1. Introduction

Across many animal species, sexual dimorphism is an important trait involved in sexual selection (Andersson, 1994). Sexually dimorphic traits in human faces have received much attention by those interested in evolutionary approaches to human preferences and perception (see e.g., Thornhill & Gangestad, 1999). Sexually dimorphic traits (relative masculinity/femininity) in human male faces has been proposed to relate to both inter-sexual selection (Little, Jones, & DeBruine, 2011; Thornhill & Gangestad, 1999), influencing attraction to the opposite sex, and intra-sexual selection (Swaddle & Reiperson, 2003), relating to competition between members of the same sex. In terms of attractiveness to the opposite sex, there are benefits that could be associated with sexual dimorphism: (1) indirect benefits, genetic benefits that are passed to offspring such as genes associated with strong immune systems, and (2) direct benefits, benefits that are directly passed to mates or offspring such as resources or avoidance of disease.

1.1. Variation in preferences for men’s masculinity

Evidence for the attractiveness of sex-typical masculine facial traits (e.g., large jaws, prominent brows) in male faces is mixed: some studies have shown masculine preferences (e.g., Cunningham, Barbee, & Pike, 1990; DeBruine et al., 2006; Grammer & Thornhill, 1994), while other studies have shown preferences for feminine faces (Perrett et al., 1998; Little & Hancock, 2002). Many studies, however, also demonstrate systematic variation in women’s preferences for male facial masculinity and the direction of preference for masculine traits does not preclude adaptive individual differences. Women prefer relatively more masculine-faced men when they think themselves or are rated as attractive (Little, Burt, Penton-Voak, & Perrett, 2001; Penton-Voak, Little, Jones, Burt, Tiddeman, & Perrett, 2003), when they already have a partner (Little, Jones, Penton-Voak, Burt, & Perrett, 2002), at peak fertility in the menstrual cycle (Penton-Voak et al., 1999; Jones, DeBruine, Perrett, Little, Feinberg, & Smith, 2008), and when rating for short-term relationships (Little et al., 2002). These findings have been interpreted as consistent with ideas that masculinity in male faces is associated with indirect benefits, (i.e., they are associated with genetic quality, Thornhill & Gangestad, 1999), as these are conditions under which we might expect women...
to be most attentive to heritable genetic benefits. Of course this does not preclude that facial masculinity is in part preferred due to direct benefits or that it plays a role in male–male competition.

1.2. Trade-offs inherent in preferences

Individual variation in attraction to masculinity may be related to a trade-off between quality and investment (Gangestad & Simpson, 2000; Little et al., 2002). High-quality individuals may invest less in each partner (and offspring) or be more likely to cheat on/desert partners. High-quality individuals may not make ideal long-term partners in a species, such as humans, with extended parental investment (Burley, 1986; Moller & Thornhill, 1998). For example, masculine-faced men are perceived as dominant but also as poor-quality parents (Perrett et al., 1998). Indeed, while masculine-faced men report better health (Thornhill & Gangestad, 2006) and are physically stronger (Fink, Neave, & Seydel, 2007) but also have more short-term partners (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008) which suggests low investment in relationships. In this framework, masculinity in men is associated with both indirect and direct benefits with a trade-off between investment and quality. For example, masculinity may be negatively linked to levels of investment (direct benefit) but also positively to quality in terms of genes for health/dominance (indirect benefits) and current health/resources (direct benefits). Such a trade-off is consistent with many aspects of masculinity preferences such as increased preferences for masculinity in short-term contexts (Little et al., 2002) or at peak fertility (Penton-Voak et al., 1999; Jones et al., 2008).

1.3. Environmental influences on preference

Previous studies have mainly focused on individual differences based on factors intrinsic to the choosing individuals (e.g., physical attractiveness), but we may also expect variation according to extrinsic ecological conditions that influence the relative value of investment versus other (e.g., good genes/dominance) benefits from partners. For example, resource scarcity and pathogen stress in the environment an individual inhabits might influence the trade-off between preferring a high-investing partner and one with a high-quality immune system or who is more dominant/healthy. Such reasoning may help explain observed cross-cultural differences in preferences for male masculinity.

Penton-Voak, Jacobson, and Trivers (2004) found stronger preferences for male masculinity in rural Jamaica than in the UK and Japan. One reason they suggested for this finding is that a higher pathogen prevalence in Jamaica may result in increased preferences for masculinity in male faces, as health benefits, both direct and indirect, may be more salient under higher disease stress. The Hadza, a tribe of African hunter gatherers, have also been found to exhibit stronger preferences for facial symmetry, another putative cue of mate quality that is also correlated with facial masculinity in Hadza men (Little et al., 2008), than do participants in the UK (Little, Apicella, & Marlowe, 2007). A difference in pathogen load between samples may also explain increased preferences for symmetry in the Hadza because individuals close to the equator have higher pathogen loads (Low, 1990) and outdoor living is likely to increase exposure to pathogens. Another study has examined a cross-cultural sample of 30 countries, calculating both the average female preference for male facial masculinity and a composite health index derived from World Health Organization statistics (DeBruine, Jones, Crawford, Welling, & Little, 2010). This study found that poorer health (i.e., higher mortality and incidence of disease) was related to stronger female preferences for male masculinity (DeBruine et al., 2010). This relationship between health factors and masculinity preferences was replicated in a follow-up study of differences in the average masculinity preference of women in US states (DeBruine, Jones, Little, Crawford, & Welling, 2011).

Results from these cross-cultural studies indicate that health risks are a potentially important determinant of mate preferences, but such studies are correlational and do not address how such associations arise. There are of course other factors that vary across culture and often co-vary with health, such as wealth. Indeed, a reanalysis of the data presented in DeBruine et al. (2010) suggested that factors associated with relative wealth and male–male competition (i.e., homicide rates) are associated with variation in preferences for face masculinity in women across cultures (Brooks, Scott, Maklakov, Kasumovic, Clark, & Penton-Voak, 2011), although this pattern was not replicated in a further study of regional differences across US states (DeBruine et al., 2011).

One way to disentangle the reasons behind such variation is through experimental exposure. If preferences are sensitive to environmental cues then we predict that preferences will vary accordingly. One study has demonstrated that imagining oneself as being in either a high- or low-resource availability scenario affected women’s preferences, with a low-resource environment leading to higher preferences for feminine-faced men for long-term partnerships (Little, Cohen, Jones, & Belsky, 2007). A harsh, low-resource environment then appears to promote a strategy wherein women favor lower-quality but potentially higher-investing men for long-term relationships. In contrast, another study demonstrated that exposure to cues of pathogens increased women’s preferences for male facial masculinity and symmetry, and hence quality over investment (Little, Jones, & DeBruine, 2011). Potentially, these patterns of data highlight different aspects of environmental influence on preferences. Resource availability and parasite prevalence may drive face preferences in different ways. Abundant resources may allow women to choose with lower concern for investment and so enable the selection of higher-quality partners whereas scarce resources may place pressure on women to choose investing partners, at the expense of quality. Parasite prevalence, on the other hand, will increase health risks/child mortality and so choosing a healthy partner may be more important than choosing an investing partner under conditions of high disease and parasite risk.

Alongside resource scarcity and parasite prevalence, the degree of male–male intra-sexual competition could also influence female preferences. Across cultures, variation in human mating systems (monogamy vs. polygny) is related to variation in male resource control according to ecological variables as well as variation in male–male competition for status (Marlowe, 2000). Where males can control resources, we expect there to be an unequal distribution of resources, as some males will be better able to control resources than others. This would lead to female preferences for male traits indicating that males can successfully compete for and control resources. In groups in which direct male–male competition is prevalent, and status, or even survival, is dependent on successful competition, we would also expect females to prefer cues of successful male competition. While cues to the ability of acquiring resources may be varied, success in direct physical competition is likely partly related to physical strength and fitness. As a man’s physical strength is positively related to ratings of facial masculinity and dominance (Fink et al., 2007), we can predict that masculinity in faces would be preferred in conditions where men physically competing with one another is more common.

1.4. The current experiments

Previous experimental work on exposure to visual cues of pathogens suggests a role of health concerns in generating preferences for masculinity. Other environmental cues of male–male competition and wealth also appear likely alter the balance of preferences for male facial masculinity according to how valuable
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