Northumbria Research Link

TAMSIN K. SAXTON [a,b]*, ANTHONY C. LITTLE [c], HANNAH M. ROWLAND [b], TING GAO [b], S. CRAIG ROBERTS [b]

[a] School of Psychology, University of St Andrews, St Mary's College, South Street, St Andrews, Fife, Scotland, KY16 9JP

[b] School of Biological Sciences, University of Liverpool, Crown Street, Liverpool, L69 7ZB

[c] Department of Psychology, University of Stirling, Stirling, FK9 4LA

* corresponding author, +44(0)1334 463044, tamsin.saxton@st-andrews.ac.uk

Trade-offs between markers of absolute and relative quality in human facial preferences

Short title: Trade-offs in human facial preferences

Individuals are attuned to cues of quality in potential mates. Mate quality is assessed on both an absolute scale, independent of the observer, and also on a relative scale, dependent upon attributes of the observer. Much research has focused on how individuals respond to either absolute or relative quality in mate choice, but how these dimensions are weighted during mate choice decisions is poorly understood and has recently attracted much theoretical interest. Here we examine the interplay between women's facial preferences for a measure of absolute quality (sexual dimorphism) and one of relative quality (self-similarity). Women rated the attractiveness of male faces that had been simultaneously manipulated along the dimensions of masculinity and

self-similarity in short-term and long-term relationship contexts. Sexual dimorphism had a greater positive effect on ratings than self-similarity, and masculinity and self-similarity had positive combinative effects on ratings of attractiveness. Women's co-expressed preferences for masculine faces combined with their lesser preference for subtly self-similar faces may reflect selection of good genes, promote optimal outbreeding, and give rise to directional selection even in the presence of a general self-similarity preference.

3

1 Successful mate choice necessitates the accurate assessment of quality in a potential

2 partner. Yet this assessment entails a paradox. Quality can be defined both with

3 reference to an absolute scale that can be measured independently of the observer,

4 such as ornamental indicator traits demonstrating good genes; and also on a relative

5 scale that cannot be assessed without consideration of the traits of the observer, such

6 as genetic compatibility (Neff and Pitcher, 2005). Potential mates are likely to score

7 differently on the two scales, and the question of how individuals trade off absolute

8 and relative quality in mate selection is of key interest to biologists but has been little

9 investigated (Colegrave et al., 2002; Mays and Hill, 2004; Roberts and Little, 2008)

10 beyond an initial study in mice (Roberts and Gosling, 2003).

11 Mays and Hill (2004) identify different scenarios that might describe how individuals

12 trade off absolute and relative quality. Firstly, individuals might privilege absolute or

13 relative quality dependent upon social, ecological or genetic context, with reference to

14 genetic diversity within the population, for instance. Alternatively, individuals might

15 employ a nested, heirarchical rule, whereby potential mates will only be assessed with

16 regards to relative quality if they exceed a certain threshold on the measure of

17 absolute quality. Both of these scenarios have been demonstrated in mice (Roberts

18 and Gosling, 2003). Finally, individuals might employ different criteria for social mates

19 compared with extra-pair mates, as has been demonstrated in passerine birds (review

20 in Mays and Hill, 2004). Humans represent an ideal model to study this trade-off

21 because preferences for absolute and relative quality may be addressed using facial

22 features (Roberts and Little, 2008). The distinction between social and extra-pair mates

4

23   can be approximated in humans by asking individuals to evaluate others for a short-

24   term compared with a long-term relationship (see e.g. Gangestad and Simpson, 2000).

25   In humans, sexual dimorphism is considered an indicator trait of absolute quality. Male

26   masculinity is associated with perceived healthiness (Rhodes et al., 2003; Rhodes et al.,

27   2007) and actual health (Rhodes et al., 2003; Thornhill and Gangestad, 2006), lower

28   levels of fluctuating asymmetry (another indicator trait) (Little et al., 2008), and higher

29   levels of testosterone (Penton-Voak and Chen, 2004), which may constitute an index of

30   'good genes' (Zahavi, 1975, 1977; Hamilton and Zuk, 1982; Maynard Smith, 1985;

31   Folstad and Karter, 1992). The manipulation of male facial masculinity in digital images

32   and the attendant implicit effects on the mate quality of the stimulus have been

33   greatly used to examine how women respond to the quality of a potential partner.

34   Relatively more masculine male faces seem to be preferred when good gene benefits

35   might be most relevant, such as when a woman is most likely to become pregnant

36   (review in Jones et al., 2008), or when she makes judgments for a short-term

37   relationship (where lasting benefits may be limited to those associated with

38   conception) compared with a long-term relationship (where lasting benefits may

39   derive from additional partner characteristics) (Penton-Voak et al., 1999a; Little et al.,

40   2002; Penton-Voak et al., 2003).

41   Alongside preferences for absolute traits, humans also assess the facial attractiveness

42   of potential partners with reference to the relative measure of self-similarity. Couples

43   exhibit physical similarity (overviews and research in e.g. Griffiths and Kunz, 1973;

44   Zajonc et al., 1987; Bereczkei et al., 2002; Little et al., 2003; Bereczkei et al., 2004;

45 Little et al., 2006) and the experimental manipulation of facial similarity generally

46 indicates that visual similarity to the rater enhances attractiveness to some degree

47 (Penton-Voak et al., 1999b; DeBruine, 2004; DeBruine et al., 2005; Bailenson et al.,

48 2006). This relative preference may have indirect benefits: since facial resemblance is

49 associated with relatedness, it may enable optimal outbreeding (Bateson, 1978, 1980,

50 1982) and influence inbreeding depression (Potts and Wakeland, 1993). Similarly, it

51 may encourage the selection of a partner from the same population who is more likely

52 to have appropriate adaptations to the local environment, thereby enabling the

53 maintenance of co-adapted genetic complexes (Read and Harvey, 1991), or enhance

54 one's own genetic representation in future generations through the selection of a

55 partner with some genetic matches (Thiessen and Gregg, 1980; Epstein and Guttman,

56 1982; Rushton, 1988; Thiessen, 1999). Recent work has suggested that genotype at the

57 major histocompatibility complex (MHC) can be discerned through facial shape,

58 providing a pathway for assortative mating at the genetic level (Roberts et al., 2005;

59 Roberts and Little, 2008). In addition, a preference for own-phenotype resemblance

60 could provide direct benefits, by enhancing trusting relationships within a partnership

61 (DeBruine, 2002, 2005; DeBruine et al., 2008; Krupp et al., 2008), or leading women to

62 seek out supportive kin during pregnancy (DeBruine et al., 2005; DeBruine et al., 2008;

63 Jones et al., 2008).

64 The present study examines the interaction between cues of absolute and relative

65 mate quality on human mating preferences. Sixty Caucasian women rated men's faces

66 that had been manipulated simultaneously to represent two levels (masculinized and

6

67 feminized) of sexual dimorphism (absolute quality) and two levels (self-similar and self-

68 dissimilar) of self-similarity (relative quality) for both short-term and long-term

69 relationships.

70

71 METHODS

72 All stimuli images were created on the basis of neutral-expression photographs taken

73 under standardized lighting conditions of white individuals aged 18 - 25 with no

74 spectacles or beards. Photographs were standardized in size with reference to pupil

75 position, and manually marked around the main features (e.g. eyes, nose and mouth)

76 and the outline of each face (e.g. jawline and hairline) using dedicated software

77 (Tiddeman et al., 2001). Twenty-four photographs of men were grouped into sets of

78 four images. For each set of four images, the average location of each point in each

79 face was calculated, and the faces of each group were morphed to this average shape.

80 Next, the four images in each group were superimposed to produce a photographic-

81 quality composite image. This technique has been used to create composite images in

82 previous studies (see Benson and Perrett, 1993; Tiddeman et al., 2001; Little and

83 Hancock, 2002). These six composite images were used as the base faces for the

84 stimuli.

85 Sixty Caucasian women aged 16 – 39 (mean ± SD = 23 ± 5 yrs) were recruited from

86 amongst university students and social contacts for a study on perceptions of

87 attractiveness; participants were not told the specific study hypotheses. Half of the

7

88 women were users of hormonal contraceptives and half were normally-cycling. Each

89 was photographed directly facing the camera with a neutral expression.

90 A unique set of 24 male facial stimuli was created for each rater. Sexual dimorphism

91 was transformed on the basis of two composite images, one derived from 50

92 symmetrized male photographs and one from 50 symmetrized female photographs.

93 The linear shape difference between the two composites was used to create two new

94 images from each of the six base faces. One image was transformed 50% towards the

95 female composite shape, and the other was transformed 50% towards the male

96 composite shape, following previous methods (see Benson and Perrett, 1991; Perrett

97 et al., 1998; Tiddeman et al., 2001). Image colors were not changed from the originals.

98 The transform thus gave rise to 12 images, composed of two images (one feminized

99 and one masculinized) for each of the six base faces.

100 Following previous methodology (Penton-Voak et al., 1999b; DeBruine, 2002, 2004),

101 facial self-similarity was manipulated using the linear shape difference between

102 feature points in the shape composite of 50 symmetrized female photographs against

103 each participant's own particular shape. Two new images were created from each of

104 the 12 images described above. One image was created by transforming the shape

105 25% towards the participant's own particular shape. The other image was created by

106 transforming the shape 25% towards the female composite image. Since the

107 participant's image may be more or less feminine than average, this self-similarity

108 transformation does not have systematic effects on facial sexual dimorphism. This

109 transform was applied uniquely to the 12 faces described above for each participant.

110   The final stimuli then constituted 24 faces for each female: six base faces by two levels

111   of sexual dimorphism (feminized and masculinized) by two levels of self-similarity (self-

112   dissimilar and self-similar) (see supplementary data, diagram 1). Images were masked

113   on the outline of the face so that hair and clothing cues were not visible. Image colors

114   were not changed from the originals.

115   A transform of 50% sexual dimorphism was chosen so the images were still

116   perceptually male when feminized, and because this size of transform has been used in

117   many previous studies of the effects of sexual dimorphism on face preference and is

118   known to affect judgments of attractiveness (Perrett et al., 1998; Penton-Voak et al.,

119   1999a). A transform of 25% self-similarity was chosen in the aim of creating

120   approximate perceptual equivalence with the 50% sexual dimorphism manipulation.

121   There is more possible variability in the face shape of any one individual compared

122   with the possible variability in the face shape of an average male or average female,

123   meaning that a 50% transform towards or away from self-similarity could result in

124   greater differences than a 50% transform along a sexual dimorphism continuum. These

125   manipulations are demonstrated in the supplementary data, diagram 2.

126   Each woman rated the attractiveness of her unique set of face stimuli separately for

127   short-term and long-term relationships. Women were told that a short-term

128   relationship might include a date or holiday romance, and a long-term relationship

129   might include marriage or shared parenting. Ratings were provided on a 7-point scale

130   anchored by the verbal descriptors 'unattractive' and 'very attractive'. Images were

131   presented in a random order. Four of the women were unavailable to come to the

132   laboratory and carried out ratings online; the remainder carried out the ratings at the

133   laboratory. Following the collection of ratings, women were interviewed regarding

134   their conception of the study hypotheses. Around a third of the participants suggested

135   that the faces were used to investigate responses to face manipulations, including size,

136   shape and masculinity manipulations. No-one suggested that the faces had been

137   manipulated to resemble the rater.

138   If the study population were systematically more or less attractive than the population

139   used to create the base faces, then this could systematically bias ratings towards or

140   away from the self-similar faces. To test this, 20 independent female raters rated the

141   attractiveness of the six composite faces that had been manipulated 25% towards or

142   25% away from an average face made from the study population. There were no

143   significant difference between the mean ratings of the six faces manipulated 25%

144   towards compared with those manipulated 25% away (paired samples t-tests; short

145   term relationship ratings: $t_{19} = 0.27$, $p = .790$; long term relationship ratings: $t_{19} = .32$, p

146    $= .756$).

147   Analysis was carried out in SPSS 15.0.

148   RESULTS

149

150   Repeated-measures ANOVA (2 x relationship term, 2 x sexual dimorphism, 2 x self-

151   similarity) revealed significant main effects of sexual dimorphism and self-similarity,

152   reflecting that masculinized faces were rated significantly more attractive than

153   feminized faces ($F_{1,59} = 19.39$, $p < .001$; $r = .50$) and that self-similar faces were rated

154 significantly more attractive than self-dissimilar ($F_{1,59}$ = 4.50, p = .038; r = .27).

155 However, these significant main effects were modified by two significant interactions.

156 First, there was an interaction between relationship term and self-similarity ratings

157 ($F_{1,59}$ = 4.48, p = .039) (Figure 1). Among self-dissimilar faces (2 x relationship term, 2 x

158 sexual dimorphism), relationship term was not significant ($F_{1,59}$ = .08, p = .784), while

159 among self-similar faces, there was a non-significant trend for faces to be given higher

160 ratings in the short-term compared with long-term context ($F_{1,59}$ = 3.43, p = .069).

161 There was no significant effect of self-similarity in long-term relationship ratings (2 x

162 sexual dimorphism, 2 x self-similarity; $F_{1,59}$ = .26, p = .615), while in short-term

163 relationship ratings self-similar faces were rated significantly more attractive than self-

164 dissimilar ($F_{1,59}$ = 6.90, p = .011).
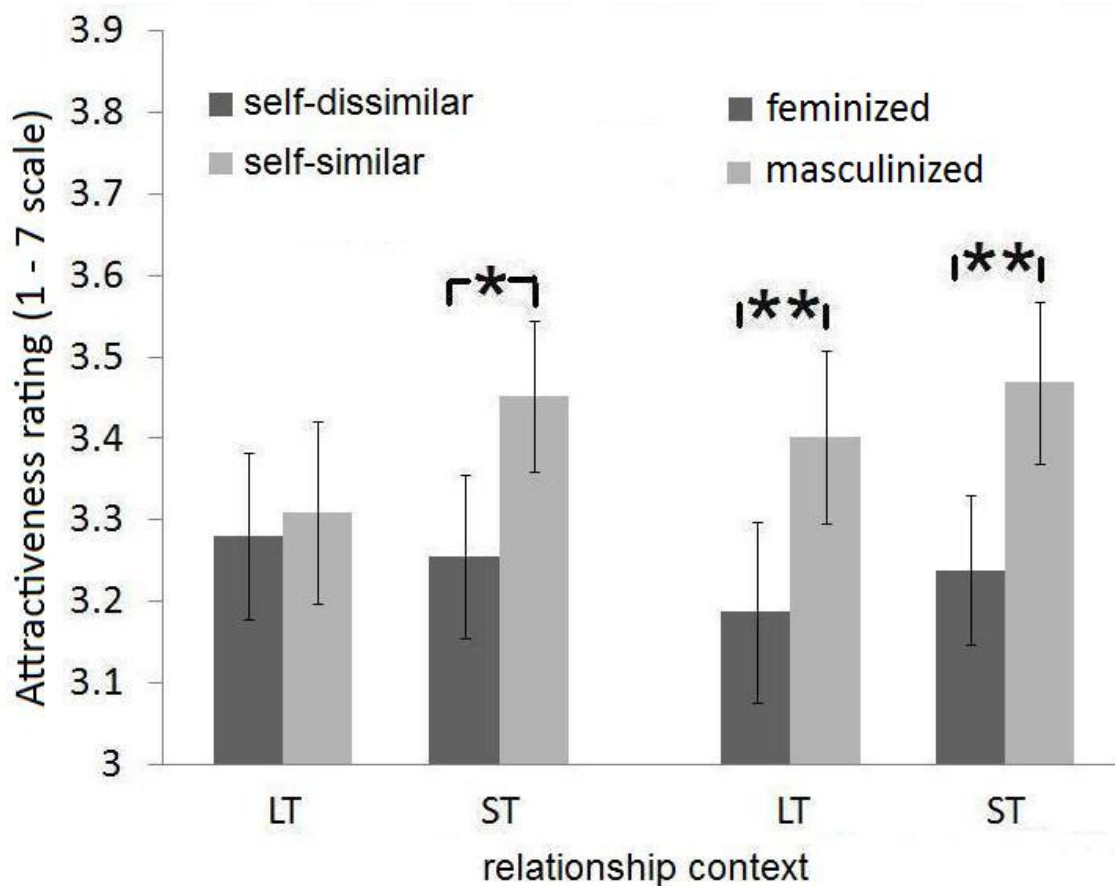
165
166 Figure 1. The effects of self-similarity and sexual dimorphism for short-term (ST) and

167 long-term (LT) relationship ratings. Bars = mean rating ± SE; * $p < .05$, ** $p < .01$

168

169 Second, there was a significant interaction between sexual dimorphism and self-

170 similarity ($F_{1,59} = 8.86$, $p = .004$) (Figure 2). Masculinized faces were rated significantly

171 more attractive than feminized faces in both self-dissimilar ($F_{1,59} = 4.52$, $p = .038$) and

172 self-similar faces ($F_{1,59} = 26.67$, $p < .001$). However, self-similarity was rated

173 significantly more attractive amongst masculinized faces ($F_{1,59} = 9.87$, $p = .003$) but

174 not amongst feminized faces ($F_{1,59} = .07$, $p = .800$).
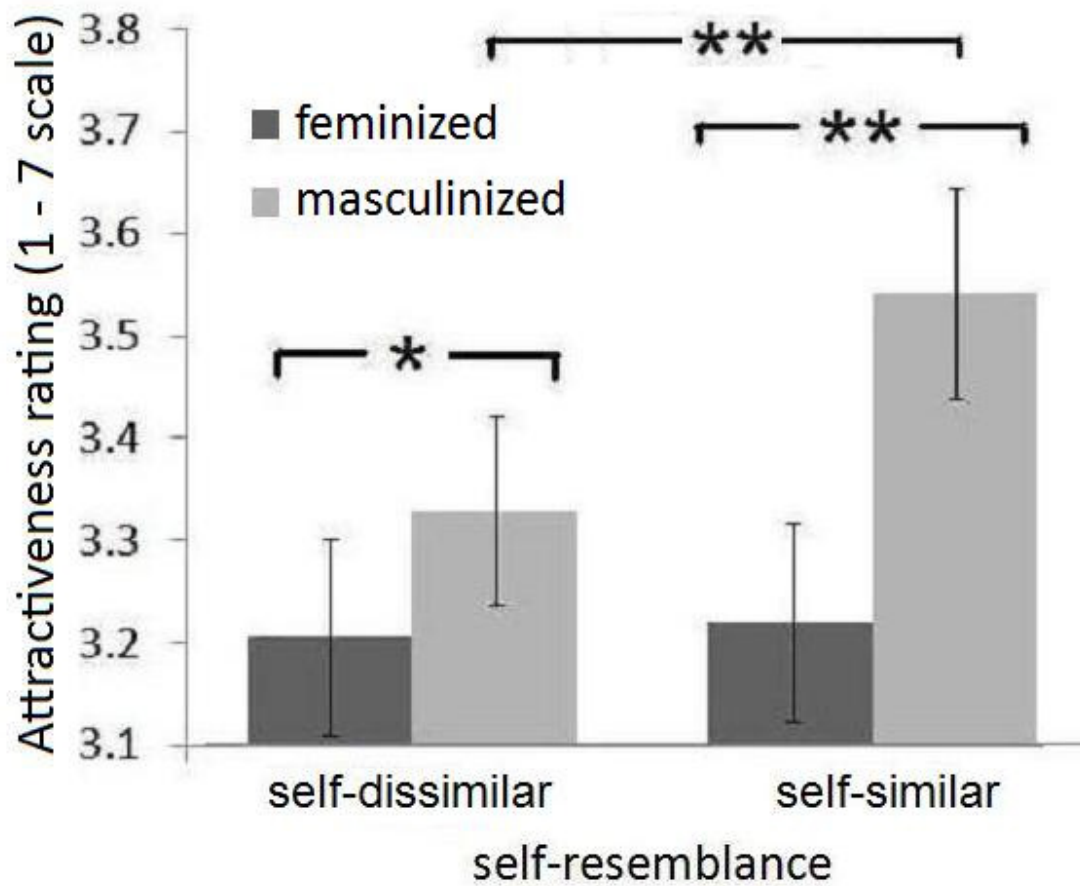
175

176 Figure 2. The effects of sexual dimorphism for each level of self-similarity (left panel)

177 and the effects of self-similarity for each level of sexual dimorphism (right panel),

178 collapsing together short-term and long-term relationship ratings. Bars = mean rating

179 ± SE; * $p < .05$, ** $p < .01$

180

181 There was no interaction between relationship term and sexual dimorphism ($F_{1,59}$ =

182 .03, $p = .861$).

183 DISCUSSION

13

184   The women rated masculinized faces as more attractive than feminized faces, and self-

185   similar faces as more attractive than self-dissimilar faces. Absolute quality (sexual

186   dimorphism) had greater influence on ratings than relative quality (self-similarity). This

187   was apparent from a comparison of the effect sizes, the statistical significance of the

188   effects, and also in the consistency of effects across relationship contexts and across

189   levels of self-similarity or sexual dimorphism.

190   The findings support predictions by Mays and Hill (2004) for a hierarchical, nested rule

191   underlying preference trade-offs. That is, our results suggest that the faces were first

192   assessed for their absolute quality (their masculinity); only faces which were high in

193   absolute quality (i.e. masculinized faces) were evaluated for relative quality (self-

194   similarity). Masculinized faces were always rated more attractive than feminized faces;

195   in contrast, self-similarity only significantly increased ratings of attractiveness in

196   masculinized and not feminized faces (Figure 2). These findings reflect results in mice,

197   where females prefer to mate with high-status males as determined by androgen-

198   dependent urinary odor cues (i.e. absolute quality), and only base their choices on a

199   relative scale, MHC dissimilarity, when there is very little variation in the genetic

200   quality of the males, or when there is large variation between the males in the extent

201   of their MHC dissimilarity (Roberts and Gosling, 2003).

202   The interaction between masculinity and self-similarity also has a possible bearing

203   upon human mate choice strategies. It has been argued that masculine men may not

204   be a viable partner option for most women because they are highly sought after (Little

205   et al., 2001; Penton-Voak et al., 2003; Scott et al., 2008). Yet where both partners have

206   a vested interest in a relationship (for example, by resemblance to each other), this

207   may limit the marketplace, and open up opportunity for women of lower quality to

208   partner more masculine men. Alternatively, or in addition, when faces are perceived as

209   attractive (here, because they are masculinized), self-similarity may become more

210   important. Further, masculinized faces that are usually avoided on the basis that they

211   are associated with negative personality traits such as dishonesty (Perrett et al., 1998)

212   may become attractive with increased self-similarity due to the pro-social traits

213   attributed to a self-similar face (review in DeBruine et al., 2008) including, in particular,

214   trustworthiness (DeBruine, 2002, 2005).

215   It has been noted previously that the use of cues of both absolute and relative mate

216   quality in mate choice may constitute a mechanism to maintain variance in mate

217   choice relevant traits, even in the presence of directional selection (Roberts and

218   Gosling, 2003; Neff and Pitcher, 2005). In humans, although greater emphasis appears

219   to be placed on masculinity than self-similarity in judgments of attractiveness, the

220   combinative effect of self-similarity and masculinity that we demonstrate would likely

221   help to maintain variance in relative levels of facial masculinity.

222   The finding that self-similarity did not increase ratings of attractiveness in feminized

223   faces might help explain the discrepancy with previous findings that manipulated self-

224   resemblance has a neutral or non-significant positive effect on attractiveness ratings

225   where facial masculinity was not simultaneously manipulated (Penton-Voak et al.,

226   1999b; DeBruine, 2005). It should be noted that there was some discrepancy between

227   the preferences of our raters and raters in previous studies. Our raters did not exhibit

228   the preference for masculinity in the context of short-term relationships compared

229   with long-term relationships that has been demonstrated previously (Little et al., 2002;

230   Penton-Voak et al., 2003).

231   Mating context (short-term or long-term relationships) also affected evaluations of

232   attractiveness, with self-similarity significantly increasing ratings of attractiveness in

233   short-term but not long-term relationships (Figure 1). Our findings contrast with

234   previous findings that self-similarity is aversive in ratings of facial attractiveness in a

235   short-term relationship context (DeBruine, 2005), or at the high-fertility phase of the

236   menstrual cycle (DeBruine et al., 2005), both contexts when genetic quality is thought

237   to be privileged (Roberts and Little, 2008). Reasons for the discrepancy could be due to

238   our simultaneous manipulations of masculinity, or to differences in the rating

239   procedure or degree of facial manipulation. The current study used manipulations of

240   25% self-similarity, whereas previous work has manipulated faces to greater degrees

241   of self-similarity. Our participants gave higher ratings to 25% self-similarity than 25%

242   self-dissimilarity, suggestive of a preference for subtle resemblance and consistent

243   with optimal outbreeding (Bateson, 1978, 1980, 1982). Previous work suggests that

244   there is an asymptotic rather than linear function of own-phenotype resemblance on

245   attractiveness ratings (Penton-Voak et al., 1999b). Our manipulation of 25% self-

246   similarity was chosen to create approximate perceptual equivalence in the difference

247   between high and low self-similarity compared with the difference between feminized

248   and masculinized faces (see Methods, and supplementary data diagram 2). However,

249   the greater effect size of the masculinity manipulation may suggest that the sexually

250   dimorphic transforms were more salient. Future work might look to investigate the

251   impact of different proportions of self-similarity, and also the effect of individual

252   differences amongst the raters on the interaction between sexual dimorphism and

253   self-similarity manipulations.

254   In sum, our results constitute the first examination of the trade-offs of absolute and

255   relative quality in human preferences, and as such provide insights into the dynamics

256   underlying the mate choice process. Overall these data demonstrate a sophisticated

257   system of preferences, whereby absolute and relative quality is assessed in faces, and

258   which may simultaneously allow for selection of good genes and the promotion of

259   optimal outbreeding.

269   REFERENCES

270

271   Bailenson JN, Garland P, Iyengar S, Yee N. 2006. Transformed facial similarity as a

272   political cue: A preliminary investigation. Polit Psychol. 27:373-385.

273   Bateson P. 1978. Sexual imprinting and optimal outbreeding. Nature. 273:659 - 660.

274   Bateson P. 1980. Optimal outbreeding and the development of sexual preferences in

275   Japanese quail. Z Tierpsychol. 53.

276   Bateson P. 1982. Preferences for cousins in Japanese quail. Nature. 295:236 - 237.

277   Benson PJ, Perrett DI. 1991. Synthesizing continuous-tone caricatures. Image Vision

278   Comput. 9:123-129.

279   Benson PJ, Perrett DI. 1993. Extracting prototypical facial images from exemplars.

280   Perception. 22:257-262.

281   Bereczkei T, Gyuris P, Koves P, Bernath L. 2002. Homogamy, genetic similarity, and

282   imprinting; parental influence on mate choice preferences. Pers Indiv Differ.

283   33:677-690.

284   Bereczkei T, Gyuris P, Weisfeld GE. 2004. Sexual imprinting in human mate choice. Proc

285   Biol Sci. 271:1129-1134.

286   Colegrave N, Kotiaho JS, Tomkins JL. 2002. Mate choice or polyandry: reconciling

287   genetic compatibility and good genes sexual selection. Evol Ecol Res. 4:911-917.

288   DeBruine LM. 2002. Facial resemblance enhances trust. Proc Biol Sci. 269:1307-1312.

289   DeBruine LM. 2004. Facial resemblance increases the attractiveness of same-sex faces

290   more than other-sex faces. Proc Biol Sci. 271:2085-2090.

291   DeBruine LM. 2005. Trustworthy but not lust-worthy: context-specific effects of facial

292   resemblance. Proc Biol Sci. 272:919-922.

293   DeBruine LM, Jones BC, Little AC, Perrett DI. 2008. Social perception of facial

294   resemblance in humans. Arch Sex Behav. 37:64-77.

295   DeBruine LM, Jones BC, Perrett DI. 2005. Women's attractiveness judgments of self-

296   resembling faces change across the menstrual cycle. Horm Behav. 47:379.

297   Epstein E, Guttman R. 1982. Mate selection in man: Evidence, theory, and outcome.

298   Soc Biol. 31:243-276.

299   Folstad I, Karter AJ. 1992. Parasites, bright males, and the immunocompetence

300   handicap. Am Nat. 139:603-622.

301   Gangestad SW, Simpson JA. 2000. The evolution of human mating: Trade-offs and

302   strategic pluralism. Behav Brain Sci. 23:573-644.

303   Griffiths RW, Kunz PR. 1973. Assortative mating: a study of physiognomic homogamy.

304   Soc Biol. 20:448-453.

305   Hamilton WD, Zuk M. 1982. Heritable true fitness and bright birds: a role for parasites?

306   Science. 218:384-387.

307   Jones BC, DeBruine LM, Perrett DI, Little AC, Feinberg DR, Law Smith MJ. 2008. Effects

308   of menstrual cycle phase on face preferences. Arch Sex Behav. 37:78-84.

309   Krupp DB, Debruine LM, Barclay P. 2008. A cue of kinship promotes cooperation for

310   the public good. Evol Hum Behav. 29:49-55.

311   Little AC, Burt DM, Penton-Voak IS, Perrett DI. 2001. Self-perceived attractiveness

312   influences human female preferences for sexual dimorphism and symmetry in

313   male faces. Proc Biol Sci. 268:39-44.

314   Little AC, Burt DM, Perrett DI. 2006. Assortative mating for perceived facial personality

315   traits. Pers Indiv Differ. 40:973-984.

316   Little AC, Hancock PJ. 2002. The role of masculinity and distinctiveness on the

317   perception of attractiveness in human male faces. Br J Psychol. 93:451-464.

318   Little AC, Jones BC, Penton-Voak IS, Burt DM, Perrett DI. 2002. Partnership status and

319   the temporal context of relationships influence human female preferences for

320   sexual dimorphism in male face shape. Proc Biol Sci. 269:1095-1100.

321   Little AC, Jones BC, Waitt C, Tiddeman BP, Feinberg DR, Perrett DI, Apicella CL,

322   Marlowe FW. 2008. Symmetry is related to sexual dimorphism in faces: Data

323   across culture and species. PLoS ONE. 3:e2106.

324   Little AC, Penton-Voak IS, Burt DM, Perrett DI. 2003. Investigating an imprinting-like

325   phenomenon in humans: Partners and opposite-sex parents have similar hair

326   and eye colour. Evol Hum Behav. 24:43.

327   Maynard Smith J. 1985. Mini review: Sexual selection, handicaps and true fitness. J

328   Theor Biol. 115:1-8.

329   Mays HLJ, Hill GE. 2004. Choosing mates: good genes versus genes that are a good fit.

330   Trends Ecol Evol. 19:554-559.

331   Neff BD, Pitcher TE. 2005. Genetic quality and sexual selection: an integrated

332   framework for good genes and compatible genes. Mol Ecol. 14:19-38.

333   Penton-Voak IS, Chen JY. 2004. High salivary testosterone is linked to masculine male

334   facial appearance in humans. Evol Hum Behav. 25:229-241.

335   Penton-Voak IS, Little AC, Jones BC, Burt DM, Tiddeman BP, Perrett DI. 2003. Female

336   condition influences preferences for sexual dimorphism in faces of male

337   humans (*Homo sapiens*). J Comp Psychol. 117:264-271.

338   Penton-Voak IS, Perrett DI, Castles DL, Kobayashi T, Burt DM, Murray LK, Minamisawa

339   R. 1999a. Menstrual cycle alters face preference. Nature. 399:741-742.

340   Penton-Voak IS, Perrett DI, Peirce JW. 1999b. Computer graphic studies of the role of

341   facial similarity in judgements of attractiveness. Current Psychology:

342   Developmental Learning Personality. 18:104-117.

343   Perrett DI, Lee KJ, Penton-Voak IS, Rowland D, Yoshikawa S, Burt DM, Henzi SP, Castles

344   DL, Akamatsu S. 1998. Effects of sexual dimorphism on facial attractiveness.

345   Nature. 394:884-887.

346   Potts WK, Wakeland EK. 1993. Evolution of MHC genetic diversity - a tale of incest,

347   pestilence and sexual preference. Trends Genet. 9:408-412.

348   Read AF, Harvey PH, 1991. Genetic relatedness and the evolution of animal mating

349   patterns. In: Mascie-Taylor CG, Boyce AJ, eds. Human Mating Patterns Oxford:

350   Oxford University Press.p. 115-131.

351   Rhodes G, Chan J, Zebrowitz LA, Simmons LW. 2003. Does sexual dimorphism in human

352   faces signal health? Biol Lett. 270:S93–S95.

353   Rhodes G, Yoshikawa S, Palermo R, Simmons LW, Peters M, Lee K, Halberstadt J,

354   Crawford JR. 2007. Perceived health contributes to the attractiveness of facial

355   symmetry, averageness, and sexual dimorphism. Perception. 36:1244-1252.

356   Roberts SC, Gosling LM. 2003. Genetic similarity and quality interact in mate choice

357   decisions by female mice. Nat Genet. 35:103-106.

358   Roberts SC, Little AC. 2008. Good genes, complementary genes and human mate

359   choice. Genetica. 132:309-321.

360   Roberts SC, Little AC, Gosling LM, Jones BC, Perrett DI, Carter V, Petrie M. 2005. MHC-

361   assortative facial preferences in humans. Biol Lett. 1:400-403.

362   Rushton PJ. 1988. Genetic similarity, mate choice, and fecundity in humans. Ethol

363   Sociobiol. 9:329-333.

364   Scott I, Swami V, Josephson SC, Penton-Voak IS. 2008. Context-dependent preferences

365   for facial dimorphism in a rural Malaysian population. Evol Hum Behav. 29:289-

366   296.

367   Thiessen D, 1999. Social influences on assortative mating. In: Corballis MC, Lea SG, eds.

368   The Descent of Mind: Psychological perspectives on hominid evolution Oxford:

369   Oxford University Press.p. 311-323.

370   Thiessen D, Gregg B. 1980. Human assortative mating and genetic equilibrium: an

371   evolutionary perspective. Ethol Sociobiol. 1:111-140.

372   Thornhill R, Gangestad SW. 2006. Facial sexual dimorphism, developmental stability,

373   and susceptibility to disease in men and women. Evol Hum Behav. 27:131-144.

374   Tiddeman B, Burt DM, Perrett D. 2001. Computer graphics in facial perception

375   research. IEEE Comput Graph. 21:42-50.

376   Zahavi A. 1975. Mate selection – a selection for a handicap. J Theor Biol. 53:205-214.

377   Zahavi A. 1977. The cost of honesty. J Theor Biol. 67:603-605.

378   Zajonc RB, Adelmann PK, Murphy ST, Niedenthal PM. 1987. Convergence in the

379   physical appearance of spouses. Motiv Emotion. 11:335-346.

380