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Abstract

Human mate choice is complicated, with various individual differences and contextual factors influencing preferences for numerous traits. However, focused studies on human mate choice often do not capture the multivariate complexity of human mate choice. Here, we consider multiple factors simultaneously to demonstrate the advantages of a multivariate approach to human mate preferences. Participants (N=689) rated the attractiveness of opposite-sex online dating profiles that were independently manipulated on facial attractiveness, perceived facial masculinity/femininity, and intelligence. Participants were also randomly instructed to either consider short- or long-term relationships. Using fitness surfaces analyses, we assess the linear and non-linear effects and interactions of the profiles' facial attractiveness, perceived facial masculinity/femininity, and perceived intelligence on participants' attractiveness ratings. Using Hierarchical Linear Modeling, we were also able to consider the independent contribution of participants' individual differences on their revealed preferences for the manipulated traits. These individual differences included participants' age, socioeconomic status, education, disgust (moral, sexual, and pathogen), sociosexual orientation, personality variables, masculinity, and mate value. Together, our results illuminate various previously undetectable phenomena, including nonlinear preference functions and interactions with individual differences. More broadly, the study illustrates the value of considering both individual variation and population-level measures when addressing questions of sexual selection, and demonstrates the utility of multivariate approaches to complement focused studies.

1.0 Introduction

Mate choice is complicated. In even the simplest of animal mating systems, the outcome of mate choice can depend on a suite of variables (Brooks & Endler, 2001b; Moller & Pomiankowski, 1993). Mate choice among humans is more complex than in almost any other species, with studies showing mate preferences for a large range of traits. This includes effects on attractiveness of wealth (Henrich, Boyd, & Richerson, 2012), status (Li, Bailey, Kenrick, & Linsenmeier, 2002), intelligence (Miller, 2000), strength (Puts, 2010), smell (Wedekind, Seebeck, Bettens, & Paepke, 1995), facial masculinity or femininity (Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Perrett et al., 1998), voice pitch (Puts, 2005), stature (Kurzban & Weeden, 2005), body shape (Singh, 1993), kindness (Li et al., 2002), and personality (Botwin, Buss, & Shackelford, 2006). This list of features considered cues for mate choice is not exhaustive and is still growing rapidly.

In addition, variation among individuals has also been shown to be important when choosing a mate. This includes whether an individual is considering a short- or long-term partner (Buss, 1989), their physical attractiveness - both self-rated (Little, Burt, Penton-Voak, & Perrett, 2001) and other-rated (Montoya, 2008) - their age (Buss & Barnes, 1986), personality (Buss & Barnes, 1986), pathogen disgust sensitivity (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010; Jones, Fincher, Little, & DeBruine, 2013), sociosexual orientation (Provost, Kormos, Kosakoski, & Quinsey, 2006; Simpson & Gangestad, 1992; Waynforth, Delwadia, & Camm, 2005), education (Mare, 1991), and, for women, whether they are at the fertile phase of the menstrual cycle (Penton-Voak et al., 1999). Adding to the complexity, contextual factors or environmental influences also play a role in moderating the strength and direction of mate preferences. Factors such as local aggregate and individual economic circumstances (Stone, Shackelford, & Buss, 2008), health conditions (DeBruine, Jones, Crawford, Welling, & Little, 2010; F. R. Moore et al., 2013), sex-ratio (Stone, Shackelford, & Buss, 2007), and gender parity (Zentner & Mitura, 2012) can influence the weighting given to different mate choice criteria. Many other individual differences or contextual effects no doubt remain to be discovered.

In addition to the multivariate nature of mate choice, individuals in search of a mate can vary in their motivation to choose, and in the strength and direction of their preferences (Jennions & Petrie, 1997). Some of this variation can arise due to genetic variation between individuals (Verweij, Burri, & Zietsch, 2012; Zietsch, Verweij, & Burri, 2012), idiosyncratic issues of adaptive compatibility (e.g. genetic compatibility; Roberts & Little, 2008), or as a plastic response to the context in which individual "choosers" find themselves (Lee & Zietsch, 2011){Little, 2007 #50;Little, 2011 #49}.

Previous studies on human mate choice have predominantly focused on one or two mate choice criteria at a time, which are useful for identifying potential effects or testing specific hypotheses, but often over-simplify the multivariate complexity of mate choice. Such a picture could be incomplete for several reasons: Firstly, multiple mate choice criteria may interact with each other in ways that cannot be detected by experimental tests of mate preferences under tightly controlled conditions. Most studies also further simplified mate choice by focusing on linear relationships, ignoring the possibility of nonlinear effects on mate preferences (such as exponential or quadratic relationships).

Multivariate studies of animal mate choice have shown that interactions between traits can add important non-linearity to the overall pattern of selection (Blows & Brooks, 2003; Blows, Chenoweth, & Hine, 2004; Brooks et al., 2005; A. J. Moore, 1990). Interactions among colour pattern traits in guppies (Blows & Brooks, 2003; Blows, Brooks, & Kraft, 2003) revealed selection on those patterns and a complex multi-peak fitness surface that linear selection analyses failed to detect (Brooks & Endler, 2001a). Likewise, simultaneous manipulations of suites of acoustic traits in crickets (Bentsen, Hunt, Jennions, & Brooks, 2006; Brooks et al., 2005) and frogs (Gerhardt & Brooks, 2009) revealed strong stabilizing selection and exponential (positive quadratic) selection that univariate manipulations had not exposed. Studies on human mate preferences have also revealed non-linear effects; for example, men's body preferences for intermediate shoulder, hip, and waist widths over larger or smaller widths (Donohoe, von Hippel, & Brooks, 2009). Other studies of human mate preferences have also found complex interactions among a handful of factors; for example Penton-Voak et al. (2003) found that women's preference for facial sexual dimorphism was influenced by an interaction between their condition and whether they were rating for short- or long-term attractiveness. Brooks, Shelly, Fan, Zhai, and Chau (2010) found that multivariate non-linear selection analyses consistently outperformed indices and ratios such as Body Mass Index (BMI), waist-to-hip ratio and age in predicting the attractiveness of scanned images of female bodies. These examples further emphasise the need to look beyond focused studies.

In addition, the different properties that alter the value of a potential mate are often correlated – sometimes positively but also sometimes negatively. Positively correlated preferences could indicate that traits are preferred because they reflect the same underlying quality (e.g., cues for the same trait). However, preference for correlated traits may also solely be driven by one of the traits (e.g., preferences for facial symmetry could be driven by preference for a correlated trait such as facial sexual dimorphism; Scheib, Gangestad, & Thornhill, 1999). Conversely, unrelated or negatively correlated traits (e.g. between a potential mate's attractiveness and faithfulness) can turn choice into an exercise in optimisation. Such possibilities cannot be captured in studies that assess effects in isolation.

The multivariate complexity of mate choice and the many sources of variation among individual choosers combine to make mate choice more complex and varied than it might appear from the experiments often used to test focused hypotheses. Fortunately, evolutionary biology has well-established multivariate methods for estimating linear and non-linear selection (fitness surfaces) on suites of correlated traits (Lande & Arnold, 1983; Phillips & Arnold, 1989), for comparing fitness surfaces among groups or experimental treatments (Chenoweth & Blows, 2005), and for visualising complex fitness surfaces (Blows & Brooks, 2003; Brodie, Moore, & Janzen, 1995). It is also possible to combine multivariate response surface analysis with independent manipulations of suites of continuous traits that are ordinarily correlated in order to establish how each trait contributes to selection (Brooks et al., 2005; Donohoe et al., 2009; Gerhardt & Brooks, 2009; Mautz, Wong, Peters, & Jennions, 2013).

Here we use a large dataset generated from an experiment testing the factorial effects of facial attractiveness, facial masculinisation or feminisation, and intelligence on the attractiveness ratings participants gave to online dating profiles. These three traits have received much attention in the mate preference literature as putative fitness indicators; it is unknown if they contribute additively or non-additively (i.e. interactively) to overall attractiveness. We also measured individual variation on 17 traits of the profile-raters and entered these traits simultaneously in a hierarchical linear model to determine how these could independently affect preference for facial attractiveness, perceived facial masculinity/femininity, and perceived intelligence of the dating profiles.

2.0 Methods

2.1 Participants

Participants were 430 men (*M* ± *SD* = 23.07 ± 4.86 years) and 422 women (*M* ± *SD* = 24.07 ± 6.80 years) who were recruited from an online survey website (http://www.socialsci.com) in return for online store credit. Participation was conditional on being heterosexual and not currently in a long-term relationship. Participants who completed the incorrect survey (i.e., males who completed the female survey and vice versa; 33 males, 5 females), did not identify as being heterosexual (34 males; 71 females), or did not report their age (6 males; 2 females) were removed from analyses. A further 1 male and 6 females were removed for completing the survey in an unrealistic time (<5min), which suggested a lack of attention to the questions, and a further 5 females were removed for substantial missing data. This reduced the sample size to 356 men (*M* ±

SD = 23.27 ± 4.93 years) and 333 women (*M* ± *SD* = 24.15 ± 6.18 years). The study was administered online and participants completed it in one sitting.

2.2 Stimuli

Participants were first asked to rate the attractiveness of a series of individuals in ostensible online dating profiles. Each profile consisted of a facial photo, as well as a short personal description embedded in a realistic dating profile template. These profiles varied independently across three dimensions: facial attractiveness, perceived facial masculinity/femininity, and perceived intelligence. Facial images were collected from stock image websites, while profile descriptions were adapted from self-descriptions obtained on real dating websites. Independent online volunteers recruited from SocialSci.com evaluated the facial attractiveness of the individuals in the photos (75 males and 65 females) and the perceived intelligence of the personal descriptions (136 males and 131 females) in the absence of other stimuli. From these ratings, 32 facial photographs and personal descriptions of each sex were chosen to represent the full spectrum of facial attractiveness and perceived intelligence (mean facial attractiveness ± *SD* = 47.21 ± 13.91 and 57.87 ± 13.68 for male and female images respectively; mean perceived intelligence ± *SD* = 54.97 ± 20.21 and 49.46 ± 20.59 for male and female descriptions respectively). Inter-rater reliability was high for both traits (α = .87 and .91 for facial attractiveness of male and female photographs respectively; α = .86 and .87 for perceived intelligence of the descriptions for male and females respectively). Perceived facial masculinity/femininity was manipulated by morphing each facial photograph with either a masculine or feminine template, which was developed through a combination of averaged male and female faces and perceived masculine and feminine caricatures as developed by Johnston, Hagel, Franklin, Fink, and Grammer (2001). Facial photographs were morphed with the template by 30% in shape and colour in the Fantamorph 4 software package, effectively masculinizing/feminizing each photograph while still maintaining each individual's identity. Photographs of attractive and less attractive individuals were morphed to be more masculine or more feminine and then randomly paired with statements that conveyed high or low perceived intelligence, which produced a total of 128 profiles of each sex. All profiles were presented in greyscale. Participants rated a subset of 32 of these profiles, such that they rated each individual only once, with the target photo either masculinized or feminized, and paired with either an intelligent or less intelligent personal description. Thus, each participant rated 16 masculinised and 16 feminised targets, as well as 16 intelligent and 16 unintelligent self-descriptions. There were no significant differences between stimuli sets on facial attractiveness, perceived masculinity/ femininity, or perceived attractiveness. Participants rated the profiles in a random order and were instructed to either rate the set of profiles' attractiveness for a long-term or short-term relationship. Thus, there were four independent manipulations: facial attractiveness of the profile picture, perceived facial masculinity/femininity of the profile picture, perceived intelligence of the profile description, and whether participants were instructed to consider the profiled individual in the context of a long-term or short-term relationships. For further details see Lee et al. (2013), and for example profiles see Figure 1.

2.3 Measures

Participants first provided demographic information, including age and sex. After rating the dating profiles on attractiveness, they were given the following measures in a randomised order.

The Three-Factor Disgust Scale. The Three-Factor Disgust Scale (Tybur, Lieberman, & Griskevicius, 2009) asked participants to rate the degree to which they find 21 statements disgusting on a 7-point scale (0 = not disgusting at all; 6 = extremely disgusting). Three domains of disgust were assessed: pathogen, moral, and sexual disgust. Pathogen disgust refers to aversion to exposure to pathogen contagions that could threaten one's health, moral disgust refers to aversion to social transgressions, and sexual disgust measured aversion to sexual deviance or unwanted sexual contact. Items for each subscale were summed to produce a score for each disgust domain.

Socioeconomic Status (SES). SES was measured via a single item (Adler, Epel, Castellazzo, & Ickovics, 2000) that asked participants to rate their perceived standing compared to others on the three dimensions of SES: income, education, and occupation, on a 10 point scale (1 = *worst off*; 10 = *best off*). Although only a single item, this measure has previously been shown to correlate with more objective measures of SES (Adler et al., 2000).

Level of Education. Educational attainment was measured via a single item that asked participants to nominate their level of education. Participants responded on a 5-point scale where 1 = *No previous qualification*; 2 = *Completed secondary education*; 3 = *Undergraduate diploma*; 4 = *Undergraduate degree*; and 5 = *Postgraduate degree or diploma*. Educational attainment is strongly correlated with IQ (Baker, Treloar, Reynolds, Heath, & Martin, 1996; Johnson, Deary, & Iacono, 2009; Lynn & Mikk, 2007), and so was used as a proxy measure for intelligence.

The Ten Item Personality Inventory (TIPI). The TIPI, a short-form of the Big Five Personality Inventory (Gosling, Rentfrow, & Swann, 2003; Rammstedt & John, 2007), was used to measure personality on five dimensions – extraversion, agreeableness, conscientiousness, neuroticism, and openness to experience. Each personality dimensions were measure by two items, where participants rate their agreement to statements about their personality on a 5-point scale (1 = *disagree strongly*; 5 = *agree strongly*). Appropriate items were reversed coded and summed to produce scores on the 5 personality factors. Although only 10-items, this short-form has been shown to have reliability and external validity comparable to the 44-item Big Five Inventory (Rammstedt & John, 2007).

The Revised Sociosexual Orientation Inventory (SOI). The SOI (Penke & Asendorpf, 2008) measured participants' orientation towards uncommitted sex in three domains: past behavioural experiences, attitudes towards uncommitted sex, and desire for sex. The behavioural subscale asked participants to select the number of previous short-term sexual partners across three items, each coded on a 9-point scale. The attitude subscale asked participant to rate their agreement to three statements regarding short-term sexual encounters (1 = *strongly disagree*; 9 = *strongly agree*). The desire subscale asked participants to rate the frequency of sexual fantasies or arousal when around someone with whom they do not have a committed romantic relationship. This included three items measured on a 9-point scale (1 = *never*; 9 = *at least once a day*). The items of each subscale were summed to produce a SOI behaviour, SOI attitude, and SOI desire score.

Masculinity Scale. We developed a masculinity scale to assess the masculinity/femininity of participants. Participants were asked to rate themselves compared to others of their age and gender on 19 traits that have been previously found to be sexually dimorphic on either physical (e.g., muscular) or psychological domains (e.g., verbally orientated). Each trait was accompanied with a short description to aid participants in rating themselves on a 5-point scale (1 = *lowest 5%*; 2 = *lower 30%*; 3 = *middle 30%*; 4 = *higher 30%*; 5 = *highest 5%*). For traits that were either clearly measuring sexual dimorphism, or described as being "typical of men" or "typical of women", men and women were given different items asking them to rate themselves on the same trait at the opposing end of the sexual dimorphism dimension (e.g., when men rated the degree to which they have the trait "deep voice", women rated the degree to which they have the trait "high-pitched voice"). Appropriate items were reversed scored and summed, such that a higher score indicated greater physical and psychological masculinity. Further detail regarding the reliability and validity of this measure and provided in the supplementary materials.

Perceived Mate Value and Attractiveness. Three measures were included that assessed participants' mate value and self-perceived attractiveness. Given the conceptual similarity of the measures, and the high correlation between them, they were combined to produce an overall Perceived Mate Value and Attractiveness score. First, the Mate Value Inventory (Kirsner, Figueredo, & Jacobs, 2003) asked participants to rate themselves on 17 traits that are typically desirable in a mate on a 7-point scale (-3 = *extremely low in this trait*; 3 = *extremely high in this trait*). Also included was a 6-item scale that assessed participant's self-perceived success with members of the opposite-sex. This involved participants rating their agreement to items such as "I am likely to date people I am interested in" on a 7-point scale (1 = *strongly disagree*; 7 = *strongly* *agree*). Finally, a single item measure was included that assessed participant's self-perceived attractiveness (Lukaszewski & Roney, 2011). This item asked participants to rate the percentage of people of the same sex and age in their area whom they are more attractive than. Participants were given a sliding bar ranging from 0 to 100 with which they could indicate their response. Scores on these three measures were combined by standardising each measure within sex, then computing the mean across the three standardised scores.

2.4 Analyses

Overall response surfaces. For each profile, we conducted separate sequential model-building exercises for each sex. First we fitted the identity of the rater as a random effect. Then, we sequentially added terms as follows: the two experimental manipulations (i.e., whether the profiles were masculinized or feminized, and whether participants were asked to rate profiles for short or long-term relationships) as fixed factors; their interaction; linear (β_i) terms for the pre-rated facial attractiveness and the pre-rated intelligence of the profile descriptions as linear covariates; the interactions between the manipulations and the linear covariates; the non-linear effect of the covariates (squared terms of each covariate and cross-product of the two covariates) and the interactions between manipulations and the non-linear terms. At each stage we tested whether the added terms significantly enhanced the model using partial F-tests (Chenoweth & Blows, 2005).

Hierarchical Linear Modelling. For the HLM analysis missing values were replaced with the grand mean for that scale from other the participants of the same sex. There were a total of 11391 and 10656 observations for males and females, respectively. These data are hierarchical in nature, such that each of the 32 attractiveness ratings of each profile made by each participant (Level 1) are nested within the participants themselves (Level 2). Therefore, to assess participants' individual differences on preferences for facial attractiveness, perceived facial masculinity/femininity, and perceived intelligence, we used Hierarchical Linear Modeling using the HLM software package (see Raudenbush & Bryk, 2002). On Level 1, participants' preferences for each trait were revealed by the associations between their attractiveness ratings of the profiles and the profiles' facial attractiveness (based on pre-ratings), perceived intelligence (based on pre-ratings), and whether the photograph had been masculinised or feminised. We tested whether Level 2 predictors (individual differences between participants) moderate these associations.

A total of 17 Level 2 predictors were included: Participants' age, SES, education, moral disgust, sexual disgust, pathogen disgust, sociosexual behaviour, sociosexual attitudes, sociosexual desires, extraversion, agreeableness, conscientiousness, neuroticism, openness, masculinity, perceived attractiveness and mate value, and whether participants rated profiles for short-term vs. long-term relationships. Separate analyses were conducted for men and women. A sequential approach to model building was also conducted; however, all random effects were found to be significant or close to significance (<.07), so all Level 1 predictors were retained, and removing Level 2 predictors that did not significantly explain variability did not change the pattern of results. Therefore, here we report models where all predictors are included simultaneously, which also allowed us to assess the unique contribution of each predictor on revealed preferences. To facilitate interpretation, all predictors were z-standardized except for the dichotomous predictors (at Level 1, whether dating profiles were masculinized or feminized, and at Level 2, whether participants were rating for short-term or long-term attractiveness). See Electronic Supplementary Material for additional detail on the analyses conducted. We also tested a model including interaction terms between whether participants' were instructed to consider short-term or long-term relationships and all remaining Level 2 factors on participants' attractiveness ratings of Level 1 characteristics of the profiles. In this latter model, no significant interactions were found; therefore, these interaction terms were dropped from the model reported here. The mean long-term and short-term ratings of the same dating profile were highly correlated (r = .94, p < .001 for male profiles, r = .82, p < .001 for female profiles).

3.0 Results

3.1 Overall response surface – men rating women's dating profiles

The best model for how male participants rated female profiles included the two manipulations (whether the face was masculinized or feminized, and whether participants rated profiles for short- or long-term relationships), their interaction, the linear (***β***) and non-linear (***γ***) effects of pre-rated intelligence and attractiveness, and the interactions between each manipulation and the linear and non-linear components of the response surface (Table 1). There was no statistical support for complex interactions between the response surface and the interaction between the manipulations. This result indicates that although each of the manipulations altered the response surface, these effects were independent of one another.

The response surfaces describing the relationship between pre-rated facial attractiveness, perceived intelligence, and participants' attractiveness ratings for each of the four manipulation combinations are shown in Figure 2. When participants were asked to rate profiles for short-term attractiveness their responses were typically more positive (i.e., male participants were less choosy when considering a short-term relationship). In all treatments facial attractiveness and perceived intelligence enhanced the ratings given to profiles, but the rise due to intelligence was much more dramatic when participants were asked to rate profiles for long-term mating prospects than for short-term mating prospects (Table 2, Figure 2). Feminization improved the attractiveness of faces, but the effects were more dramatic when the profile suggested high intelligence and when the pre-rated facial attractiveness was low.

3.2 Overall response surface – women rating men's dating profiles

The analysis of male profiles rated by women was somewhat simpler. Again, the manipulation effects and the covariates (both linear and non-linear terms) significantly affected attractiveness. Only the linear parts of the response surface interacted with whether women were considering long-term or short-term relationships. There was no interaction between linear or non-linear terms with the perceived facial masculinity/femininity manipulation of the dating profiles (See Tables 1 and 2).

Both manipulations influenced attractiveness but their effects did not interact (Table 1). Instead they were additive (note the parallel contours within each panel of Figure 2). Masculinization raised attractiveness by up to 5 points at some places, and women gave slightly higher ratings for the same profile when asked to consider short-term (as opposed to long-term) attractiveness. Intelligence and facial attractiveness both increase attractiveness ratings of male profiles.

The only differences in slopes of the fitness surfaces in Figure 2 are differences in the linear slopes of the preferences for attractiveness and intelligence between raters asked to evaluate profiles for short-term and long-term relationships (Table 2). The intelligence slope is steeper and the attractiveness slope less steep when women are asked to rate males for long-term matings. This suggests a straightforward shifting of priorities from facial attractiveness in short-term matings to intelligence in long-term matings. While masculinisation or feminisation affected the attractiveness of a given face, the effect was additive: the slope did not differ between surfaces with masculinized or feminized faces (Figure 2). The non-linear selection gradients were not significant, nor did they differ between the levels of the two manipulated factors or with the interaction between those factors.

3.3 Hierachical Linear Modelling – Men's ratings of women's profiles

An empty model of male participants' attractiveness ratings of women's dating profiles with no predictors found that the intra-class correlation (i.e., the proportion of the total variance accounted for by between-individual variance) was .25. This indicates that variance exists at both levels, further confirming that HLM is the appropriate analysis of this data. Analysis of variance components suggest that 35% of variance can be explained by Level 1 predictors (i.e., variation between dating profiles). See the Electronic Supplementary Material for variance components.

The γ coefficients from the HLM analysis are reported in Table 3. For each trait, the intercept indicates the main effect of that trait on participants' attractiveness ratings; thus, increased facial attractiveness, perceived intelligence, and feminization of profile pictures led to increased attractiveness ratings from male participants. A significant *t*-statistic indicates that the Level 2 predictor moderated the relationship between the Level 1 predictor and participants' attractiveness ratings of the dating profiles. The results show that male preference for facial attractiveness was significantly greater in participants with higher pathogen disgust, unrestricted sociosexual desire, and neuroticism, and decreased in participants who were older, more sensitive to moral disgust, more open to new experiences, and in participants who were rating profiles for short-term attractiveness. Preference for feminized profiles increased when men reported more unrestricted sociosexual desire and higher perceived mate value, and decreased only when men reported more restricted sociosexual attitudes. Men's preference for perceived intelligence was stronger in participants more sensitive to moral disgust and more open to new experiences, and in participants who were rating profiles for a long-term relationship. However, preference for perceived intelligence was significantly lower in younger participants, and in participants low in self-reported masculinity. No other effects were significant for men.

3.4 Hierarchical linear modeling – Women's ratings of men's profiles

An empty model of women's attractiveness ratings of men's dating profiles with no predictors found that the intra-class correlation (i.e., the proportion of the total variance accounted for by between-individual variance) was .22. Analysis of variance components suggest that 42% of the variance can be explained by Level 1 predictors (i.e., variation between dating profiles). See the Electronic Supplementary Material for variance components.

The γ coefficients from the HLM analysis are reported in Table 3. Significant intercepts were found for all three traits, such that women's attractiveness ratings increased when profiles were higher in facial attractiveness, perceived intelligence, or had been facially masculinized.

Women's preference for facial attractiveness was higher in women more sensitive to pathogen disgust, less sensitive to moral disgust, and high in neuroticism. Preference for masculinized profiles was higher in participants who reported high subjective SES, and low sociosexual attitudes. Women's preference for perceived intelligence was higher in participants more sensitive to moral disgust, and less sensitive to sexual disgust. No other effects were significant for women.

4.0 Discussion

Our experiment is unusual in that it combines factorial manipulations (facial masculinity/femininity and whether we were asking participants to rate profiles for short-term or long-term mating) and continuous variation in the independently rated attractiveness of faces and intelligence of profile descriptions. This combination allowed us to infer, with some of the precision inherent to experimental methods, the complex interactions between various determinants of attractiveness inherent in mate choice decisions. We were also able to test how individual differences influenced these nuanced and complex choices. We found an intermediate level of complexity in the preferences we measured: there were significant linear and non-linear preference functions, and in some cases these were altered between levels of the manipulated factors. But the highest-order interactions between combinations of factors and preference functions were generally not significant. The preferences involving men choosing women were slightly more complex than those involving women choosing men.

4.1 Overall response surfaces

The results of our overall response-surface analysis suggest that the kind of relationship (short vs long) participants were asked to consider, the experimental masculinization or feminization of the face, the pre-rated attractiveness of the face before experimental masculinization/feminization, and the perceived intelligence of the profile statement all contributed to the rating participants gave a particular profile. Moreover these factors interacted in interesting ways with one another. There were some informative similarities and some equally revealing differences between the sexes in these effects.

Experimental masculinization of male faces and feminization of female faces increased participants' ratings of attractiveness, effecting an increase of five or more points – this effect was more pronounced for men rating profiles of women. These results support the view that male facial masculinity can influence attractiveness when present with other information (e.g., information in the dating profile, or other aspects of the facial photograph), contrary to recent suggestions that masculine characteristics in men's faces only matter when they are considered in isolation (Scott, Clark, Boothroyd, & Penton-Voak, 2012). Similarly, profiles tended to get higher ratings when participants were asked to rate profiles for a short-term relationship than when participants rated profiles for a long-term relationship, indicating increased choosiness when considering long-term partners.

The overall response surface analyses reveal that both men and women show an increase in attractiveness ratings for intelligent, facially attractive profiles of the opposite sex members. By manipulating the perceived intelligence of the profile statement independent of the facial attractiveness of the picture, we showed that both traits contribute to the perceived attractiveness of a profile. While both facial attractiveness and perceived intelligence elevated ratings that male faces received from females, the effects were linear and did not interact. Thus, a given increment in either intelligence or attractiveness raised the rating by a predictable amount independent of the effects of the other trait. However, the effect of facial attractiveness and perceived intelligence on the attractiveness ratings of the female profiles by male raters was non-linear, and this non-linearity included interactions (i.e., correlational selection) between the two traits. This interaction indicated that women in the upper half of the distribution of pre-rated attractiveness enjoyed a greater elevation in their ratings when paired with an intelligent profile statement than did women with less attractive faces. This could represent a threshold effect, where men first look to secure an acceptable level of physical attractiveness before considering perceived intelligence when making attractiveness judgements – a prediction that could be tested in the future.

Experimentally feminized female faces receive comparable ratings to masculinized faces when those faces were high in pre-rated facial attractiveness, but ratings for the masculinized faces drop off far more rapidly as pre-rated facial attractiveness drops off. Given the tight association between facial femininity and attractiveness in women (Perrett et al., 1998), presumably the women with high pre-rated facial attractiveness were more feminine to begin with, and this may have reduced the effect of masculinization on participants' attractiveness ratings. On the other hand, masculinized male faces received higher ratings, but the effects of manipulated perceived facial masculinity/femininity were independent (additive) of the effects of pre-rated facial attractiveness and perceived intelligence.

In both sexes, participants asked to consider a long-term relationship weighted perceived intelligence more heavily than those asked to rate profiles for a short-term liaison, which is consistent with previous research using self-reported preferences (Prokosch, Coss, Scheib, & Blozis, 2009). For women rating men, the greater weighting on perceived intelligence accompanied a simple reduction in the weighting on pre-rated facial attractiveness, perhaps reflecting a trade-off or optimisation process between the two preferences.

These interactions between the facial attractiveness/perceived intelligence response surface and the two experimental conditions (masculinization/feminization and short vs long-term mating) reveal shifts in the relative importance of facial attractiveness and perceived intelligence. The two manipulations, however, did not interact with one another to change the response surface, suggesting that the effects of the manipulations were independent.

4.2 Hierarchical Linear Modelling

Using HLM, we were able to consider the unique contribution of 17 individual difference variables on preferences for facial attractiveness, perceived intelligence, and perceived facial masculinity/femininity. Here, we replicated several previous findings, even when considering multiple variables. We found an association between pathogen disgust and preference for facial attractiveness in both men and women (Park, van Leeuwen, & Stephen, 2012; Young, Sacco, & Hugenberg, 2011), and with stronger male preference for facial femininity (Jones, Fincher, Welling, et al., 2013; Little, DeBruine, & Jones, 2011). However, no relationship was found between women's pathogen disgust and preference for male facial masculinity, in contrast with the findings of a number of recent studies (DeBruine, Jones, Crawford, et al., 2010; DeBruine, Jones, Tybur, et al., 2010; Jones, Fincher, Little, et al., 2013; Little et al., 2011; F. R. Moore et al., 2013). Also, women who reported low subjective SES significantly preferred more feminine male faces, which is thought to be associated with good parental ability (Little, Cohen, Jones, & Belsky, 2007). While more focused analyses of pathogen disgust and SES using this dataset were presented in Lee et al. (2013), here we show that the observed associations with mate preferences were not due to confounds involving other personality, mating, or demographic variables. Women's preference for facial masculinity is complex and potentially influenced by multiple factors, of which the underlying mechanisms are not yet understood (Lee et al., in press; Scott et al., 2012), thus, further multivariate investigation into preference for facial masculinity is required.

In turn, some associations identified in previous research failed to replicate in our analysis. We failed to find homophily for intelligence (Watson et al., 2004), as no association was found between participants' education (a proxy measure for their intelligence) and a preference for perceived intelligence. While this lack of association in our analysis does not indicate that homophily for intelligence does not exist, further research is needed to explore how strong homophily is in more complex choice scenarios such as the one we present here, or whether this relationship could be explained by a third variable.

Additionally, our analyses were able to identify possible relationships that potentially could be fruitful for further investigations. For instance, research has focused on the influence of pathogen disgust on mate preferences; however, we find that moral disgust has as much, or even more influence in preference for facial attractiveness and perceived intelligence. Perhaps those with higher moral disgust place more importance on intrinsic traits such as intelligence than on more superficial traits such as physical appearance, but further research would be needed to test this.

For women, we found a negative relationship between unrestricted sociosexual attitudes and preference for facial masculinity of male profiles. This is contrary to previous findings that suggest more masculine men are preferred for short-term relationships (Little et al., 2007; Provost et al., 2006; Waynforth et al., 2005). For men, we also found that unrestricted sociosexual attitudes were associated with lower preference for facial femininity; however, we also found a positive relationship between unrestricted sociosexual desire and preference for facial physical attractiveness and facial femininity. These seemingly contradictory findings, in combination with previous research suggest a need for further research to clarify the effects of sociosexual attitudes on desire on preferences.

Associations were also found between Big Five personality traits and preference for facial attractiveness; specifically, neuroticism was associated with preference for facial attractiveness, but the relationship was positive for men and negative for women. In addition, men's openness to experience was associated with less importance placed on facial attractiveness and more importance on perceived intelligence, perhaps suggesting shifting values among men who are more open to new experience. Previous findings that extraversion and openness to experience influenced women's preference for facial sexual dimorphism (Welling, DeBruine, Little, & Jones, 2009) were not supported.

Men's masculinity was also negatively associated with preference for perceived intelligence. Given that men place less importance on intelligence in a partner compared to women (evident in the current data as well as the findings of Li et al., 2002), the association between men's masculinity and intelligence preferences may reflect within-sex variation in sexual dimorphism in mate preference for intelligence. Individual levels of physical or psychological sexual dimorphism and associations with sex-typical preferences have rarely been investigated, and present another avenue for possible research.

The complex ways in which individual differences altered the preferences we observed suggest that variation among individuals in mate choice might be an important source of variation in sexual selection, as it is thought to be in other animals (Brooks & Endler, 2001b; Chaine & Lyon, 2008; Forsgren, Amundsen, Borg, & Bjelvenmark, 2004; Jennions & Petrie, 1997). Further, the pattern of sexual selection inferred from the overall response surface analysis above is an aggregate outcome of the individual ratings of different participants. Changes in the composition of the population sampled or in the environmental factors (e.g. triggers of moral disgust, or economic inequality) could alter the overall pattern of sexual selection.

4.3 Conclusion

Several considerations warrant caution when interpreting these results. First, the dating profiles varied in numerous ways that were not strictly controlled for (e.g., extraneous information in personal descriptions or profile photographs). Also, recent work has suggested that facial appearance from unstandardized images, such as images used in this study, may not reflect as stable of a representation of a person's attractiveness compared to more standardised images (Jenkins, White, Van Montfort, & Burton, 2011; Morrison, Morris, & Bard, 2013). Although these variations had the advantage of enhancing realism, they also introduced noise that could have obscured subtle associations. We attempt to minimise this issue by testing a large sample, such that even small associations could be detected, although we note that this may have also increased the chances of detecting artefacts of subtle confounds that could have been introduced by idiosyncrasies of the stimuli – future research could address this by using a larger stimuli set. Also, we did not consider an exhaustive list of variables that could influence preference for facial attractiveness, perceived facial masculinity/femininity, or perceived intelligence. However, these analyses include many more factors than have previously investigated in human mate choice, and demonstrate the value of considering multiple preferences simultaneously and allowing for nonlinear preference functions and moderating effects of individual differences. This approach allowed us to identify relationships previously undetectable by more focused studies that investigate linear relationships. Our results also illustrate the value of considering both individual variation and population-level measures of likely sexual selection. Because mate choice in humans is so complex, the current findings suggest that we should complement focused studies with multivariate approaches.

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Figure Legends

Figure 1. Examples of dating profiles with male (top) and female (bottom) profile pictures, as well as masculinized and intelligent (left) and feminized and less intelligent (right) pictures and personal descriptions. Note varying degrees of facial attractiveness and intelligence were used, and all 3 dimensions were counterbalanced when shown to participants.

Figure 2. The response surfaces describing the relationship between participants' attractiveness ratings of the online profiles (contour lines) and the four manipulations: 1) the pre-rated facial attractiveness (x-axis); 2) The pre-rated perceived intelligence (y-axis); 3) the facial masculinization (blue and green contours) or feminization (red or yellow contours); and 4) whether participants were instructed to consider a short-term (left) or long-term (right) relationship.