural Selection. Natural Selection was based on three main principles: variation, inheritance, and selection. He noticed that beyond the variation that existed between species, individuals within the same species demonstrated variation too. Hence he then proposed that some of that variation was inherited, i.e. passed down from parents to their offspring, and then passed them on to their offspring down through the generations. Based on the adaptation abilities provided by those inherited traits, related to survival and reproduction, only some individuals of the species would generate offspring. Selection occurred through differential reproductive success, with more adapted individuals gaining more opportunities to pass on their inherited qualities to future generations.

The inherited traits are more commonly taken as morphological, but behavioural patterns also constitute important adaptations, leaving as exclusion the developmental modifications as non-heritable. Darwin himself, acknowledging this fact wrote: “In the distant future I see open fields for more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history” (Darwin, 1859, p. 488). Psychology does now recognise the evolutionary roots of behaviour, seeking its possible origins and adaptive significance, namely through a relatively recent field: Evolutionary Psychology.

Known behavioural adaptations in humans are for example the fear of snakes (Seligman, 1971), disgust towards rotting meat and faeces (V. Curtis, Aunger, & Rabie, 2004) and preference for sweet. Without cognitive awareness of their adaptive functions, humans usually experience these emotions and preferences that assure our distance from poisonous species and contamination but also the demand for high energy food supplies, without realising its importance to individual and species survival.

1.2. SEXUAL SELECTION

Along with natural selection, there is another Darwinian principle that explains morphological and behavioural adaptations that do not serve individuals survival. The development of the peacock's tail and its preference by peahens intrigued Darwin as being potentially costly in case of a need to escape from predators (Buss, 1999). Why would male peacocks maintain a trait that can warn predators about its presence? Why would peahens be attracted to individuals that had a higher probability of getting killed? Another thing he noticed was that the peacocks' brilliant plumage was only present in male individuals and that peahens had a much more discrete appearance. These observations were then explained by the principle of sexual selection (Darwin, 1871) which states that some phenotypic traits arise as a consequence of successful mating.

Sexual selection operates through two main processes: intrasexual competition and intersexual competition (Buss, 2006; Darwin, 1871). Intrasexual competition represents the competitive battles in which same-sex members fight for mating opportunities. The traits that allow individuals to win contests, as strength, are passed on to the next generation given its contribution to enhancing mating opportunities (Buss, 1999). Intrasexual competition is responsible for the appearance of armamentation traits as the large and threatening deer's antlers. Deer with large antlers intimidate their opponents and win more fights, gaining more frequent access to females. Armamentation is used not only to fight over access to the other sex but also to control territory, resources, and status which in turn also attracts the opposite sex. Similarly, cues of physical strength in men assure their superiority in physical contests and are also usually perceived as attractive by women (Sell, Tooby, & Cosmides, 2009). Although in the majority of mammalian species, intrasexual competition is more frequent in males, given the lower female reproductive potential compared to the other sex (Buss, 2005), research is starting to recognise its presence between human females (Stewart-Williams & Thomas, 2013). Intrasexual competitiveness in women includes, for example, displaying physical attractiveness (Buss, 1988) and derogating female rivals (Schmitt & Buss, 1996).

Intersexual selection is the process whereby certain traits (that do not need to have direct survival value) are preferred by opposite-sex mating partners, resulting in the spreading or maintenance of those traits through generations (Buss, 2005). Those traits are ornamentation traits and are usually illustrated by the already referenced example of the peacock's tail. One example of ornamentation in humans is the presence of secondary sexual characteristics which is called by sexual dimorphism. Sexual dimorphism is defined by the "distinct difference in size or appearance between the sexes of an animal in addition to the sexual organs themselves" ("Sexual dimorphism," 2016). In humans, increased levels of sexual hormones (namely oestrogens and testosterone), during puberty, are responsible for the development of physical and sexual maturity of the secondary sexual characteristics. Those include a voice change, development of facial hair, and greater skeletal and muscle growth in the upper torso in males and breast growth, widening of the pelvic bones and increased fat deposits in the hips in females (Susman & Rogol, 2004). Feminine facial traits in women, such as a smaller chin and higher cheekbones, are clearly attractive for men (Johnston & Franklin, 1993; Perrett et al., 1998; Perrett, May, & Yoshikawa, 1994). Also, masculine body shape (Little, Jones, & Burriss, 2007) and voice pitch (Collins, 2000) in men are considered attractive by the opposite sex.

Darwin (1871) did not use the term intersexual selection and chose 'female choice' instead, since, in most species, the female individuals tend to be more discriminating or choosy about whom they want to mate with. Females have lower reproduction capacity and deal with higher costs of impregnation (e.g. gestation), meaning that they have to choose wisely before engaging in the act of intercourse. Similarly, human females are also 'picky' since they have to handle a nine-month gestation, investment through breastfeeding, and lost mating opportunities during a considerable amount of time. Men, in turn, have a greater desire for sexual variety than women (Buss, 2013) probably because, in ancient times, they experienced lower costs after conception. Even though nowadays, parental investment tends to approach equality between sexes (Stewart-Williams & Thomas, 2013), sexual strategies were shaped over many years in our evolutionary past and might still resist recent patterns of behaviour. Because of these differences in sexual strategies between men and women, and also because the work of this thesis focuses on mating preferences, the participants were mainly females since women are predicted to be pickier than men in mate choice.

1.3. 'PARENTAL INVESTMENT' THEORY

Robert Trivers (1972) proposed a theory that emphasises the sex differences in mating strategies that were mentioned previously. This theory aimed to explain the conditions under which sexual selection would occur for each sex. The 'parental investment' theory proposes that the relative proportion of parental investment varies between males and females. Parental investment is considered the time, physical effort and risks to life, involved in procreation, feeding, nurturing and protecting the offspring. According to this theory, the sex that invests less in the offspring is intrasexually more competitive, aiming to gain reproductive access to other sex individuals. On the other hand, the sex that invests more in offspring is predicted to be choosier in mate selection. This difference is particularly visible in species where males' body size differentiates more from females' (Stewart-Williams & Thomas, 2013). Some of the most persuasive evidence for 'parental investment' theory comes from observation of sex-role reversed species – species where males are the heavy investing parent [e.g. red-necked phalarope (Reynolds, 1987), stickleback (Svensson, 1988), and seahorse (Trivers, 1985; although see Vincent, 1994)]. In these species, as predicted by Trivers' theory, males are more discriminating than females in terms of mating.

Trivers acknowledges 4 different pairing strategies – Polygyny (practice of one male taking two or more female partners), monogamy (practice of one male taking one only female partner), polyandry (practice of one female taking two or more male partners) and polygynandry (two or more males have an exclusive sexual relationship with two or more females). Because of the sex differential in parental investment, polygyny is the most common reproductive strategy among humans (over 80% of cultures) (Buss, 2005). Because of the lower parental investment of males, they can engage in sexual relationships with multiple partners and fulfil the need of enhancing reproductive success. Nevertheless, despite the difference in parental investment in our species, human males compared to other animals, invest heavily as parents. Probably because of that, monogamy is the second most common reproductive strategy.

1.4. SEXUAL DIMORPHISM

Exaggerated sexually dimorphic traits are believed to signal genetic fitness. According to the 'handicap' theory (Folstad & Karter, 1992; Hamilton & Zuk, 1982; Zahavi, 1975) more masculine men normally possess more genetic quality since they can deal with the immunosuppression effects of testosterone and remain healthy. The 'testosterone immunosuppressive' theory has been supported, for example, by the fact that females are often more susceptible to autoimmune disorders (Grossman, 1990). Although this subject has been a matter of discussion (Prall & Muehlenbein, 2014; M. L. Roberts, 2004; Scott, Clark, Boothroyd, & Penton-Voak, 2013a), recent studies have corroborated this idea. Foo, Nakagawa, Rhodes, and Simmons (2016), in their meta-analyses, reported good evidence that testosterone suppresses the immune function, especially in studies with experimental designs (where testosterone levels are manipulated through supplementation), although lower effect sizes are found in correlational studies. Testosterone immunosuppression might then result in greater vulnerability to pathogen or parasite attack wherein only high-quality males, with good genes, can afford to display sexual characteristics fully without suffering large parasite loads (Folstad & Karter, 1992).

In the women's case, oestrogens might be handicapping sex hormones in a similar way that testosterone is for men (Thornhill & Gangestad, 1999a). Since oestrogens prepare women's body for reproduction and allocate energy resources for this task, energy provided to the immune system will be scarce, which in turn might result in a health decrease. Therefore, only high-quality females may be able to display fertility signs, as oestrogens displays, and remain healthy. However, it is possible that, in women's case, reproductive health or fertility might be more relevant than immunity or other health measures within the context of mate choice (Law Smith et al., 2006). Indeed both oestrogen and progesterone play a core role in a successful conception (Baird et al., 1999) and faces of women with higher levels of late follicular oestrogen are perceived as more feminine, attractive and healthy (Law Smith et al., 2006).

Therefore, sexually dimorphic traits in both sexes might then be taken as genetic cues of fitness and become attractive. Both men and women are prone to perceive such traits as beautiful or attractive, in other sex mates, as they assure direct and/or indirect benefits. Direct benefits provide direct gains to the partner as survival, reduced risk of infection and increased resources. On the other hand, indirect benefits are, for example, disease resistance, that assumes major importance as being transmitted to the offspring (Little, Jones, & DeBruine, 2011). Assuring individual and offspring survival are the ultimate evolutionary goals, and, as such, humans might feel attracted to anything that promotes those goals even without conscious aware of it.

1.4.1. Femininity

A universal preference for signs of femininity on women is almost unquestionable given the amount of evidence from men's attractiveness judgments (Perrett et al., 1998; G. Rhodes, 2006). It has been suggested that this prevalence is justified by the adaptive value of choosing a female mate that is better able to procreate (D. Jones, 1995). At puberty, the release of oestrogens in pubertal girls causes a fat deposition on the lower trunk, namely in their hips and upper thighs. This causes women's volume of body fat in these regions to be 40 percent greater than for men (Buss, 2008). Consequently, men are attracted to those femininity signs in women's body, namely waist curves in an hourglass fashion (Singh, 2002). Curvier women are believed to have higher levels of female reproductive hormones (Jasieńska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004) and hence advertise fertility. The waist-to-hip ratio (WHR) has been suggested to be a good predictor of women's attractiveness (Penton-Voak et al., 2003; Singh, 1993). The WHR is given by the "circumference of the waist measured at its narrowest point, divided by the circumference of the hips measured at their widest point" (Lee, Brooks, Potter, & Zietsch, 2015, p. 480). A high (unattractive) WHR is linked to reduced pregnancy rates in women undergoing in vitro fertilisation (Wass, Waldenström, Rössner, & Hellberg, 1997). Conversely, in a study by Singh (2004), women figures with low WHR were judged to be more attractive by male participants than figures with high WHR (although see Yu & Shepard, 1998). Also, women with low WHR demonstrate stronger preferences for masculine men than women with high WHR (Penton-Voak et al., 2003) even when controlling for body mass index (BMI) (Smith, Jones, Welling, et al., 2009). These last findings are interpreted as a sign of mate value in women, as explained bellow in 1.6.2 section. Recent findings have shown that men's attractiveness judgments do not rely exclusively on strategic depositions of fat in females' body but also on spine morphology (D. M. G. Lewis, Russell, Al-Shawaf, & Buss, 2015). A specific lumbar curvature angle in women seems to be attractive as it allows them to deal better with the forward-shifted centre of mass during pregnancy. Men are thought to prefer and select women with optimal lumbar curvature as they might be perceived as less vulnerable to spinal injuries, better at foraging during pregnancy, and better able to sustain multiple pregnancies without debilitating injury.

Besides paying attention to female's body, men are believed to infer cues of fertility by focusing on women's face traits. Oestrogen levels at puberty time determine the maintenance of a 'neotenous' look (from the Greek meaning "extended youth") in women's faces, which includes less prominent brows and jaws, thicker lips, smaller nose and head size, high eyebrows and large eyes (Law Smith et al., 2006; Perrett, 2010). Youth is attractive to the other sex since women's reproductive value declines steadily with increasing age after twenty (Buss, 2008). Hence, experiments show that judgments of facial attractiveness decline with the increasing age of the photographed women (Jackson, 1992). People with 'baby-like' faces are usually perceived as warmer, honest, sincere but also naïve and physically weaker comparing to more mature looking faces (Berry & McArthur, 1985; McArthur & Apatow, 1983; McArthur & Berry, 1987). Babyness can also signal 'incompetence' which becomes unwanted when a man is looking for a woman able to raise offspring. So, babyness features are only considered as attractive when combined with high and prominent chick bones. Prominent check bones are believed to develop by the influence of female sex hormones during women's maturation

(Symons, 1995). This combination of both traits is called the ‘sexy-scheme’ and includes both youth and maturity signals (Grammer, Fink, Møller, & Thornhill, 2003).

1.4.2. Masculinity

Similarly to women, men also undergo morphological transformations during puberty that not only alter their bodies’ morphology but also impacts their facial features. Testosterone’s increase during this process causes boys faces to grow prominent eyebrow ridges, large jawbones and to increase the width of the upper face. This last trait refers to a sexually dimorphic characteristic of the face that is independent of body size: the facial width-to-height ratio (fWHR). Weston, Friday, and Liò (2007) found that the growth trajectories of bizygomatic width start to diverge between males and females at puberty, which does not happen for the upper facial height (from the upper lip to the mid-brow), leading to a width-to-height facial dimorphism (greater ratio in men). Men with high fWHR have been reported to be more aggressive in sports and to be perceived as more dominant (Carré & McCormick, 2008) and aggressive (Carré, McCormick, & Mondloch, 2009) by others. High fWHR has also been associated with low trustworthiness (Stirrat & Perrett, 2010), deception (Haselhuhn & Wong, 2011), but also positive traits as achievement drive (G. J. Lewis, Lefevre, & Bates, 2012) and generosity to the in-group (Stirrat & Perrett, 2012).

However, more recent approaches have questioned the assumption that fWHR is sexually dimorphic (Lefevre et al., 2012; Özener, 2012). Such inconsistencies might be due to confounders in fWHR calculation or to different methodologies of testosterone’s level measurement (Lefevre, Lewis, Perrett, & Penke, 2013). A possible confounder is facial adiposity, which is sexually dimorphic itself, with women having larger fat deposits than men, particularly around the cheek area (Enlow & Moyers, 1982). Facial adiposity in women might be mistaken by larger bone structure, causing fWHR to be perceived as similar between the sexes. On the other hand, some researchers reported non-significant relationships between testosterone levels and perceived facial masculinity (Peters, Simmons, & Rhodes, 2008). However, according to the ‘challenge’ hypothesis (Archer, 2006; Wingfield, Hegner, Dufty, & Ball, 1990), associations between masculinity traits and testosterone should not be based on baseline values but rather on reactive testosterone. The ‘challenge’ hypothesis claims that testosterone rises as a consequence of a physiological mechanism that is activated during challenging situations related to intrasexual competition. Hence, when analysing the association between testosterone and masculinity, researchers should collect testosterone measures after participants’ confrontation with a situation where they would be competing with same-sex opponents. Pound, Penton-Voak, and Surridge (2009) found that the level of facial masculinity was not associated with pre-task (baseline) testosterone levels, but was associated with testosterone levels after success in the competitive task. Later, fWHR, in particular, was found to be associated with reactive testosterone too (Lefevre et al., 2013).

Masculinity traits, namely facial masculinity, may then be used as a cue to competitive-seeking behaviours. Masculinity influences perceived dominance (Boothroyd, Jones, Burt, & Perrett, 2007; Perrett et al., 1998; Swaddle & Reierson, 2002) and humans can judge physical strength and fighting ability just by looking at male faces (Sell, Cosmides, et al., 2009). Testosterone levels are associated with aggression (Archer, 2006) and competition (Booth, Shelley, Mazur, Tharp, & Kittok, 1989; Gonzalez-Bono, Salvador, Serrano, & Ricarte, 1999) in men. Puts (2010) claimed that masculinity evolved mainly and primarily as armament through intrasexual competition. According to this view, because women invest more in offspring and have a slower reproductive rate, there will always be fewer females than males available for mating. This causes men to induce in mating competition, aiming to exclude competitors by force or threat. Thus, masculine features such as men's beards and deep voices are designed specifically to help increase apparent size and dominance, in order to threat other males. Besides, size and musculature may serve as weapons to increase fighting ability (Puts, 2010). These armaments are thought to be sexually selected as females become attracted to dominant males that are more able to provide access to better resources and territory. The same males can also offer protection from rape and harm to offspring (Smuts, 1996). Accordingly, dominance does seem to predict the number of sexual partners in males (Puts, Hodges, Cárdenas, & Gaulin, 2007) and is considered attractive for fertile women (Puts et al., 2016; Snyder, Kirkpatrick, & Barrett, 2008).

Other evidence of how masculinity and testosterone are related to male dominance and physical strength comes from research focused on the ratio of the lengths of the second to fourth manual digits (2D:4D). 2D:4D has shown to be sexually dimorphic, with males having a lower ratio than women (Manning, Scutt, Wilson, & Lewis-Jones, 1998). Variation in this ratio is thought to reflect the influence of prenatal testosterone during development (Manning, Scutt, Wilson, et al., 1998) and may be established prenatally by the 13th or 14th-week post conception (Garn, Burdi, Babler, & Stinson, 1975; Phelps, 1952). In particular, high prenatal testosterone, low prenatal oestrogens, or both, cause a low (masculine) 2D:4D (Manning, Scutt, Wilson, et al., 1998). Low 2D:4D has been associated with facial masculinity (Fink et al., 2005), aggressive behaviour (A.

A. Bailey & Hurd, 2005) and heterosexual orientation (Putz, Gaulin, Sporter, & McBurney, 2004). Similar to fWHR, 2D:4D seems to be related to testosterone increase after ‘challenging’ conditions such as aggressive and sexual encounters, as predicted by the ‘challenge’ hypothesis (Wingfield et al., 1990).

Researchers have also been studying masculinity, namely perceived masculinity, through computer-based techniques that allow them to take the geometrical differences between average male and female face shapes and apply this difference to new faces, making masculine or feminine versions of original faces. In other words, the resulting faces can represent a degree of masculinity that lies between a typical female face and a typical male face. With this technique, researchers can create two versions of the same original face, or even create several versions of the same face diverging in masculinity. This methodology of manipulating masculinity has the major advantage of allowing masculinity preferences to be assessed independently of other facial traits that could be correlated with masculinity (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010). Perrett et al. (1998) asked their participants to alter faces along a shape masculinity continuum to obtain an optimal level of attractiveness. According to the ‘handicap’ theory, female participants were expected to masculinise the faces demonstrating a preference for cues of good genes and dominance. However, both participants from the UK and Japan preferred faces that were slightly feminised in shape. This contradiction was then explained by the ‘trade-off’ theory (Gross, 1996).

1.5. THE ‘TRADE OFF’ THEORY

Choosing a mate with exaggerated sexually dimorphic traits is not enough to ensure reproductive success as there are other physical and behavioural cues that might also be relevant to that purpose. Women, when choosing a partner that might later be the father of their children, cannot rely only on health and resources and probably need someone kind and supportive. Masculine men are perceived by women as less honest, less warm, less cooperative and with lower parenting abilities (Boothroyd et al., 2007; Perrett et al., 1998). This perception seems to be somehow accurate since men with high circulating testosterone are associated with troubled interpersonal relationships, infidelity, violence, and divorce (Booth & Dabbs, 1993) and weaker preferences for long-term relationships (Boothroyd et al., 2005).

The need for a supporting and caring partner is, according to the ‘trade-off’ theory (Gross, 1996), the reason why women might find facial femininity in men attractive. In fact, more feminine men are perceived as warmer, more emotional, honest, cooperative and as potential better parents (Perrett et al., 1998). The idea is that women, in certain contexts, might trade-off the desire for good genes and dominance for the desire of a cooperative partner. Contextual factors, like fertility, relationship goals and environmental harshness, alter the relative importance of the benefits and costs associated with choosing a more masculine partner and consequently influence attractiveness preferences. For example, Moore, Law Smith, Cassidy, and Perrett (2009) asked women what was their ideal number of children and then tested their preferences for masculine male face shapes. They found that women who desire a higher number of children preferred more feminine male face shapes and ranked cues of parental care over cues to immunocompetence in a partner. Hence, in cases similar to these, women seem to trade-off the benefits associated with partner's masculinity in exchange for paternal investment (Gangestad & Simpson, 2000).

1.6. STRATEGIC PLURALISM

1.6.1. Relationship context

Women seem to show different preferences according to individual and environmental circumstances, which implies that they do not adopt a single mating strategy but rather a strategic pluralism (Gangestad & Simpson, 2000). Namely, women seem to adopt different tactics and preferences based on whether they are looking for a partner to spend the night or a lifetime. Buss and Schmitt (1993) have found that women do place greater emphasis on a male's physical attractiveness and physical prowess in the context of a short-term relationship. Short-term mating is believed to have served, in ancestral women, the core purpose of reproduction. A short-term partner was needed for intercourse and then could be dismissed or replaced. By contrast, a long-term partner would be expected to parent the offspring, protect the family and stay supportive at least until the offspring's independence. Given these requirements, good quality masculine men are supposedly a good bet for a short-term relationship since they can transmit good genes/immunity to descendants. However, given their limited ability for parenting, masculine men might not be so suitable for long-term relationships. In this case, more feminine men would assure the protection and support so that the offspring can survive over the course of its development.

Penton-Voak and co-workers (1999), in their second experiment, gave participants a task similar to the one already mentioned from Perrett et al. (1998). Participants were given a chance to alter male face shapes along a masculinity continuum, according to their attractiveness preferences. However, this time, participants were asked to do this task considering short- or/and long-term relationship goals. Results showed that fertile women preferred more masculine male faces when considering short-term relationships than when considering a long-term relationship context. Relationship context was then analysed in subsequent studies (Little, Burt, Penton-Voak, & Perrett, 2001; Penton-Voak et al., 2003) that found consistent results. After that, researchers have taken relationship context to the equation when analysing women's preference for various types of attractiveness traits (e.g. Little, Cohen, Jones, & Belsky, 2007; Little & Jones, 2012; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Scott, Swami, Josephson, & Penton-Voak, 2008; Smith, Jones, Little, et al., 2009; Vukovic et al., 2011).

1.6.2. Mate value

Even when considering the same relationship goal, women report individual differences in what they find attractive. These individual differences may in part be due to the extent with which a woman is personally affected by the positive and negative traits associated with masculinity (Little et al., 2001) which depends on individual mate value. Own mate value is generally analysed through attractiveness ratings made by others or by the self. Researchers usually ask participants to rate their own attractiveness on a Likert scale from 'very unattractive' to 'very attractive' or else ask others to look at the participants' face and do the same procedure. Given the importance of women's attractiveness to men's mate choice, women might take into account their self-attractiveness when judging other-sex faces (and other traits), to increase their reproductive success. Once again, this process occurs without conscious intervention, and women do not explicitly think something like: "This one is more attractive because the others are out of my league". Without acknowledging it, women that differ in self-attractiveness do seem to be attracted by different features in men.

As mentioned before, masculine men are thought to be less prone to long-term relationships and have lower parenting abilities (Kruger, 2006). High quality (more attractive) females are thought to prefer more masculine males since their own mate quality guarantees their ability to compete for, retain, and/or replace masculine partners. They might also have the capacity to bridge the need of a supporting mate by being able to invest more than other females (Little et al., 2001). On the contrary, low-quality females will have more difficulties dealing with males' desertion and probably look for someone more cooperative, who will not abandon them and the offspring (Little et al., 2001). Because of that, self-attractiveness effects are normally visible only in the context of long-term relationships (Burriss, Welling, & Puts, 2011b; Penton-Voak et al., 2003) since choosing a masculine man as a short-term partner does not involve the risks mentioned for either high or low-quality females. This way, both more and less attractive women are attracted to more masculine men in short-term relationships, probably enhancing the probability of gaining genetic benefits. However, when attractiveness judgments are pondered for long-term relationships, less attractive women enhance preferences for femininity in males, while highly attractive women maintain their preferences at the same level of masculinity.

Perceived self-attractiveness is not constant, being influenced by the exposure to the attractiveness of other individuals in the same population. Several studies have shown that when exposed to photographs of individuals with variable attractiveness, participants adjust their perceived self-attractiveness in accordance (Cash, Cash, & Butters, 1983; Kenrick & Gutierres, 1980; Thornton & Moore, 1993). Exposure to photographs of physically attractive others generally decreases self-ratings of attractiveness, whereas exposure to less attractive others might increase ratings of self-attractiveness. Therefore, individuals ‘choosiness’ will also be influenced by this kind of exposing experiences. Little and Mannion (2006) altered the self-attractiveness perceptions of female participants by exposing them to same-sex images that could be very or not at all attractive, and asked them to choose between masculinised and feminised versions of several faces. Results showed that women, when exposed to highly attractive women’s faces, lowered self-rated attractiveness and preferences for male facial masculinity, while the opposite happened when exposed to unattractive same-sex pictures. This occurs because mate choice happens within a biological marketplace in which mate value is determined by the laws of supply and demand (Pawłowski & Dunbar, 1999). Market value changes, along with the level of intrasexual competition, based on perceived relative number of attractive or unattractive individuals within the population.

1.6.3. Menstrual Cycle

This strategic pluralism in women does not depend exclusively on relationship context and self-attractiveness. Human females also seem to adjust their preferences according to the phase of the menstrual cycle (Gangestad, Thornhill, & Garver, 2002; B. C. Jones et al., 2008; Penton-Voak et al., 1999). The benefits of copulating with a male with good gene markers are only meaningful if conception is achieved, which leads females to be more attracted to masculine men in the fertile (follicular) phase of the menstrual cycle. It is possible that men may have the ability to sense when women are in the follicular phase since in a Burriss and Little's study (Burriss & Little, 2006) male participants rated masculine males as more dominant if their female partners were fertile. Other evidence comes from a study of Miller, Tybur, and Jordan (2007) who found that strippers earned more tip money per night when they were in their most fertile period. However, there is the possibility that men are only reacting to changes in women's behaviour that happen in specific phases of the menstrual cycle. In fact, women are more likely to engage in extra-pair copulations (EPCs) when fertile (Bellis & Baker, 1990) and to pursue non-genetic benefits, as resources and support, when not fertile.

However, some authors have questioned the cycle shifts on women's preferences. Wood, Kressel, Joshi, and Louie (2014) claimed that previous findings are most possibly false positives and that support for effects was largely due to publication bias. Other studies (e.g. Harris, Pashler, & Mickes, 2014) have argued that assessments of women's fertility have been the target of several different calculations, allowing researchers to search for favourable results. Given this, methodological standards for accessing preference shifts over menstrual cycle need to be revised (Gangestad et al., 2016; although see Gildersleeve, Haselton, & Fales, 2014) and, meanwhile, hormonal influence may be studied through periods in women's reproductive life with more extreme variation. Increased preference for facial masculinity have been reported comparing peri vs. post-pubescence (Little et al., 2010), post-partum vs. pregnancy (Cobey, Little, & Roberts, 2015) and circum vs. peri-menopause (B. C. Jones, Vukovic, Little, Roberts, & DeBruine, 2011; Little et al., 2010; Vukovic et al., 2009). This evidence supports the idea that the benefits of choosing a masculine partner become diminished when conception is not a relevant concern.

1.6.4. Hormonal contraception

Variations based on female's menstrual cycle seem to be exclusive to when there is no use of hormonal contraception. Wedekind, Seebeck, Bettens, and Paepke (1995) found oral hormonal contraceptive use in women to be associated with preference for body odours of men who share a relatively high proportion of genes with them. Because genetic variability is desired to assure offspring viability and health, this pattern was taken as disruptive. The oral contraceptive pill changes the normal hormonal state of the menstrual cycle by mimicking pregnancy (Alvergne & Lummaa, 2010). In normally cycling women, during the middle phase of the cycle, occurs a pick of luteinizing hormone (LH) causing ovulation. After ovulation, the formation of *corpus luteum* causes a progesterone increase. If implantation does not occur, the *corpus luteum* degenerates, causing a sharp drop in levels of both progesterone and oestrogens and ultimately menstruation happens. Because contraceptive pill inhibits the release of LH and FSH (follicle-stimulation hormone), fluctuations of progesterone and oestrogens are softened, and approximate the hormonal state of pregnancy (Alvergne & Lummaa, 2010). Because of that, pill users' may not show preferences for signs of genetic dissimilarity in partners during mid-cycle and might keep attracted by men traits that ensure parenting and support (as they would if pregnant). Also, women might decrease their preference for masculine traits in men, in order to retain the benefits of more feminine supportive men. Little, Burriss, Petrie, Jones, and Roberts (2013) conducted a study comparing masculinity preferences in women before and after they started taking the pill and found that participants decreased their preferences for facial masculinity after approximately three months of use. In a second experiment they also found that women that were taking the pill during formation of current partnerships, were dating more feminine-faced men than women that were not. A later study found that women's sexual satisfaction in long-term relationships was influenced by changes in hormonal contraceptive use (S. C. Roberts et al., 2014). Such findings showed that if women were taking the pill at the moment where they started their current romantic relationship but stopped during it, reported lower sexual satisfaction than women that were still currently taking it or had never used the pill at any point.

It remains to be determined which hormone, our group of hormones mediate the changes in women's attractiveness preferences and general sexuality (Cobey et al., 2015). Some research presents testosterone as the more viable mediator, namely because it increases near ovulation in women (Alexander, Sherwin, Bancroft, & Davidson, 1990; Dabbs Jr, 1990) and is also increased in post-pubescent comparing to peri-pubescent girls (Angold, Costello, Erkanli, & Worthman, 1999). Also, although not rapidly decreasing after the beginning of menopause, testosterone does decrease with age (Zumoff, Strain, Miller, & Rosner, 1995). However more research is needed, namely to understand the effects of other hormones, such as progesterone and oestrogens, over women's lifespan. Also, there is the possibility that much of the reported findings on preference differences between pill and non-pill users are due to pre-existing behavioural patterns that distinguish those groups of women. For example, Guillermo, Manlove, Gray, Zava, and Marrs (2010) reported that women using hormonal contraceptives show greater interest in engaging in short-term sexual relationships and Little et al. (2002) found that oral contraceptive use was associated with a greater number of reported sexual partners. It remains to be known if women with such characteristics are more predisposed to start using hormonal contraceptives or if it is the use of the pill that leads to such behaviours and interests.

1.6.5. Partnership status

Partnership status may also cause differentiated preferences for sexually dimorphic cues since studies report a higher preference for facial masculinity when female participants are currently in a relationship (Little et al., 2002). At the fertile phase of their menstrual cycle, committed women are thought to increase their preference for facial traits of masculinity in male faces as a representation of what they would like to pursue in a man for an EPC. Although this mechanism may also serve to maximise genetic benefits in offspring for women without partners, Little and colleagues (2002) found that this preference was significantly superior in women within committed partnerships. Note that partnered female participants in this study reported to be happy in their current relationships, which supports the idea that the preferences observed may indeed represent a strategy for EPCs. B. C. Jones, Little, Boothroyd, DeBruine, et al. (2005) found that women reported themselves to be less committed to their partners in the fertile phase of in their cycles when compared with the luteal phase.

1.6.6. Environmental factors

Women also seem to adjust their preferences according to environmental demands (Little, Cohen, et al., 2007; Penton-Voak, Jacobson, & Trivers, 2004). Gangestad and Buss (1993) proposed that people who lived in areas with high pathogen incidence would show preferences for mates with enhanced pathogen resistance. Therefore, they found a positive association between parasite prevalence and the strength of both male and female preferences for attractive and healthy individuals. Later, DeBruine, Jones, Crawford, Welling, and Little (2010), using a large, cross-cultural sample of individuals, investigated the relationship between women's preferences for male facial masculinity and National Health Index of each participant's nationality. Their main finding was that masculinity preference increased as health decreased, indicating that women in environments with a high prevalence of pathogens and inaccessible or poor healthcare prefer masculine men. They assumed that since masculine men signal immunocompetence, such men would be more likely to father healthy offspring. Besides increasing offspring survival, preference for healthy masculine men may also include infection avoidance, which enables women to stay healthy and provide long-term parental investment (Little, DeBruine, & Jones, 2011). Given this, differences in pathogen prevalence are likely to result in cross-cultural differences and within-cultural agreement in mate preferences and mating systems (DeBruine, Jones, Tybur, et al., 2010). In fact, differences were found between Jamaican and UK participants in a study of Penton-Voak and colleagues (2004), with Jamaican women preferring more masculine faces than the other group. Intra-individual differences may arise from similar explanations based on disgust sensitivity. Women that score higher in the Three Domains of Disgust Scale (Tybur, Lieberman, & Griskevicius, 2009) prefer signs of masculinity in faces (DeBruine, Jones, Tybur, et al., 2010), bodies and voices (B. C. Jones et al., 2013) (although findings seem exclusive to younger adults and the forced-choice preference measure (Lee & Zietsch, 2015)).

Brooks et al. (2011) reanalysed DeBruine Jones, Crawford, et al. (2010) data, including further information, namely about income inequality, homicide rates and women's empowerment and education. They found that income inequality was a better predictor of masculinity preferences in women than national health status. Such findings were interpreted as a preference by less empowered women, living in unequal societies where homicide rates are higher (related with higher levels of intrasexual competition in men), for more dominant/ high-status men. Because of that, DeBruine and co-workers, in response, presented additional analyses of the original data, but still reported evidence of the superiority of health when predicting mate preferences (DeBruine, Jones, Little, Crawford, & Welling, 2010). They showed that health measures (comparing to income inequality) are better predictors of women's preference for facial masculinity among different US states. This incongruence of results raises the possibility that both health and male-male competition explain different amounts of variance in mate preferences, depending on the population of study, which makes it difficult to infer which is the best predictor (DeBruine, Jones, Little, et al., 2010).

Apart from that, correlational studies on the influence of environmental factors feature another divergence on how they affect mate choice. Two main factors may drive preferences in opposite ways: the already mentioned pathogen incidence and resource scarcity. While pathogen incidence is believed to be positively related to masculinity preferences as an adaptive preference for healthy resistant mates, resource scarcity might bias women's mate choice towards femininity traits that advertise male investment, relationship commitment and parental qualities (Lee & Zietsch, 2015). Accordingly, studies analysing resource harshness reported a positive relationship with women's preferences for femininity in males (e.g. Little, Cohen, et al., 2007; Watkins, DeBruine, Little, Feinberg,

& Jones, 2012). Resource harshness is believed to lead women to prefer investing/stable partners that can help them during pregnancy and provide necessary resources for eventual reproduction and offspring survival (Little, Cohen, et al., 2007). However, such interpretation is not consensual since other studies claim that resource scarcity could as well lead to an enhanced preference for masculinity (Lee & Zietsch, 2015). In a harsh environment with high mortality, the probability of offspring survival decreases. Consequently, it could be beneficial to focus on acquiring good genes for the offspring to allow them to thrive in the hostile environment.

An alternative explanation for cross-cultural differences may reside on the technology access of each population. Women seem to prefer more feminine men on low developed environments (with low urbanisation) (Scott et al., 2014) and in populations without internet access (Batres & Perrett, 2014). Although Batres and Perrett (2014) findings were interpreted as related to resource scarcity, it is possible that the main influence comes from media exposure. Media exposure may lead people to inaccurately perceive the range and prevalence of desirable others (Kenrick & Gutierres, 1980; Kenrick, Neuberg, Zierk, & Krones, 1994) and that affects the 'choosiness' of individuals as discussed in section 1.6.2. Therefore, women that live in developed countries and have frequent access to the internet, because they are exposed to a high range of unfamiliar attractive faces, may prefer more masculine faces given their biased perception of own market-value.

More studies are needed to understand better which environmental factors do influence mate choice and the weight of each of them. The use of experimental methods, where the perception of environmental factors is manipulated, might shed some light in the inconsistencies found so far in correlational studies (DeBruine, Jones, Little, et al., 2010). Either way, it is important to note that although different results and explanations have been presented, "variation in women's masculinity preferences is systematic, rather than arbitrary" (DeBruine, Jones, Little, et al., 2010, p. 2), which validates the need for further research.

1.6.7. Strategic pluralism in men

Intrasexual variation in attractiveness preferences of men is weaker than women's as femininity is consistently preferred across studies (G. Rhodes, 2006). Men do place great weight on attractiveness in the appearance of women while women sometimes might prioritise status and resources (Buss, 2008) and it is all supposedly given to the inequality in parental investment between sexes. While a woman feels the need to choose a high-quality partner for impregnation but also someone who provides the care and the protection required to guard the offspring that took her so much investment to raise, ancestral men could afford to focus more exclusively on finding fertile and healthy female mates. That may be the main reason why it is common to see attractive young women becoming romantically involved with much older men who happen to be wealthy. Consistently, women report more emotional distress when men lie about their social status, their financial resources, or the depth of their romantic commitment, whereas men are most upset with women's deception about sexual access and sexual infidelity (Haselton, Buss, Oubaid, & Angleitner, 2005). However, when considering short-term partners, women value physical attractiveness just as much as men (Li & Kenrick, 2006).

However, there is some evidence that men also engage in strategic pluralism to enhance their reproductive success. Nowadays, men, similarly to women, do place greater weight on kindness and intelligence when considering a long-term relationship while focusing mainly on physical attractiveness for a one-night stand (Li & Kenrick, 2006). Also, because humans have bi-parental care and men often invest in raising their children, men are expected to value cues to mothering ability and a cooperative personality in long-term relationships (Little, Jones, Feinberg, & Perrett, 2013). Evidence suggests that men give higher importance to body attractiveness in short-term relationships (Confer, Perilloux, & Buss, 2010; Currie & Little, 2009).

Besides being influenced by relationship context, men's attractiveness preferences also depend on own mate quality (Pawłowski & Dunbar, 1999), and the interaction between the two (Burriss et al., 2011b; Little, Jones, et al., 2013; Regan, 1998). Burriss and co-workers (2011b) found that attractive men tend to express higher preferences for femininity comparing to less attractive ones, particularly when considering a short-term relationship. Less attractive men are probably dissuaded from pursuing feminine/highly attractive females since such women will be interested in masculine/attractive men. Hence, such mating effort towards high-quality women would be unproductive and doomed to failure (Burriss et al., 2011b). Also, because attractive/feminine women are more likely to cheat on their partners (Buss & Haselton, 2005), particularly if they are less attractive than them (Gangestad, Thornhill, & Garver-Apgar, 2005), low-quality men face higher risk of raising a child which is not their own. Accordingly, low-quality men score lower in the Sociosexual Orientation Inventory (SOI), meaning that they report less desire to engage in sex without closeness and commitment (Simpson, Gangestad, Christensen, & Leck, 1999). A subsequent study found similar evidence regarding relationship context and mate value (Little, Jones, et al., 2013), and showed that men's preferences for facial femininity are influenced by partnership status too. Partnered men prefer more feminine women for short-term partners (possible EPCs) given their need to be choosier and guarantee that such risky behaviour will result in a successful impregnation.

Lastly, men are also influenced by environmental harshness in their attractiveness preferences. Little, Cohen, et al. (2007) reported men favouring femininity in their short-term preferences, especially under a harsh hypothetical scenario comparing to a supposedly safe situation. In Lee and co-workers' study (2015) men reporting enhanced pathogen disgust, preferred women with lower WHR. Since lower WHR is positively associated with women's health and fertility (Jasieńska et al., 2004; Singh, 1993, 2002; Wass et al., 1997), this indicates that men that score high in pathogen avoidance are placing greater importance on such benefits (Lee et al., 2015). In contrast, resource scarcity enhanced preferences for high WHR, which was interpreted as men's preference for more masculine females that would be more able to help in competing and acquiring resources. These two studies again claim different conclusions, which highlight the need for further investigation on the influence of environmental harshness.

1.7. SEXUAL DIMORPHISM AND HEALTH: COLOUR CUES

Many examples of sexually dimorphic features that occur on the animal kingdom rely on manifestations of colour. The mentioned case of the peacock is a prime example since its plumage has more bright colours than the peahens' (Zi et al., 2003). Other examples of sexual dichromatism are frequently found in other bird species (Bortolotti, Negro, Tella, Marchant, & Bird, 1996; Dale, Dey, Delhey, Kempenaers, & Valcu, 2015). For example, male blue tits are chromatically more yellow than females (Slagsvold & Lifjeld, 1985). Also, sexual dichromatism has been reported in several amphibians, as in frogs (Bell & Zamudio, 2012), many fish species (Kodric-Brown, 1998) and other vertebrates. Similarly to sexually dimorphic morphology, colour is believed to be an honest signal of the individual's condition. In most of the cases, males display more bright and colourful phenotypes than females (Folstad & Karter, 1992). Interestingly, the species that have the opposite pattern (females been brighter than males), as phalaropes and jacanas, have been associated with sex-role reversal (females are larger, more competitive, and more ornamented than males, and males invest more on offspring) (Eens & Pinxten, 2000; although see Heinsohn, Legge, & Endler, 2005). In primates, colour also seems to influence attractiveness between the sexes. For example, female rhesus macaques exhibit preferences for the red versions of male faces (Waitt et al., 2003).

Recently, several studies have reported the importance of skin colour in human attractiveness (e.g. Fink, Bunse, Matts, & D'Emiliano, 2012; Fink, Grammer, & Matts, 2006; B. C. Jones, Little, Burt, & Perrett, 2004; Matts, Fink, Grammer, & Burquest, 2007). The multi-million industry of facial cosmetics is itself a proof of how much skin colour influences the perception of facial beauty, and much of its use seems to serve the purpose of exaggerating sexually dimorphic differences (Russell, 2009). Also, skin colour is believed to influence facial attractiveness given the fact that it also is somehow altered by owners' health. Fink, Grammer, and Thornhill (2001) presented participants with several face stimuli and found out that attractiveness ratings were positively correlated with the homogeneity of skin colour distribution. B. C. Jones and co-workers (2004) tested if humans could tell how sexually attractive were other individuals just by looking at small patches of their skin. Participants did respond as predicted and attractiveness ratings of all face photos were correlated with colour and texture of the patches.

Much of the colour displayed by animals comes from the presence of pigments as carotenoids. Carotenoids are yellow-red organic pigments that are ingested through the animal's diet and assume an important function of health maintenance, helping to protect against oxidative damage (Dowling & Simmons, 2009). The same applies to humans, that normally increase the numbers of carotenoids through ingestion of fruit and vegetables (Alaluf, Heinrich, Stahl, Tronnier, & Wiseman, 2002). There is a possibility that carotenoids are important for the human reproductive system, as they are for other species of mammals, birds and fish (Biard, Surai, & Møller, 2005; Chew, 1993; Pike, Blount, Lindström, & Metcalfe, 2009). Human participants, when given the opportunity to adjust face skin yellowness, choose to increase it in order to enhance perceived healthiness and attractiveness (Stephen, Coetzee, & Perrett, 2011; Stephen, Law Smith, Stirrat, & Perrett, 2009; Whitehead, Re, Xiao, Ozakinci, & Perrett, 2012). In times of illness, carotenoids are depleted (Whitehead, Ozakinci, & Perrett, 2012), namely in the case of HIV and malaria (Stephen et al., 2011). However, certain exceptions can occur under which exaggerated skin yellowness may also be linked to unhealthy conditions (e.g. jaundice) (Knudsen, 1990). The presence of carotenoids in the body contributes to a yellower appearance of faces but, as it also associates with skin blood perfusion and oxygenation, increased carotenoids results also in a redder hue. Stephen, Coetzee, Law Smith, and Perrett (2009) gave participants the opportunity to adjust skin colour redness of Caucasian faces, simulating changes of oxygenated (red tinted skin) and deoxygenated blood (blue tinted skin), in order to increase their apparent health. They found that participants when searching for the healthiest appearance, chose to increase oxygenated blood colour but to decrease the deoxygenated blood colour (when allowed to adjust both).

Skin redness is also affected by the presence of haemoglobin in the blood and consequent skin vascularization and blood perfusion (Piérard, 1998). High blood oxygenation is increased by aerobic exercise becoming consequently associated with cardiovascular fitness (Armstrong & Welsman, 2001). Redness is lowered in acute sickness and cardiovascular disease (Stephen, Coetzee, et al., 2009). Redness has been associated not only with health but also to dominance and masculinity. Male rhesus macaques show facial reddening in the mating season, in response to increased levels of testosterone (L. Rhodes et al., 1997). In mandrills, red facial colour is related to male's rank (Setchell & Jean Wickings, 2005; Setchell, Smith, Wickings, & Knapp, 2008). Likewise, in humans, the colour red tends to be associated with physical dominance and aggressiveness. In combat and team sports, wearing red enhances the probability of winning (Attrill, Gresty, Hill, & Barton, 2008; Hagemann, Strauss, & Leißing, 2008; R. A. Hill & Barton, 2005; Rowe, Harris, & Roberts, 2005). Also, skin reddening happens as consequence of increased blood flow and is associated with anger responses (Drummond & Quah, 2001). Stephen, Oldham, Perrett, and Barton (2012) conducted an experiment where female participants were allowed to manipulate skin colour of male faces in a red-green axis to maximise their perceived dominance, aggression, and attractiveness. They found that the highest levels of red were associated with aggression, followed by dominance, and the least but still positively with male attractiveness. Accordingly, facial skin redness is sexually dimorphic, with men being redder than women (Edwards & Duntley, 1939).

Another component of skin colour that has been studied in humans is its luminance. Skin luminance depends on the presence of melanin in the skin (Stamatas, Zmudzka, Kollias, & Beer, 2004), since melanin darkens the skin tone. Melanin is beneficial to the human body since it plays an important role in immunity (Burkhart & Burkhart, 2005) and protection against UV radiation (Brenner & Hearing, 2008). Nonetheless, melanin also associates with health costs since it impairs the photoproduction of vitamin B, potentially leading to defective bone mineralisation (Murray, 1934). Sun-tanning increases skin melanin and it is currently fashionable in Western, Caucasian populations (Melia & Bulman, 1995), being considered unattractive, however, in other populations for its stereotypical association with lower social classes (Hulse, 1967). Also, skin luminance seems to be sexually dimorphic with women being lighter than men, and with light skin being considered more attractive in female faces (Edwards &

Duntley, 1939; Hulse, 1967; Russell, 2003; Van den Berghe & Frost, 1986). Hence, light skin in women has been taken as a sign of fecundity (Aoki, 2002). Van de Berghe and Frost (1986), in their first article as co-workers, cite a testimony from a Hopi member, an indigenous tribe of United States of America. This man stated: “I preferred a light complexion, for we say that women with a dark skin may be half of men” (Talayesva, 1942, pp. 281-282). The use of skin lightening products is common among black South Africans, especially for upwardly mobile, educated women (Glenn, 2008). In contrast, a darker hue may be desirable in male individuals. According to Frost’s proposal (1994), a darker man is perceived as a potential rival by same-sex individuals and as a high-quality potential future mate by the opposite sex.

Based on the mentioned evidence, there are reasons to believe that colour is sexually dimorphic in humans as it is in other animals. Sex differences in individual colours have already been reported, as in redness and luminance (Edwards & Duntley, 1939). Skin colour has also been reported as influenced by women’s menstrual cycle phase (Prokop, Pazda, & Elliot, 2015) and mate-value, namely by individual differences in WHR (B. C. Jones, Little, Boothroyd, Feinberg, et al., 2005). However, since then, a more recent and unified analysis of skin colour as contributing to attractiveness was missing. A recent proposal claimed skin colour, as an indicative of current health condition, to be more determinant on perceived attractiveness than shape masculinity (Scott, Pound, Stephen, Clark, & Penton-Voak, 2010; Stephen, Scott, et al., 2012). However, another hypothesis relies on the possibility that skin colour itself may be a masculinity/femininity index, advertising mate quality too.

1.8. FACE ATTRACTIVENESS: OTHER BIOLOGICALLY BASED TRAITS BESIDES SEXUAL DIMORPHISM

1.8.1. Averageness

Former investigations have searched for an optimal geometric formula that could represent facial beauty. A popular proportion that was advertised as the secret for facial beauty is the golden ratio. Euclid of Alexandria (300 B.C), the founder of geometry, was the first to give a clear definition of what the golden ratio was (Livio, 2008). Antique Greeks defined the golden ratio as a representation of a rectangle where the ratio of the smaller side to the longer side was the same as the ratio of the longer side to the longer and shorter sides put together[1] (Perrett, 2010). This ratio has been applied to human faces by some researchers. They divide the face into parts and, for example, consider the lower face relative to the whole face, and analyse the relative proportions of those parts. As appealing as this notion can be, there is no evidence that such ratio is more frequent in attractive faces than unattractive ones, and there are several ratios, that one can calculate in the human face, that do not resemble in any way the golden ratio. However, there are other kind of proportions in the human face that have been linked to higher attractiveness and beauty.

Humans tend to find faces with familiar proportions (average faces) as attractive. Averageness refers to the resemblance of one specific face to the majority of faces within a population (Little, Jones, et al., 2011). Galton (1879) first noted that if he blended several faces together, then the resulting face was perceived as more attractive than the individual faces he used. Similar findings were later encountered with more recent computer-based techniques. Faces averaged digitally do look more attractive than the unmanipulated individual ones, and this effect is amplified as the number of faces included in the averages increases (Langlois & Roggman, 1990; Langlois, Roggman, & Musselman, 1994). However, Alley and Cunningham (1991) noted that, as the number of faces that were included in the average increased, the smoother the skin texture became. Could the attractiveness effect be due to the appearance of the skin of the resulting face? The response to this question seems to be negative, since later studies proved that even when the colour/texture of the face is controlled, the average face was still perceived as more attractive (Apicella, Little, & Marlowe, 2007; P. Benson & Perrett, 1992; Little & Hancock, 2002; G. Rhodes & Tremewan, 1996).

Theorists have proposed that averageness advertises developmental stability, i.e. the ability to deal with environmental or genetic stress during development (Thornhill & Møller, 1997). Other proposal claims that averageness promotes the optimal performance of bodily functions (Symons, 1979). Thus, as an example, an average phenotypic form of the nose would allow better breathing. Also, Thornhill and Gangestad (1993) hypothesised that average faces might be attractive since they denote heterozygosity. Since heterozygosity ensures genetic diversity, the preference for this trait would allow better defence against parasites and promote healthy offspring. It could be argued that average faces are more attractive simply because they are more symmetrical than others. However, studies that manipulated both traits individually found that averageness and

[1] $(a + b) / a = a / b$ or $a = 1.618 \times b$

symmetry had independent influences in face attractiveness (B. C. Jones, DeBruine, & Little, 2007; G. Rhodes, Sumich, & Byatt, 1999).

Some researchers debated the contribution of averageness to attractiveness since although averaging faces result in an attractive mean face, attractive faces are not necessarily average. Perrett et al. (1994) showed that the average of a set of individual faces is less attractive than the average of only the attractive individuals of the same set. Besides that, they noticed that the exaggeration of the features that were exclusive to the attractive individuals (what distinguished them from the others), also enhanced perceived attractiveness. So, apparently, in this case, distinctiveness and not averageness was associated with optimal attractiveness (DeBruine, Jones, Unger, Little, & Feinberg, 2007). In fact, face averageness may only partially explain what it takes to make a beautiful face.

1.8.2. Symmetry

Symmetry is considered another trait that advertises the biological quality of the individuals and hence influences their attractiveness as mates. Fluctuating asymmetries (FAs) are non-directional (random) deviations from symmetry on individuals' phenotype (G. Rhodes, 2006). Symmetry has been proven to relate with genetic endurance since FAs are supposedly originated by inbreeding, homozygosity, parasite load, poor nutrition and genetic mutations (Møller, 1997; Møller & Swaddle, 1997; Parsons, 1990; Polak, 2003). Accordingly, symmetry is considered as a sign of developmental stability and mate quality. It signals increased ability to deal better with environmental and genetic pressures during development. More symmetric individuals are thought to provide mates with direct (disease contagion avoidance) and indirect benefits (healthy genes supply to offspring) (Little, Jones, et al., 2011). In humans, body symmetry is positively related to sperm number, speed, and migration in men (Manning, Scutt, & Lewis-Jones, 1998) and with fecundity in women (especially breast symmetry) (Manning, Scutt, Whitehouse, & Leinster, 1997). It also seems to relate positively with the total number of sexual partners of men (Thornhill & Gangestad, 1994) and women seem to experience more orgasms if their partners are symmetrical (Thornhill, Gangestad, & Comer, 1995). When it comes to face symmetry, studies have found that it correlates positively with some health measures (e.g. respiratory health) (Thornhill & Gangestad, 2006).

Mealey, Bridgstock, and Townsend (1999) measured face symmetry of monozygotic twins and found that it correlated positively with face attractiveness ratings, wherein the more symmetric of the twins was rated as more attractive than the other. Because monozygotic twins share the same DNA but different developmental pathways, the effect was assigned to developmental stability. Other studies, also using unmanipulated faces, found the same positive correlation between symmetry and attractiveness (Grammer & Thornhill, 1994; Scheib, Gangestad, & Thornhill, 1999). In later studies, researchers altered faces to get perfect symmetry, using vertically bisected half-faces aligned with its mirror image. Those studies, using this type of 'chimeric' face images, did not find the same positive contribution of symmetry in face attractiveness. However, such methodology was criticised since 'chimeric' face images contain unnatural proportions that are not viable in real life, consisting in structural abnormalities (Perrett et al., 1999). More recent studies used improved methodological techniques that consisted on calculating a symmetric shape of the face by averaging of the height and lateral position of corresponding pairs of features on the left and right sides of the face, and then remapping the original face image according to such calculation (Perrett et al., 1999). When using this type of methodology, results do show a positive relation between face symmetry and attractiveness (Little & Jones, 2003, 2006; Perrett et al., 1999; G. Rhodes, Proffitt, Grady, & Sumich, 1998).

Previous authors have argued the preference for face symmetry not to be due to evolutionary reasons towards optimal mate choice, but instead, it was merely a by-product of the design of our perceptual system (Enquist & Arak, 1994; Johnstone, 1994). According to them, symmetry was preferred just because it was more readily perceived by the visual system. However, such hypothesis could not explain Gangestad and Thornhill's (1998; 1999b) and Rikowski and Grammer's (1999) findings. In these studies, women preferred the body odour of more symmetric men even without ever seeing them. This evidence supports the idea that symmetry does advertise mate quality and might be sexually selected.

1.9. ATTRACTIVENESS THROUGH SCENT

As mentioned in the previous section, women were shown to prefer the scent of more symmetrical men. This experiment was first conducted by Gangestad and Thornhill (1998), who hypothesised that women should be more attracted by the odours of symmetrical men, especially during ovulation. Women were asked to smell and rate the attractiveness of t-shirts that were worn by men during two nights in a row. Attractiveness ratings were then compared to men's FA. According to their predictions, t-shirts worn by more symmetric men were rated as more attractive than the ones from less symmetrical men but only by female participants that were in the fertile phase of their menstrual cycle. Similar findings were found by the same authors in a subsequent replication of the study

(Thornhill & Gangestad, 1999b) and Rikowski and Grammer (1999). Thornhill and co-workers (2003) reporting similar findings of female preference for odours of more symmetric men, found that contrary to previously mentioned studies, even women with low conception risk (non-pill users that were not in their fertile phase of the menstrual cycle) exhibited the same preference for odours of symmetry. Apparently, pill use does seem to interfere with female odour choice, while the effect of the menstrual cycle is more controversial.

Other studies have also found evidence that olfaction cues may be used for mate-choice. Male body odour attractiveness has been found to correlate positively with ratings of male physical attractiveness (S. C. Roberts et al., 2011) and male dominance (Havlíček, Roberts, & Flegr, 2005). Other evidence comes from studies investigating odour preferences and MHC (major histocompatibility complex) compatibility. The MHC is a group of genes with the important immunologic function of recognising foreign molecules in vertebrates' body (Thornhill et al., 2003). In non-human animals, studies have shown that preferences for individuals with different MHC-congenic strains are mediated by chemosensory urinary cues. Preferences for individuals with different MHC-congenic strains have been reported in mice (Yamazaki et al., 1976) and also in several species of fish, reptiles, and birds (S. C. Roberts, Gosling, Carter, & Petrie, 2008). Preferences for immunologic dissimilar males were thought to lead to heterozygotic offspring, which would have increased resistance to infectious diseases (Potts & Wakeland, 1990). Preference for MHC-dissimilar individuals might prevent kin-matings ('inbreeding avoidance' hypothesis) (J. L. Brown & Eklund, 1994). Evolutionary scientists believed that our ancestors relied more on the sense of smell than we do today since they lived in groups with their extended kin and needed to avoid inbreeding. Inbreeding leads to MHC homozygosity which in turn may lead to susceptibility to infectious diseases (Potts, Manning, Wakeland, & Hughes, 1994). The best-known study acknowledging body odour preferences, already mentioned in section 1.6.4, was conducted by Wedekind and colleagues (1995). In their study, women were asked to smell T-shirts that have been worn by men during a two night period. Results showed that women who were not using the contraceptive pill (but not pill-users) rated as more pleasurable the odours from t-shirts of MHC-dissimilar men (see also Wedekind & Füri, 1997). Interestingly, these women also reported that the odours of MHC-dissimilar men reminded them of their current or previous partners. However, several studies have reported null effects when trying to replicate Wedekind and colleagues (1995) findings (e.g. S. C. Roberts et al., 2008; Thornhill et al., 2003).

Odour preferences in humans is a new ground area of research with much more to be explored. Communication between members of our species might happen through the olfaction perception of chemical signals. Rhesus monkeys (*Macaca mulatta*) were found to produce volatile, short-chained fatty acids in their vaginal secretions that influence males' sexual interest (Michael & Keverne, 1968), which were later named 'copulins' (R. F. Curtis, Ballantine, Keverne, Bonsall, & Michael, 1971). Similar substances have been reported as present in human females (Michael, Bonsall, & Kutner, 1975), with varying composition throughout the menstrual cycle (Preti & Huggins, 1975) and thought to influence male attractiveness judgments (Grammer, Fink, & Neave, 2005), although this last hypothesis remains unproved. Copulins are also referred to as belonging to the general group of 'pheromones' (Kohl, Atzmueller, Fink, & Grammer, 2001).

The word 'pheromone' was only invented in 1959, to represent a chemical signal emitted by one individual that alters either the behaviour or physiology of another individual (Karlson & Luscher, 1959). Butenandt, Beckmann, Stamm, and Hecker (1959) discovered the first sex pheromone in silkworms. Since then, several pheromones have been identified through the animal kingdom, namely in mammals (Wyatt, 2015). As mammals, there are strong indications that humans might have pheromones too. Several molecules have been presented by research as human 'putative' pheromones, namely androstenone (5α-androst-16-en-3-one), androstenol (5α-androst-16-en-3α-ol), androstadienone (Δ4,16-androstadien-3-one) as male, and estratetraenol (estra-1,3,5(10),16-tetraen-3-ol) as female (Wyatt, 2015). Female preferences for androstenone have been reported to change with menstrual cycle phase and with pill use (Grammer, 1993; Hummel, Gollisch, Wildt, & Kobal, 1991; Renfro & Hoffmann, 2013). Cornwell and co-workers (2004) found that pleasantness ratings of androstadienone and estratetraenol correlated with female and male preferences, respectively, for sexually dimorphic shape in opposite-sex faces. Other studies have failed to find preferences for the identified putative pheromones (e.g. Black & Biron, 1982). According to Wyatt (2015), although evolutionary psychologists have been doing a very good job, conducting well-designed experiments to test preferences for pheromones, it remains to be scientifically proven that those molecules are real human pheromones.

Given this limitation, perhaps the most valid way to study human chemical communication, at least for now, is through analyses of body odours preferences. Body odours are caused by the presence of bacteria in the secretions of the sebaceous and apocrine glands which, in turn, are very frequent in human armpits (Leyden, McGinley, Hölzle, Labows, & Kligman, 1981). It is believed that no human smells the same and that we all have a ‘body odour signature’, that is produced in our armpits (Lenochova & Havlíček 2008). Because sebaceous and apocrine glands develop during puberty (Wyatt, 2015) simultaneously with the development of secondary sexual characteristics, it is possible that body odour communicates the masculinity/ femininity of the individual. Previous studies have looked for women’s preferences for faces of men with high testosterone. Findings indicate that women’s risk of conception (measured by the presence of oestrogen levels) covaries with preferences for faces of men with high testosterone (Roney & Simmons, 2008; Roney, Simmons, & Gray, 2011). Likewise, Thornhill, Chapman, and Gangestad (2013) searched for women’s preferences for high testosterone men through the perception of body odours and found that women in the fertile phase of their cycle demonstrated similar preferences (although see Rantala, Eriksson, Vainikka, & Kortet, 2006). Further studies are needed to investigate if preferences for other sexually dimorphic traits can be accessed through the perception of smell.

1.10. SEXUAL ORIENTATION - *THE DARWINIAN PARADOX*

Sexual orientation refers to a person’s preference for emotional and sexual relationships with individuals of the same sex (homosexual), the other sex (heterosexual), or either sex (bisexual). Despite these categorizations, recent approaches take sexual orientation as a continuum. This revolutionary way of seeing sexual orientation was first due to a pioneer study of Kinsey and his colleagues (Kinsey, Pomeroy, & Martin, 1948; Kinsey, Pomeroy, Martin, & Gebhard, 1954), in which they found that people who define themselves as heterosexuals have had homosexual experiences — and vice versa. Accordingly, they created a seven-point scale (from 0 to 6) to describe people’s sexual orientation. Kinsey’s proposal was then supported by Robert Epstein’s work (2007) that gathered data from over 18000 people who characterised themselves as gay, straight, or bisexual and then responded to a questionnaire about their sexual desires and experiences. Epstein found an overlap where people that claim different sexual orientations reported similar sexual behaviours and fantasies (e.g. some heterosexual individuals reported having homosexual fantasies or behaviour as some homosexual individuals reported having heterosexual tendencies). These results support the idea that sexual orientation should be viewed as a continuum rather than a matter of discrete categories.

Apart from that, sexual orientation is definitely puzzling for evolutionary psychologists (Buss, 1999). Evolutionary theories do go in line with the observation of superiority of heterosexuality in human cultures and argue that heterosexuality is a psychological adaptation since it enables reproductive success. However, the presence of other sexual orientations, even if comparatively small, challenges evolutionary predictions. Homosexual behaviours are not only exclusive of the human species, and have been observed across a wide range of other animals (Sommer & Vasey, 2006). Acknowledging this fact, Muscarella (2000) proposed the 'alliance formation' theory in which homoerotic behaviour had a specific function: alliance formation. According to this theory, homoerotic behaviour between young and older men allowed the younger men to gain allies, status, and sexual access to females. However, evidence for this advantage seems to be restricted to some cultures and does not apply to a vast number of cases.

Another proposed explanation relies on the 'kin selection' hypothesis (E. O. Wilson, 1975, 1978). According to this hypothesis, homosexuals are 'non-reproducers' who contribute to the well-being of their genetic relatives, namely their siblings. The families with homosexual members would gain 'special' reproductive advantages (in comparison to families without homosexuals), resulting in the indirect replication of genes for homosexuality through sibling lineages. However, this theory has received mixed empirical support, with studies failing to find significant differences between the dedication to siblings between homosexual and heterosexual men (e.g. Rahman & Hull, 2005).

Another explanation is the 'female fertility' hypothesis, which suggests that genes for male homosexuality can evolve by increasing fecundity of female relatives. Camperio-Ciani, Corna, and Capiluppi (2004) found that female maternal relatives of homosexuals have higher fecundity than female maternal relatives of heterosexuals. The 'female fertility' hypothesis suggests that the genes responsible for male homosexuality, although decreasing male's reproductive success, confer a general benefit outcome, by the compensating increased reproductive rate in the female relatives.

Recently, Kuhle and Radtke (2013) proposed the 'alloparenting' hypothesis to explain the sexual fluidity typical of women. Women are thought to be more sexually fluid since they fluctuate between heterosexual and homosexual preferences and desires more frequently than men (Diamond, 2008). The 'alloparenting' hypothesis explains this phenomenon as a means for ancestral mothers, when faced with paternal desertion, death, or divestment of resources, to get support from same-sex individuals on raising offspring. In other words, sexual fluidity promoted the acquisition of alloparenting care from other female friends. This strategy would be very beneficial given the extreme dependence of human infants on caregivers to survive and the high frequency of rape in ancestral times (Kuhle & Radtke, 2013). We can conclude that, based on the number of theories presented to explain the origin of homosexual orientation, more research is needed to understand the origin of the so-called ‘Darwinian paradox.'

Maybe because of this puzzling nature of sexual orientation, studies in evolutionary psychology about homosexual preferences are scarce. Some researchers claim that homosexual men have attraction patterns similar to heterosexual men, as both emphasise attractiveness over status and change preferences from relatively older to younger partners with age (J. M. Bailey, Gaulin, Agyei, & Gladue, 1994; Kenrick et al., 1994). Lesbians are reported to have similar preferences to heterosexual women by placing little emphasis on physical appearance, although doing it even less than heterosexuals (Buss, 2008). Meanwhile, other studies, especially with psychophysiology or neuropsychological measures, found attractiveness preferences in homosexual individuals to be somewhat similar to those of opposite-sex heterosexuals. Homosexual men, like heterosexual women, were found to have increased activation in the hypothalamus when smelling putative male pheromones (Savic, Berglund, & Lindström, 2005). Studies with fMRI measures have demonstrated that the homosexual’s response to faces is modulated by sexual preference, but not necessarily by gender per se (Ishai, 2007; Kranz & Ishai, 2006). Also, homosexual men are attracted to masculine body traits as muscularity the same way as heterosexual women do (Levesque & Vichesky, 2006).

Although the participants of the studies presented in the following chapters were mainly heterosexual, acknowledging the preferences of people with different sexual orientations and the evolutionary explanations for such behaviours, helps us understand the phenomenon of human attraction in a more comprehensive way.

1.11. INTERSEXUAL SELECTION BASED ON SOCIAL ATTRIBUTION: THE EFFECT OF PERCEIVED TRUSTWORTHINESS

Regardless of sex, gender or sexual orientation, humans use others’ physical traits, namely faces, to predict other’s behaviour and personality. As previously said, masculinised faces of men and women are perceived as less honest, warm, cooperative and emotional (Perrett et al., 1998). Highly masculine men tend to be perceived as more aggressive and dominant (Carré & McCormick, 2008; Carré et al., 2009). Facial appearance can even be used as a cue to other’s willingness to be in long-term relationships. Boothroyd, Jones, Burt, DeBruine, and Perrett (2008) presented participants with composite and real faces, and in both types of stimuli, they were able to identify restricted (participants reporting higher preference for long-term relationships) vs.

unrestricted individuals (participants reporting higher preference for short-term relationships) with no other information besides facial images.

Much of the personality attributions are based on perceived attractiveness. There is a well-known phenomenon that influences how we perceive other's character which is the 'What is beautiful is good' stereotype (Dion, Berscheid, & Walster, 1972; Eagly, Ashmore, Makhijani, & Longo, 1991; Feingold, 1992; Langlois et al., 2000). Also claimed as a 'halo effect', it refers to the tendency to automatically ascribe more positive traits to attractive people. When judging faces, humans appear to parse attractiveness with socially desirable traits. In their study, Eagly and colleagues (1991) found that participants associated attractive individuals with more prestigious occupations, happier marriages with more competent spouses and with better prospects for personal fulfilment, just by looking at their faces. This effect has been extensively investigated given its social implications. For example, good looking people tend to be perceived as less likely to commit murder and armed robbery (Saladin, Saper, & Breen, 1988) which might lead to condemnation of innocent unattractive individuals and forgiveness of attractive but guilty ones. The 'halo effect' itself goes in line with the evolutionary predictions regarding mate value. As noticed, attractiveness serves the function of helping individuals to acquire high-quality mates, hence relying on attractiveness as signalling good attributions is clearly adaptive.

People are very confident when judging character by 'reading faces' (Hassin & Trope, 2000) and normally are also very consistent in their judgments (although not necessarily correct) (Langlois et al., 2000; Penton-Voak, Pound, Little, & Perrett, 2006). Physiognomy, the pseudoscience of reading faces, reached its apogee in the 19th century when Johann Lavater published his book "Essays on Physiognomy: For the promotion of the knowledge and the love of mankind" (1775-1778) in which he detailed how to relate facial features to personality traits. In his autobiography, Darwin reported that he was almost impeded from boarding on the historical *Beagle* by the captain, a fan of Lavater's work, who did not believe that a person with such a nose would possess "sufficient energy and determination" for the voyage (as cited in Todorov, 2008, p. 208). Francis Galton also conducted work on physiognomy, trying to identify face traits associated with antisocial behaviour. He did it by 'blending' faces of criminals, with a similar, while less sophisticated, technique to the one used currently in face research (Perrett, 2010). In spite of Galton's failure in finding the 'face of crime' and the demise of physiognomy in science (Cleeton & Knight, 1924), it is true that humans do infer personality from faces and use such information in their daily social relationships (Hassin & Trope, 2000).

One of the important social judgments that humans make when meeting someone new, almost instantaneously (Willis & Todorov, 2006), is inferences about trustworthiness. The importance of trustworthiness relies on its impact on basic approach-avoidance responses (Todorov, 2008), used by individuals to decide whether to approach or to avoid a stranger or, as the present work proposes, a new partner. Researchers have identified which structural facial traits contribute to a more trustworthy appearance, which are high inner eyebrows, pronounced cheekbones, wide chins and shallow nose sellion. On the contrary, faces with low inner eyebrows, shallow cheekbones, thin chins and deep nose sellion tend to be perceived as less trustworthy (Todorov, Baron, & Oosterhof, 2008). Facial width also influences trustworthiness perceptions, with men with wider faces, which is a masculine trait, being perceived as less trustworthy (Stirrat & Perrett, 2012). Finally, trustworthiness judgments are influenced by emotion cues even in neutral faces, with untrustworthy faces appearing angry and being characterised by V-shaped brows and ∩-shaped mouths, and trustworthy faces appearing happy and being characterised by Λ-shaped brows and U-shaped mouths (Oosterhof & Todorov, 2009). While structural features of trustworthiness reveal the negative association between trustworthiness and masculinity (Oosterhof & Todorov, 2008), expressive cues of trustworthiness highlight the strict relation between trustworthiness and emotion. Smiling faces are perceived as more trustworthy (Krumhuber et al., 2007) while low trustworthy ones evoke anger attributions (Winston, Strange, O'Doherty, & Dolan, 2002). Either way, some researchers claim that trustworthiness inferences are unlikely to be derived by emotion alone (Bzdok et al., 2011) since trustworthiness judgments have been shown to be separable from the effects of facial emotion (Adolphs, 2002; Winston et al., 2002).

Trustworthiness judgments, and other typical social inferences as attractiveness, approachability, distinctiveness, and intelligence, were shown to reach above chance levels of agreement with previous ratings of the faces just about 100 ms of stimulus exposure (Santos, 2003; see also Willis & Todorov, 2006). Later research showed that discriminations between trustworthy and untrustworthy faces can happen after only 33 ms of exposure (Todorov, 2008). Interestingly, these trustworthiness judgments are quite invariant since people tend to show equivalent responses even if more time is provided, with additional time only serving to increase confidence in judgments (Willis & Todorov, 2006). Todorov, Pakrashi, and Oosterhof (2009) presented participants with extremely trustworthy or untrustworthy versions of faces for 20 ms that were immediately masked by the neutral version of the face, which was presented for 50 ms. Participants were asked to judge the trustworthiness of the last face presented. They found that those neutral faces were perceived as more trustworthy when preceded by trustworthy primes than when preceded by untrustworthy primes. So trustworthiness decisions do happen very fast and might influence later social inferences and perceptions. Again, it is important to note that trustworthiness assessments, although rapid and consistent, are not always valid concerning the real personality of others (Rule, Krendl, Ivcevic, & Ambady, 2013).

Todorov's team has been extensively working on the identification of the configurations of facial features that lead to specific social attributions. They started by presenting computer-generated faces to participants while asking them to describe spontaneously the person they saw. Later, they asked another group of participants to look at emotionally neutral faces and rated them in the traits (e.g. emotional stability, attractiveness, aggressiveness, intelligence) identified by the previous group. Lastly, they used a Principal Components Analysis (PCA) of these ratings to identify main dimensions of trait judgments of faces and understand how they relate to each other. Oosterhof and Todorov (2008) found two main components that accounted for most of the variance in judgments: valence/trustworthiness and power/ dominance. A similar technique had been previously used in Fiske, Cuddy, and Glick's study (2007) that identified warmth (closely related to approachability and trustworthiness) and competence (closely related to dominance) as the main universal dimensions of social cognition. Fiske and co-workers claimed that such dimensions reflected evolutionary pressures given the individuals' need to determine whether they were encountering a friend or foe (warmth) and how effectively any such intentions could be enacted (competence). Recently, Sutherland and colleagues (2013), also using data-driven methods, replicated the two-dimensional structure of social judgments proposed by Todorov's team. However, instead of using computer-generated faces, they used real faces drawn from the Internet. Probably because real faces vary in different aspects not included in Todorov's artificial faces, a new dimension aroused, which they called youthfulness-attractiveness. Within their model, older faces were perceived as less attractive, more trustworthy (when female), and more dominant (when male). Independently of the model in consideration, it is notable that trustworthiness is one of the main social attributions that humans make when observing others' faces.

It is possible that trustworthiness perceptions were also important to our ancestors, given its associations to one of the primitive structures in our brain, the amygdala. Adolphs, Tranel, and Damasio (1998) first showed that bilateral amygdala damage patients had their capacity of evaluating the trustworthiness and approachability of faces impaired. Comparing to other brain damage controls and normal controls, these patients tended to give higher ratings of trustworthiness and approachability to faces that were evaluated as untrustworthy and unapproachable by the other two groups. Several later fMRI (functional magnetic resonance imaging) studies confirmed the involvement of the amygdala in trustworthiness judgments, claiming an enhanced activity in this brain region during the exposure to untrustworthy faces (Engell, Haxby, & Todorov, 2007; Winston et al., 2002). Recent studies have questioned this linear amygdala response to face trustworthiness, reporting U-shaped quadratic responses, where both trustworthy and untrustworthy faces elicit larger activations than faces in the middle of the continuum (Mattavelli, Andrews, Asghar, Towler, & Young, 2012; Said, Baron, & Todorov, 2008; Todorov, Said, Engell, & Oosterhof, 2008). Quadratic effects in the amygdala have also been found for face attractiveness (Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007), with increased activation to both very attractive and unattractive faces. Another similarity between inferences about attractiveness and trustworthiness comes from evidence of studies manipulating oxytocin levels (Theodoridou, Rowe, Penton-Voak, & Rogers, 2009). Oxytocin administration seems to increase both ratings of trustworthiness and attractiveness of male and female faces when rated by both sex participants. Trustworthiness and attractiveness ratings are positively correlated (Todorov, Said, et al., 2008). This means that trustworthy faces tend to be perceived as attractive and vice-versa.

The relationship between trustworthiness and attractiveness has also been analysed in studies involving self-resembling faces. DeBruine (2005) used computer-based techniques to create female versions of male participant's faces and asked them to rate the attractiveness of those images. She found that, when participants considered a short-term relationship, where the sexual appeal is the dominant criterion, facial resemblance decreased attractiveness while increasing trustworthiness. However, other studies have shown that human attractiveness preferences sometimes happen towards familiarity with parental traits, a phenomenon named imprinting. Imprinting preferences have been reported in non-human animals (Kendrick, Hinton, Atkins, Haupt, & Skinner, 1998; Lorenz, 1943) and humans (Bereczkei, Gyuris, Koves, & Bernath, 2002; Bereczkei, Gyuris, & Weisfeld, 2004). Little, Penton-Voak, Burt, and Perrett (2003) found evidence that humans tend to choose partners with identical hair and eye colour of the opposite-sex parent and that we are also attracted to age cues consistent with our parent's age when we were born (see also Perrett et al., 2002). Imprinting effects are, in turn, affected by the quality of the relationship with the parent. Daughters are more likely to choose mates who are similar to their fathers if their relationship was good during childhood and if the father provided great emotional support (Bereczkei et al., 2004; Wiszewska, Pawlowski, &

Boothroyd, 2007). Assortative mating (pairing with similar partners) may be beneficial for long-term relationships since it increases genetic compatibility between mates (Tregenza & Wedell, 2000). It also might ensure that mate choice is made based on successful/ trustworthy parents as models (Todd & Miller, 1993). Given the costs associated with inbreeding, discussed earlier, Bateson (1978) proposed 'optimal-outbreeding' (an optimal equilibrium between genetic dissimilarity and assortment) to be the most adaptive choice.

Given this, it is possible that cues to trustworthiness might be taken into consideration for mate-choice, particularly when participants ponder a long-term relationship. Personality traits are proven to be very important in mate choice for both sexes (Buss, 1989; Buss & Barnes, 1986), and trustworthiness may be one of the desired features. If that is the case, trustworthiness traits would be expected to be attractive, which seems to be true since attractive faces are trusted (R. K. Wilson & Eckel, 2006). Trustworthiness may even be considered in mate choice as it is linked with sexual dimorphism, with less trustworthy faces being perceived as more masculine (Oosterhof & Todorov, 2008). In fact, Campbell and co-workers (2009) found that female faces with more masculine appearance are perceived as less desirable as long-term partners and also as less trustworthy. Such results were interpreted as a way for men to increase the probability of paternity. Because increased levels of testosterone in women are associated with increased number of sexual partners and more unrestricted sociosexual orientation (Cashdan, 1995; van Anders, Hamilton, & Watson, 2007), men might prefer more feminine/trustworthy females to reduce the risk of cuckoldry. Cuckoldry is believed to be very costly for males who, when engaging in a long-term relationship, take the risk of providing paternal care for unrelated offspring. The sentence "Mama's baby, papa's maybe" illustrates the reason for the men's need to be highly attentive to signals of sexual betrayal (Buss, 2008) and hence may prefer trustworthy females. However, future research needs to further investigate this hypothesis between perceived trustworthiness and frequency of EPCs.

Women, while always certain of their maternity, might be especially sensitive to emotional betrayal because if the man connects emotionally with another woman, he might desert the current mate, and eventually start to invest in offspring sired with another woman (Buss, Larsen, Westen, & Semmelroth, 1992). This interpretation goes in line with Perrett and colleagues' (1998) results and claims about women preferring more feminine-faced men to select possible mates with socially desirable traits. Hence, women might also prefer males with good parenting skills, who are also honest and trustworthy.

1.12. OVERVIEW OF THE CURRENT WORK

The current work took the information presented in this first chapter as the foundation for the formulation of unrevealed questions concerning the evolutionary view over human attractiveness and focused on the effect of two main domains: sexual dimorphism and trustworthiness. The next four chapters will address such questions, by describing four main studies conducted during this Ph.D. period.

The second chapter intended to contribute to a better understanding of the perception of face sexual dimorphism. Several studies have reported behavioural evidence about female and male preferences for sexually dimorphic shape traits in faces (e.g. Perrett et al., 1998). However, as previously mentioned, it is still a matter of debate whether women do prefer feminised faces in men and the underlying reasons for such preference (Scott et al., 2010). Thus, the first study aimed to contribute to this discussion by analysing the electrophysiological correlates of the perception of both female and male faces manipulated to appear more masculine or more feminine. Results showed differentiated responses between male and female participants and were discussed in line with the previous literature.

The study described in the third chapter aimed to explore another facial characteristic, besides shape, that could be potentially sexually dimorphic. Skin colour is presented as being significantly different from men and women, and attractiveness preferences results showed that, in line with preferences for other traits as voice and body shape, and contrary to findings regarding face shape, masculinity in colour is considered attractive. Preferences for facial shape mimic previous findings (Perrett et al., 1998). Effects of relationship context and mate value were also taken into account.

In the fourth chapter, the results of chapter 3 were used to consider a new hypothesis regarding preferences for body odours. Female participants were asked to smell body odours from men, which were previously measured in their skin colour masculinity. The results of attractiveness ratings turned out as predicted, with women preferring the smell of more masculine men. Other types of ratings were discussed according to a possible bias in more abstract attributions to body odours.

The fifth chapter addressed another possibly important inference made in mate choice which is perceived trustworthiness. Trustworthiness is taken as a face trait which both sexes prefer, contrasting to the sex divergences reported in the previous chapters. Men and women were asked to alter the shape of several faces according to their attractiveness preferences without being aware that the underlying modifications represented a trustworthiness continuum. Both sexes increased trustworthiness appearance when looking for attractive hypothetical partners. Individual differences were found concerning social interaction anxiety. We found that individuals that scored higher in social interaction anxiety preferred more trustworthy looking faces than less anxious participants. Once again, relationship context was considered.

Finally, the sixth chapter presents the reflections made from the results of all four studies and the possible conclusions of this work. Theoretical implications of our findings are also discussed along with suggestions for future work in the field.

Chapter 2. Event-related potentials modulated by the perception of sexual dimorphism: The influence of attractiveness and sex of the face

2.1. INTRODUCTION

The human face provides important social information to the observer, assuming an essential relevance in contexts of mate choice (Thornhill & Gangestad, 1999a). One of the reasons why face perception is so important in mate choice is because face attractiveness advertises mate quality (Little, Jones, et al., 2011). Therefore, facial attractiveness perception in heterosexual individuals is particularly relevant towards opposite-sex faces, since they might be potential mates (Little & Jones, 2003). This assumption is supported by previous research about ERP (event-related potentials) of face perception that investigated how women and men perceive opposite and same-sex faces. Results from such studies indicate the existence of specialized processing of faces of possible mates (Oliver-Rodríguez, Guan, & Johnston, 1999; van Hooff, Crawford, & van Vugt, 2011).

One of the variables that are believed to influence face attractiveness is sexual dimorphism, i.e. the presence of secondary sexual characteristics in faces. The shape of mature men's and women's faces tends to be different, with men having larger jawbones, more prominent cheekbones and thinner cheeks (Enlow, 1990). The perception of sexually dimorphic traits is thought to influence mating preferences as they are honest signals of health and immunity in both sexes (Folstad & Karter, 1992) and/or intrasexual competitiveness, particularly in men (Puts, 2010; Scott et al., 2013a; Swaddle & Reierson, 2002). Femininity in female faces is considered attractive by male counterparts (Perrett et al., 1998) possibly because it indicates health and fertility (Law Smith et al., 2006). Women with more feminine faces are believed to have a better reproductive health (Baird et al., 1999; Thornhill & Gangestad, 1999a), but also seem to evoke positive attributions, such as warmth, honesty, cooperativeness and youthfulness (Law Smith et al., 2006; Perrett et al., 1998). On the other hand, masculinity in male face shape is found to be attractive to women in some studies (DeBruine et al., 2006; Johnston, Hagel, Franklin, Fink, & Grammer, 2001) while others report a preference for more feminine male faces (DeBruine, Jones, Smith, & Little, 2010; Perrett et al., 1998). Although masculinity in males is expected to be attractive for being associated with good genes and indirect benefits to the offspring (Kirkpatrick & Ryan, 1991; Zahavi, 1975), women's preference for shape femininity in male's faces has been justified as a strategic trade-off when searching for a more cooperative partner (Gangestad & Simpson, 2000). Less masculine males are thought to be less aggressive, more honest, more cooperative and to have an increased parenting ability (Perrett et al., 1998). Because of that, less masculine males are perceived as more attractive, especially if women are considering long-term relationships

(Little & Hancock, 2002). Given the importance of sexual dimorphism on mating decisions, its perception assumes a biological relevance that we expect to emerge even at early stages of visual processing.

To our knowledge, there are just two published studies that have investigated the neurophysiological correlates of the perception of sexual dimorphism in faces (Cellerino et al., 2007; Freeman, Ambady, & Holcomb, 2010). Cellerino and colleagues (2007) addressed face sexual dimorphism by presenting participants gender-ambiguous face stimuli which they had to classify as male or female. Although using event-related potentials (ERPs), they focused mostly on defining specific brain regions implicated in face gender and masculinity processing. Through independent component analyses, they found that the perceived facial masculinity correlated with one of the components, that had a parieto-temporal source and latency of about 170 ms. The other study, from Freeman and colleagues (2010) used artificial face stimuli manipulated to appear “less gendered” and found that sex-typicality of faces modulated P1 latency and N170 amplitude. However, the results from the later study are difficult to interpret as the sex of participants was not discriminated, especially taking into account the evidence that women and men respond differently to faces from different sexes (e.g. Godard & Fiori, 2010; Tiedt, Weber, Pauls, Beier, & Lueschow, 2013).

This study aimed to investigate in detail the time course of the electrophysiological correlates of the processing of faces that vary in masculinity/femininity and understand whether these correlates differ between male and female participants. Also, we investigated how this perception is modulated by the type of judgment, namely whether participants are making attractiveness judgments or sex discrimination judgments. To do so, we carried out an ERP experiment and analysed early and late potentials that are related either to more automatic or to more conscious mental processes during the perception of sexually dimorphic traits in faces, under different processing conditions (judge sex or judge attractiveness). To that end, we focused our analyses in the following potentials: P1, N170, P2, EPN, and LPP.

The P1 is an early visual ERP component, peaking around 100 ms at occipital electrodes, which is commonly thought to reflect low-level stimulus features processing and seems to be involved in early stages of attentional gain control (Hillyard, Vogel, & Luck, 1998). The P1 ERP component has also been shown to be linked to face perception (Itier & Taylor, 2004). Previous studies have reported modulations of P1 waves by the perception of sexual dimorphism in faces (Freeman et al., 2010) and also contingently on participants’ sex (Dzhelyova, Perrett, & Jentzsch, 2012; Hahn et al., 2016).

Occipito-temporal cortex responses occurring approximately at 170 ms after stimulus onset (a component known as the N170) are thought to reflect the structural encoding stage in face perception (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000). According to Bruce & Young's (1986) model of face recognition, the direct encoding module, which is responsible for sex categorization, follows the structural encoding of facial features. Accordingly, the N170 component should be insensitive to sex categorization but several findings have challenged this idea reporting N170 modulations by face gender (Sun, Gao, & Han, 2010) and other high-level social features of faces, as emotion (Frühholz, Jellinghaus, & Herrmann, 2011; Wieser, Pauli, Reicherts, & Mühlberger, 2010) and attractiveness (Hahn et al., 2016; Zhang & Deng, 2012).

P2 is a visual potential that peaks around 200 ms after stimulus onset over parieto-occipital sites and has been associated with implicit selective attention to 'emotionally distinct' stimuli (Carretié, Martín-Loeches, Hinojosa, & Mercado, 2001). Enhanced P2 amplitudes were found in response to both attractive and unattractive opposite sex faces (van Hooff et al., 2011). Larger P2 responses were also elicited for male comparing to female faces in a sample of female participants (Ito & Urland, 2003).

The early posterior negativity (EPN) is an enhanced negativity at temporo-occipital electrodes, peaking approximately at 260-280 ms after stimulus onset (Schupp, Öhman, et al., 2004), although some studies have reported that the EPN peaks at 300 ms (e.g. Schupp, Junghöfer, Weike, & Hamm, 2004). It is suggested to result from reflex-like visual attention to emotional stimuli, which facilitates sensory encoding processes. The amplitude of the EPN has been reported as more pronounced for stimuli of high evolutionary significance, namely erotic images and pictures of mutilations (Junghöfer, Bradley, Elbert, & Lang, 2001). Werheid et al. (2007) revealed that attractive, as opposed to unattractive, faces elicited a larger EPN component.

Finally, LPP (late positive potentials) occur around 350-400 ms at centro-parietal sites, lasting for several hundred milliseconds, in response to emotionally arousing pictures (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000) and aesthetically pleasing images (Höfel & Jacobsen, 2007). Augmented LPP amplitudes have been reported particularly to faces expressing anger or fear (Schupp, Öhman, et al., 2004). Enlarged LPP amplitudes have also been identified as indices of selective attentional processing in the domain of explicitly directed attention, that is, when subjects are instructed to selectively attend to certain stimulus features (Schupp, Junghöfer, et al., 2004).

The aim of this study was to explore the electrophysiological correlates of the perception of both female and male faces that were masculinised or feminised, focusing on the previously mentioned ERP components, which have been associated with sex and/or attractiveness processing. Participants performed two different tasks: in the attractiveness task, participants were asked to evaluate each face as attractive or unattractive, whereas in the sex discrimination task they were asked to indicate if the presented face was male or female. Regarding the attractiveness task, we expected participants to consider feminised female faces more frequently as attractive since femininity has been shown to clearly enhance attractiveness in female faces (Law Smith et al., 2006). Given the inconsistency in previous studies' conclusions regarding the influence of face shape masculinity on men's attractiveness, we do not hold a specific prediction on how sexual dimorphism will affect attractiveness evaluations of male faces. Regarding the sex discrimination task, although studies have shown that humans are very proficient at recognising the sex of faces (Bruce et al., 1993), we expected participants to perform slightly worse when visualising feminised male faces and masculinised female faces (as these could be considered as sex incongruent stimuli). Considering the effects on the ERP components, we expect to observe specific modulations by sexual dimorphic differences in faces, especially towards opposite-sex stimuli, which may indicate the presence of attentional mechanisms related with mate-choice.

2.2. EXPERIMENT 1

2.2.1. Methods

2.2.1.1. Participants

Forty-four participants took part in the experiment but four were excluded from the analyses as they did not fulfil the criterion of 5 % maximum of omissions (no responses) in both experimental tasks or the criterion of 10 % maximum of bad channels during EEG (electroencephalography) recording (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007). Other five were excluded for being left-handed. The remaining 35 right-handed participants (M_{age} = 22.94, *SD* = 3.93, Range: 18 - 31), 18 men and 17 women, were included in the analyses. All participants reported being Caucasian and exclusively or predominantly heterosexual (≤ 2 in a scale from 0 as "exclusively heterosexual" to 6 as "exclusively homosexual").

2.2.1.2. Stimuli

Sixty facial photographs selected from a database of Portuguese young adult faces, 30 male, and 30 female, were delineated with 192 points (with X and Y coordinates) using Psychomorph software (Tiddeman, Burt, & Perrett, 2001). This delineation intended to delimit the different face areas, a process which is required to posterior averaging processes and sexually dimorphic transformations. For each sex of faces, groups of four different facial photographs were averaged together to create 121 composite male faces and 121 composite female faces. Composite faces were used in preference to the original individual faces since composites are not recognisable as familiar individuals and assure lower levels of inter-individual differences.

The facial shape of each of the 242 composite faces was manipulated towards higher masculinity or higher femininity according to the shape difference between the male and female prototype faces. Each of the two prototypes consisted in the average of all same-sex faces of the original set. Although faces vary in several traits besides sexual dimorphism, when averaging all of them according to sex, the final appearance will contain the mean structural features that represent each sex, with all other variations being lost as noise during the averaging process. Using these face prototypes, we created a feminised version (-50% masculinity) and a masculinised version (+ 50% masculinity) of each composite face (see Figure 1). The hair, neck, ears and background were occluded with an oval black mask. The total of the 484 images was converted to grey scale and resized to 719 x 1200 pixels, with a resolution of 300 x 300 dpi.

Figure 1. Example of the sexually dimorphic shape transform applied to faces in Experiment 1. The left images represent increased feminisation (- 50% masculinisation) and the right images represent increased masculinisation (+ 50% masculinisation).

2.2.1.3. Procedure

Participants were sat in a dim lit and sound-attenuated room with 80 cm distance from the computer screen. Initially, participants performed a training block with four trials in which they were instructed to press one of the two mouse buttons to judge the attractiveness of faces. They were told to follow their first impression and respond quickly. The instruction was to press one of the buttons if the face was judged as attractive and the other button for unattractive evaluations. It was stressed that during the training block, responses would not be considered for further analyses and that EEG recordings were still inactive. The faces presented during the training block (2 male and two female faces) were different from the ones presented in the experimental phase.

In the experimental phase, participants were asked to perform a similar attractiveness judgment task and also a sex discrimination task in separate blocks. EEG recording was carried out during this phase. Exclusively in the attractiveness task, it was explained that there were no right or wrong answers as it depended on their own judgment. Two blocks of 120 face images (60 female faces and 60 male faces), performing a total of 240 face images, were presented in each of the experimental tasks (attractiveness and sex discrimination tasks). Half of the faces were masculinised versions of the composite faces, and the other half were feminised versions of the same faces. Task, block and image order were randomised, and response key mapping was counterbalanced across participants. Participants were allowed to take a break with no fixed duration after each block. Each trial started with a fixation cross (500 ms) followed by the face image (250 ms) and then participants were instructed to respond (2000 ms maximum time allowed). Answers were only allowed after the face disappeared from the screen. Responses were followed by a 1000 ms blank screen (see Figure 2). Each face was presented only once.

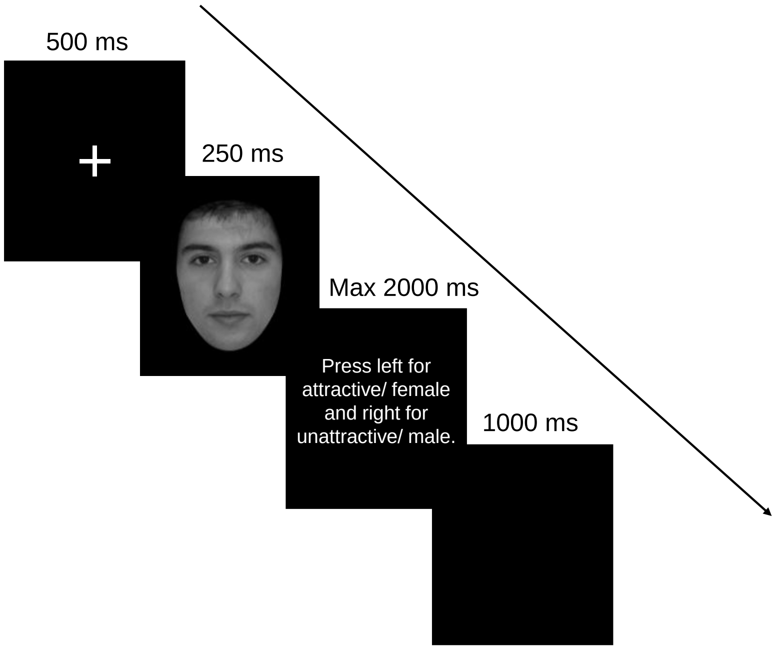

Figure 2. Representation of the sequence of events in both tasks of Experiment 1.

EEG recordings

EEG activity was recorded using *Neuroscan* software (Scan 4.3) and a Quick-cap with 64 Ag/AgCl electrodes located according to the 10/10 International System. Signal was amplified with a SynAmps2 system. Vertical eye movements were recorded using two electrodes placed above and below the left eye. Two electrodes placed in the external corner of each eye were used to record horizontal eye movements. The EEG signals were measured relative to a reference electrode positioned on the tip of the nose and a notch filter for 50 Hz was applied online. For all electrodes, impedance was kept under 5kΩ.

2.2.1.4. ERP analyses

Offline analyses included a band-pass filtering from 0.1 to 30 Hz. Offline epochs were generated lasting 1050 ms and starting 150 ms before stimulus onset. Baseline correction was carried out by subtracting the average pre-stimulus amplitude value. EEG data were analysed only for correct response trials in the sex discrimination task and for all the answered trials in the attractiveness task. EEG waveforms were averaged separately for all conditions (masculinised female face, feminised female face, masculinised male face, feminised male face) of each task (attractiveness and sex discrimination tasks). For early components (P1, N170, and P2), peak amplitude was analysed within the respective time window, while mean amplitudes in specific time windows were computed for EPN and LPP components. Considering the topographical characteristics of the grand average waveforms and the locations and latencies where the components were more conspicuous, each of these potentials was analysed in the following electrodes and time windows: P1 (90 – 140 ms; electrodes O1, OZ and O2); N170 (140 – 200 ms; electrodes PO7, PO8, O1, OZ and O2); P2 (200 – 260 ms; electrodes PO3 and PO4); EPN (260 – 340 ms; electrodes P7, P8, PO7 and PO8); LPP (330–430 ms, 430–530 ms, 530–630 ms, 630–730 ms; electrodes CP1, CPZ, CP2).

2.2.2. Results

2.2.2.1. Behavioural data

2.2.2.1.1. Attractiveness task

2.2.2.1.1.1. Percentage of faces evaluated as attractive

The mean percentage of faces in each condition that were evaluated as attractive was analysed. Before the analysis, data were arcsine transformed to fulfil the normality demands of parametric tests. For ease of interpretation, reported mean values and standard deviations correspond to the untransformed data. A 3-way mixed ANOVA [between-subjects factor: sex of participant; within-subjects factors: sex of the face and sexually dimorphic transform] revealed a main effect of sex of the face, F (1, 33) = 53.50, p < .001, η_p^2 = .619, indicating that female faces (M = 53.41, SE = 3.66) were associated with a higher percentage of attractive evaluations comparing to male faces (M = 22.37, SE = 3.01). The effect of sex of participant was not significant, F (1, 33) = .22, p = .641, η_p^2 = .007. There was a significant interaction effect between sex of participant and sex of the face, *F* (1, 33) = 15.53, $p < .001$, $\eta_p^2 = .320$. Male participants gave a higher percentage of attractive evaluations to female faces (*M* = 63.15, *SE* = 5.11) than to male faces (*M* = 16.94, *SE* = 4.19), and this difference was much larger than for female participants, despite the fact that they also gave a higher percentage of attractive evaluations to female faces (*M* = 43.68, *SE* = 5.26) than to male faces (*M* = 27.79, *SE* = 4.31). There was also a significant main effect of sexually dimorphic transform, *F* (1, 33) = 13.76, $p = .001$, $\eta_p^2 = .294$, with feminised faces (*M* = 40.50, *SE* = 2.87) being overall associated with a higher percentage of attractive evaluations than masculinised faces (*M* = 35.28, *SE* = 2.74). The interaction between sex of the face and sexually dimorphic transform was marginally significant, *F* (1, 33) = 4.09, $p = .051$, $\eta_p^2 = .110$, with feminised female faces (*M* = 57.32, *SE* = 3.83) being considered as attractive more frequently than masculinised female faces (*M* = 49.51, *SE* = 3.66) (no difference was found for male faces).

2.2.2.1.1.2. Reaction times

Reaction times on the attractiveness task were analysed through a 3-way mixed ANOVA [between-subjects factor: sex of participant; within-subjects factors: sex of the face and sexually dimorphic transform]. Data were log transformed to fulfil the normality demands of parametric tests. Again, reported mean values and standard deviations correspond to the untransformed data. The effect of sex of the face was statistically significant, *F* (1, 33) = 4.53, $p = .041$, $\eta_p^2 = .121$, as participants responded faster when visualising male faces (*M* = 420.84 ms, *SE* = 28.91) comparing to when seeing female faces (*M* = 447.26 ms, *SE* = 25.17). There was also a significant interaction between sex of participant and sex of the face, *F* (1, 33) = 6.19, $p = .018$, $\eta_p^2 = .158$, indicating that the previous effect was mainly due to responses of male participants (female participants were equally fast judging the attractiveness of male and female faces).

The effect of sexually dimorphic transform was statistically significant, *F* (1, 33) = 4.77, $p = .036$, $\eta_p^2 = .126$, with faster responses occurring to masculinised faces (*M* = 428.12 ms, *SE* = 24.86) than to feminised faces *M* = 439.98 ms, *SE* = 27.38). Also, the interaction effect between sex of the face and sexually dimorphic transform revealed statistical significance, *F* (1, 33) = 12.56, $p = .001$, $\eta_p^2 = .276$, with faster responses given to masculinised male faces (*M* = 407.47 ms, *SE* = 27.62) than to feminised male faces (*M* = 434.21 ms, *SE* = 30.51). Participants were equally fast judging the attractiveness of feminised and masculinised female faces.

2.2.2.1.2. Sex discrimination task

2.2.2.1.2.1. Accuracy

The percentage of correct responses in the sex discrimination task was analysed for the participants of each sex in each experimental condition. Because Shapiro-Wilk tests revealed that distributions were not normal for neither of the conditions and because no data transforms were able to correct this problem, non-parametric tests were applied. In order to analyse the effect of sex of the face, we calculated the overall mean accuracy for male faces and female faces. Wilcoxon tests, $Z = -3.07$, $p = .002$, showed that participants were better at discriminating male faces (*Mdn* = 97.50%) than female faces (*Mdn* = 95.00%). To analyse the effect of sexually dimorphic transform we performed two Wilcoxon tests, using a Bonferroni corrected alpha of .025. There was a statistically significant difference for male faces, $Z = -2.24$, $p = .025$, with masculinised faces (*Mdn* = 98.33%) being better discriminated than feminised faces (*Mdn* = 96.67%), and also for female faces, $Z = -5.03$, $p < .001$, with feminised faces (*Mdn* = 98.33%) being better discriminated than masculinised faces (*Mdn* = 91.67%). Mann-Whitney tests showed that male and female participants did not differ in the percentage of correct responses for any of the face conditions.

2.2.2.1.2.2. Reaction times

The reaction times for correct responses in the sex discrimination task were log transformed and analysed with a 3-way mixed ANOVA [between-subjects factor: sex of participant; within-subjects factors: sex of the face and sexually dimorphic transform]. Once more, reported mean values and standard deviations correspond to the untransformed data. The effect of sex of the face was statistically significant, F (1, 33) = 8.16, $p = .007$, $\eta_p^2 = .198$, with faster responses given to male faces (M = 255.71 ms, SE = 15.00) comparing to female faces (M = 276.81 ms, SE = 15.51). The interaction between sex of the face and sexually dimorphic transform was also statistically significant, F (1, 33) = 41.21, $p < .001$, $\eta_p^2 = .555$. Participants gave faster responses to masculinised male faces (M = 242.27, SE = 14.26) comparing to feminised male faces (M = 269.14, SE = 16.15), and to feminised female faces (M = 260.40, SE = 14.92) comparing to masculinised female faces (M = 293.22, SE = 16.78). No other effect reached statistical significance.

2.2.2.2. Event-related potential data

ERP data were analysed through mixed ANOVAs [between-subjects factor: sex of participant; within-subjects factors: task, sex of the face, sexually dimorphic transform and electrode]. Peak amplitude was analysed for P1, N170, and P2 and mean amplitude was considered for EPN and LPP potentials. The Greenhouse-Geisser correction was used for violations of sphericity and corrected degrees of freedom are reported. Bonferroni corrections were used in pairwise comparisons to explore significant effects. Table 4, in the appendix section, shows results of all analyses performed for all components. Figures 3 and 4 represent the topographical scalp maps for the attractiveness (Figure 3) and sex discrimination (Figure 4) tasks for female and male participants.

P1 (90 – 140 ms; electrodes O1, OZ, and O2)

For the P1 component, there was a significant interaction between task and sex of the face, F (1, 33) = 5.59, p = .024, η_p^2 = .145. In particular, for the sex discrimination task, P1 amplitude was more positive for male faces (M = 8.11 μV, SE = 1.07) than female faces (M = 7.35 μV, SE = .97). No significant differences were found in the attractiveness task. A significant interaction between sex of the face and electrode emerged, F (2, 66) = 3.19, p = .048, η_p^2 = .088, although following pairwise comparisons were not significant. Lastly, an interaction between sex of participant, task, sex of the face, sexually dimorphic transform and electrode, F (1.63, 53.77) = 3.87, p = .035, η_p^2 = .105, demonstrated that for women, in the attractiveness task, when judging female feminised faces, P1 amplitude was more positive in OZ comparing to O2.

N170 (140 – 200 ms; electrodes PO7, PO8, O1, OZ, and O2).

The N170 potential revealed enhanced amplitudes over parieto-occipital electrodes (PO7 and PO8), compared to other locations, F (1.94, 64.17) = 27.86, p < .001, η_p^2 = .458. Peak amplitudes were larger for female faces (M = -10.07 μV, SE = 1.00) than for male faces (M = -8.96 μV, SE = 1.04), F (1, 33) = 20.80, p < .001, η_p^2 = .387, and such difference was significant in all five locations (significant interaction effect between sex of the face and electrode, F (2.02, 66.49) = 3.53, p = .035, η_p^2 = .097). The effect of sex of the face was also more evident for female participants, F (1, 33) = 5.41, p = .026, η_p^2 = .141, and more prominent in the sex discrimination task, F (1, 33) = 6.09, p = .019, η_p^2 = .156. There was an interaction effect between task, sex of the face and sexually dimorphic transform, F (1, 33) = 7.94, p = .008, η_p^2 = .194, although there were no differences between feminised and masculinised faces of either sexes. There was a significant interaction between sex of participant and electrode, F (1.94, 64.17) = 6.13, p = .004, η_p^2 = .157, although there were no differences between sexes in either of the locations.

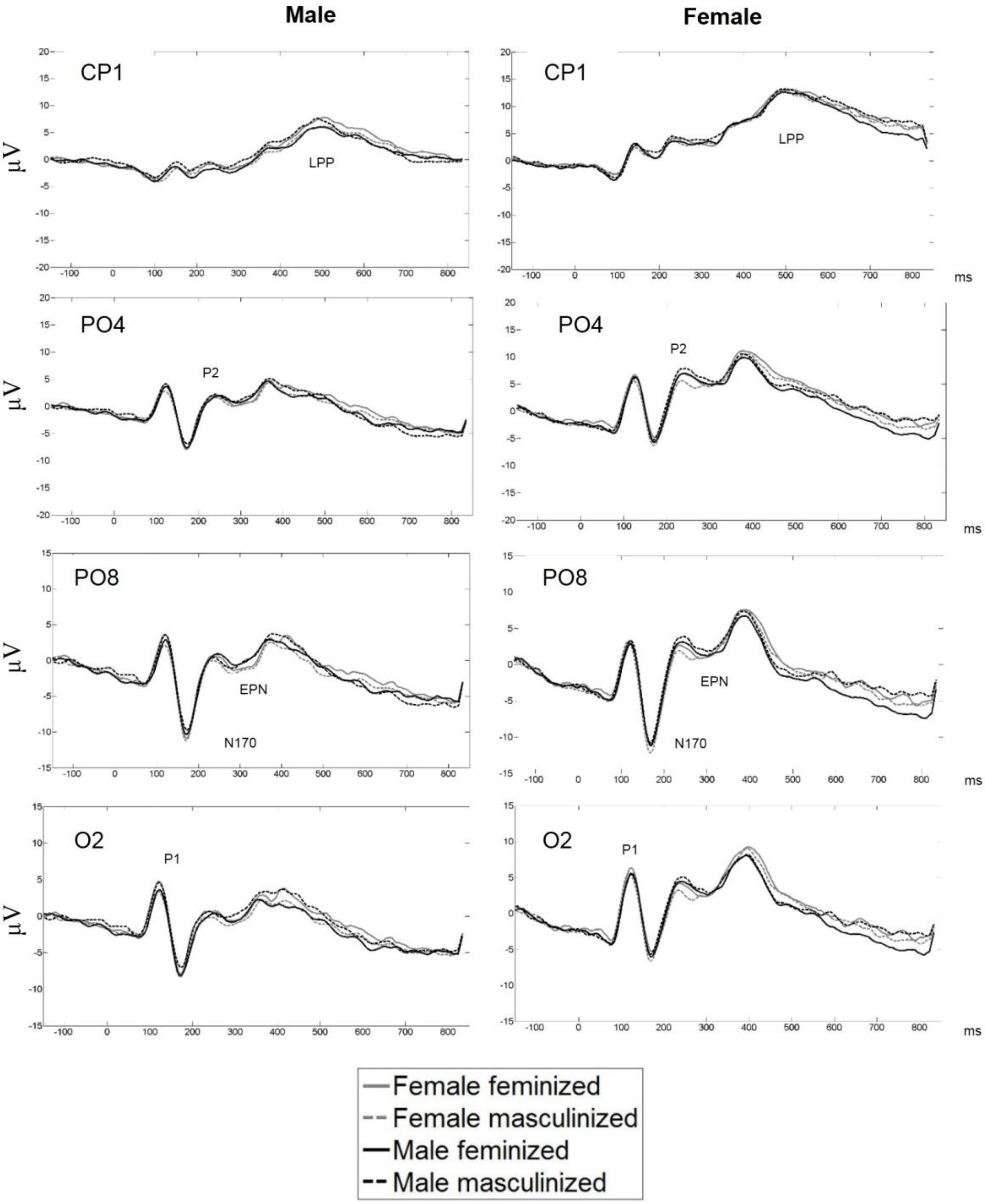

Figure 3. Grand-average waveforms in the attractiveness task in Experiment 1, for male (left panel) and female participants (right panel) over centro-parietal, parieto-occipital and occipital sites.

P2 (200 – 260 ms; electrodes PO3 and PO4)

Regarding P2 amplitude, there was a significant effect of sex of participant, *F* (1, 33) = 8.80, *p* = .006, η_p^2 = .211, wherein more positive amplitudes were observed for female participants (*M* = 9.66 μV, *SE* = 1.40) comparing to male participants (*M* = 3.87 μV, *SE* = 1.36). Male faces elicited larger amplitudes (*M* = 7.30 μV, *SE* = 1.04) than female faces (*M* = 6.23 μV, *SE* = .94), *F* (1, 33) = 9.38, *p* = .004, η_p^2 = .221, mainly in female participants, *F* (1, 33) = 4.30, *p* = .046, η_p^2 = .115 and in the sex discrimination task, *F* (1, 33) = 7.80, *p* = .009, η_p^2 = .191. There was a significant interaction effect between sex of the face and sexually dimorphic transform, *F* (1, 33) = 6.18, *p* = .018, η_p^2 = .158, and a significant interaction effect between sex of participant, sex of the face and sexually dimorphic transform, *F* (1, 33) = 4.83, *p* = .035, η_p^2 = .128. The later effect showed that masculinised male faces (*M* = 11.17 μV, *SE* = 1.54) elicited more positive P2 amplitudes than feminised male faces (*M* = 9.93 μV, *SE* = 1.48), in female participants. No differences were found for female faces or male participants.

EPN (260 – 340 ms; electrodes P7, P8, PO7 and PO8)

The EPN mean amplitude was more negative in the attractiveness task (*M* = -.15 μV, *SE* = .84) than in the sex discrimination task (*M* = .88 μV, *SE* = .68), *F* (1, 33) = 4.58, *p* = .040, η_p^2 = .122. Also, more negative amplitudes emerged for female faces (*M* = -.19 μV, *SE* = .79) than to male faces (*M* = .92 μV, *SE* = .67), *F* (1, 33) = 13.50, *p* = .001, η_p^2 = .290, mainly in the sex discrimination task, *F* (1, 33) = 6.05, *p* = .019, η_p^2 = .155, and over all four locations, *F* (1.99, 65.53) = 6.93, *p* = .002, η_p^2 = .174. An interaction effect between task, sex of the face and electrode confirms such results, *F* (1.69, 55.62) = 4.71, *p* = .017, η_p^2 = .125. Higher amplitudes for female faces in the sex discrimination task were also mainly attributed to female participants, *F* (1, 33) = 4.87, *p* = .034, η_p^2 = .129. An interaction effect between sex of participant, sex of the face and sexually dimorphic transform, *F* (1, 33) = 4.38, *p* = .044, η_p^2 = .117, showed that only women had a larger EPN response when visualising feminised male faces (*M* = 2.00 μV, *SE* = 1.03) than when visualising masculinised male faces (*M* = 3.45 μV, *SE* = 1.04), with no differences found for female faces. Amplitudes were in general more negative over parietal locations (P7 and P8), *F* (2.00, 66.06) = 9.26, *p* <.001, η_p^2 =.219, and also more negative for male participants (*M* = -1.23 μV, *SE* = 1.01) comparing to female participants (*M* = 1.96 μV, *SE* = 1.04), *F* (1, 33) = 4.83, *p* = .035, η_p^2 = .128.

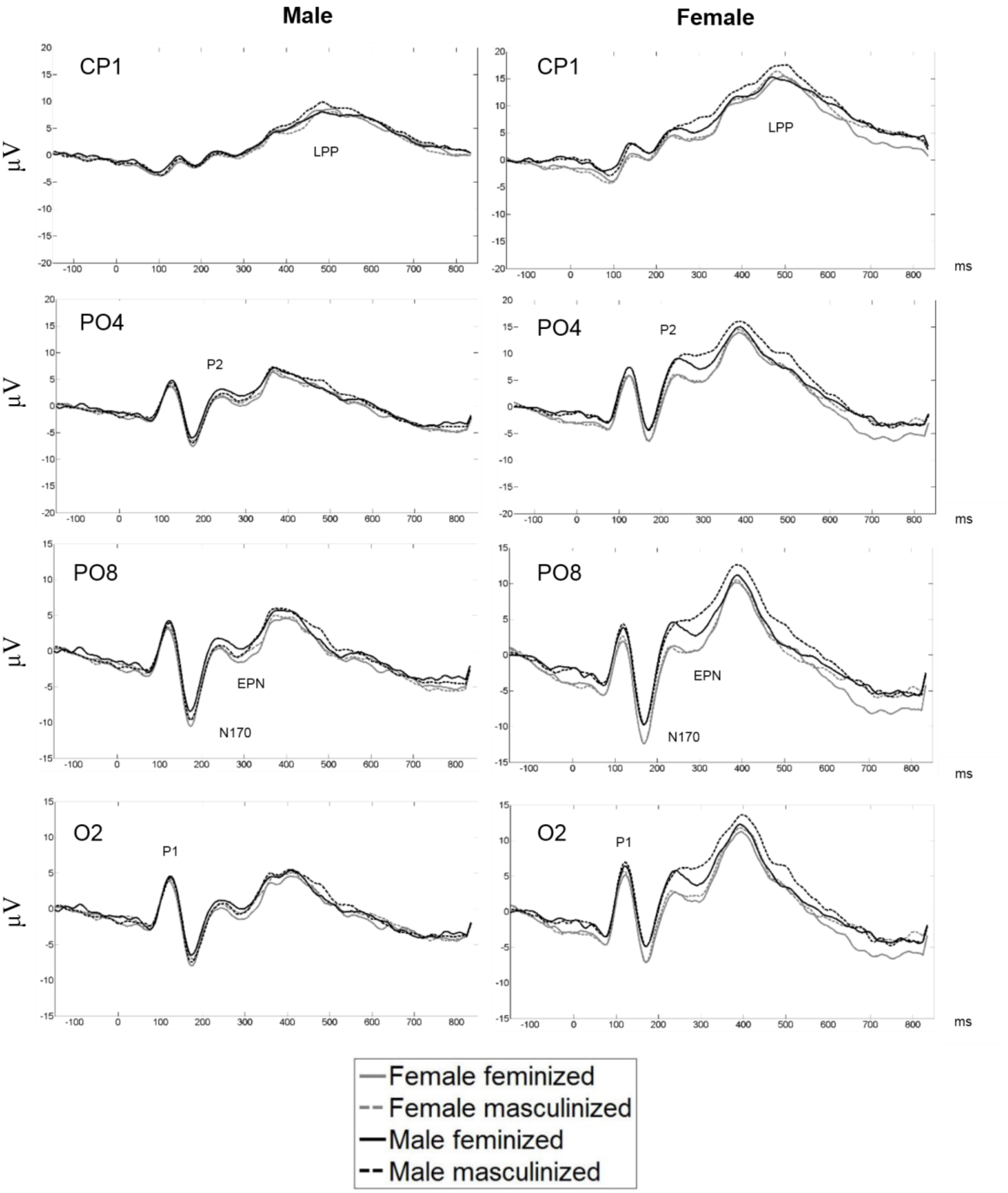

Figure 4. Grand-average waveforms for the sex discrimination task in Experiment 1, for male (left panel) and female participants (right panel) over centro-parietal, parieto-occipital and occipital sites.

LPP (330–430 ms, 430–530 ms, 530–630 ms, 630–730 ms; electrodes CP1, CPZ, CP2)

LPP mean amplitudes were constantly superior for female participants compared to male participants (see Table 1). In the first three time windows, the sex discrimination task elicited larger amplitudes than the attractiveness task. However, female participants exhibited larger amplitudes for the attractiveness task between 630 and 730 ms. During the first two time periods, masculinised male faces elicited larger amplitudes compared to feminised male faces. Between 530 and 630 ms, male faces were associated with larger amplitudes than female faces exclusively in the sex discrimination task. Despite the fact that, in the first time window, LPP amplitudes were superior over CP1, in the following 3 time windows, LPP were more positive over CPZ.

Table 1. Significant effects found in the results of ANOVAs, in Experiment 1, analysing the mean amplitudes of the LPP (late positive potentials) in the considered time windows.

		LPP			
		330 – 430 ms	430 – 530 ms	530 – 630 ms	630 -730 ms
Sex of participant	F (1, 33)	10.64**	17.62***	20.84***	20.21***
	p	.003	< .001	< .001	< .001
	η_p^2	.244	.348	.387	.380
Sex of the face x Sexually dimorphic transform	F (1, 33)	6.36*	10.32**	.82	.26
	p	.017	.003	.372	.611
	η_p^2	.161	.238	.024	. 008
Task	F (1, 33)	21.26***	15.72***	4.21*	.04
	p	< .001	< .001	.048	.851
	η_p^2	.392	.323	.113	.001
Task x Sex of participant	F (1, 33)	2.20	1.15	3.47	7.55**
	p	.148	.292	.072	.010
	η_p^2	.062	.034	.095	.186
Task x Sex of the face	F (1, 33)	1.06	1.38	4.39*	3.47
	p	.311	.248	.044	.071
	η_p^2	.031	.040	.118	.095
Electrode	F (2, 66)	4.10*	19.26***	24.80***	29.20***
	p	.021	< .001	< .001	< .001
	η_p^2	.111	.369	.429	.469

Note: * $p < .05$; ** $p < .01$; *** $p < .001$.

2.3. DISCUSSION

This study aimed to understand the effect of sexually dimorphic facial traits on sex discrimination and attractiveness judgments, analysing both behavioural and electrophysiological measures. The analyses of attractiveness judgments showed that regardless of the sex of participant, the highest number of attractive evaluations was attributed to female faces when compared to male faces. Feminised faces of both sexes were also considered to be attractive more frequently than masculinised faces by both male and female participants. Apparently, the attractiveness of female and male faces seems to be accessed somewhat similarly by men and women. Thus, both male faces and masculinised stimuli, in general, were associated with faster reaction times, possibly demonstrating that both male and female participants take more time visualising female and overall feminised faces, which, for being considered more attractive, may assume a rewarding effect (Aharon et al., 2001; Leder, Tinio, Fuchs, & Bohrn, 2010).

Similar findings, with no behavioural differences between men and women evaluating attractiveness of both sex faces, have been reported in previous research (Levy et al., 2008), namely in studies using eye-tracking (Alexander & Charles, 2008) and fMRI (Bray & O'Doherty, 2007; Kranz & Ishai, 2006). Men are believed to have an increased motivational drive towards opposite-sex faces, when compared to women, interpreted as a gender difference in the incentive salience of beauty (Levy et al., 2008). The lower female motivation for the pursuit of heterosexual beauty might be explained by frequent bisexual interest among heterosexual women that drives them not to show a differentiated response (Rupp & Wallen, 2007). In turn, this female bisexual interest has been justified as an alloparenting strategy proposed by recent evolutionary theories (Kuhle & Radtke, 2013). According to this theory, women may engage in romantic bonds with same-sex individuals that could help them rear their children.

The effect of sexual dimorphism on attractiveness judgments was mainly visible for female faces, with femininity clearly increasing attractiveness in those faces as predicted by previous studies (G. Rhodes, 2006). The non-significant effect of sexually dimorphic transform in male faces possibly represents the absence of consensus among female participants that show different preferences towards masculinity according to own condition and environmental influences (Gangestad & Simpson, 2000). A tendency to prefer masculinity traits in male faces is usually found in women who consider themselves attractive (Little et al., 2001), who are seen as attractive by others (Penton-Voak et al., 2003), who are ovulating (Gildersleeve et al., 2014), when are considering short-term relationships (Penton-Voak & Perrett, 2000) and when having a stable partner (Little et al., 2002), among other factors. Women in opposite situations tend to prefer more feminine males that are perceived as more cooperative, warm and honest (Perrett et al., 1998). Such diversified preferences between women in addition to the general men’s dislike of male faces, caring little if they were feminised or masculinised, possibly caused sexual dimorphism not to influence attractiveness judgments in a specific direction.

Regarding the sex discrimination task, there were no differences between the sexes in the percentage of correct responses, as found in previous research (O’Toole et al., 1998), which shows that both men and women are extremely good discriminating the sex of faces. Also, as expected, congruent stimuli (feminised female faces and masculinised male faces) were associated with the highest levels of correct responses and fastest reaction times, as found in previous studies (e.g. Freeman et al., 2010), suggesting a possible beneficial effect of congruent sexual dimorphism on this categorization decision. Higher levels of accuracy and faster responses were associated with male comparing to female faces, as reported in other studies (Dzhelyova et al., 2012; O'Toole et al., 1998).

In contrast with this lack of differentiated behavioural responses between participant sexes, namely in attractiveness judgments and sex discrimination, different results in ERPs were found for female and male participants. In fact, compared to male participants, women exhibited more differentiated responses in N170, P2, EPN and LPP amplitudes, when visualising female and male faces. Also, as in previous research (e.g. Sun et al., 2010), the N170 component was modulated by the sex of the face, with larger N170 amplitudes for female compared to male faces, especially for women. The fact that such difference was especially evident for female participants goes in line with previous claims of women responding more strongly to social stimuli than men (Proverbio, Zani, & Adorni, 2008).

Similarly to the N170, both P2 and EPN components were associated with differences in amplitudes according to the sex of faces, particularly in the sex discrimination task and for female participants, which again supports the idea that women are more sensitive to social categorization decisions (Sun et al., 2010), such as the sex of the face. As both components are thought to be linked to attentional processes (Carretié et al., 2001; Schacht, Werheid, & Sommer, 2008), we can conclude that although men and women did not perform differently in the sex discrimination task, ERP data suggests that there are differences in the way women attend to information about the sex of faces that does not seem to be evident in men. Both components were also influenced by face shape sexual dimorphism, which means that such information starts to be integrated in the brain around 200 ms after stimulus onset. Importantly, significant interactions between sex of participant, sex of the face and sexually dimorphic transform in those components (EPN and P2), with pairwise comparisons only significant for opposite-sex faces, may indicate a specific effect of sexual dimorphism on the perception of faces of possible mates. The absence of significant differences for same-sex faces implies that masculinity assumes special relevance when participants visualise individuals that could constitute partners. Such effect was only visible for female participants, which means that although they do not overtly discriminate male face attractiveness based on masculinity traits, they are attending to it when perceiving male faces.

The EPN and LPP were modulated by the type of task that the participant was performing. These effects might represent a top-down influence on those later potentials, where participants' expectations make them respond differently according to instructions, by focusing the visual attention conditionally on the task announced (Clark, Fan, &

Hillyard, 1994; Shulman et al., 1997). Masculinised male faces were associated with larger LPP amplitudes compared to feminised male faces between 330 and 530 ms. Given that facial threat also elicits augmented LPP (Schupp, Öhman, et al., 2004), this result might be due to increased attention to apparently threatening males. Such might happen because of the positive relation between masculinity and perceived anger (Hess, Adams, Grammer, & Kleck, 2009) and reduced trustworthiness (Oosterhof & Todorov, 2008).

At first sight, our results seem contradictory to Cellerino et al. (2007) and Freeman et al. (2010) findings, as we did not find a modulation of the N170 component by the sexually dimorphic transform. However, we believe that Cellerino et al.'s (2007, p. 516) "correlates for the perception of sexual dimorphism" do correspond to our correlates of the sex discrimination process. As they used gender-ambiguous stimuli, and participants were asked to judge faces as female or male, their N170 effect probably corresponds to the identification or attribution of a sex category to faces. Thus, as we also found a significant difference in N170 amplitude contingent to the sex of the face, we believe that our results do coincide. Regarding Freeman and colleagues' (2010) work, their manipulation of "face typicality" does resemble our sexually dimorphic manipulation within each sex category of faces. The differences between our findings and theirs may be due to methodological divergences in the manipulation of masculinity/femininity of faces, although we cannot confirm such assumption as the authors did not address how this transform was carried out by the software used. Also, the fact that we used composites of real faces while they used computer generated faces could also be the cause of the differentiated findings.

2.4. CONCLUSIONS

This study aimed to shed some light over the time course of the neurophysiological processes underlying the perception of sexually dimorphic traits in faces. Expected preferences for femininity in female faces were found. Also as expected, we found evidence for the advantage of congruency between sex of the face and sexually dimorphic traits in a sex discrimination task. ERP results showed that sexual dimorphism modulates P2, EPN and LPP responses. Moreover, P2 and EPN amplitudes were modulated by masculinity specifically when female participants visualised opposite-sex faces. Such effects may indicate that the perception of masculine traits in faces may hold a special relevance in faces of potential mates. However, this difference was not visible in male participants.

Since this study focused exclusively on face shape and recent studies have shown that human faces are also sexually dimorphic in terms of reflectance (Said & Todorov, 2011), future research could try to repeat this study using faces with more masculinised/feminised colouration. Also, it would be of interest to investigate if individual differences in women, as in self-attractiveness level, relationship status, menstrual cycle phase or relationship goal, do influence electrophysiological correlates as they have been proven to influence behavioural responses (Little, Jones, et al., 2011).

In sum, the evidence found suggests that masculinity/femininity facial features seem to contribute to decisions regarding sex discrimination as well as to attractiveness judgments. Although the relationship between attractiveness and sexual dimorphism is evident given the numerous behavioural findings in previous studies, its relation with sex categorization and the neurophysiological correlates of these processes have seldom been investigated. This study helps to understand the first stages of face perception that ultimately precede mating decisions.

Chapter 3. The role of sexually dimorphic skin colour and shape in attractiveness of male faces

The work presented in this chapter was fully published in the article below: Carrito M. L., Santos, I. M., Lefevre, C. E., Whitehead, R. D., Silva, C. F., Perrett, D. I. (2016). The role of sexually dimorphic skin colour and shape in attractiveness of male faces, *Evolution and Human Behavior*, *37* (2), 125-133, 10.1016/j.evolhumbehav.2015.09.006.

3.1. INTRODUCTION

The role of sexual dimorphism in male facial attractiveness is still equivocal (DeBruine, Jones, Smith, et al., 2010; Little & Hill, 2007). While some work shows positive associations between masculinity and attractiveness (DeBruine et al., 2006; Little & Mannion, 2006), other findings suggest a negative (Little & Hancock, 2002; Perrett et al., 1998) or no association (Scott et al., 2010; Stephen, Scott, et al., 2012). However, most research to date has failed to address the possible independent effects of sexual dimorphism in facial shape and facial skin colour on attractiveness perception, despite findings indicating the importance of skin colour on attractiveness judgments (Matts et al., 2007; Russell, 2003; Scott et al., 2010; Stephen, Scott, et al., 2012). Moreover, a lack of preference for masculinity in male faces may be observed by virtue of conflicting preferences for relatively feminine shape but also relatively masculine skin colour (Said & Todorov, 2011). Here we investigated this idea formally, addressing two questions: 1) Is masculinity in face colour attractive when judging male faces? 2) How does sexually dimorphic colour relate to attraction to sexually dimorphic shape? To answer these questions we examined preferences for colour and shape separately and simultaneously.

3.1.1. Women's preferences and sexual dimorphism

Sexual dimorphism is believed to signal health and contribute to the attractiveness of male faces. This position has been justified by the association between both baseline and reactive testosterone and masculine facial appearance (Lefevre & Lewis, 2013; Pound et al., 2009) and by the immunosuppressive effects of testosterone (Grossman, 1985; Wedekind, 1992; Zahavi, 1975) (but see M. L. Roberts, 2004; Scott et al., 2010). According to the immunocompetence handicap hypothesis, since only males with relatively high genetic quality can sustain the immunosuppression associated with high levels of testosterone and remain healthy, masculinity may, therefore, signal mate value (Little, Jones, et al., 2011). It follows that women should benefit from choosing a partner with sexually dimorphic masculine features as these would indicate long-term healthiness and ability to provide direct and indirect genetic benefits to her offspring (Kirkpatrick & Ryan, 1991; Little, Jones, et al., 2011).

An alternative conceptualization regarding the value of facial masculinity relies on the possibility that masculine traits may signal intrasexual competitiveness and dominance. In fact, owners of masculine faces are perceived as dominant (Boothroyd et al., 2007; Perrett et al., 1998; Stirrat & Perrett, 2010) and aggressive (Lefevre & Lewis, 2013; Stirrat, Stulp, & Pollet, 2012). Perceived facial dominance is associated with status in some human hierarchies (Muller & Mazur, 1997). Masculine facial traits could be a cue for competitive status-seeking behaviours (Scott et al., 2013a) and are therefore attractive to women that desire a dominant mate who will ensure access to resources and protection (Puts, 2010).

There are some factors influencing women's preferences for facial masculinity including women's self-attractiveness and the relationship context of hypothetical unions. Women who regard themselves as attractive (Little et al., 2001; Little & Mannion, 2006) and women who are rated as more attractive by others (Penton-Voak et al., 2003) prefer more masculine and symmetrical faces than less attractive women. This difference is seen in the context of a long- but not a short-term relationship.

Although high partner masculinity may confer benefits (health, good genes), masculinity may also have potential costs because it is related to reduced paternal skills, cooperativeness and trustworthiness (Perrett et al., 1998). Less attractive women may prefer a male with a more feminine face for a long-term relationship because such a man may invest more in the relationship and be less likely to desert (Penton-Voak et al., 2003). Conversely, attractive women may prefer more masculine male faces because they can cope with their lower parental ability and may even persuade them to invest more (Little et al., 2001). This assumption is featured in the Trade-off Theory (Gangestad & Simpson, 2000; Gross, 1996) which suggests that women may trade heritable immunity benefits against the costs of lack of paternal investment.

3.1.2. Colour as a sexually dimorphic cue

Recent research has suggested that face colour has an impact on attractiveness that may be more pronounced than face shape (Said & Todorov, 2011; Stephen, Scott, et al., 2012) as it may be a more reliable index of current health compared to shape (Scott et al., 2010). Overall, skin colour (Stephen, Coetzee, et al., 2009) and colour distribution (Fink et al., 2006; Matts et al., 2007) have strong effects on apparent health and attractiveness in human faces.

The CIE L*a*b* colour space is commonly used in human perceptual studies and includes 3 main axes: L*(0 = dark, 100 = light), a* (negative = green, positive = red) and b* (negative = blue, positive = yellow). For Caucasian skin colour, the redness component (a*) is formed primarily by haemoglobin in the blood vessels (Stephen, Coetzee, et al., 2009), and the yellowness component (b*) by the presence of carotenoid and melanin pigments (Alaluf et al., 2002; Stephen, Law Smith, et al., 2009). Skin lightness (L* values) is decreased primarily by the presence of melanin in the skin (Stamatas et al., 2004).

Skin CIE L*a*b* values have been associated with human health but also appear to be sexually dimorphic and related with reproductive health and dominance (Little, Jones, et al., 2011). Carotenoid levels are reduced in infertile men, and carotenoid supplements can improve men's fertility (Eskenazi et al., 2005). For female faces, light skin may be taken as a sign of fecundity (Aoki, 2002; Van den Berghe & Frost, 1986) and skin lightness affects attractiveness (Russell, 2003). Skin colour varies considerably between people from different regions of the globe but is sexually dimorphic within a specific region, with men having darker (lower L*) and redder (higher a*) skin compared to women (Jablonski & Chaplin, 2000; Russell, 2003; Van den Berghe & Frost, 1986). Madrigal and Kelly (2007) analysing the prevalence of sexually dimorphic colour in different areas with different solar radiation, concluded that hormonal factors might be a more reliable explanation of differences between sexes. Indeed, according to H. Hill, Bruce, and Akamatsu (1995), discrimination of human sexes relies more on colour information than on face shape.

Red stimuli, in general, are associated with increased perceived dominance, an advantage in intra-sexual competition and access to resources (Stephen, Oldham, et al., 2012). Men wearing red are more likely to win physical competitions even when controlling for ability and are perceived as more aggressive and more dominant (Feltman & Elliot, 2011; Little & Hill, 2007). The red colour is associated with attractiveness, and women perceive men to be more attractive and sexually desirable when seen on a red background or in red clothing (Elliot et al., 2010).

The effect of sexual dimorphism in skin colour on attractiveness has not been investigated directly, but differences in skin lightness and redness (components of dimorphism) have pervasive roles in perception, and preliminary research indicated that a darker photograph contributed to male facial attractiveness (Frost, 1994). Therefore, skin colour seems to be sexually dimorphic, providing cues to health and, possibly, to dominance. While skin colour has clear effects on attractiveness, the effect of sexual dimorphism in skin colour on attractiveness is not known.

3.1.3. Current study

This study aims to define the influences of sexually dimorphic skin colour and face shape on women's attractiveness judgments. Said and Todorov (2011) developed a model of attractiveness in which, by determining the position of each face in a face space, it was possible to predict its attractiveness. Their face space incorporated 25 shape dimensions and 25 colour dimensions. According to the authors, the mixed results of previous studies regarding masculinity and male attractiveness may reflect competing effects of shape and colour. After analysing the separate contributions of these sexually dimorphic dimensions, the authors concluded that, for male faces, masculinity is attractive in colour properties whereas femininity is attractive in shape. Their model predicts that, compared to the average male face, “attractive male faces have darker skin, more beard, darker brows and eye lines and less bulk around the cheeks and upper neck” (Said & Todorov, 2011, p. 1186). The authors also reported that attractive female faces were feminine in both face shape and colour.

Said and Todorov (2011) used artificial facial stimuli (synthetic models with bald heads) and noted that it is possible that real faces’ attractiveness is rated differently. Since colour properties of the face stimuli were encoded in 25 principal component dimensions, it was not possible within their approach to resolve the contribution of any single sexually dimorphic feature such as a specific skin hue or the presence of a beard.

In the present study, we aimed to test predictions for the attractiveness of sexually dimorphic face shape and colour using composites of real human faces. Note that even though computer graphic techniques were used to manipulate sexually dimorphic traits in faces, this work aimed to use more ecologically valid stimuli than Said and Todorov (2011). Furthermore, we integrate attractiveness preferences in a mating context to ensure that perceptive mechanisms involved are related to sexual selection.

Our goal was to understand how the two dimensions of sexual dimorphism, skin colour and shape, contribute to women’s judgments of male facial attractiveness. Following the conclusions of previous studies, we hypothesised that relative femininity in face shape will be attractive in both male and female faces and that masculinity in skin colour will be attractive for male faces. Additionally, we expected our participants to feminise male faces less than female faces in shape and masculinise them more than female faces in colour. The prediction for the attractiveness of female facial colour is unclear[2].

Although preferences for feminine traits in male faces have been reported as previously mentioned, when it comes to other sexually dimorphic characteristics, such as the voice, women who perceive masculine male voices as more dominant prefer them

[2] Said and Todorov’s (2011) model predicted that feminisation of 25 dimensional colour (reflectance) makes female faces more attractive but they also found that attractive female faces had darkened skin.

compared to more feminine male voices (Vukovic et al., 2008). The reason why face shape behaves differently from other sexually dimorphic variables is not known, but it may be due to the relationship between masculinity and facial expressions of emotion. Angrier faces are perceived as more masculine and happier faces are perceived as more feminine (Hess et al., 2009). Hence, feminine shape faces may be more attractive since happier faces are also more attractive (Mueser, Grau, Sussman, & Rosen, 1984). Other sexually dimorphic characteristics are less related to emotion so preferences for male masculinity can prevail.

In the first experiment, we investigated women's preferences for sexually dimorphic colour in male faces. In the second experiment, participants manipulated faces in either sexually dimorphic skin colour or shape in different tasks. In the last experiment, participants were able to manipulate both sexually dimorphic variables simultaneously while considering short- or long-term relationship contexts. In this experiment, we included a 'friendship' control condition with female faces. In all three experiments, we also examined the effect of self-perceived attractiveness on face preferences. We predict that women who rate themselves high in attractiveness will prefer male faces that are more masculinised in shape and skin colour in virtue of their ability to deal with partner's lower parental investment.

3.2. EXPERIMENT 2

3.2.1. Method

3.2.1.1. Participants

One hundred and forty-two Caucasian students, 101 women and 41 men, from St Andrews University, UK, volunteered for the skin colour measurements (M_{age} = 20.29, *SD* = 1.79). Another 72 Caucasian students from St Andrews University, UK, 36 women and 36 men, were photographed voluntarily (M_{age} = 20.28, *SD* = 1.69) (see Whitehead, Re, et al. (2012) for procedures). Lastly, 48 heterosexual Caucasian female participants (M_{age} = 22.65, *SD* = 6.60) voluntarily took part in the online experiment that is described in the procedure.

3.2.1.2. Colour Measurement

For details of colour measurement procedures see Whitehead, Re, et al. (2012).

From a total of 142 participants, 103 that reported no use of a solarium, fake tan or sunbathing in the previous month and had skin colour values that lay within three standard deviations of the mean were selected for analysis. After exclusions, there were 75 women and 28 men left to calculate mean CIE L*a*b* face skin values (across the three face regions) for the male and female faces. Average male face skin colour was L*= 63.39, a*= 13.53 and b*= 15.06 and average female colour was L*= 66.81, a*= 11.48 and b*= 13.91. Average male face skin luminance (L*) was significantly different from female average ($Z = -6.23$, $p < .001$), and the same was true for a* ($Z = -5.63$, $p < .001$) and b* ($Z = -3.99$, $p < .001$) parameters.

3.2.1.3. Stimuli

Individual photographed faces were colour calibrated before manipulation (see Whitehead, Re, et al. (2012) for detailed procedures). Twelve composite female faces and 12 composite male faces were used for perceptual judgments; each composite face was an average of 3 photographed faces of different individuals. These groups of three faces were randomly selected from the 36 photographs of the same sex individuals mentioned in 3.2.1.1 Different combinations were used for short- and long-term stimuli. The averaging procedure aimed to reduce individual differences in colour and shape of the face stimuli without the need to use other procedures that would increase the artificiality of the faces. One hundred and ninety-two landmarks were marked on each face image to delineate the facial features that would be transformed.

Two face uniform colour masks were created in Psychomorph (Tiddeman et al., 2001) to represent the average male and female skin colour from the L*a*b* values reported above. The skin portions including lips and eyebrows but excluding eyes (sclera, iris, and pupil) of the composite faces were manipulated according to the colour difference between the two endpoint colour masks. We obtained a set of 21 images for each face, ranging from -200% masculinised to 200% masculinised, with the middle image being the original composite face. The colour continuum represented a total range of +/-1.710 L* units, +/-1.024 a* units and +/-0.577 b* units. Finally, the hair, neck, ears and background were occluded from view (see Figure 5).

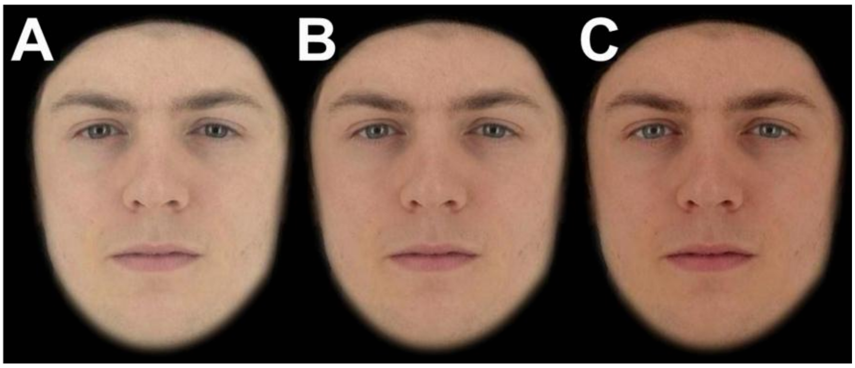

Figure 5. Coloration applied to faces along sexually dimorphic colour axis in Experiment 2. A represents low masculinisation (-200%), B is the original image and C represents high masculinisation (+200%).

3.2.1.4. Procedure

Participants were asked to answer a short computer-based questionnaire with demographic information including a 7-point scale for self-rated attractiveness. Participants then performed two facial manipulation tasks, where they were asked to "make the face look as attractive as possible". The tasks consisted of manipulating face images along colour masculinity to maximise the attractiveness of the faces from the range available. Horizontal mouse movement allowed participants to change the colour of the presented face, similar to previous studies (Little et al., 2002; Penton-Voak et al., 2003; Perrett et al., 1998; Whitehead, Re, et al., 2012).

Faces were presented in random order in two counterbalanced blocks of 12 male and 12 female faces. Participants selected, via horizontal movements of a mouse cursor, the position along the colour axis. The direction of movement, axis centre location and axis arrangement (left movement increasing or decreasing masculine colour) were randomised.

3.2.2. Results

3.2.2.1. Colour masculinity preferences

For each participant the mean degree of masculinisation considered to be maximally attractive, was calculated for male and female faces independently. Distributions were normal (Kolmogorov-Smirnov tests $p > 0.2$). A significant preference for masculinity was found for male faces ($M = 81.74\%$, $SD = 69.23$, one sample t-test against no change in masculinity, *t* (47) = 8.18, *p* < .001, *d* = 1.18) and for female faces (*M* = 59.27%, *SD* = 83.5, *t* (47) = 4.92, *p* < .001, *d* = .71). Participants masculinised male faces more than female faces, *t* (47) = -2.47, *p* = .017, *d* = 0.36 (Figure 6).

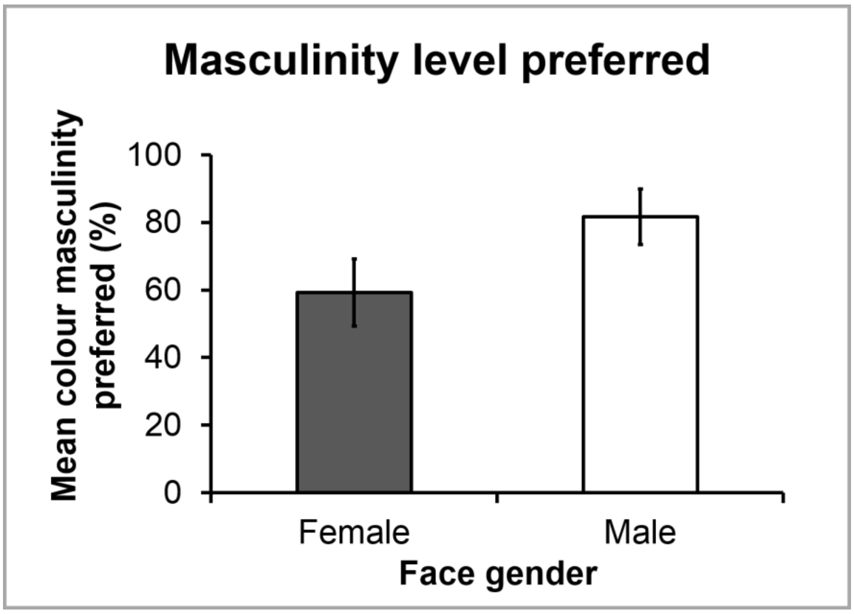

Figure 6. Mean masculinity level preferred in colour according to the sex of the face stimuli in Experiment 2. Error bars show standard errors of the mean.

3.2.2.2. Self-rated attractiveness.

Self-reported attractiveness of women did not correlate with the level of colour masculinity chosen for the male faces (Spearman's rank correlation (r_s) = .005, *p* = .974) or the female faces (r_s = - .074, *p* = .619).

3.2.3. Discussion

In Experiment 2, we found a preference for more masculine colour in male faces compared to female faces. While participants chose to masculinise both male and female faces, this tendency was exaggerated in male faces. This outcome may reflect skin colour acting as a signal of mate quality through the owner's health or status (Scott et al., 2010; Whitehead, Re, et al., 2012).

Our colour measurements indicate that men have darker (lower L*), redder (higher a*) and yellower (higher b*) facial skin colouration compared to women. Frost (1994) suggests that in our ancestral environment, the darker faces of men might be perceived as stronger potential rivals for other men and hence better future mates for women.

Lightness is more attractive in female faces compared to male faces and is more naturally pronounced in women's than in men's faces (Frost, 1988; Van den Berghe & Frost, 1986). Redness of male facial skin is related to important traits including perceived dominance and attractiveness (Matts et al., 2007; Re, Whitehead, Xiao, & Perrett, 2011) and, along with yellowness, might signal mate quality (Stephen, Scott, et al., 2012). Hence males with colour masculinised faces may be more attractive because their colour is associated with health or dominance and ability to access resources (Puts, 2010).

Female faces had less masculine colour applied than male faces but were still subject to an increase in masculinisation of skin colour for optimal attractiveness. This is likely to reflect the fact that skin colour cues convey similar health information in men and women. Blood flow to the skin and hence skin redness is linked with health and cardiovascular fitness (Re et al., 2011). Skin yellowness depends on carotenoids from a healthy diet and lifestyle (Alaluf et al., 2002; Whitehead, Ozakinci, et al., 2012; Whitehead, Re, et al., 2012).

3.3. EXPERIMENT 3

The aim of this experiment was to explore preferences for sexual dimorphism in skin colour (as Experiment 2) and in face shape from the same participants. We explored preferences for sexual dimorphism in skin colour with an extended colour range. It is possible that in Experiment 2, face colour preferences were limited by the truncated range available to participants. Experiment 3, therefore, tested whether an increased range of face colour would affect the masculinity level preferred by participants.

3.3.1. Method

3.3.1.1. Participants

Sixty-one volunteer female participants (M_{age} = 20.11, *SD* = 4.26) took part in the experiments online. All participants reported heterosexual orientation and Caucasian ethnicity.

3.3.1.2. Stimuli

The 24 base images (12 female) from Experiment 2 were used.

3.3.1.2.1. Shape Manipulation

The facial shape of each of the 24 faces was manipulated according to the shape difference between Penton-Voak and colleagues' (2003) average male and average female face shapes. A continuum of 11 images was created for each face ranging from +100% masculinised to -100% masculinised (see Figure 7).

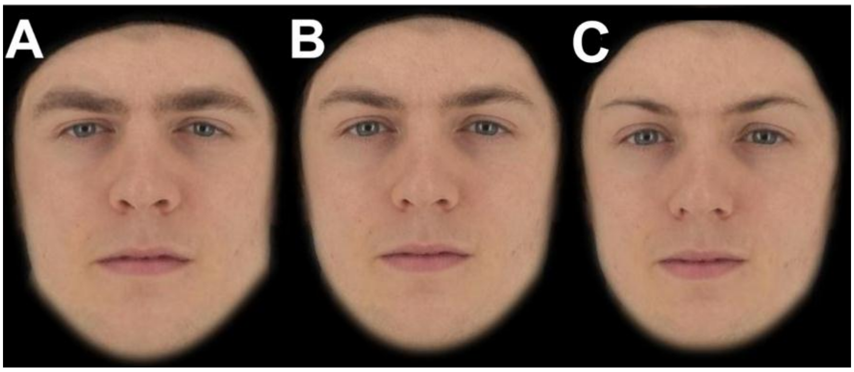

Figure 7. Shape transform applied to faces along sexually dimorphic shape axis in Experiment 3. A represents high masculinisation (+100%), B is the original image and C represents low masculinisation (-100%).

3.3.1.2.2. Colour Manipulation

The skin portions of the same 24 faces were manipulated according to the colour difference between the two endpoint colour masks from Experiment 2 in order to obtain a set of 21 images each, ranging from -300% to +300% masculinised.

3.3.1.3. Procedure

Participants performed two facial manipulation tasks where they were asked to "make the face look as attractive as possible", with appearance varying either in the colour or shape continuum. As in Experiment 2, horizontal mouse movement allowed participants to manipulate the colour (or shape) of the test face. Faces were presented in random order and shape, and colour blocks were counterbalanced.

3.3.2. Results

3.3.2.1. Preferences for masculinity in male and female faces

For each participant the mean preferences for sexually dimorphic colour and shape across male and female faces were calculated. Values were normally distributed

(Kolmogorov-Smirnov, $p > .05$) except for male colour which showed acceptable skewness of -.75 (*SE* = .31) and kurtosis of .17 (*SE* = 0.60). A significant preference for colour masculinity was found in male faces (*M* = 121.27%, *SD* = 81.2, $t(60) = 11.66$, $p < .001$, $d = 1.49$) and in female faces (*M* = 103.77%, *SD* =85.58, $t(60) = 9.74$, $p < .001$, $d = 1.21$) (Figure 8).

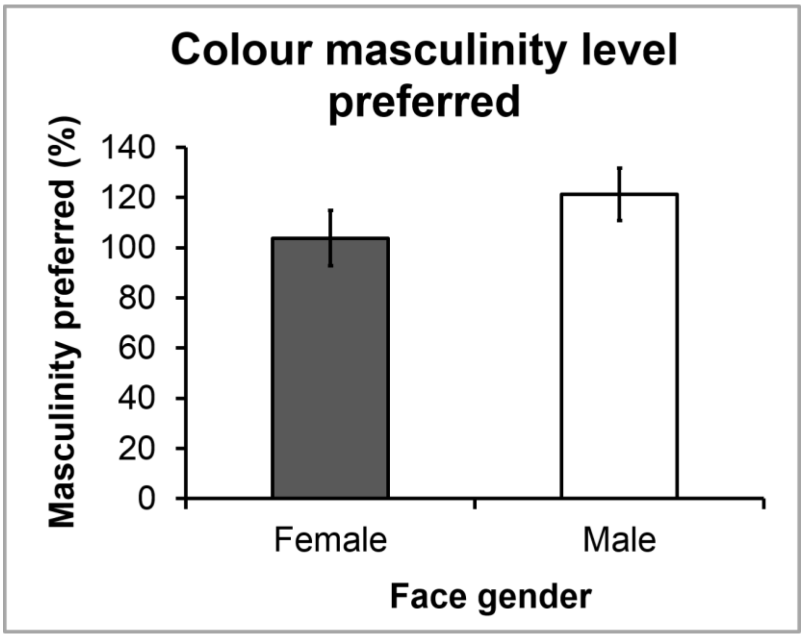

Figure 8. Mean masculinity level preferred in colour according to the sex of the face stimuli in Experiment 3. Error bars show standard errors of the mean.

Furthermore, a significant preference for femininity in shape was found in male faces (*M* = -11.83%, *SD* =33.75, $t(60) = -2.74$, $p < .001$, $d = -.35$) and in female faces (*M* = -43.28%, *SD* = 19.21, $t(60) = -17.60$, $p < .001$, $d = -2.25$) (Figure 9).

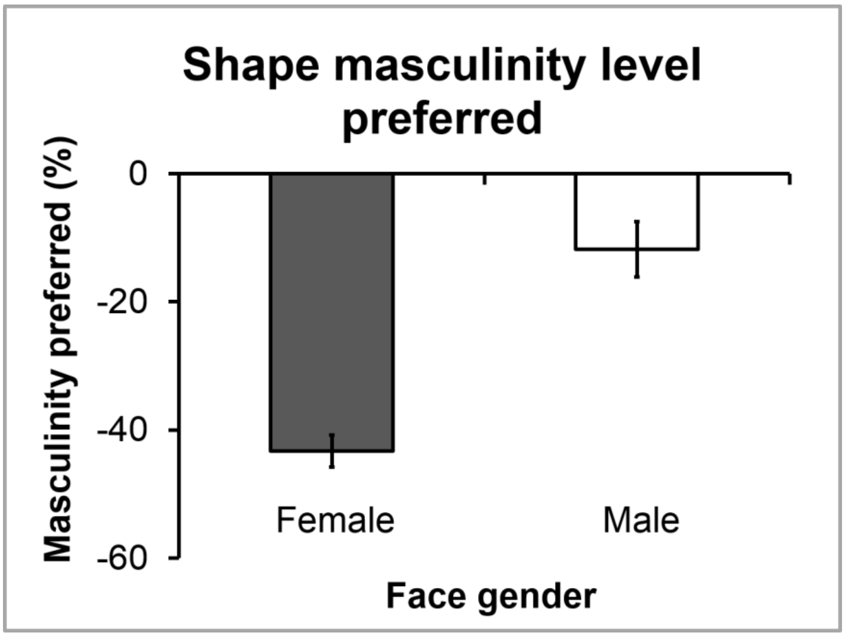

Figure 9. Mean masculinity level preferred in shape according to the sex of the face stimuli in Experiment 3. Error bars show standard errors of the mean.

There was a significant effect of sex of the face on colour preferences, (paired *t* (60) = -2.10, *p* = .04, Figure 8) reflecting greater masculinity preferences in male faces. There was also a significant effect of sex of the face on shape preferences (*t* (60) = -6.8, *p* < .001, Figure 9) reflecting greater femininity preferences in female faces.

Preferences for sexually dimorphic shape did not correlate with preferences for sexually dimorphic colour across individuals, neither for female faces (*r* = .06, *p* = .648) nor male faces (*r* = .17, *p* = .191).

3.3.2.2. Self-rated attractiveness

Self-rated attractiveness did not correlate significantly with the levels of skin colour masculinity chosen for female faces (r_s = -.01, *p* = .936) or male faces (r_s = .017, *p* = .891). Self-rated attractiveness also did not correlate significantly with the levels of shape masculinity preferred for female faces (r_s = -.114, *p* = .345) or male faces (r_s = .178, *p* = .137).

3.3.3. Discussion

Experiment 3 tested skin colour preferences with an extended colour range. The increased manipulation range (-300% to +300%) allowed participants to indicate preferences for slightly higher degrees of colour masculinisation. Since preferences fell below +150%, there did not seem to be a ceiling effect. Therefore, it is not possible to draw conclusions about the absolute level of preferred sexual dimorphism in skin colour since this may depend on the colour range available. However, it is noteworthy that participants in Experiments 2 and 3 preferred a similar difference of colour masculinity between female and male faces, which indicates that participants prefer different skin colour in men and women. Indeed the preferred level of skin colour masculinisation tended to be 20% greater for men's faces than for women's faces.

Women chose to feminise the shape of both female and male faces to maximise their attractiveness. Such preferences for a feminised male face shape have been reported in several studies (DeBruine, Jones, Smith, et al., 2010; Little et al., 2001; Little et al., 2002; Perrett et al., 1998). Said and Todorov (2011) also found that male facial attractiveness was associated with feminisation in shape, but masculinisation was preferred in terms of colour.

3.4. EXPERIMENT 4

Experiment 4 permitted simultaneous manipulation of sexual dimorphism in both skin colour and face shape. This allowed participants to search for an optimal combination of the two cues and could potentially reveal interactions in attraction to the sexually dimorphic traits. Face colour range was restricted to +/-200% (as in Experiment 2) since in Experiment 3, participants maintained preferences below +/-150%.

Experiment 4 also investigated between-subjects the influence of short- or long-term relationship context. We predicted a preference for higher levels of masculinisation in the short-term context and that own attractiveness would correlate with masculinity preferences in the long-term context.

3.4.1. Method

3.4.1.1. Participants

Fifty-two female undergraduate students at the University of Aveiro, Portugal (M_{age} = 20.39, *SD* = 2.95) participated in the experiment, 26 in each experimental condition (short- and long-term relationship contexts). All participants were Caucasian and reported being heterosexual.

3.4.1.2. Stimuli

We employed the 24 composite base faces (12 female) from the previous two experiments.

3.4.1.2.1. Shape Manipulation and Colour Manipulation

Psychomorph (Tiddeman et al., 2001) was used to construct the average shape of 36 women and 36 men. These averages were used for shape transforms (as described in Experiment 3) to obtain 11 images for each base face ranging from -100% to 100% shape masculinised. The colour masks from Experiment 2 were used for colour transformation. The skin portions of each of the 11 shape transformed images per face were manipulated to obtain 21 images ranging from -200% to 200% colour masculinised. Thus 231 images (11 x 21 images) varying in shape and colour were prepared for each base face (see Figure 10).

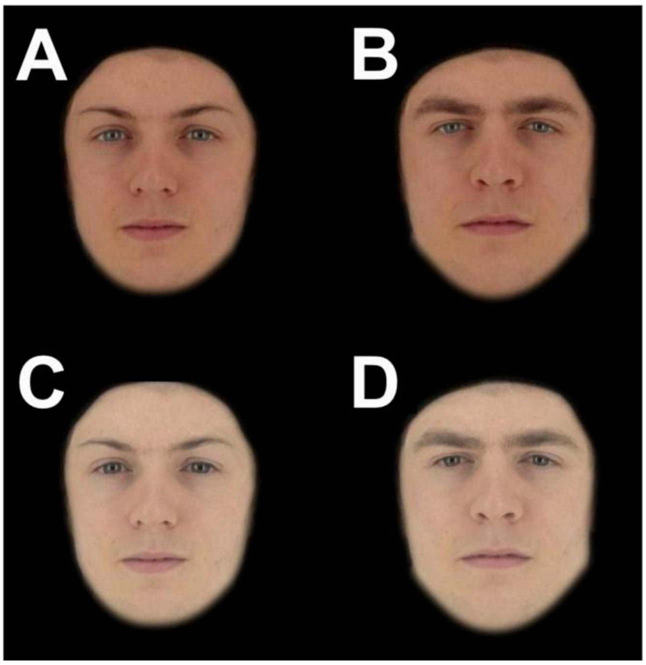

Figure 10. Sexually dimorphic shape and colour transforms of male facial appearance in Experiment 4. A represents high masculinisation of colour (+200%) and low masculinisation in shape (-100%), B represents high masculinisation of colour (+200%) and high masculinisation in shape (+100%); C represents low masculinisation of colour (-200%) and low masculinisation in shape (-100%); D represents low masculinisation of colour (-200%) and high masculinisation in shape (+100%).

3.4.1.3. Procedure

Participants answered a short questionnaire and then performed the face manipulation tasks. On each trial, participants were able to manipulate both face colour and shape, from the range available, in order to maximise its attractiveness.

When manipulating the 12 male faces, participants were instructed to assume either a short-term or a long-term relationship context as defined previously (Penton-Voak et al., 2003). Participants judged male faces in only one of the two relationship contexts, and in addition judged 12 female faces in a friendship condition. For the different conditions, the instruction was respectively: “Please alter the face until you think it is the closest to the appearance you would find attractive for a partner in a short-term (or long-term) relationship / for a friendship”.

The order of presentation of stimuli blocks (female or male) was counterbalanced across participants and trials order was randomised. Mouse movement direction was also randomised, where horizontal movement could alter the shape, and vertical movement could alter the colour of the face randomly from masculine to feminine or from feminine to masculine.

3.4.2. Results

3.4.2.1. Preferences for masculinity in male and female faces

Initial analyses examined preferences for male facial masculinity in male or female faces, collapsing data across short- and long-term relationship contexts for the male faces. A significant preference for colour masculinity was found in male faces (M = 108.85%, SD = 56.94, t (51) = 13.79, p < .001, d = 1.91) and in female faces (M = 92.92%, SD = 59.3, t (51) = 11.30, p < .001, d = 1.57).

Furthermore, a significant preference for shape femininity was found in male faces (M = - 40.67%, SD = 27.05, t (51) = -10.84, p < .001, d = -1.5) and in female faces (M = - 48.30%, SD = 29.85, t (51) = - 11.67, p < .001, d = -1.62).

As in experiments 2 and 3, participants masculinised male faces more than female faces but this time, the results did not reach statistical significance for colour preferences (paired t (51) = -1.43, p = .16) or shape preferences (t (51) = -1.45, p = .15) (Figure 11).

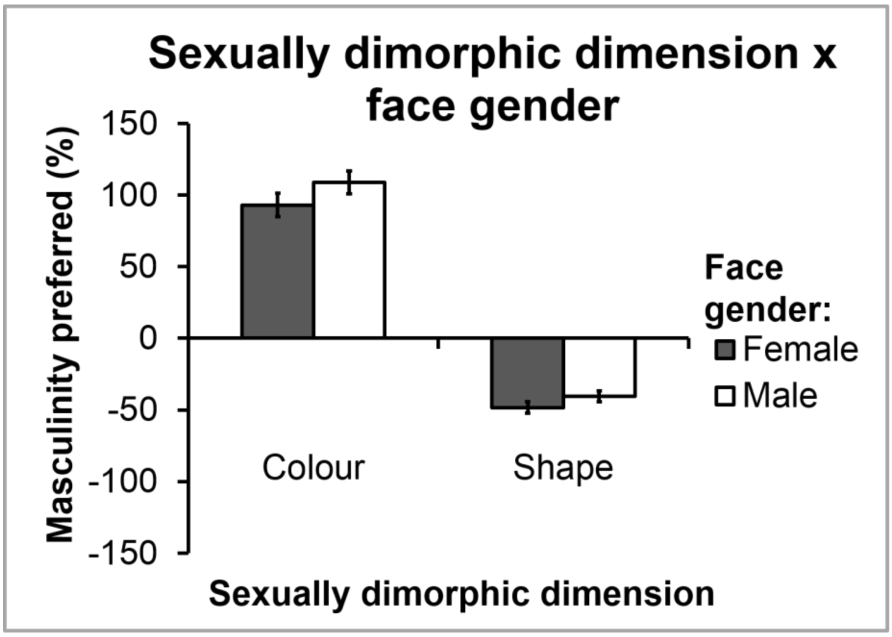

Figure 11. Mean masculinity level preferred (in colour and shape) according to the sex of the presented stimuli in Experiment 4. For male faces, preferences for a short-term and for long-term relationships are combined. For female faces, preferences are for friendship. Error bars show standard errors of the mean.

Preferences for colour masculinisation correlated negatively with preferences for shape masculinisation in female faces (r = - .414, p = .002). However, this correlation was not significant for male faces (r = - .136, p = .336).

3.4.2.2. Relationship context

T-tests for independent samples examined the association between each sexually dimorphic dimension (colour and shape) and relationship context (short- or long-term) for male faces. The effect of relationship context was not significant for male colour (t (50) = 2.12, p = .152) or male shape (t (50) = 0.52, p = .82) (Figure 12).

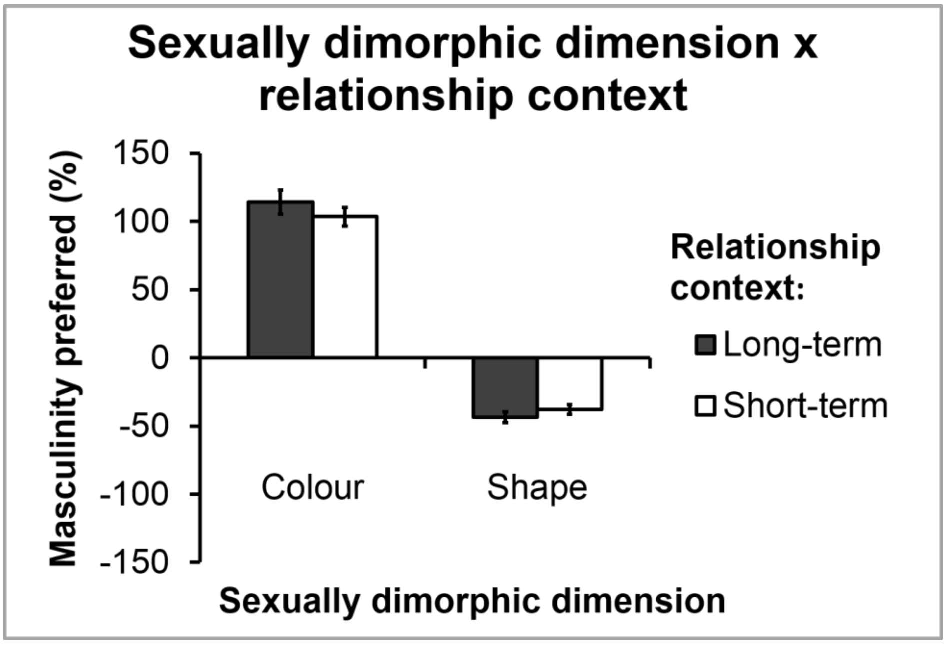

Figure 12. Mean masculinity level preferred (in colour and shape) for male faces according to long- and short-term relationship contexts considered by female participants in Experiment 4. Error bars show standard errors of the mean.

3.4.2.3. Self-rated attractiveness

When considering the short-term context group, self-rated attractiveness did not correlate significantly with shape or colour masculinisation of the male faces (r_s = -.151, *p* = .462; r_s = .103, *p* = .617, respectively). By contrast, when considering the long-term context group, self-rated attractiveness was positively correlated with shape masculinisation of the male faces (r_s = .482, *p* = .013) but not with colour masculinisation of the male faces (r_s = -.093, *p* = .652). Self-rated attractiveness did not correlate with the chosen level of masculinity in shape (r_s = -.022, *p* = .877) or colour (r_s = -.172, *p* = .223) for female faces.

3.4.3. Discussion

As in the two previous experiments, results indicate that masculinisation is generally preferred in face skin colour and feminisation is desirable in face shape. Moreover, in line with the hypothesis that reproductive strategy and mate choice depend on own-condition (Gross, 1996; Penton-Voak et al., 2003), there was a significant positive association between preferred masculinity in face shape and self-rated attractiveness for long-term relationships, such that participants who considered themselves more attractive preferred more masculine-shaped male faces. This may happen because attractive females are more able to compete more successfully for markers of quality or dominance in men (Penton-Voak et al., 2003). As expected, the influence of self-rated attractiveness only emerged for participants who considered a long-term relationship: a context that requires investment from the male partner. However, an association with self-rated attractiveness was not present when considering face skin colour.

3.5. GENERAL DISCUSSION

3.5.1. Masculinity preferences

Previous research by Said and Todorov (2011) suggested that masculinity in male faces is attractive in terms of colour properties, but that femininity is attractive in shape properties. Here we investigated sexual dimorphism in skin colour along with face shape to understand how each variable may influence female mate choice.

Based on the latest models of face attractiveness, we expected to find a preference for masculine colouration of male faces. That was the case since, in all three experiments, participants increased colour masculinity of faces to make them look more attractive. The advantage of preferring a masculine colour, which is darker, yellower and redder, may be linked with a preference for health and/or personality traits such as dominance (Stephen, Oldham, et al., 2012). Masculine traits, including a deep voice and muscular build, may have evolved in the context of intrasexual competition, and secondarily become sexually attractive to women (Puts, 2010). Hence, women's preferences for masculine male skin colour may also underlie the pursuit of a dominant mate.

Our participants also showed a preference for masculine skin colour in female faces. This is at first surprising, but it is not without precedent. Indeed Said and Todorov's (2011) figure 4a shows that direction of maximal increase in attractiveness from the average female face includes a darkening of the facial skin. Men have higher skin melanin than women (Jablonski & Chaplin, 2000), yet Lefevre and Perrett (2015) found that increased melanin levels in both male and female faces make them look healthier. Indeed, raised a* and b* levels, which are components of masculinity in skin colour, are attractive in both sexes since both increase perceived health (Stephen, Coetzee, et al., 2009; Stephen et al., 2011). Therefore, participants may enhance skin colour masculinity in female faces to increase perceived health. Importantly, the preferred colour masculinity level for female faces was lower than the masculinity level preferred for male faces (although this effect did not reach significance in Experiment 4); hence participants amplify sex differences in skin colour when maximising attractiveness in male and female faces.

For face shape, following Said and Todorov's (2011) findings, we expected our participants to prefer feminine-shaped male faces as potential partners. Indeed, as predicted, our participants did consider feminised male faces as more attractive (Experiments 3 and 4). Consistent with this model, we also found a preference for masculinisation in the colour component relative to the shape component for male faces. Moreover, preferences in colour and shape masculinisation did not correlate for male faces, which may support the claim that shape and colour have different weights on attractiveness (Said & Todorov, 2011).

If dimorphism in skin colour contributes to judgments of masculinity in male or female faces, colour variation can lead to discrepant conclusions about the contribution of masculinity to male facial attractiveness. The majority of studies using natural images (varying in intensity and colouration) reported a positive correlation between attractiveness and perceived masculinity (G. Rhodes, 2006). Studies manipulating face shape while keeping colour constant are less consistent in reporting masculinity contributing to male facial attractiveness (G. Rhodes, 2006). Studies of natural image allow preferences for masculinity in male skin colouration to be manifest, while studies manipulating or measuring masculinity in face shape cannot reflect an attraction to masculine skin colouration.

3.5.2. Own attractiveness

According to the Trade-off Theory (Gross, 1996; Little et al., 2001; Penton-Voak et al., 2003), we expected that participants who rated themselves as more attractive would show preferences for more masculinised faces, especially when considering a long-term mate. The absence of significance for the effect of self-rated attractiveness on preferred masculine face shape and colour in Experiments 2 and 3 may be because a relationship context was not specified (although in Experiment 3 there was a non-significant, but positive, correlation between self-attractiveness and shape masculinisation). Experiment 4 did show the expected correlation between self-rated attractiveness and preference for shape masculinisation in the long-term partnership contexts. This effect, however, was not apparent in preferences for male face colour in long- or short-term contexts.

3.5.3. Limitations and future studies

A limitation of the current research is that we did not control variations in participant's own skin colour (beyond restricting the analysis to those reporting ethnicity as 'White'). Melanin levels vary considerably with latitude and population. Individuals used to a darker-skinned population may have higher preferences for masculinised skin colour (in both male and female faces). Such variation can potentially disrupt detection of relationships between preferred masculinity in skin colour and other variables including self-rated attractiveness.

Comparing the results of the three experiments, we found different mean values of preferred face masculinity for each group of participants. Such variation could be due to the stimulus range or the experimental setting, i.e., participation online or in the lab, since online participants were worldwide, whereas attendees in the lab had perhaps more similar cultural backgrounds. Differences between Experiments 2 and 4 could also reflect a trade-off between masculinity cues, with higher colour masculinity selected for faces with low shape masculinity.

Nonetheless, the goal of the present studies was not to determine an absolute value of masculinity for optimal attractiveness but to explore the roles of sexual dimorphism in skin colour and face shape in attractiveness judgments. We confirmed a preference amongst Caucasian women for masculinity of skin colour in men's faces. Additionally, we found that the attraction to masculinisation of skin colour co-exists with a preference for femininity in face shape.

Future research is required to resolve the question of why femininity is found attractive in one trait (male face shape) while preference for masculinity is evident in other traits such as skin colour. Further research will also be necessary to establish the impact of sexually dimorphic skin colour on: (a) social attributions, (b) attractiveness in different populations and (c) individual differences in attraction more generally, as a result of partnership status, menstrual cycle, other-rated attractiveness, sexual orientation and hormonal contraceptive use.

3.6. CONCLUSION

This work is the first to investigate the attractiveness of skin colour, as a sexually dimorphic variable, in composites of real faces, and it sheds light on the reasons for the equivocal results in the role of sexual dimorphism in male facial attractiveness. The divergent results found in previous studies may, at least in part, be explained by the apparent trade-off between preferences for masculine facial colouration but feminine facial shape.

This study highlights the importance of analysing face skin colour along with shape when studying the attractiveness of faces. We show that when women are given the opportunity to adjust sexually dimorphic skin colour and shape of a male face to maximise attractiveness, masculine skin colour and feminine face shape are the preferred traits.

Chapter 4. Do masculine men smell better? An association between skin colour masculinity and female preferences for body odour

The work presented in this chapter was accepted for publication as the article below:

Carrito, M. L., Santos, I. M., Alho, L., Ferreira, J., Soares S. C., Bem-Haja, P., Silva, C. F., Perrett, D. I. (2017). Do masculine men smell better? An association between skin color masculinity and female preferences for body odor. *Chemical Senses*. 10.1093/chemse/bjx004.

4.1. INTRODUCTION

Several studies have demonstrated that olfactory cues seem to have an important role in human sexual behaviour (Kohl et al., 2001; Lübke & Pause, 2015), especially in women's mate choice (Havlíček et al., 2008; Herz & Cahill, 1997; Herz & Inzlicht, 2002). Women show superiority in sensitivity-detection and recognition-identification body odour tasks compared to men (Brand & Millot, 2001) and seem to be more sensitive to the influence of body scents in their sexual interest (Herz & Cahill, 1997). In fact, female participants seem to prefer the odours of men that are more dominant (Havlíček et al., 2005) and more symmetric (Thornhill & Gangestad, 1999b). During puberty, when sexually dimorphic traits begin to emerge, the development of sebaceous and apocrine skin glands occurs which suggests that masculinity may be imprinted in human odour (Wyatt, 2015).

Heterosexual women might feel attracted to masculine traits in men, namely scent cues, since masculinity is believed to signal genetic fitness and/or intrasexual competitiveness. The preference for masculinity traits in sexual partners might lower the risk of infection for women, since masculine healthy males may be less likely to contract and spread diseases (Kirkpatrick & Ryan, 1991) or at least ensure protection and resources for them and their offspring (Puts, 2010). Several studies have reported that preferences for masculinity, especially in odour cues, are dependent on the menstrual cycle of the female participants (Havlíček et al., 2005; Thornhill & Gangestad, 1999b). Those studies report that women prefer the scent of more masculine males only near ovulation, and this occurs only for non-pill users. However, other studies have failed to find differences across the ovulatory cycle (Rantala et al., 2006).

To our knowledge, Allen, Cobey, Havlíček, and Roberts (2016), while studying the effect of artificial fragrances on preferences for human body odours, were the first to investigate how perceived facial masculinity correlates with perceived body odour masculinity. They found a positive correlation between face masculinity ratings given by both sex participants with odour masculinity ratings given by female participants. Other studies explored the preference for masculinity in odour cues relying on men's testosterone levels (Thornhill et al., 2013), 2D:4D (S. C. Roberts et al., 2011), or women's exposure to androstenone (Cornwell et al., 2004; Grammer, 1993), androstenol (Savic & Berglund, 2010) or androstadienone (Cornwell et al., 2004). Acknowledging the debate on whether these last chemicals do in fact represent real human pheromones (Wyatt, 2015) and the inconsistent results regarding the attractiveness level of face shape masculinity, with some studies reporting preferences for femininity (DeBruine, Jones, Smith, et al., 2010; Little & Hancock, 2002; Perrett et al., 1998) and others suggesting a preference for masculinity (e.g. DeBruine et al., 2006; Little & Mannion, 2006) in male faces, it becomes important to consider other measures of masculinity when investigating odour preferences for sexually dimorphic cues. In this study, we measured masculinity through a new trait which has received little attention: sexually dimorphic skin colour.

One of the most typical sexual dimorphic traits that distinguishes males and females throughout the animal kingdom is phenotypic colour. Sexual dichromatism is frequent between species of birds (Bortolotti et al., 1996; Dale et al., 2015) , amphibians (Bell & Zamudio, 2012) and fish (Kodric-Brown, 1998). Human skin colour, apart from being an important indicator of current health (Fink et al., 2012; Re et al., 2011; Stephen, Law Smith, et al., 2009; Whitehead, Ozakinci, et al., 2012), has been shown to be different between human females and males (Van den Berghe & Frost, 1986) but also to be considered attractive in mate preferences (Carrito et al., 2016). The multi-million industry of facial cosmetics is itself a proof of how much skin colour influences the perception of facial beauty, and much of cosmetics use seems to serve the purpose of exaggerating sexual dimorphic differences (Russell, 2009). A recent proposal claimed skin colour, as an indicator of current health condition, to be a stronger determinant of perceived attractiveness than shape masculinity (Scott et al., 2010; Stephen, Scott, et al., 2012). In a previous study of Carrito and colleagues (2016), participants chose to masculinise the colour of male faces more than the colour of female faces when asked to modify the faces to define the most attractive appearance. A masculine skin colour that is darker, yellower and redder than a more feminine skin colour, might represent direct benefits to the female partner and hence be attractive for women.

Accordingly, the goal of our study was to investigate whether the odour of men with more masculine facial skin colour would be more attractive to heterosexual women. We expected odours of donors with more masculine skin colour to be preferred by female raters compared to the ones from men with less masculine skin colour. Along with attractiveness, women were asked to rate other characteristics of the odours: pleasantness, sexiness, health, familiarity, intensity, arousal, masculinity and dominance.

4.2. EXPERIMENT 5

4.2.1. Method

4.2.1.1. Participants

Detailed written informed consent was obtained from all participants prior to enrollment, and all aspects of the study were performed in accordance with the Declaration of Helsinki for experimentation with human subjects. The study was part of a project that was approved by the Scientific Council of the University of Aveiro, which assessed its ethical, formal and scientific aspects. A socio-demographic questionnaire open to the academic community was available online, in order to recruit female participants for the experimental task. Forty-two women, aged between 18 and 39 (M_{age} = 24.24 years, *SD* = 6.43), from a total of 116, were selected to participate in the study.

The inclusion criteria were ethnicity (Caucasian), age (between 18 and 40 years old), health status (not reporting any physical, neurological or mental disease), not being pregnant and not currently taking any medication. The upper limit in age was a deliberate choice aiming to avoid the possible influence of hormonal effects related with participants' menopause (Cobey et al., 2015; B. C. Jones et al., 2011). The absence of use of hormonal contraceptives was also a requirement since it has been shown that hormonal contraceptives influence sensitivity to olfactory stimuli (Lundström, McClintock, & Olsson, 2006; Renfro & Hoffmann, 2013) and also attractiveness judgments in other domains (Little, Burriss, et al., 2013; S. C. Roberts et al., 2014). All participants reported having regular menstrual cycles (28 – 40 days). Participants were asked about the date of the onset of their last menstruation (day 1). Fertile women were considered when being in days 9–15 of their cycle at the time of the experiment (N = 10) while others were considered to be in non-fertile phases of the cycle (N = 31) (Havlíček & Lenochová, 2006). One participant could not recall the date of the onset of her last menstruation and her fertility status was not considered.

Participants were asked to refrain from eating (e.g., gum, candies), drinking coffee, or using any scented products that could interfere with their olfactory ability for 1 hour before testing.

4.2.1.2. Materials

4.2.1.2.1. Skin colour measurements

The first phase of this work focused on trying to establish a measure of facial skin colour sexual dimorphism for the young adult Portuguese population. To do so, it was necessary to collect a sample of skin colour measurements of men and women in order to calculate a representative skin colour average, according to the International Commission on Illumination (CIE) L*a*b* values, typical of the male and female population. The CIELab colour space is defined by L*, a*, and b* values (L* reflects degrees of lightness and positive values of a* and b* reflect degrees of redness and yellowness, respectively) (Whitehead, Ozakinci, et al., 2012) and is designed to be perceptually uniform, with a change of one unit appearing to be of approximately the same magnitude regardless of its dimension (Martinkauppi, 2002). Therefore, skin colour measurements were taken from 100 Caucasian university students, 50 women (aged between 18 and 37; M_{age} = 21.14, *SD* = 3.89) and 50 men (aged between 19 and 31; M_{age} = 22.98, *SD* = 2.65) who volunteered for skin colour measurements. Exclusion criteria included the use of self-tanning products, recent physical effort, skin or infectious disease. The experimenter cleaned the skin on the forehead of each student with cotton and alcohol. Skin colour was measured using a Konica Minolta Chroma Meter CR-400. The aperture of the Chroma meter was lightly held against the skin, in order to minimise pressure-induced blanching. White-point calibration was conducted before recording sessions. Recordings were repeated three times on the participant's forehead, and the most divergent value of the three was excluded from the analyses. Two men and 3 women were later excluded from the sample because the Euclidean (ΔE^*) distance between their two remaining skin colour measurements was larger than 2. Finally, we averaged the two remaining values to obtain a unique L* a* b* set of values for each participant.

Through this process of skin colour measurement, average CIE L*a*b* values were assessed for male (n = 48) and female (n = 47) participants. Average male face skin colour was L*= 65.37, a*= 12.52 and b*= 17.05 and average female colour was L*= 67.82, a*= 11.02 and b*= 15.85. Average male face skin luminance (L*) was significantly different from female average (t (93) = - 4.51, p < .001), and the same was true for the a* (t (93) = 3.77, p < .001) and b* (t (93) = 3.08, p < .001) colour axes.

Logistic regression was conducted in order to posteriorly calculate skin colour masculinity scores of the male body odour donors. To do so, we considered the L* a* b* values as predictors and the sex of participant as the outcome (men were scored as 1 and women as 0). The resulting model was significant, χ^2 (3) = 26.96, $p < .01$, R^2 (Nagelkerke) = .329, and was represented by the following equation: Sex = constant + *B*1 x L* + *B*2 x a* + *B*3 x b*, in which the constant = 7.2, *B*1 = -.22, *B*2 =.25 and *B*3 =.27. Logistic regression analyses revealed that skin colour (L*, a* and b*) predicted the sex correctly for 69.5% of participants.

A similar skin colour measurement procedure was adopted to collect skin colour measurements of the male body odour donors. Thirty-two male students volunteered, 14 of them being later excluded based on several criteria as described below. Male volunteers filled a socio-demographic questionnaire and two Visual Analogue Scales (VAS, 0 - 100 mm) that measured their own perceived stress and anxiety levels during the tasks. Only participants that reported low levels of stress or anxiety (< 50 in the stress/anxiety scales) were selected. Additional inclusion criteria were: ethnicity (Caucasian), age (over 18 but under 40 years old), avoidance of sun-tanning activities, health status (not reporting physical, mental or neurological diseases) and not currently taking any medication. The 18 male volunteers that fulfilled all requirements (aged between 18 and 34; *M* = 23.83, *SD* = 3.94) were selected for subsequent skin colour measurements and body odour sampling. Regarding the skin colour measurements, CIE L*a*b* values of participants' forehead skin were used to estimate the degree of skin colour masculinity of each of the 18 donors. Based on the model presented previously, we calculated the masculinity score of each of the body odour donors (*M* = 1.63, *SD* = 1.08, Range: -0.31 – 3.86).

4.2.1.2.2. Sampling of donors' body odour

For the body odour sampling procedure, donors were given a kit with two cotton pads (Mercurochrome) and medical adhesive tape in a zip bag, a white cotton t-shirt, a towel and a hypoallergenic scent free gel wash (*Lactacyd Derma Gel*). Donors were instructed to refrain from using fragrant hygiene products (e.g., perfume, body lotions), smoking, eating spicy foods, garlic, and drinking alcohol, the day before the body odour sampling and until the end of the sampling, in order to avoid alterations of their natural body odour (Alho et al., 2015).

Donors were instructed to bathe early in the morning with the *Lactacyd Derma Gel* and to put in place the cotton pads under both armpits. After they had put on the white cotton t-shirt supplied, donors could also wear their personal clothes if they were clean (and fragrance-free). Body odours were collected on the cotton pads attached to their armpits (Alho et al., 2015; Mitro, Gordon, Olsson, & Lundström, 2012). Donors wore the t-shirts for periods of 4 hours. The cotton pads were then collected, divided into equal-size quadrants, stored in a closed zip-locked bag and frozen at -20°C.

The samples were thawed 1 hour before the experimental task. Four pad quadrants were placed separately in wide-mouthed glass jars with lids and were used as body odour samples. In order to prevent contamination, odour samples were always handled with surgical gloves. Also, the time interval between storage and the last defrosting was less than 6 months (Lenochova, Roberts, & Havlíček 2009).

4.2.1.3. Procedure

In the odour rating task, participants smelled each body odour sample for 3 seconds and rated them on their perceived attractiveness, sexiness, healthiness, familiarity, intensity, pleasantness, masculinity, dominance and arousal using a VAS (0-100 mm). The anchor points for the ratings were not attractive and very attractive for "attractiveness", and the same format was applied to the rest of the traits. The specific instructions were as follows: "Place a mark on the lines below in order to indicate your judgment about the various characteristics of this odour". The order of presentation of the traits to be rated was randomised between trials for each sample for each participant. Also, the order of presentation of the 18 odours was randomised and different for each participant. This task was repeated 18 times (one time for each odour sample).

4.2.2. Results

4.2.2.1. Notes on data analysis

All the analyses were performed using SPSS with Amos (v.22). Primary descriptive and correlational analyses considered male body odour donors as units of analyses (section 4.3.2), averaging the scores given by all female participants. However, because this methodology does not take into account the variability stemming from individual differences between raters, further analyses were performed taking into account the absolute values of the ratings given by each female rater for each odour sample. Multilevel analyses allowed the consideration of both the effect of female raters (n = 42; level 1) and the effect of male body odour donors (n=18; level 2) to be analysed simultaneously rather than aggregating data by either one of them (Gildersleeve, Haselton, Larson, & Pillsworth, 2012). This test was repeated for each of the dependent variables considered, addressing how the skin colour masculinity score predicted each one of the ratings.

In order to avoid repeating conceptually similar evaluations and increasing the probability of one of the judgments becoming significant by chance, the ratings considered in all analyses were previously submitted to a dimension reduction procedure. Exploratory factor analyses allowed the extraction of two factors and the model was posteriorly improved using confirmatory factor analyses. Hence the dependent variables considered in the previously mentioned multilevel analyses were not the individual ratings initially collected but the dimensions determined by the latter model.

4.2.2.2. Descriptive statistics and correlations between ratings

In the first analyses performed, body odour donors were considered as units of analysis (n = 18), to investigate possible associations between the collected ratings. Table 2 shows descriptive statistics for all the rated traits.

Table 2. Descriptive statistics of the male odour ratings in Experiment 5.

	Mean	SD	Range
Attractiveness	27.13	10.27	8.85 - 45.83
Pleasantness	33.84	13.56	7.26 - 53.29
Sexiness	25.35	9.20	9.70 - 43.55
Health	45.17	8.86	28.57 - 57.29
Masculinity	51.68	15.58	32.21 - 77.22
Dominance	36.44	9.48	24.12 - 53.45
Intensity	46.83	21.54	17.71 - 83.52
Arousal	34.78	9.73	20.14 - 51.62
Familiarity	27.90	6.66	20.02 - 46.83

Since the rating values were normally distributed (Shapiro-Wilk, $p > .05$), except for pleasantness, which showed acceptable skewness of .96 (SE = .54) and kurtosis of -.11 (SE = 1.04), Pearson correlations were performed. As observed in Table 3, there are multiple significant correlations between the ratings.

Table 3. Correlations between odour ratings when considering male body donors as units of analysis in Experiment 5.

	ATTR	PLEA	SEXI	HEAL	MASC	DOMI	INTE	AROU	FAMI
ATTR	---								
PLEA	.899**	---							
SEXI	.948**	.783**	---						
HEAL	.880**	.926**	.806**	---					
MASC	-.507*	-.783**	-.373	-.686**	---				
DOMI	-.385	-.651**	-.255	-.606**	.934**	---			
INTE	-.624**	-.835**	-.511*	-.814**	.948**	.878**	---		
AROU	-.329	-.622**	-.195	-.600**	.878**	.872**	.895**	---	
FAMI	-.201	-.482*	-.125	-.430	.715**	.664**	.659**	.750**	---

Note: * $p < .05$; ** $p < .01$. ATTR = Attractiveness; PLEA = Pleasantness; SEXI = Sexiness; HEAL = Health; MASC = Masculinity; DOMI = Dominance; INTE = Intensity; AROU = Arousal; FAMI = Familiarity.

4.2.2.3. Ratings – Dimension reduction

Analyses were performed considering both body odour donors and female raters as units of analysis. Exploratory factor analysis, with Principal Component Analysis (PCA) as extraction method and varimax rotation with suppression of small coefficients (< .40), allowed the extraction of two main components: one including attractiveness, pleasantness, sexiness and health ratings; the other including masculinity, dominance, intensity and arousal ratings. To confirm the validity of these latent factors and to verify if the observed variables are legitimate representations of their latent factors, we conducted a confirmatory factor analysis. A new model, excluding both health and arousal, showed higher factor weights and individual reliabilities. Following the procedure used by Gildersleeve, Haselton, Larson, and Pillsworth (2012), we have grouped the attractiveness, pleasantness and sexiness ratings in a single latent factor which was called “Likeability”. In addition, we grouped the masculinity, dominance and intensity ratings in a factor called “Maleness”. The two-factor model (see Figure 13) revealed a good goodness-of-fit index (GFI = .901). Additionally, all the items of the two factors obtained high factor weights ($\lambda \geq .5$) and appropriate individual reliabilities ($R^2 \geq .25$) showing good local adjustment and factorial validity (Figure 13).

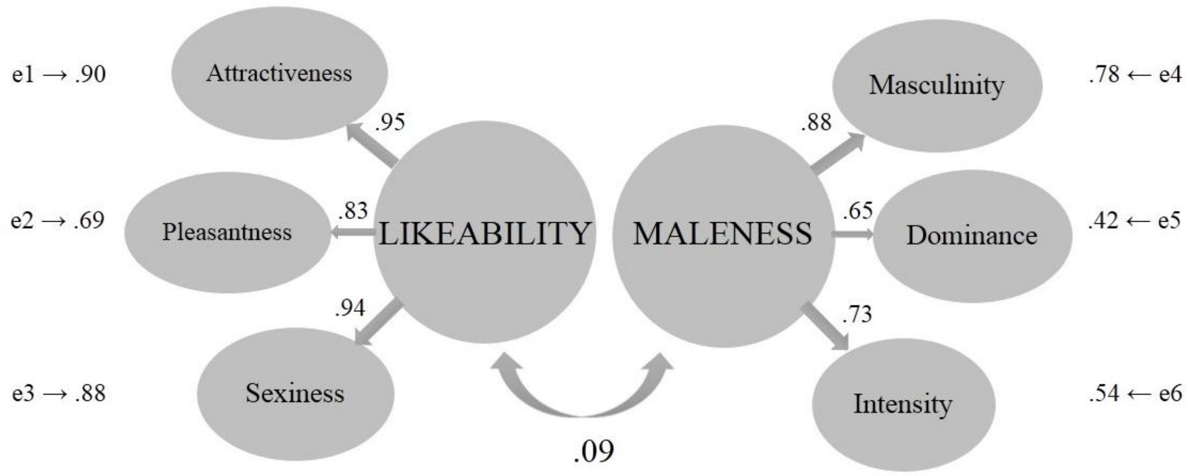

Figure 13. Confirmatory factor analysis of the factors, Likeability and Maleness, in Experiment 5. Proportions represent, from centre to periphery, the correlation between factors, factor weights and individual reliabilities, respectively.

The discriminant validity (which assesses whether the items/variables present in a particular factor are not correlated with other factors) was calculated by comparing the Average Variance Extracted (*AVE*) of each factor with the square of the correlation between the two factors (Anderson & Gerbing, 1988). *AVEs* were evaluated as described by Fornell and Larcker (1981). The resulting value (.0081) was far below that of the AVE values ($AVE_{Likeability}$ =.83; $AVE_{Maleness}$ =.58), confirming discriminant validity.

The Cronbach alpha was calculated to assess the internal consistency of the items in each factor. The values obtained for the two factors were above .7 (Nunnally, 1975) indicating an appropriate reliability ($Cronbach\ \alpha_{Likeability}$ = .929; $Cronbach\ \alpha_{Maleness}$ = .793). Thus, the values of likeability and maleness were calculated taking into account the factor weights of each variable (for example: Likeability = Sexiness*.94 + Pleasantness*.83 + Attractiveness*.95).

4.2.2.4. The influence of skin colour masculinity on odour ratings

The following multilevel analyses took into consideration likeability, maleness, arousal, familiarity and health as dependent variables (separate analysis were performed for each of the variables). The colour masculinity score predicted positively both likeability (Unstandardized β = 4.44 +/- 1.944, Wald Chi-square = 5.228, *df* = 1, *p* = .022) and health (Unstandardized β = 2.102 +/- .756, Wald Chi-square = 7.731, *df* = 1, *p* = .005). Maleness was predicted negatively by the colour masculinity score (Unstandardized β = -8.403 +/- 1.464, Wald Chi-square = 32.924, *df* = 1, *p* <.001). Finally, colour masculinity score did not predict ratings of familiarity (Unstandardized β = -.643 +/- .849, Wald Chi-square = .573, df = 1, p = .449) or arousal (Unstandardized β = 1.756 +/- .955, Wald Chi-square = 3.377, df = 1, p = .066).

4.3. ADDITIONAL SURVEY

With the aim of better understanding the reason why donors with high skin colour masculinity had their body odours rated as less masculine and less dominant, an online survey was conducted to investigate the stereotypical notion of what masculine/dominant men smell like. Questions were formulated about judgments of male odour intensity and unpleasantness, considering the masculinity and dominance of the donor.

4.3.1. Method

4.3.1.1. Participants

A hundred and sixty-six women responded voluntarily to one of four questions. All of them were Caucasian and were more than 18 years old but less than 38 (M_{age} = 24.13; SD = 4.84). The number of participants that responded to each of the four questions was 43 for question 1; 40 for question 2; 43 for question 3; and 40 for question 4.

4.3.1.2. Procedure

The questions/answers were formulated with a common starting scenario: “Imagine that you are sensing the odour of two different men (natural odour – without perfume or deodorant)”. Participants responded to only one of the following questions:

1. Which of the odours is more intense? Possible answers: (a) the more masculine; (b) the less masculine.
2. Which of the odours is more intense? Possible answers: (a) the more dominant; (b) the less dominant.
3. Which of the odours is more unpleasant? Possible answers: (a) the more masculine; (b) the less masculine.
4. Which of the odours is more unpleasant? Possible answers: (a) the more dominant; (b) the less dominant.

4.3.2. Results

The “more masculine man” option was selected by 93.02% of participants for the more intense odour scenario (Figure 14) and by 65% of participants for the more unpleasant odour scenario (Figure 15). Similarly, the “more dominant man” option was selected by 85% of participants for the more intense odour scenario (Figure 16) and by 65% of participants for the more unpleasant odour scenario (Figure 17).

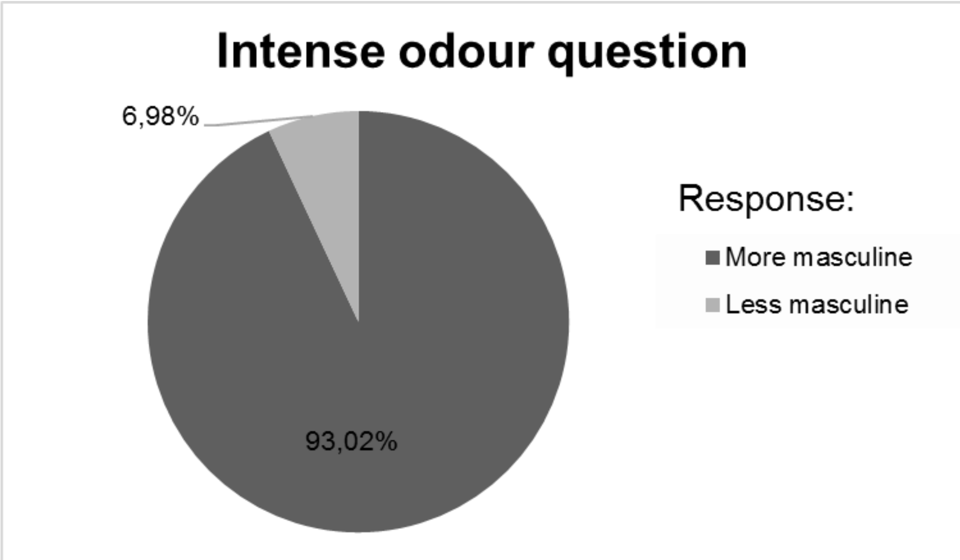

Figure 14. Percentage of more masculine and less masculine responses to the hypothetical scenario of sensing an intense body odour in the additional survey.

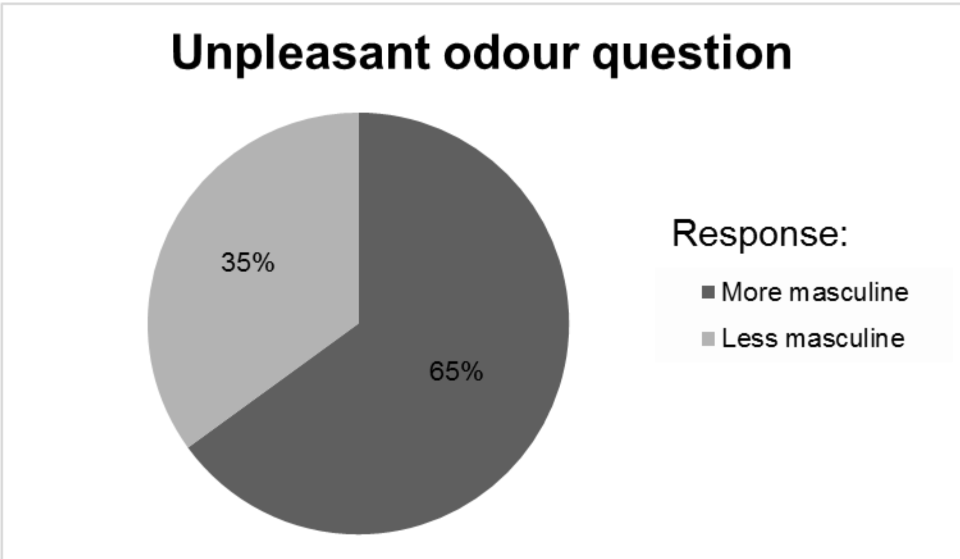

Figure 15. Percentage of more masculine and less masculine responses to the hypothetical scenario of sensing an unpleasant body odour in the additional survey.

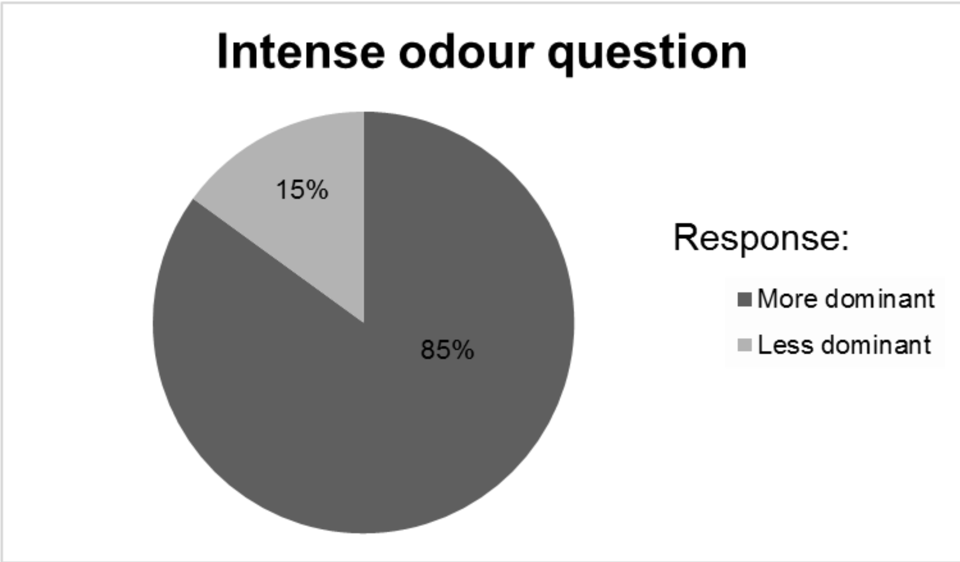

Figure 16. Percentage of more dominant and less dominant responses to the hypothetical scenario of sensing an intense body odour in the additional survey.

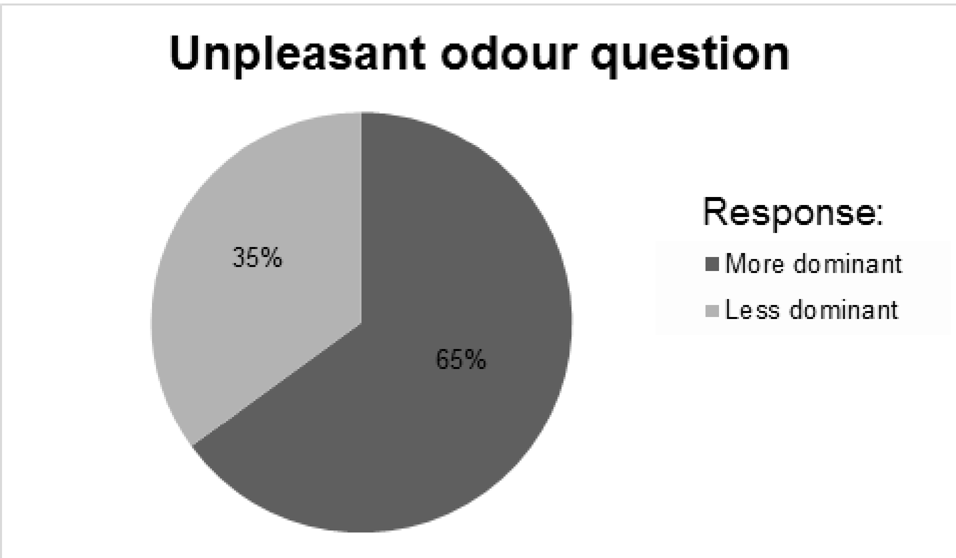

Figure 17. Percentage of more dominant and less dominant responses to the hypothetical scenario of sensing an unpleasant body odour in the additional survey.

As predicted, women associated the intense and unpleasant odours to more masculine/ dominant males.

4.4. DISCUSSION

The main aim of this work was to explore if skin colour masculinity had any association with odour judgments of the same participants. To do so, we measured skin colour L*a*b* values of male donors and calculated their masculinity index according to a regression model of skin colour sexual dimorphism. The body odours of each donor were rated by female participants. Results showed that the donors' skin colour masculinity index predicted positively their likeability (attractiveness, pleasantness and sexiness) and health ratings, but negatively their maleness (masculinity, dominance and intensity) ratings.

Skin colour has been reported as an important determinant of perceived health (Re et al., 2011; Stephen, Coetzee, et al., 2009; Stephen et al., 2011; Stephen, Law Smith, et al., 2009). Skin colour is also related to reproductive life (B. C. Jones et al., 2015) and plays an important role in the perception of face attractiveness (Fink et al., 2012; Fink et al., 2006; Matts et al., 2007). It has been found that the way in which skin colour influences attractiveness seems to be different for each sex (Russell, 2003, 2009). Previous studies from Van den Berghe and Frost (1986) and Frost (1988, 1994) have suggested that skin colour is sexually dimorphic and that a more typical colour of the respective sex is attractive for the opposite sex. According to Carrito et al. (2016), a more masculine skin colour tends to be attractive for both sexes yet more so for male faces. Using the same methodology of skin colour measurement, we found that men with highly masculine colour have a body odour perceived not only as more attractive, pleasant and sexy, but also as healthier.

Consistent findings have been reported that more dominant men have a sexier smell than less dominant men (Havlíček et al., 2005). Dominant and masculine men might constitute a beneficial choice as partners since they ensure access to resources and protection (Puts, 2010). In fact, a recent explanation regarding the mate value of masculinity emphasises its relation to competitive status-seeking behaviours, more than actual immunocompetence (Scott et al., 2010). Despite the controversy surrounding the exact function of masculinity (whether it relates to health and/or competitiveness), masculinity does seem to be attractive when considering preferences for body shape (Little, Jones, et al., 2007), voice (Vukovic et al., 2008) and skin colour (Carrito et al., 2016). It remains unclear why studies exploring face shape report inconsistent results but these might reflect methodological issues (G. Rhodes, 2006).

How skin colour is related to body odour production also remains to be known. A recent study by Zuniga and coworkers (2016) found skin yellowness to be positively correlated with body odour hedonic evaluations when female participants rated odours of male donors. The authors claimed that such result represented a preference for odours of possible healthy mates that had a rich diet in fruit and vegetables. However, self-reported fruit and vegetable consumption did not predict the participants' affective evaluation of the odours. Because skin yellowness is sexually dimorphic, as we observed in section 4.2.1.2.1, it is possible that Zuniga et al.´s (2016) findings represent a preference for odours of men with more masculine colour, similarly to our study. Body odours are caused by the presence of bacteria in the secretions of the sebaceous and apocrine glands which, in turn, are very frequent in human armpits (Leyden et al., 1981). Because sebaceous and apocrine glands develop during puberty (Wyatt, 2015), simultaneously with the development of secondary sexual characteristics, it is possible that body odour communicates sexual maturity of the individual. On the other hand, considering the possibility that masculinity is indeed related to health and fitness, the relationship between skin colour and odour production may be indirect, with men with more masculine skin colour being healthier and consequently having a different odour. The health of the individual is believed to influence body odour, as disease can significantly alter the smell of sweat (Olson & Marshuetz, 2005; Shirasu & Touhara, 2011), so heterosexual women may feel attracted to odours of more masculine, healthier men.

Concerning the results related to the maleness factor, previous findings have demonstrated that the odour of more dominant men is less intense (Havlíček et al., 2005) and a similar result was found in the present study for skin colour masculinity. An inverse relationship between odour pleasantness and intensity has been reported in other studies (Doty, Orndorff, Leyden, & Kligman, 1978; Havlíček, Dvořáková, Bartoš, & Flegr, 2006; Mutic, Moellers, Wiesmann, & Freiherr, 2016). Here, skin colour masculinity negatively predicted the maleness factor that included masculinity, dominance and intensity ratings. At first sight, this result might seem unexpected, but it is probably due to the influence of a stereotype from female raters. It is possible that attributions of masculinity to odours are based on an overgeneralization of the stereotypic assumption that men smell worse than women. By such stereotypical overgeneralization more masculine men should, therefore, smell (even) worse than feminine men. Unable to find literature that supports the existence of the stereotype “Masculine men smell intensely and badly”, we conducted an online survey where female participants, facing an imaginary odour presentation, had to say if the intense/unpleasant odours normally belong to more or less masculine/dominant men (see data in the additional survey). As predicted, women associated the intense and unpleasant odours to hypothetical more masculine and dominant males. By this, we conclude that these findings probably result from the influence of a stereotype. This conclusion is supported by Mutic and co-workers' findings (2016) that suggest that both women and men are unable to correctly attribute masculinity ratings to odours. They found a masculinity bias in human odour since body odours tended to be rated as masculine, regardless of the sex of the donor. Their results were also interpreted as resulting from masculine gender stereotypes, with intense body odour being judged as originating from dominant and physically strong men.

More studies exploring the association between preferences for facial masculinity and odour preferences are needed since, to our knowledge, there is little evidence of this relationship. Despite the number of studies linking (face and body) symmetry and odour attractiveness (Rikowski & Grammer, 1999; Thornhill et al., 2013; Thornhill & Gangestad, 1999b; Thornhill et al., 2003), facial masculinity has been neglected by recent studies of odours (except for Allen et al., 2016). As mentioned before, higher masculinity, when measured through the levels of testosterone, seems to enhance the attractiveness of odours (Thornhill et al., 2013). Other studies have investigated sexually dimorphic preferences in odour cues, through preferences for putative pheromones (Cornwell et al., 2004). The use of putative pheromones has been criticised by some authors who claim that there is insufficient evidence that the compounds identified so far are actual pheromones (Wyatt, 2015). For this reason, studies that use body odours are more ecologically valid than studies of preferences for putative pheromones.

It would also be of interest to test preference for odours of same-sex individuals to evaluate whether the preferences reported here and in similar studies (e.g. Zuniga et al., 2016) do in fact represent mate choice mechanisms or if they simply account for a need of individuals to be surrounded by healthy others in order to avoid infectious diseases. Carrito et al. (2016), when evaluating preferences for skin colour masculinity in faces, found that female participants masculinised both male and female faces, noticing, however, that male faces were consistently more masculinised than the other face group. This difference in face colour preferences, showed skin colour masculinity to be especially important when women judge male faces, which might be taken as a possible mate choice strategy. Regarding odour preferences, if such difference was evident between same and other-sex odours, similar conclusions could be reached, and a mate choice relevance would be indicated. Future studies should also try to understand if the menstrual cycle phase of the raters influences their preferences for odours of men varying in skin colour masculinity. Such analyses were not performed in this work given the unequal number of female participants present in each group (only 10 female raters were in the fertile phase while the other 31 were in the non-fertile phase of their menstrual cycle).

To our knowledge, this study was the first to explore the relationship between skin colour masculinity and odour attractiveness. The results show that females prefer the odour of men with more masculine face skin colour. Our findings support the idea that chemosensory communication is important in the context of reproductive success (Lübke & Pause, 2015) and that humans, like other animals, use olfactory signals for the transmission of information that is biologically relevant (Grammer et al., 2005).

Chapter 5. Individual differences in attraction to face trustworthiness: The effect of social interaction anxiety

5.1. INTRODUCTION

There is evidence that humans may feel attracted by different facial features depending on the type of relationship context they are considering. Studies show that women tend to prefer more masculine / symmetrically faced men for a short-term partner, prioritizing genetic quality, as opposed to the preference for more feminine (and trustworthy looking) male faces when considering a long-term mate (Little et al., 2001; Little & Jones, 2012; Penton-Voak et al., 2003). Concerning men's preferences, although some studies show no effects of relationship context when considering sexually dimorphic features (Burriss et al., 2011b; Scott et al., 2008), others do. Some studies also claim that men place great weight on kindness and honesty when considering a partner for a long-term relationship and prioritize other characteristics, like physical attractiveness, for short-time relationships (Li, Bailey, Kenrick, & Linsenmeier, 2002; Li & Kenrick, 2006; Regan, Levin, Sprecher, Christopher, & Gate, 2000). Therefore, even if men and women differ in terms of preferences for sexually dimorphic traits when considering the two relationship contexts, they may have similar preferences for features perceived as affording high trustworthiness for a long-term *versus* a short-term relationship.

Trustworthiness judgments are made very rapidly when meeting someone for the first time (Willis & Todorov, 2006) and serve the important social function of helping to decide whether to approach or avoid that person (Todorov, 2008). Hence, trustworthiness may be an important indicator taken into account in mate choice. There are several structural facial features that may contribute to perceptions of trustworthiness. Faces with high inner eyebrows, pronounced cheekbones, wide chins and U-shaped mouths are perceived as more trustworthy as opposed to faces with lower eyebrows, shallow cheeks, thin chins and ∩-shaped mouths (Todorov, Baron, et al., 2008). The perception of these features, which also approximate to negatively and positively valenced expressions, may trigger avoidance and approach responses (Oosterhof & Todorov, 2008). Negatively and positively valenced expressions may also decrease and increase perceived attractiveness (Jaensch et al., 2014).

Although there are cues that are universally perceived as attractive (e.g. symmetry), studies have identified individual differences that influence the strength of those preferences (Little, Burt, & Perrett, 2006; Little & Perrett, 2002; Welling, DeBruine, Little, & Jones, 2009). Social anxiety is characterised by an excessive fear of being exposed to the scrutiny of others (American Psychiatric Association, 2013). This condition seems to bias the perception of certain emotional face expressions, making them look more threatening (Staugaard, 2010). Social phobics seem to show increased sensitivity to threat since, when asked to make a quick assessment of a neutral face slowly changing into a negative expression, they identify angry faces at a lower intensity of change (Joormann & Gotlib, 2006). Social phobia is believed to be related to a dysregulation of the amygdala function (Amaral, 2002). Patients with bilateral damage of the amygdala have also shown an impairment in their ability to assess whether a person looks trustworthy compared to a control group (Adolphs et al., 1998). Social interaction anxiety, in particular, refers to “distress when meeting and talking with other people, be those people members of the opposite sex, strangers, or friends” (Mattick & Clarke, 1998, p. 457). Therefore, social interaction anxiety may influence mate preferences towards individuals who vary in their level of perceived facial trustworthiness.

The present study assessed whether attractiveness preferences for faces that vary in perceived trustworthiness change when considering short- and long-term relationship contexts and how these preferences can be influenced by social interaction anxiety. Unfamiliar faces were presented to heterosexual participants of both sexes, who were asked to consider them as potential mates and to adjust the shape of each face until it looked the most attractive. The faces changed along a perceived trustworthiness continuum. These choices were made considering a partner for both a short-term and a long-term relationship. We predicted that higher levels of perceived trustworthiness would be preferred for long-term relationships compared to short-term ones. We expected this to occur both for male and female participants since both sexes were observed to place greater importance on trustworthiness when considering long-term relationships (Fletcher, Tither, O’Loughlin, Friesen, & Overall, 2004).

This study also explored the association between face preferences and individual differences in social interaction anxiety. We hypothesised that those with high social interaction anxiety would choose faces displaying cues of higher perceived trustworthiness.

5.2. EXPERIMENT 6

5.2.1. Method

5.2.1.1. Participants

Ninety-four students volunteered to participate in the experimental task, 46 women (M_{age} = 21.37, *SD* = 2.29) and 48 men (M_{age} = 21.13, *SD* = 2.33). Participants reported being exclusively or mainly heterosexual (≤ 1 in a scale from 0 as “Exclusively heterosexual" to 6 as "Exclusively homosexual"), and Caucasian. Participation did not involve any kind of compensation (incentives were not provided).

5.2.1.2. Materials

5.2.1.2.1. Stimuli

Individually photographed faces (30 male and 30 female faces), taken under standard pose and illumination conditions, and displaying a neutral facial expression, were used. Each one of the 60 faces was delineated with 192 points (with x and y coordinates) in order to delimit the face areas that would be transformed. Delineation and face transformation were done using Psychomorph software (Tiddeman et al., 2001). For both sexes, groups of three different facial photographs were averaged together, to create 20 composite male faces and 20 composite female faces. Averaging faces is possible by reshaping ('warping') each face into the average shape and then blending images together digitally (P. J. Benson & Perrett, 1993). Composite faces were used instead of the original individual faces since composites are not recognisable as familiar individuals and assure lower levels of inter-individual differences.

Two uniform face shape masks, representing an average face of high perceived trustworthiness and an average face of low perceived trustworthiness, were used to manipulate the shape of the composite faces. Each one of the masks was an average of 10 Caucasian faces developed by Todorov, Baron, et al. (2008) using FaceGen software (www.facegen.com), previously rated as high or low in perceived trustworthiness (for more details, see Dzhelyova, Perrett, & Jentzsch, 2012). The manipulation of the composite faces was based on the shape difference between those two endpoint shape masks, resulting in a set of 11 images for each face, ranging from -50% trustworthiness to +50% trustworthiness, with the middle image being the original composite face, as exemplified in Figure 18. Finally, the hair, neck, ears and background were occluded with an oval black mask.

5.2.1.2.2. Questionnaires

Participants were asked to complete a demographics questionnaire including information about age, sex, ethnicity and sexual orientation. Participants also responded to the Portuguese version of the Social Interaction Anxiety Scale (SIAS) (Mattick & Clarke, 1998; Pinto-Gouveia & Salvador, 2001). The SIAS assesses anxiety in interpersonal interactions. This questionnaire has good levels of internal consistency and adequate construct validity (E. J. Brown et al., 1997). We obtained a Cronbach's α of 0.90 for our sample and a mean sum value of 29.35 (SD = 11.7, range 6–55).

Figure 18. Example of the trustworthiness transformation in Experiment 6. The image on the left represents the most untrustworthy version (-50% transformation), the one in the middle is the original composite face, and the face on the right represents the most trustworthy version (+50% transformation).

5.2.1.3. Procedure

Participants started by signing an informed consent form, after which they were asked to complete a number of self-report questionnaires, including SIAS. After concluding the questionnaires, participants performed a face manipulation task, where they were told to alter each of the faces until they found the most attractive face within the range available. The faces presented were of the opposite sex of the participant. To be able to visualise the face changing, participants were required to move the mouse horizontally across the image and background, which resulted in a gradual morphing effect with 11 different frames. The chosen face was selected by pressing the left key of the mouse. The starting frame was randomised, and there was no time limit for the task. The 20 composite faces were presented one at a time. Underlying changes in apparent trustworthiness level were not mentioned explicitly to the participants. Half of the faces should be considered as possible mates for a short-term relationship, and the other half should be considered as possible long-term mates. For the different conditions, the instruction was, respectively, "Please alter the face until you think it is the closest to the appearance you would find attractive for a partner in a short-term (or long-term) relationship”. Short- and long-term relationship contexts were defined and described to the participants as in previous research (Penton-Voak et al., 2003). The sets of 10 faces associated with each relationship context were counterbalanced between participants. The order in which participants did the task in terms of relationship context (short- or long-term) and the order of the faces presented within each set were randomised.

5.2.2. Results

5.2.2.1. Overall preferences and effects of sex of participant and relationship context

For each participant, the mean degree of perceived trustworthiness considered to be maximally attractive was calculated. One sample t-tests revealed that preferences for more trustworthy looking faces were greater than chance (i.e. 0%, which would mean a choice not different from the original face) for both short-term [t (93) = 6.88, p < .001, d = 1.419, M = + 14.19%] and long-term relationship contexts [t (93) = 9.97, p < .001, d = 2.056, M = + 18.7%].

Distributions were normal (Kolmogorov-Smirnov tests, p > .11), and homogeneity of variances was assumed (Levene’s tests, p > .12). Perceived trustworthiness preferences were examined via a mixed ANOVA [dependent variable: trustworthiness level preferred; within-subjects factor: relationship context (short- and long-term); between-subjects factor: sex of participant]. This analysis yielded a significant main effect of relationship context, F (1, 92) = 8.62, p = .004, η_p^2 = .086, with higher levels of perceived trustworthiness being more attractive for long-term relationships (M = + 18.59%, SE = 1.81) than short-term relationships (M = + 14.10%, SE = 2.03). A significant main effect of sex of participant also emerged, F (1, 92) = 6.96, p = .01, η_p^2 = .07, such that men selected a higher level of perceived trustworthiness in opposite sex faces as more attractive (M = + 21%, SE = 2.47) compared to women, who preferred comparatively lower levels of perceived trustworthiness (M = + 11.70%, SE = 2.52). The interaction between relationship context and sex of participants was not significant, F (1, 92) = .30, p = .58, η_p^2 = .003 (see Figure 19).

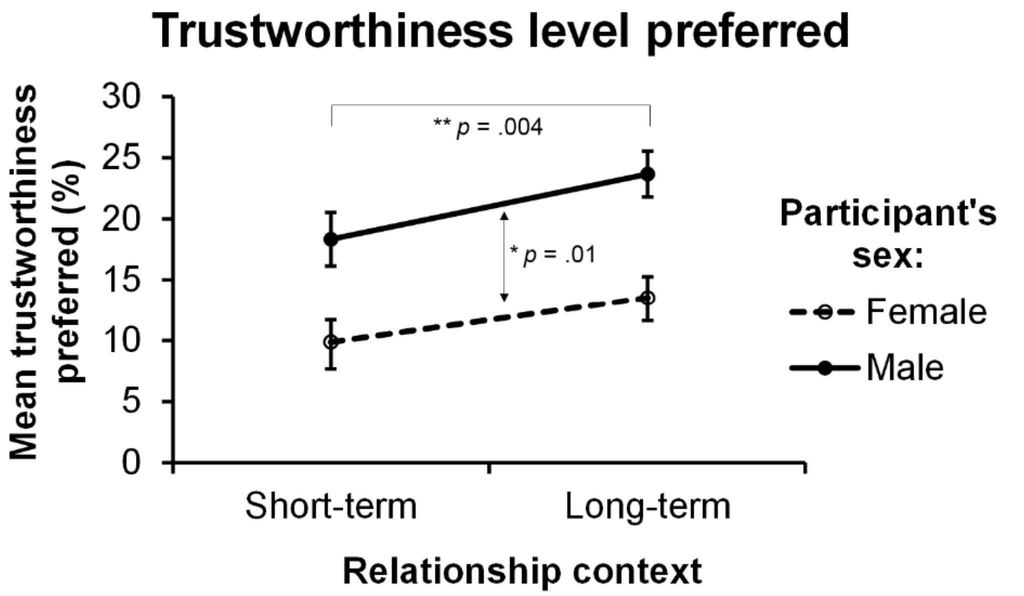

Figure 19. Mean perceived trustworthiness level preferred as a function of relationship context (short- or long-term) and sex of the participant in Experiment 6. Error bars show standard errors of the mean.

5.2.2.2. Social interaction anxiety

First, sex differences in social interaction anxiety were explored through a t-test analysis. Social interaction anxiety values were standardised by being converted to z-scores. No differences in the level of social interaction anxiety were found between male (*M* = 28.75, *SE* = 11.32) and female participants (*M* = 29.98, *SE* = 12.20), *t* (92) = .506, p = .614, *d* = .10. Then, the relation between preferred level of apparent trustworthiness and individual differences in social interaction anxiety was examined through ANCOVA analyses [dependent variable: trustworthiness level preferred; within-subjects factor: relationship context (short- and long-term); between-subjects factor: sex of participant; covariate: social interaction anxiety]. This analysis revealed a significant effect of relationship context on trustworthiness preferences, *F* (1, 91) = 8.56, *p* = .004, η_p^2 = .086, with higher levels of perceived trustworthiness being again more attractive for long-term relationships (*M* = + 18.59%, *SE* = 1.76) than short-term relationships (*M* = + 14.10%, *SE* = 2.00). There was also a significant effect of sex of participant, *F* (1, 91) = 8.02, *p* = .006, η_p^2 = .081, with male participants (*M* = 21.22%, *SE* = 2.41) preferring higher levels of trustworthiness in opposite sex faces compared to female participants (*M* = 11.47%, *SE* = 2.46). Also, there was a significant effect of the covariate (social interaction anxiety), *F* (1, 91) = 5.9, *p* = .017, η_p^2 = .061.

Although the interaction effect between relationship context and social interaction anxiety was not significant, *F* (1, 91) = .36, *p* = .548, η_p^2 = .004, parameter estimation revealed a significant effect of social interaction anxiety on long-term relationship context, t (91) = 2.64, *p* = .01, η_p^2 = .071, but not on short-term relationship context, t (91) = 1.86, *p* = .067, η_p^2 = .036. Figures 20 and 21 represent the relationship between the social interaction anxiety levels and the trustworthiness preferences when considering both relationship contexts.

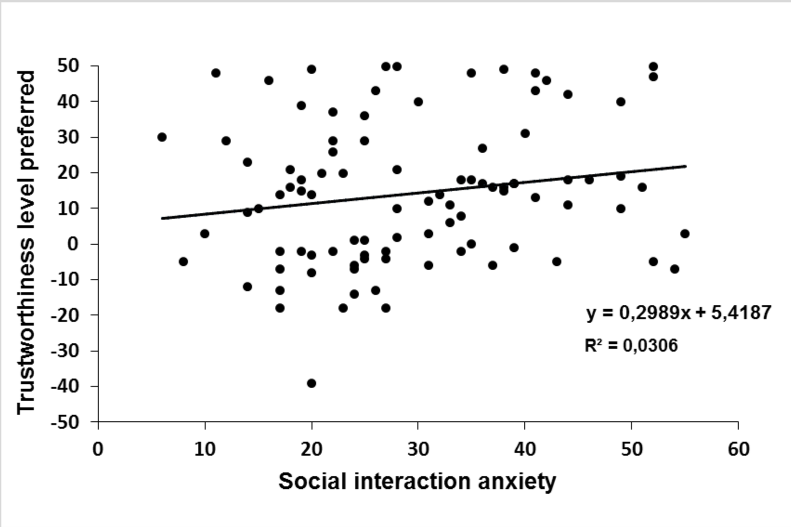

Figure 20. The relation between social interaction anxiety (unstandardized values) and trustworthiness preferences when considering short-term relationship contexts in Experiment 6.

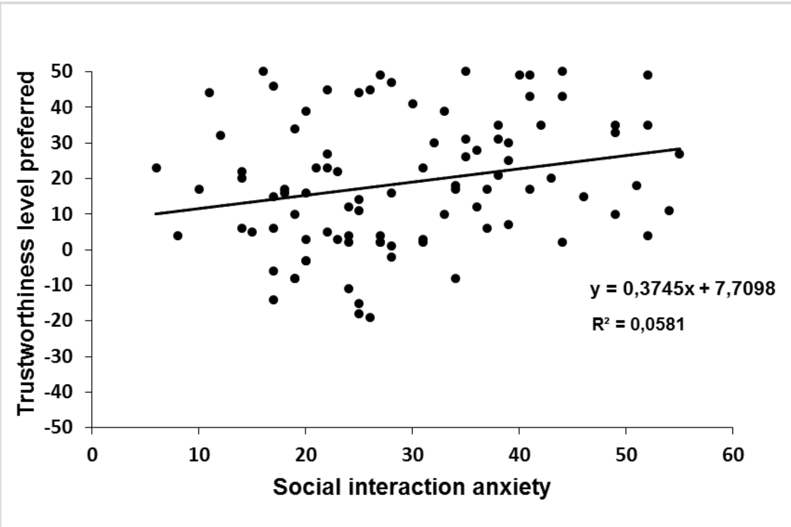

Figure 21. The relation between social interaction anxiety (unstandardized values) and trustworthiness preferences when considering long-term relationship contexts in Experiment 6.

5.3. DISCUSSION

The results of this study provide a broad understanding of male and female preferences for face cues of apparent trustworthiness in mating contexts. Participants seemed to show different preferences for faces that varied in their perceived trustworthiness level depending on the relationship context involved. Specifically, participants preferred more trustworthy looking faces when choosing a partner for long-term relationships, compared to short-term relationships. Similarly to previous research (Little et al., 2002), this result indicates the presence of differential mating strategies which are dependent on relationship goal. Previous research has suggested that signs of genetic fitness become more attractive for short-term relationships, whereas other features often related with trustworthiness become more attractive for long-term relationships. Previous studies have also reported that both women and men place greater weight on "good-genes" cues when considering a short-term relationship and tend to prioritise other traits for long-term relationships (Fletcher, Simpson, Thomas, & Giles, 1999; Little, Cohen, et al., 2007). When choosing a partner for a long-term relationship, a preference for more trustworthy partners that are committed to the relationship and prone to take care of the living offspring might be adaptive (Andersson, 1994).

On the other hand, analyses also showed that women preferred lower levels of perceived trustworthiness in opposite-sex faces compared to men, probably in order to retain some benefits from more masculinised males. According to Oosterhof and Todorov (2008), masculinity is inversely proportional to perceived trustworthiness and because of that, women searching for signs of genetic fitness in men's faces may have tolerated lower levels of trustworthiness. Note that genetic fitness integrates not only signs of health but also dominance (Puts, 2010). Since trustworthiness goes along with femininity in female faces (Oosterhof & Todorov, 2008), it is possible that men preferred more trustworthy faces because they were not forced to make any trade-off. Such conclusions should perhaps be taken with caution because face stimuli were different between groups once men and women manipulated opposite-sex faces.

Subsequent analyses explored the effects of social interaction anxiety on facial preferences. It appears that trustworthiness preferences increase alongside the social interaction anxiety of the individuals, regardless of their sex or relationship context goals. This result was expected since socially anxious individuals date less and have fewer sexual relationships (Alden & Taylor, 2004) and may search for someone very trustworthy who will not trigger their fears. This hypothesis is supported by evidence that highly socially anxious individuals show stronger avoidance tendencies towards angry faces

(Heuer, Rinck, & Becker, 2007; Roelofs et al., 2010). In fact, social anxiety was found to be negatively related to a secure attachment style and positively related to avoidant and anxious styles (Mickelson, Kessler, & Shaver, 1997) and also related to impaired relationship functioning (Hart, Turk, Heimberg, & Liebowitz, 1999).

The attentional bias theory proposes that socially anxious individuals have a higher propensity to be attentive to threatening cues in the environment (Staugaard, 2010). If socially anxious individuals are extra-vigilant to threats, and are characterised by a negative biased processing of social information (Cooney, Atlas, Joormann, Eugène, & Gotlib, 2006), they are also likely to be more sensitive to cues of untrustworthiness and may thus prefer a face that is clearly trustworthy looking when considering someone for a long-term relationship. The present results support this hypothesis.

To the best of our knowledge, this is the first study to acknowledge the influence of relationship context on attractiveness preferences for perceived trustworthy face traits. Previous studies regarding preferences for perceived face trustworthiness also did not consider the possible influence of individual differences, such as social interaction anxiety. The present results have shown that trustworthy-looking facial features are favoured by those with high levels of social interaction anxiety. Overall, this study provides further evidence that strategies underlying mate choice depend partially on individual characteristics and highlights the importance of a trustworthy appearance for attraction.

Chapter 6. General discussion and conclusions

6.1. SUMMARY OF FINDINGS AND FUTURE STUDIES

This work aimed to contribute to a deeper understanding of what drives human attractiveness judgments, considering that physical attractiveness has a core role in mating decisions. Mating assumes a major importance within Evolutionary Psychology since it strongly predicts evolutionary fitness (i.e. the individual's contribution to the gene pool in the following generations (Lee et al., 2015)). On the other hand, face and odour attractiveness are necessarily implicated in mating decisions because they are believed to advertise the genotypic quality of potential partners (Little, Jones, et al., 2011; S. C. Roberts et al., 2008).

Most of the work presented in this thesis focused on the effect of the perception of sexually dimorphic traits on attractiveness judgments. Sexual dimorphism is considered to signal mate quality (Thornhill & Gangestad, 1996) and is consequently attractive as predicted by the sexual selection theory (Andersson, 1994). Previous studies have focused on exploring the effect of face masculinity/ femininity on perceived attractiveness, analysing the preferences of both sexes. Prior investigations have reported a clear male preference for signs of femininity in female faces. However, research on face masculinity has been characterised by inconsistent findings. Some studies reported women's preferences for male faces with a more masculine shape (e.g. DeBruine et al., 2006; Little & Mannion, 2006), or male faces with a more feminine shape (e.g. DeBruine, Jones, Smith, et al., 2010; Little & Hancock, 2002; Perrett et al., 1998), while others reported null effects (Scott et al., 2010; Swaddle & Reierson, 2002; Thornhill & Gangestad, 2006). The work presented in the second chapter tested the contribution of sexually dimorphic shape to face attractiveness judgments, as in previous studies, and also to sex discrimination processes. The original contribution of this study, comparing to prior research, was the collection of EEG signal during experimental tasks that allowed to identify the ERP associated with the perception of sexually dimorphic traits. Participants were asked to visualise unfamiliar faces and to decide whether the face was female or male and also, in a separate task, whether it was attractive or unattractive. We collected information about event-related potentials that were elicited while participants were performing such tasks.

Results showed that sexual dimorphism enhances accuracy in sex discrimination of faces and also confirmed previous findings that femininity is attractive in female faces (G. Rhodes, 2006). We found no effect of masculinity on overt attractiveness preferences for male faces which was interpreted as a consequence of the diverse trade-off strategies adopted by different women. The 'trade-off' theory mentioned in Chapter 1, predicts that some women may prefer signs of femininity in opposite-sex members as a way of retaining the benefits of less masculinised men (e.g. warmth, emotionality, honesty, cooperativeness) and avoiding the detriments associated with more masculine ones (lower preference for long-term relationships, aggressiveness, and lower parenting skills). Such preference combined with the choices of women that do prefer signs of masculinity (and who supposedly gather the conditions needed to deal better with the detriments of more masculine men) may have led to this null effect. Another possible reason lies in the fact that a forced choice paradigm might not be the best design to explore the already recognised complexity of preferences for sexually dimorphic traits in men's faces (although see DeBruine, 2013). Despite that, sexual dimorphism was found to modulate both early (P2, EPN) and late event-related potentials (LPP). More importantly, the amplitude of P2 and EPN was modulated by masculinity when female participants judged opposite sex faces, which may represent an adaptive increased attentional processing in order to enhance reproductive success. Increased attention to fitness signals may allow individuals to choose healthy mates, who will guaranty an equally healthy offspring.

According to Said and Todorov (2011), the mixed results regarding the effect of masculinity on face attractiveness may reflect competing effects of shape and colour. Based on such claim, the work presented in the third chapter aimed to investigate the influence of both sexually dimorphic dimensions on attractiveness preferences, separately manipulating those factors. First, we confirmed that skin colour is sexually dimorphic, with men having a darker, redder and yellower hue than women. Secondly, in 3 subsequent experiments, we allowed our participants to change both sexually dimorphic colour (all experiments) and shape (Experiments 3 and 4) of faces, in order to increase their attractiveness. We found that participants preferred feminised shape versions of both male and female' faces. Preferences for sexually dimorphic colour were in the opposite direction, with a clear tendency to masculinise both female and male faces. Importantly, although transformations in same and opposite-sex faces were in the same direction, participants significantly amplified sex differences in both shape and colour. In other words, although participants increased face skin colour masculinity and decreased face shape masculinity of both sex faces, they increased more the colour masculinity and decreased less the shape masculinity of male stimuli comparing to female stimuli. This difference between preferences in male and female faces indicates that, in this case, opposite-sex preferences do represent adaptations to identify high-quality mates.

The reason why both characteristics (shape and colour) elicit differentiated responses remains to be explored. It should be taken into consideration that male facial sexual dimorphism is the only trait that seems to be associated with mixed results in the literature, since masculinity in males seems to be consistently preferred when considered in voices (Feinberg, 2008; B. C. Jones, Feinberg, DeBruine, Little, & Vukovic, 2010; Puts et al., 2007) and body shape (Little, Jones, et al., 2007; Peters, Simmons, & Rhodes, 2009). Although believing that manipulations done on facial masculinity do correspond to real life variation, since they seem to positively correlate with other masculine traits as voice (Feinberg, DeBruine, Jones, & Little, 2008), it is possible that they elicit simultaneously other attributions besides masculinity, which influences the direction of preferences. Future studies should try to determine what it is with facial shape masculinity that justifies female preferences for femininity. The holistic character of face perception (Abbas & Duchaine, 2008; Todorov, Loehr, & Oosterhof, 2010) makes it almost impossible to isolate the features that contribute to each specific attribution. Perceptions of face emotionality may be a possible confound in face preferences. Masculinised faces tend to be perceived as angrier (Hess et al., 2009) which may elicit avoidance responses to masculinity by female participants. Another possible variable that may influence women's preferences for masculinity traits is facial adiposity. Masculinity face traits, namely fWHR, are associated with larger chin width (Lefevre et al., 2013), and manipulation of facial width may, sometimes, be perceived as increased facial adiposity. Since high facial adiposity is usually unattractive in men, by signalling poor health (Coetzee, Perrett, & Stephen, 2009), it is possible that women willing to decrease facial adiposity are forced to prefer more feminised men. Another possible explanation is that female participants decrease the masculinity of male faces in order to increase youthfulness since feminised faces are also perceived as younger (Perrett et al., 1998). However, such hypotheses would also need to be studied in future investigations.

The study reported in Chapter 3 also analysed the occurrence of differential preferences according to own and environmental conditions (strategic pluralism) when participants manipulated the masculinity of faces. Namely, we explored the effect of self-attractiveness and relationship context (Experiment 4) on women's preferences for sexually dimorphic shape and colour. Although the relationship context effect and the correlation between self-attractiveness and masculinity preferences were not significant, we did find a correlation between self-attractiveness on face shape preferences in one of the relationship contexts. Self-attractiveness correlated positively with preferences for masculinity in participants that considered a long-term relationship effect. This was expected since, in long-term relationships, only the high-quality females are able to deal with the disadvantages of dating a more masculine male (Little et al., 2001). The reason why this effect was not visible in preferences for skin colour masculinity is unknown.

Strategic pluralism does seem to be evident in other domains besides preferences for face shape, namely in vocal and body masculinity preferences (Feinberg, 2008; Feinberg et al., 2012; Little, Jones, et al., 2007). It is possible that the absence of differential strategies according to relationship context and self-attractiveness in preferences for sexually dimorphic skin colour are just due to lack of statistical power of such effects. Zietsch, Lee, Sherlock, and Jern (2015) have recently proposed that context-dependent effects may have a lower impact than genetic factors (although see Germine et al., 2015). This implies that, although preferences may be modulated by such variables, the limited effect size of this modulation may produce visible effects in some cases while not in others.

In the following study (Chapter 4), we took into account the previous conclusions on sexually dimorphic skin colour and hypothesised that it could be related to attractiveness in body odours. Other investigations have found a positive link between the attractiveness of men's body odour and their dominant personality (Havlíček et al., 2005) and face symmetry (Thornhill & Gangestad, 1999b). If skin colour masculinity is attractive for female counterparts, it is possible that skin colour masculinity represents direct or indirect benefits in the mating context that could also be advertised by other means besides physical appearance. Hence, men with more masculine skin colour might be perceived as attractive even by their body odours. To investigate this possibility we asked female participants to rate men's body odours in several characteristics, such as attractiveness, sexiness, pleasantness, health, intensity, dominance and masculinity. Later, we compared such ratings with men's masculinity index calculated based on their skin colour. As expected, odours of men with more masculine skin colour were perceived as more likeable (attractive, sexy and pleasant) and more healthy. Such finding may indicate that women also access the mate value of possible partners through the sense of smell and that chemosignals may incorporate information about owners' reproductive and/or heritable health or intrasexual competitiveness. Future studies should explore if skin colour masculinity does, in fact, relate to androgen levels in men's body and also with increased health and dominance in the same individuals.

Odours of men with more masculine skin colour were also perceived as less intense and as belonging to less masculine and dominant males. In the discussion of Chapter 4, we proposed that such counterintuitive findings might be due to a stereotypical notion of what masculine male odour should smell like. The data presented in the additional survey proved the existence of such stereotypes, since our female participants, just by imagining intense and unpleasant body odours, associated them with more masculine/ dominant men. As the assessment of the odour's masculinity and dominance during the experimental phase were not positively associated with the skin colour masculinity scores of our donors, we hypothesise that women may not be able to correctly judge the masculinity of odours, at least in a conscious way. Based on Mutic and co-worker's argument (2016), it is also possible that women stereotypically relate masculinity with intense odours, relying on the premise that more masculine/dominant men engage in more physically demanding activities that cause sweating and consequently increase the odour's intensity and unpleasantness. However, in this study, in particular, body odour donors had to refrain from doing intense physical activities, so this association does not necessarily lead participants to accurate conclusions. However, this should not have a significant impact on the reproductive success of women since they still seem to be attracted by the smell of more masculine men. Therefore, it is important that women do feel a mating drive towards healthy masculine men, even if they cannot accurately judge its masculinity level.

Lastly, the study reported in Chapter 5 focused in another trait that modulates attractiveness inferences in humans: trustworthiness. As we have seen, the future partner's personality is also important when choosing a mate (Buss, 1988) and that is one of the reasons why women may forego of masculinity benefits, mainly if they are considering a long-term relationship (Little et al., 2002). In this kind of relationship, choosing a trustworthy mate might be an adaptive choice, since a supportive partner may be more likely to ensure continued protection and parental care. In fact, trustworthiness perception influences attractiveness judgments, with trustworthy faces being perceived as more attractive than untrustworthy ones (R. K. Wilson & Eckel, 2006). Our study aimed to explore which facial appearance would be preferred in faces when the underlying manipulation consisted of changes in perceived trustworthiness. As expected, both women and men increased perceived trustworthiness when looking for the most attractive appearance, and did so especially when considering a long-term partner. Male participants increased perceived trustworthiness more than female participants, possibly because increasing trustworthiness also leads to an increase in face femininity. Also, we found that individual differences in social interaction anxiety modulated face preferences of participants of both sexes. Social interaction anxiety correlated positively with the level of trustworthiness preferred in faces, which may imply that more socially anxious individuals do place extra caution when choosing a partner comparing to the other participants. Again, this effect of social interaction anxiety goes in line with the previously proposed notion of strategic pluralism (Gangestad & Simpson, 2000). Humans may agree about the overall attractiveness of faces, but individual differences may arise according to own conditions and environment. If the environment triggers stress/ anxious responses, individuals should adapt their mating preferences accordingly. Thus, individuals with high social interaction anxiety may prefer trustworthy partners because they make them feel safer.

6.2. METHODOLOGICAL ISSUES

The work reported in Chapters 2, 3 and 5, focused on face preferences considering sexually dimorphic and trustworthiness cues. In all three studies, faces were altered using computer graphic techniques. Stimuli manipulation was performed by considering the geometrical differences between prototype average faces and applying a transformation to the new faces according to this difference. The use of this methodology assumes that extreme masculinity face shape can be generated by a linear extrapolation of the differences between prototypical faces (DeBruine et al., 2006). The same assumption was considered for perceived trustworthiness in Chapter 5. This technique primarily developed in Perrett et al. (1998) and others (Cornwell et al., 2004; Penton-Voak et al., 2001) has been criticized by some authors that claim that inconsistencies in studies investigating the impact of sexually dimorphic shape on face attractiveness are linked with such methodological choice (e.g. Johnston et al., 2001; Swaddle & Reierson, 2002) and not with individual differences instigated by strategic pluralism. Johnston et al. (2001), for example, claimed that the complexity of the interaction between sex and growth hormones, responsible for the development of a masculine look on faces, cannot be represented by such a simplistic function. These researchers proposed that the manipulation of sexual dimorphism on face shape should rely on perceived masculinity, using averages of faces scored high or low in perceived masculinity as extremes. So this criticism would only be valid for Chapters 2 and 3, as in our study with trustworthiness (Chapter 5), the manipulation is based on a perceived trait. However, a later study from DeBruine et al. (2006) challenged this view, showing that both methodologies produce similar correlated results, and arguing that differences reported in different studies are more likely to result from individual differences.

G. Rhodes (2006), in her meta-analysis, suggested that the methodology we used could also influence women’s attractiveness choices in men’s faces since the created composite faces tend to have smoother skin texture and jaw lines. In her view, this fact could “bias responses against the masculinised shapes that are inconsistent with the feminine skin textures displayed” (G. Rhodes, 2006, p. 210). However, as DeBruine

(2014) argues, composite faces actually tend to elicit stronger, instead of weaker, preferences for masculinity in men's faces (see Scott & Penton-Voak, 2011). While there is a possibility that methodological issues do influence the outcome of investigations, it is unlikely that they are the reason for some studies to report preferences for femininity while others report preferences for masculinity in male faces, if even studies using the same methodology find conflicting results (e.g. DeBruine et al., 2006; Perrett et al., 1998).

Another criticism of this methodology resides in the validity of the attempt to manipulate faces on a single dimension (Scott et al., 2013a; Scott, Clark, Boothroyd, & Penton-Voak, 2013b). In the authors' words, "experiments that use isolated manipulations cannot demonstrate that a trait is important in the context of naturally varying stimuli, even if they elicit significant effects" (Scott et al., 2013b, p. 596). Although this argument is invariably right, it is a criticism transversal to all field of experimental psychology that already recognises its limitations on ecological validity.

Acknowledging such controversies, although research on attractiveness preferences is vast, it is clear that there are still questions in discussion that should be acknowledged in future studies.

6.3. OTHER POTENTIAL CRITICISMS

Research on mate preferences tends to be criticised based on the gap between attractiveness preferences and actual mate choice. It is true that most of us find the 'sex symbols' portrayed in the media as attractive which does not mean that we end up dating such individuals. But is it valid to disregard the evolutionary importance of attractiveness preferences just because it may not translate directly on mate choice? First of all, there is evidence suggesting that mate preference and mate choice do correlate positively. Female preferences for masculinity in male faces were found to correlate positively with actual and ideal partner masculinity (DeBruine et al., 2006) and with their pathogen disgust (B. C. Jones et al., 2013). Female preferences for masculinity also seem to be predicted by partner's self-rated masculinity (Burriss, Welling, & Puts, 2011a). In a recent study, Conroy-Beam and Buss (2016) developed a Euclidean algorithm to predict mate preferences and found that people who scored high in mate value according to the same model are better able to attract mates in real life who better fulfil their preferences.

Another typical misconception related with the evolutionary theory of mating is the idea that if attractive individuals have more reproductive success, then humans should become more and more attractive over time. Although appealing, that is not what Evolutionary theories predict given the host-parasite co-evolution (Gangestad & Simpson, 2000; Grammer et al., 2003). The genes considered ‘good’ today, might not be the ‘good genes’ of tomorrow because selection pressures are in constant change and parasites tend to evolve and be more effective fighting the common host genotypes. This means that genes that are currently selected may not be so in the future and, on the other hand, other genotypes that are not attractive today may be so later on. No gene is inherently better, and no phenotype is inherently more attractive, and that is why we will not become fitter with the passage of time.

6.4. CONCLUSIONS

Altogether, the findings described in Chapters 2 – 5 add evidence to the idea that beauty or attractiveness although lying in the eyes of the beholder, as David Hume (1965) argued, “those eyes and the minds behind the eyes have been shaped by millions of years of human evolution” (Buss, 2008, p. 53). Hume was right when saying that there was no quality in things themselves. For example, as previously mentioned, the sweet taste only tastes good because sweetness was associated throughout our evolutionary past with high energy foods crucial to survival. Similarly, faces, bodies or odours are not beautiful in themselves. They are perceived as beautiful because the preference for such traits in our ancient times led to reproductive advantages and healthy offspring (Grammer et al., 2003).

The first two experimental chapters investigated the role of sexual dimorphism (masculinity and femininity) on perceived attractiveness. Although several past studies aimed to understand its effect on attractiveness, there are still questions to be asked and problems to be solved. Since most of the previous work looked for behavioural responses, the study in Chapter 2 tried to shed light on this issue by exploring the neurophysiological correlates of the perception of faces varying in sexually dimorphic shape. Both early and later components were found to be modulated by differences in masculinity/ femininity in shape of faces, with P2 and EPN showing differentiated amplitudes, particularly for opposite-sex faces. Those modulations, when participants observed opposite sex faces, may indicate that mate value, accessed by perceptions of sexually dimorphic traits, do take place as early as 200 ms after stimulus visualisation.

Previous studies have extensively focused on face shape when investigating the effects of sexual dimorphism on attractiveness. Chapter 3 explored the possibility that masculinity/femininity may also manifest itself on skin colour cues. Our findings confirmed such hypothesis and showed that women are attracted by a masculine colouration in male faces. Participants seem to prefer a feminine shaped male face but with a masculine skin tone. In Chapter 4, this preference for men with masculine skin colour was later proved to be present even when female participants do not observe men's faces, and only get the chance to smell their body odour. Participants rated the odour of men with more masculine skin colour as more likeable and healthy, even though incorrectly accessing their masculinity. This study demonstrated that the features identified as influencing human attractiveness are not restricted to visual perception but also include other senses, such as the sense of smell.

The findings in chapters 2 - 4, besides proving the importance of sexual dimorphism in human attractiveness, they also identified some circumstances where masculinity may be less desirable, namely when people consider long-term relationships (Chapter 3). Relationship context and individual differences may alter mate preferences, leading other traits, besides masculinity, to also affect attractiveness. The last study in Chapter 5, investigated this possibility by focusing on preferences for perceived trustworthiness in faces. Facial trustworthiness has been previously investigated as influencing several dimensions on human relationships, namely politics, but little is still known about its possible impact on mate choice. Our results showed that perceived trustworthiness is attractive in opposite-sex faces, especially when considering long-term relationships and by individuals with higher social interaction anxiety. Other studies should continue to investigate the influence of sexual dimorphism, trustworthiness, as well as other factors, in human attractiveness, aiming for a better understanding of sexual selection mechanisms in humans and possible implications for individual, couples and group dynamics.

Future research would clearly benefit from interdisciplinary investigations, gathering psychologists, biologists, anthropologists, and sociologists, namely to try to understand how the evolution of mate preferences can influence the human relationships in the days to come. Because evolution happens at a slow pace, we are necessarily shaped by ancient selection pressures and may not be optimally dealing with the constant change in our social environments. This does not mean that we cannot adjust our preferences according to new scenarios, but we will have some limitations while having a "Stone Age brain in a modern environment" (Buss, 1999, p. 19). This fact is believed to be influencing human partnerships today and will have a significant impact in the future.

From what I learnt, Evolutionary Psychology does not only allow us to understand the ancient and current minds, but it might also shed light on where the *Beagle* goes.

Chapter 7. References

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Chapter 8. Appendix

Table 4. Results from ANOVAs performed with ERP data in Experiment 1.

		P1	N170	P2	EPN	LPP			
						330 - 430	430 - 530	530 - 630	630 - 730
Task	F	.62	.80	.05	4.58	21.26	15.72	4.21	.04
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.437	.377	.833	.040	< .001	< .001	.048	.851
	η_p^2	.018	.024	.001	.122	.392	.323	.113	.001
Task x Sex of participant	F	.00	.40	.46	.73	2.20	1.15	3.47	7.55
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.977	.533	.503	.399	.148	.292	.072	.010
	η_p^2	.000	.012	.014	.022	.062	.034	.095	.186
Sex of the face	F	.88	20,80	9.38	13.50	3.33	.29	.41	.20
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.355	< .001	.004	.001	.077	.592	.526	.661
	η_p^2	.026	.387	.221	.290	.092	.009	.012	.006
Sex of the face x Sex of participant	F	.34	5.41	4.30	1.77	.35	.13	2.46	1.90
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.565	.026	.046	.192	.559	.717	.126	.178
	η_p^2	.010	.141	.115	.051	.010	.004	.069	.054
SD transform	F	.01	.30	.10	3.26	.77	2.45	.47	.62
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.920	.589	.750	.080	.386	.127	.497	.436
	η_p^2	.000	.009	.003	.090	.023	.069	.014	.018
SD transform x Sex of participant	F	.06	.14	.14	2.36	.89	.70	.80	1.79
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.803	.715	.716	.134	.354	.409	.379	.190
	η_p^2	.002	.004	.004	.067	.026	.021	.024	.052
Electrode	F	1.28	27.86	.06	9.26	4.10	19.26	24.80	29.20
	df	2, 66	1.94, 64.17	1, 33	2.00, 66.06	2, 66	2, 66	2 .66	2, 66
	p	.285	< .001	.808	< .001	.021	< .001	< .001	< .001
	η_p^2	.037	.458	.002	.219	.111	.369	.429	.469
Electrode x Sex of participant	F	.79	6,13	.31	1.18	.48	.61	1.17	2.22
	df	2, 66	1.94, 64.17	1, 33	2.00, 66.06	2, 66	2, 66	2, 66	2, 66
	p	.456	.004	.585	.315	.621	.547	.316	.117
	η_p^2	.023	.157	.009	.034	.014	.018	.034	.063

Task x Sex of the face	F	5.59	6.09	7.80	6.05	1.06	1.38	4.39	3.47
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1.33
	p	.024	.019	.009	.019	.311	.248	.044	.071
	η_p^2	.145	.156	.191	.155	.031	.040	.118	.095
Task x Sex of the face x Sex of participant	F	3.57	2.69	1.67	4.87	1.18	.36	.00	.15
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.068	.111	.205	.034	.285	.551	.990	.698
	η_p^2	.098	.075	.048	.129	.035	.011	.000	.005
Task x SD transform	F	.00	.01	.13	1.59	.17	1.50	1.78	.65
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.979	.936	.722	.216	.682	.230	.191	.425
	η_p^2	.000	.000	.004	.046	.005	.043	.051	.019
Task x SD transform x Sex of participant	F	1.58	,22	.95	1.15	.31	.37	.19	.53
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.218	.642	.338	.292	.584	.548	.669	.471
	η_p^2	.046	.007	.028	.034	.009	.011	.006	.016
Sex of the face x SD transform	F	2.71	.02	6.18	.71	6.36	10.32	.82	.26
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.110	.879	.018	.406	.017	.003	.372	.611
	η_p^2	.076	.001	.158	.021	.161	.238	.024	.008
Sex of the face x SD transform x Sex of participant	F	.14	.04	4.83	4.38	.39	.79	.04	.02
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.710	.848	.035	.044	.539	.382	.848	.889
	η_p^2	.004	.001	.128	.117	.012	.023	.001	.001
Task x Sex of the face x SD transform	F	1.23	7.94	3.08	.07	.07	.00	1.05	1.57
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.276	.008	.089	.798	.787	.963	.314	.220
	η_p^2	.036	.194	.085	.002	.002	.000	.031	.045
Task x Sex of the face x SD transform x Sex of participant	F	.46	,28	.03	2.20	.37	.24	.01	3.53
	df	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33	1, 33
	p	.504	.602	.854	.147	.550	.625	.944	.069
	η_p^2	.014	.008	.001	.063	.011	.007	.000	.097
Task x Electrode	F	1.15	.63	1.39	.40	2.16	.17	.98	.04
	df	1.54, 50.79	2.18, 72.03	1, 33	1.63, 53.89	2, 66	2, 66	2, 66	2, 66

	p	.313	.550	.247	.634	.124	.846	.380	.960
	η_p^2	.034	.019	.040	.012	.061	.005	.029	.001
Task x Electrode x Sex of participant	F	2.77	.34	.14	.42	2.63	.56	.14	1.47
	df	1.54, 50.79	2.18, 72.03	1, 33	1.63, 53.89	2, 66	2, 66	2, 66	2, 66
	p	.85	.730	.708	.616	.079	.577	.871	.238
	η_p^2	.077	.010	.004	.013	.074	.017	.004	.043
Sex of the face x Electrode	F	3.19	3.53	3.64	6.93	1.79	.41	.18	.04
	df	2, 66	2.02, 66.49	1, 33	1.99, 65.53	2, 66	1.54, 50.82	1.61, 52.95	1.57, 51.76
	p	.048	.035	.065	.002	.175	.610	.791	.933
	η_p^2	.088	.097	.099	.174	.051	.012	.005	.001
Sex of the face x Electrode x Sex of participant	F	2.20	.53	.00	1.48	1.76	2.99	2.95	1.23
	df	2, 66	2.02, 66.49	1, 33	1.99, 65.53	2, 66	1.54, 50.82	1.61, 52.95	1.57, 51.76
	p	.119	.590	.984	.235	.181	.072	.072	.293
	η_p^2	.062	.016	.000	.043	.051	.083	.082	.036
Task x Sex of the face x Electrode	F	.11	1.07	2.02	4.71	1.37	1.19	.12	.49
	df	1.40, 46.09	2.45, 80.75	1, 33	1.69, 55.62	1.55, 51.27	1.64, 54.26	2, 66	2, 66
	p	.829	.358	.164	.017	.260	.304	.891	.613
	η_p^2	.003	.031	.058	.125	.040	.035	.003	.015
Task x Sex of the face x Electrode x Sex of Participant	F	.34	.95	.46	2.06	2.35	2.08	1.05	2.02
	df	1.40, 46.09	2.45, 80.75	1, 33	1.69, 55.62	1.55, 51.27	1.64, 54.26	2, 66	2, 66
	p	.634	.405	.501	.145	.117	.143	.355	.141
	η_p^2	.010	.028	.014	.059	.066	.059	.031	.058
SD transform x Electrode	F	2.05	.96	.14	1.37	.15	.12	.82	.02
	df	1.51, 49.77	2.38, 78,39	1, 33	2.04, 67.25	2, 66	2, 66	2, 66	2 .66
	p	.15	.400	.712	.262	.865	.885	.446	.978
	η_p^2	.059	.028	.004	.040	.004	.004	.024	.001
SD transform x Electrode x Sex of Participant	F	.48	.71	.46	.43	.34	.08	.00	.13
	df	1.51, 49.77	2.38, 78.39	1, 33	2.04, 67.25	2, 66	2, 66	2, 66	2, 66
	p	.566	.519	.501	.655	.713	.919	.999	.880
	η_p^2	.014	.021	.014	.013	.010	.003	.000	.004

	F	.43	.41	.01	1.17	.28	.76	1.06	.63
Task x SD transform x Electrode	df	1.21, 39.89	2.37, 78.20	1, 33	1.81, 59.62	2, 66	2, 66	1.70, 56.19	1.59, 52.35
	p	.552	.703	.931	.313	.755	.472	.345	.503
	η_p^2	.013	.012	.000	.034	.008	.022	.031	.019
Task x SD transform x Electrode x Sex of Participant	F	.55	1.47	.13	3.07	1.24	4.20	1.49	1.51
	df	1.21, 39.89	2.37, 78.20	1, 33	1.81, 59.62	2, 66	2, 66	1.70, 56.19	1.59, 52.35
	p	.493	.234	.719	.059	.295	.019	.235	.231
	η_p^2	.017	.043	.004	.085	.036	.113	.043	.044
Sex of the face x SD transform x Electrode	F	.17	.64	.01	.24	2.10	.73	.47	.26
	df	1.68, 55.36	1.84, 60.84	1, 33	1.52, 49.98	2, 66	2, 66	2, 66	2, 66
	p	.804	.517	.906	.725	.131	.484	.627	.773
	η_p^2	.005	.019	.000	.007	.060	.022	.014	.008
Sex of the face x SD transform x Electrode x Sex of Participant	F	.67	.54	.22	1.58	1.35	1.53	.69	.29
	df	1.68, 55.36	1.84, 60.84	1, 33	1.52, 49.98	2, 66	2, 66	2, 66	2, 66
	p	.493	.572	.639	.218	.266	.224	.506	.749
	η_p^2	.020	.016	.007	.046	.039	.044	.020	.009
Task x Sex of the face x SD transform x Electrode	F	1.03	1.42	1.11	.10	1.24	1.06	.73	.25
	df	1.63, 53.77	2.67, 88.16	1, 33	2.03, 67.10	2, 66	2, 66	2, 66	2, 66
	p	.352	.244	.299	.904	.297	.353	.485	.779
	η_p^2	.030	.041	.033	.003	.036	.031	.022	.008
Task x Sex of the face x SD transform x Electrode x Sex of Participant	F	3.87	1.98	.01	.41	1.68	1.14	.11	.18
	df	1.63, 53.77	2.67, 88.16	1, 33	2.03, 67.10	2, 66	2.66	2 .66	2, 66
	p	.035	.129	.927	.668	.195	.325	.893	.837
	η_p^2	.105	.057	.000	.012	.048	.033	.003	.005

Note: SD transform = Sexually dimorphic transform