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Abstract

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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.

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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

59 weighting given to different mate choice criteria. Many other individual differences or contextual
60 effects no doubt remain to be discovered.

61 In addition to the multivariate nature of mate choice, individuals in search of a mate can
62 vary in their motivation to choose, and in the strength and direction of their preferences (Jennions &
63 Petrie, 1997). Some of this variation can arise due to genetic variation between individuals
64 (Verweij, Burri, & Zietsch, 2012; Zietsch, Verweij, & Burri, 2012), idiosyncratic issues of adaptive
65 compatibility (e.g. genetic compatibility; Roberts & Little, 2008), or as a plastic response to the
66 context in which individual “choosers” find themselves (Lee & Zietsch, 2011){Little, 2007
67 #50;Little, 2011 #49}.

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

76 Multivariate studies of animal mate choice have shown that interactions between traits can
77 add important non-linearity to the overall pattern of selection (Blows & Brooks, 2003; Blows,
78 Chenoweth, & Hine, 2004; Brooks et al., 2005; A. J. Moore, 1990). Interactions among colour
79 pattern traits in guppies (Blows & Brooks, 2003; Blows, Brooks, & Kraft, 2003) revealed selection
80 on those patterns and a complex multi-peak fitness surface that linear selection analyses failed to
81 detect (Brooks & Endler, 2001a). Likewise, simultaneous manipulations of suites of acoustic traits
82 in crickets (Bentsen, Hunt, Jennions, & Brooks, 2006; Brooks et al., 2005) and frogs (Gerhardt &
83 Brooks, 2009) revealed strong stabilizing selection and exponential (positive quadratic) selection
84 that univariate manipulations had not exposed. Studies on human mate preferences have also

85 revealed non-linear effects; for example, men's body preferences for intermediate shoulder, hip, and
86 waist widths over larger or smaller widths (Donohoe, von Hippel, & Brooks, 2009). Other studies
87 of human mate preferences have also found complex interactions among a handful of factors; for
88 example Penton-Voak et al. (2003) found that women's preference for facial sexual dimorphism
89 was influenced by an interaction between their condition and whether they were rating for short- or
90 long-term attractiveness. Brooks, Shelly, Fan, Zhai, and Chau (2010) found that multivariate non-
91 linear selection analyses consistently outperformed indices and ratios such as Body Mass Index
92 (BMI), waist-to-hip ratio and age in predicting the attractiveness of scanned images of female
93 bodies. These examples further emphasise the need to look beyond focused studies.

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

103 The multivariate complexity of mate choice and the many sources of variation among
104 individual choosers combine to make mate choice more complex and varied than it might appear
105 from the experiments often used to test focused hypotheses. Fortunately, evolutionary biology has
106 well-established multivariate methods for estimating linear and non-linear selection (fitness
107 surfaces) on suites of correlated traits (Lande & Arnold, 1983; Phillips & Arnold, 1989), for
108 comparing fitness surfaces among groups or experimental treatments (Chenoweth & Blows, 2005),
109 and for visualising complex fitness surfaces (Blows & Brooks, 2003; Brodie, Moore, & Janzen,
110 1995). It is also possible to combine multivariate response surface analysis with independent

111 manipulations of suites of continuous traits that are ordinarily correlated in order to establish how
112 each trait contributes to selection (Brooks et al., 2005; Donohoe et al., 2009; Gerhardt & Brooks,
113 2009; Mautz, Wong, Peters, & Jennions, 2013).

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

123

124 2.0 Methods

125

126 2.1 Participants

127 Participants were 430 men ($M \pm SD = 23.07 \pm 4.86$ years) and 422 women ($M \pm SD = 24.07$
128 ± 6.80 years) who were recruited from an online survey website (<http://www.socialsci.com>) in
129 return for online store credit. Participation was conditional on being heterosexual and not currently
130 in a long-term relationship. Participants who completed the incorrect survey (i.e., males who
131 completed the female survey and vice versa; 33 males, 5 females), did not identify as being
132 heterosexual (34 males; 71 females), or did not report their age (6 males; 2 females) were removed
133 from analyses. A further 1 male and 6 females were removed for completing the survey in an
134 unrealistic time (<5min), which suggested a lack of attention to the questions, and a further 5
135 females were removed for substantial missing data. This reduced the sample size to 356 men ($M \pm$

136 $SD = 23.27 \pm 4.93$ years) and 333 women ($M \pm SD = 24.15 \pm 6.18$ years). The study was
137 administered online and participants completed it in one sitting.

138

139 2.2 Stimuli

140 Participants were first asked to rate the attractiveness of a series of individuals in ostensible
141 online dating profiles. Each profile consisted of a facial photo, as well as a short personal
142 description embedded in a realistic dating profile template. These profiles varied independently
143 across three dimensions: facial attractiveness, perceived facial masculinity/femininity, and
144 perceived intelligence. Facial images were collected from stock image websites, while profile
145 descriptions were adapted from self-descriptions obtained on real dating websites. Independent
146 online volunteers recruited from SocialSci.com evaluated the facial attractiveness of the individuals
147 in the photos (75 males and 65 females) and the perceived intelligence of the personal descriptions
148 (136 males and 131 females) in the absence of other stimuli. From these ratings, 32 facial
149 photographs and personal descriptions of each sex were chosen to represent the full spectrum of
150 facial attractiveness and perceived intelligence (mean facial attractiveness $\pm SD = 47.21 \pm 13.91$
151 and 57.87 ± 13.68 for male and female images respectively; mean perceived intelligence $\pm SD =$
152 54.97 ± 20.21 and 49.46 ± 20.59 for male and female descriptions respectively). Inter-rater
153 reliability was high for both traits ($\alpha = .87$ and $.91$ for facial attractiveness of male and female
154 photographs respectively; $\alpha = .86$ and $.87$ for perceived intelligence of the descriptions for male and
155 females respectively). Perceived facial masculinity/femininity was manipulated by morphing each
156 facial photograph with either a masculine or feminine template, which was developed through a
157 combination of averaged male and female faces and perceived masculine and feminine caricatures
158 as developed by Johnston, Hagel, Franklin, Fink, and Grammer (2001). Facial photographs were
159 morphed with the template by 30% in shape and colour in the Fantamorph 4 software package,
160 effectively masculinizing/feminizing each photograph while still maintaining each individual's
161 identity. Photographs of attractive and less attractive individuals were morphed to be more

162 masculine or more feminine and then randomly paired with statements that conveyed high or low
163 perceived intelligence, which produced a total of 128 profiles of each sex. All profiles were
164 presented in greyscale. Participants rated a subset of 32 of these profiles, such that they rated each
165 individual only once, with the target photo either masculinized or feminized, and paired with either
166 an intelligent or less intelligent personal description. Thus, each participant rated 16 masculinised
167 and 16 feminised targets, as well as 16 intelligent and 16 unintelligent self-descriptions. There were
168 no significant differences between stimuli sets on facial attractiveness, perceived masculinity/
169 femininity, or perceived attractiveness. Participants rated the profiles in a random order and were
170 instructed to either rate the set of profiles' attractiveness for a long-term or short-term relationship.
171 Thus, there were four independent manipulations: facial attractiveness of the profile picture,
172 perceived facial masculinity/femininity of the profile picture, perceived intelligence of the profile
173 description, and whether participants were instructed to consider the profiled individual in the
174 context of a long-term or short-term relationships. For further details see Lee et al. (2013), and for
175 example profiles see Figure 1.

176

177 *2.3 Measures*

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

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

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

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

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

207 *The Revised Sociosexual Orientation Inventory (SOI)*. The SOI (Penke & Asendorpf, 2008)
208 measured participants' orientation towards uncommitted sex in three domains: past behavioural
209 experiences, attitudes towards uncommitted sex, and desire for sex. The behavioural subscale asked
210 participants to select the number of previous short-term sexual partners across three items, each
211 coded on a 9-point scale. The attitude subscale asked participant to rate their agreement to three
212 statements regarding short-term sexual encounters (1 = *strongly disagree*; 9 = *strongly agree*). The

213 desire subscale asked participants to rate the frequency of sexual fantasies or arousal when around
214 someone with whom they do not have a committed romantic relationship. This included three items
215 measured on a 9-point scale (1 = *never*; 9 = *at least once a day*). The items of each subscale were
216 summed to produce a SOI behaviour, SOI attitude, and SOI desire score.

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

230 *Perceived Mate Value and Attractiveness.* Three measures were included that assessed
231 participants’ mate value and self-perceived attractiveness. Given the conceptual similarity of the
232 measures, and the high correlation between them, they were combined to produce an overall
233 Perceived Mate Value and Attractiveness score. First, the Mate Value Inventory (Kirsner,
234 Figueredo, & Jacobs, 2003) asked participants to rate themselves on 17 traits that are typically
235 desirable in a mate on a 7-point scale (-3 = *extremely low in this trait*; 3 = *extremely high in this*
236 *trait*). Also included was a 6-item scale that assessed participant’s self-perceived success with
237 members of the opposite-sex. This involved participants rating their agreement to items such as “I
238 am likely to date people I am interested in” on a 7-point scale (1 = *strongly disagree*; 7 = *strongly*

239 *agree*). Finally, a single item measure was included that assessed participant's self-perceived
240 attractiveness (Lukaszewski & Roney, 2011). This item asked participants to rate the percentage of
241 people of the same sex and age in their area whom they are more attractive than. Participants were
242 given a sliding bar ranging from 0 to 100 with which they could indicate their response. Scores on
243 these three measures were combined by standardising each measure within sex, then computing the
244 mean across the three standardised scores.

245

246 *2.4 Analyses*

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

257 *Hierarchical Linear Modelling.* For the HLM analysis missing values were replaced with
258 the grand mean for that scale from other the participants of the same sex. There were a total of
259 11391 and 10656 observations for males and females, respectively. These data are hierarchical in
260 nature, such that each of the 32 attractiveness ratings of each profile made by each participant
261 (Level 1) are nested within the participants themselves (Level 2). Therefore, to assess participants'
262 individual differences on preferences for facial attractiveness, perceived facial
263 masculinity/femininity, and perceived intelligence, we used Hierarchical Linear Modeling using the
264 HLM software package (see Raudenbush & Bryk, 2002). On Level 1, participants' preferences for

265 each trait were revealed by the associations between their attractiveness ratings of the profiles and
266 the profiles' facial attractiveness (based on pre-ratings), perceived intelligence (based on pre-
267 ratings), and whether the photograph had been masculinised or feminised. We tested whether Level
268 2 predictors (individual differences between participants) moderate these associations.

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

289

290

3.0 Results

291

292 *3.1 Overall response surface – men rating women’s dating profiles*

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

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

311

312 *3.2 Overall response surface – women rating men’s dating profiles*

313 The analysis of male profiles rated by women was somewhat simpler. Again, the
314 manipulation effects and the covariates (both linear and non-linear terms) significantly affected
315 attractiveness. Only the linear parts of the response surface interacted with whether women were
316 considering long-term or short-term relationships. There was no interaction between linear or non-

317 linear terms with the perceived facial masculinity/femininity manipulation of the dating profiles
318 (See Tables 1 and 2).

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

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

335 336 *3.3 Hierarchical Linear Modelling – Men's ratings of women's profiles*

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

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

359
360 *3.4 Hierarchical linear modeling – Women's ratings of men's profiles*

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

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

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

374

375

4.0 Discussion

376

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

389

390 *4.1 Overall response surfaces*

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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

395 to the rating participants gave a particular profile. Moreover these factors interacted in interesting
396 ways with one another. There were some informative similarities and some equally revealing
397 differences between the sexes in these effects.

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

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

421 acceptable level of physical attractiveness before considering perceived intelligence when making
422 attractiveness judgements – a prediction that could be tested in the future.

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

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

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

443

444 *4.2 Hierarchical Linear Modelling*

445 Using HLM, we were able to consider the unique contribution of 17 individual difference
446 variables on preferences for facial attractiveness, perceived intelligence, and perceived facial

447 masculinity/femininity. Here, we replicated several previous findings, even when considering
448 multiple variables. We found an association between pathogen disgust and preference for facial
449 attractiveness in both men and women (Park, van Leeuwen, & Stephen, 2012; Young, Sacco, &
450 Hugenberg, 2011), and with stronger male preference for facial femininity (Jones, Fincher, Welling,
451 et al., 2013; Little, DeBruine, & Jones, 2011). However, no relationship was found between
452 women's pathogen disgust and preference for male facial masculinity, in contrast with the findings
453 of a number of recent studies (DeBruine, Jones, Crawford, et al., 2010; DeBruine, Jones, Tybur, et
454 al., 2010; Jones, Fincher, Little, et al., 2013; Little et al., 2011; F. R. Moore et al., 2013). Also,
455 women who reported low subjective SES significantly preferred more feminine male faces, which
456 is thought to be associated with good parental ability (Little, Cohen, Jones, & Belsky, 2007). While
457 more focused analyses of pathogen disgust and SES using this dataset were presented in Lee et al.
458 (2013), here we show that the observed associations with mate preferences were not due to
459 confounds involving other personality, mating, or demographic variables. Women's preference for
460 facial masculinity is complex and potentially influenced by multiple factors, of which the
461 underlying mechanisms are not yet understood (Lee et al., in press; Scott et al., 2012), thus, further
462 multivariate investigation into preference for facial masculinity is required.

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

470 Additionally, our analyses were able to identify possible relationships that potentially could
471 be fruitful for further investigations. For instance, research has focused on the influence of pathogen
472 disgust on mate preferences; however, we find that moral disgust has as much, or even more

473 influence in preference for facial attractiveness and perceived intelligence. Perhaps those with
474 higher moral disgust place more importance on intrinsic traits such as intelligence than on more
475 superficial traits such as physical appearance, but further research would be needed to test this.

476 For women, we found a negative relationship between unrestricted sociosexual attitudes and
477 preference for facial masculinity of male profiles. This is contrary to previous findings that suggest
478 more masculine men are preferred for short-term relationships (Little et al., 2007; Provost et al.,
479 2006; Waynforth et al., 2005). For men, we also found that unrestricted sociosexual attitudes were
480 associated with lower preference for facial femininity; however, we also found a positive
481 relationship between unrestricted sociosexual desire and preference for facial physical
482 attractiveness and facial femininity. These seemingly contradictory findings, in combination with
483 previous research suggest a need for further research to clarify the effects of sociosexual attitudes
484 on desire on preferences.

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

493 Men's masculinity was also negatively associated with preference for perceived intelligence.
494 Given that men place less importance on intelligence in a partner compared to women (evident in
495 the current data as well as the findings of Li et al., 2002), the association between men's
496 masculinity and intelligence preferences may reflect within-sex variation in sexual dimorphism in
497 mate preference for intelligence. Individual levels of physical or psychological sexual dimorphism

498 and associations with sex-typical preferences have rarely been investigated, and present another
499 avenue for possible research.

500 The complex ways in which individual differences altered the preferences we observed
501 suggest that variation among individuals in mate choice might be an important source of variation
502 in sexual selection, as it is thought to be in other animals (Brooks & Endler, 2001b; Chaine & Lyon,
503 2008; Forsgren, Amundsen, Borg, & Bjelvenmark, 2004; Jennions & Petrie, 1997). Further, the
504 pattern of sexual selection inferred from the overall response surface analysis above is an aggregate
505 outcome of the individual ratings of different participants. Changes in the composition of the
506 population sampled or in the environmental factors (e.g. triggers of moral disgust, or economic
507 inequality) could alter the overall pattern of sexual selection.

508

509 *4.3 Conclusion*

510 Several considerations warrant caution when interpreting these results. First, the dating
511 profiles varied in numerous ways that were not strictly controlled for (e.g., extraneous information
512 in personal descriptions or profile photographs). Also, recent work has suggested that facial
513 appearance from unstandardized images, such as images used in this study, may not reflect as stable
514 of a representation of a person's attractiveness compared to more standardised images (Jenkins,
515 White, Van Montfort, & Burton, 2011; Morrison, Morris, & Bard, 2013). Although these variations
516 had the advantage of enhancing realism, they also introduced noise that could have obscured subtle
517 associations. We attempt to minimise this issue by testing a large sample, such that even small
518 associations could be detected, although we note that this may have also increased the chances of
519 detecting artefacts of subtle confounds that could have been introduced by idiosyncrasies of the
520 stimuli – future research could address this by using a larger stimuli set. Also, we did not consider
521 an exhaustive list of variables that could influence preference for facial attractiveness, perceived
522 facial masculinity/femininity, or perceived intelligence. However, these analyses include many
523 more factors than have previously investigated in human mate choice, and demonstrate the value of

524 considering multiple preferences simultaneously and allowing for nonlinear preference functions
525 and moderating effects of individual differences. This approach allowed us to identify relationships
526 previously undetectable by more focused studies that investigate linear relationships. Our results
527 also illustrate the value of considering both individual variation and population-level measures of
528 likely sexual selection. Because mate choice in humans is so complex, the current findings suggest
529 that we should complement focused studies with multivariate approaches.

530

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535

536

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537

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742

Figure Legends

743

744

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

749

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

755