ARTICLE IN PRESS

ENS-05506; No of Pages 8



Evolution and Human Behavior xx (2008) xxx-xxx

Evolution and Human Behavior

Correlated preferences for men's facial and vocal masculinity

David R. Feinberg^{a,*}, Lisa M. DeBruine^b, Benedict C. Jones^b, Anthony C. Little^c

^aDepartment of Psychology, Neuroscience, and Behaviour, McMaster University, Canada ^bSchool of Psychology, University of Aberdeen, UK ^cSchool of Psychology, Stirling University, UK

Initial receipt 8 June 2007; final revision received 21 December 2007

Abstract

Previous studies have reported variation in women's preferences for masculinity in men's faces and voices. Women show consistent general preferences for vocal masculinity, but highly variable general preferences for facial masculinity. Within individuals, men with attractive voices tend to have attractive faces, suggesting common information may be conveyed by these cues. Here we tested whether men and women with particularly strong preferences for male vocal masculinity also have stronger preferences for male facial masculinity. We found that masculinity preferences were positively correlated across modalities. We also investigated potential influences on these relationships between face and voice preferences. Women using oral contraceptives showed weaker facial and vocal masculinity preferences and weaker associations between masculinity preferences across modalities than women not using oral contraceptives. Collectively, these results suggest that men's faces and voices may reveal common information about the masculinity of the sender, and that these multiple quality cues could be used in conjunction by the perceiver in order to determine the overall quality of individuals.

© 2008 Published by Elsevier Inc.

Keywords: Face; Voice; Femininity; Hormonal contraceptive; Birth control; Pill

21

22

23

24

25

26

27

28

29

30

31

32 33

34

35

36

37

9

10

11

12

13

14

15

16

17

18 19

20

1. Introduction

Among humans, face, voice, and body attractiveness are influenced by their degree of masculinity or femininity (DeBruine et al., 2006; Fan, Dai, Liu, & Wu, 2005; Fan, Liu, Wu, & Dai, 2004; Feinberg, DeBruine, Jones, & Perrett, in press; Feinberg et al., 2006b; Feinberg, Jones, Little, Burt, & Perrett, 2005b; Perrett et al., 1998; Rhodes, Hickford, & Jeffery, 2000). In turn, it has been demonstrated that sex hormones (primarily testosterone, progesterone, and estrogen) are related to the degree of masculinity and femininity displayed by men's and women's faces (Law-Smith et al., 2006: Penton-Voak & Chen. 2004: Roney, Hanson, Durante. & Maestripieri, 2006), voices (Abitbol, Abitbol, & Abitbol, 1999; Alonso & Rosenfield, 2002; Brukert, Lienard, Lacroix, Kreutzer, & Laboucher, 2006; Dabbs & Mallinger 1999; Feinberg, Jones DeBruine, et al., 2006), and bodies (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). It is likely that males displaying testosterone-dependent traits 39 to a greater degree can afford to produce such traits despite 40 the immunosuppressive effects (Folstad & Karter, 1992; 41 Thornhill & Gangestad, 1999), antisocial behavior (Archer, 42 Birring, & Wu, 1998; Book, Starzyk, & Quinsey, 2001; 43 Gonzalez-Bono et al., 1999; O'Connor, Archer, & Wu, 2004; 44 Rowe, Maughan, Worthman, Costello, & Angold, 2004; 45 Studer, Aylwin, & Reddon, 2005; Tremblay et al., 1998), and 46 tendency to take risks (Archer, 1999; Booth et al., 1999) that 47 are thought to be associated with high testosterone levels. 48 Thus, facial and vocal masculinity may be considered cues of 49 costly testosterone levels. Furthermore, men in a natural- 50 fertility population with low voice pitch have higher 51 reproductive success than men with relatively high voice 52 pitch do (Apicella et al. In Press).

There is substantial evidence that people who are 54 attractive in one domain (e.g., face, voice, or body) are 55 also attractive in other domains (Collins & Missing, 2003; 56 Feinberg, Jones, DeBruine et al., 2005; Hughes, Dispenza, 57 & Gallup, 2004; Saxton, Caryl, & Roberts, 2006; Thornhill 58 & Grammer, 1999). Indeed both men's (Saxton et al., 59 2006) and women's (Collins & Missing, 2003; Feinberg, 60

^{*} Corresponding author. E-mail address: feinberg@mcmaster.ca (D.R. Feinberg).

61

62

63

65

66

67

68

69

70

71

72

73

74

75

76

77

78

79

80

81

82

83

84

85

86

87

88

89

90

91

92

93

94

95

96

97

99

100

101

102

103

104

105

106

107

108

109

110

111

112

113

114

115

116

Jones, DeBruine, et al., 2005) facial attractiveness are positively correlated with the attractiveness of their voices. Both men and women with attractive voices and faces also tend to have attractive body configurations, such as low fluctuating asymmetry (Hughes, Harrison, & Gallup, 2002) in women and a masculine upper-body shape in men (Hughes et al., 2004).

The findings described above suggest that humans display multiple cues to the same underlying quality. However, a few key questions regarding the evolution of multiple quality cues in humans remain unresolved. While many studies show that women have consistent preferences for masculine men's voices across studies (Collins, 2000; Feinberg, Jones, Law-Smith, et al., 2006; Feinberg et al., 2004; Saxton et al., 2006), different studies have yielded preferences in women for masculine (DeBruine et al., 2006; Johnston, Hagel, Franklin, Fink, & Grammer, 2001), average (Cornwell et al., 2004; Swaddle & Reierson, 2002), and feminine (Perrett et al., 1998; Rhodes, Hickford, & Jeffery, 2000) men's faces. It has been suggested that differences in the computer graphic methods that have been used in different studies of preferences for masculinity in men's faces may explain these variable findings for women's face preferences (Penton-Voak & Chen, 2004; Rhodes, 2006; Swaddle & Reierson, 2002). However, studies using the same method to manipulate masculinity in male faces have found different general preferences: DeBruine et al. (2006) reported a general preference for masculinity among women, Cornwell et al. (2004) found that average faces were generally preferred by women to feminized or masculinized versions, and Perrett et al. (1998) reported that women demonstrated strong aversions to masculinity in men's faces. More important, DeBruine et al. (2006) compared the strength of women's preferences for masculine faces using different types of computer graphic methods, finding that women who preferred facial masculinity did so for each type of manipulation.

Given that both male vocal and facial masculinity are influenced by testosterone, and masculinity and femininity affect voice and face attractiveness, why are women's preferences for masculinity in the voice consistently above chance, but women's preferences for masculinity in the face vary considerably more from study to study? Studies have revealed a great deal of individual variation in female preferences for both facial and vocal masculinity. Sources of variation in women's preferences for male vocal masculinity that have been identified to date include relationship context (Puts, 2005), menstrual cycle phase (Feinberg, Jones, Law-Smith, et al., 2006; Puts, 2005), and height (Feinberg, Jone, Little, et al., 2005). Women prefer masculinity more when in the most fertile menstrual cycle phase (Feinberg, Jones, Law-Smith, et al., 2006; Puts, 2005) and when rating voices as potential short-term partners (Puts, 2005). Taller and heavier women also prefer men with voice characteristics rated as more masculine sounding (Feinberg, Jone, Little, et al., 2005). Similar sources of systematic variation in face

preferences have also been found (see Table 1 for an 117 extensive list of studies).

This overlap in sources of individual differences (i.e., 119 menstrual cycle and relationship context) between face and 120 voice is consistent with the hypothesis that preferences for 121 masculinity in men's faces and voices may be concordant, 122 despite variation across studies in women's generalized 123 preferences for male facial masculinity. Indeed, previous 124 studies showing positive associations between the strength 125 of women's preferences for masculinity in men's faces and 126 both putative male pheromones (Cornwell et al., 2004) and 127 the reported masculinity of partnered women's romantic 128 partners (DeBruine et al., 2006) suggest correlated prefer- 129 ences for masculinity in different domains. Nevertheless, 130 while Feinberg, Jones, Law-Smith, et al. (2006) found that 131 women with the lowest average estrogen levels demonstrated 132 the largest cyclic shifts in vocal masculinity preferences, 133 Welling et al. (in press) found that women with the highest 134 Q1 average estrogen levels demonstrated the largest cyclic shifts 135 in facial masculinity preferences (see also Johnston et al., 136 2001, for further evidence that particularly feminine women 137

Table 1 t1.1 Potential sources of variation in women's preferences for male facial masculinity t1.2 Direction of Potential source t1.3relationship of variation in with facial facial masculinity masculinity preference Study preferences Being in a Little et al. (2002) t.1.4committed relationship Rating faces in a t1.5relationship context Little et al. (2002) Short-term t1.6 Long-term t1.7Oral Can mask Little et al. (2002) t1.8masculinity contraceptive use preferences Self-rated Little et al. (2001) t1.9 attractiveness Women's Penton-Voak et al. (2003) t1.10 attractiveness as rated by men Waist-hip ratio Penton-Voak et al. (2003) t1.11 Menstrual-cycle - at nonfertile Frost (1994). t1.12Johnston et al. (2001). phase phases Penton-Voak and Perrett (2000), Penton-Voak et al. (1999) Jones, Little, et al. (2005) t1.13 State progesterone - as progesterone level increases State testosterone Welling et al. (2007) + as testosterone t1.14level increases Second-to-fourth Scarbrough and t1.15digit ratio Johnston (2005) Little et al. (2001) t1.16

Penton-Voak et al. (2004) t1.17

Paternal investment

show larger cyclic shifts in preferences for faces of masculine men).

180

165

166

167

168

170

171

172

173

174

176

177

178

179

180

181

182

183

184

185

187

188

189

190

191

192

193

194

195

196

197

198

199

200

201

202

203

204

205

206

208

210

211

212

213

214

215

216

Since any costs of producing multiple ornaments will outweigh the benefits of redundant ornaments, why would men produce more than one cue to testosterone levels? While both facial and vocal masculinity are influenced by testosterone, neither facial nor vocal masculinity is perfectly correlated with testosterone levels. In other words, each cue also has a degree of error (Candolin, 2003; Møller & Pomiankowski, 1993). Indeed, people can modify their voice pitch (within physiological constraints) and their apparent facial masculinity (e.g., altering brow height; Campbell, Benson, Wallace, Doesbergh, & Coleman, 1999). Thus, it is possible that there remains selection pressure from receivers for senders to produce multiple cues to the same underlying quality in order to (a) more easily detect dishonesty, (b) reduce error in cue perception, or both. Both proximate explanations result in an ultimate effort to evoke a more robust assessment of the sender's overall quality. If multiple quality cues are used by receivers to detect dishonest cues, it may then be an evolutionarily stable strategy (Maynard-Smith, 1976) for senders to produce consistent multiple quality cues. Alternatively, senders' multiple quality cues could merely demonstrate to receivers that they are of such quality that they can spend their resources on more than one ornament if such ornaments themselves are costly.

There is evidence of inconsistencies between generalized vocal and facial masculinity preferences and also inconsistencies in the nature of individual differences in the strength of masculinity preferences. Furthermore, although it has been demonstrated numerous times that people are sending multiple quality cues across visual and vocal domains, it is unknown if these cues are used in a consistent manner. To address these issues, we examined the extent to which the strength of men's and women's preferences for male facial masculinity is associated with the strength of their preferences for male vocal masculinity. As studies have shown that hormonal contraception is associated with a disruption of potentially adaptive facial masculinity preferences (Little, Jones, Penton-Voak, Burt, & Perret, 2002) and a disruption of correlations between preferences for maletypical putative pheromones and facial masculinity preferences (Cornwell et al., 2004), we investigated whether women using hormonal contraceptives have similar face and voice masculinity preferences to those not using hormonal contraceptives. As others have found that relationship status (partnered vs. single) affects facial masculinity preferences (Little et al., 2002), we also investigated the role of relationship status on the association between facial and vocal masculinity preferences.

2. Methods

Protocols were approved by the ethics committee at the School of Psychology, University of Aberdeen (UK).

2.1. Participants

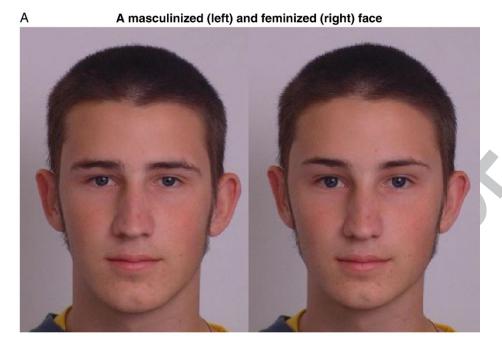
As Internet research on face attractiveness is common- 219 place and produces results similar to those of laboratory 220 studies (Feinberg, Jones DeBruine, et al., 2005; Feinberg 221 et al., in press; Jones et al., in press; Wilson & Daly, 2004), 222 the experiment was run online. Recent research has also 223 demonstrated that Internet-based studies on voice attractive- 224 ness (using voice pitch manipulations of the same strength as 225 used in the current study) reveal preferences that are 226 consistent with laboratory studies, and that the use of varied 227 computer speakers in these studies does not affect the ability 228 to perceive voice attractiveness, femininity, and age in a 229 manner consistent with use of sets of identical, professional- 230 quality headphones (Feinberg et al., in press). Data from 231 repeat user IDs were excluded from analysis (following 232 Kraut et al., 2004). Participants were 1759 people (age range 233 17-40 years; mean age=24.3 years, S.D.=6.042 years; 1213 234 women) recruited from lists of online psychology experi- 235 ments and through the media.

2.2. Stimuli 237

Here we used face stimuli from DeBruine et al. (2006) to 238 test preferences for facial masculinity. These were six male 239 faces that had been masculinized and feminized by changing 240 two-dimensional (2-D) shape by $\pm 50\%$ of the vector shape 241 differences between an average male face and an average 242 female face. This technique is also identical to facial 243 masculinity manipulations used in many other studies of 244 preferences for masculinity in male faces (see DeBruine 245 et al., 2006 , for a review). DeBruine et al. (2006) have 246 previously demonstrated that the versions of these face 247 images with increased masculinity of 2 -D shape are 248 perceived as more masculine and dominant than the versions 249 in which masculinity of 2 -D shape was reduced (see also 250 Welling et al., in press).

To create masculine and feminine voices, six men's 252 voices (spanning the normal range of male voice pitch) 253 were manipulated in pitch (i.e., perception of fundamental 254 frequency and corresponding harmonics) ±20 Hz, using 255 methods identical to those of Feinberg, Jones, Little, et al. 256 (2005). Briefly, Praat's (Boersma & Weenink, 2007) pitch- 257 synchronous overlap add algorithm was applied to the 258 signal to manipulate the fundamental frequency and 259 corresponding harmonics independently of other acoustic 260 features (i.e., formant frequencies) associated with per-261 ceived masculinity (Feinberg, Jones, Little, et al., 2005), 262 These methods have not only been used in several studies 263 of attractiveness and dominance judgments of human voices 264 (Feinberg, Jones, Law-Smith, et al., 2006; Feinberg et al., 265 2005b; Puts, Gaulin, & Verdolini, 2006), but also by several 266 researchers studying the relationship between perceptions of 267 these acoustic manipulations and social behavior in red deer 268 (Reby et al., 2005) and rhesus macagues (Fitch & Fritz, 269 2006; Ghazanfar et al., 2007). See Fig. 1 for illustrations of 270 face and voice stimuli.

D.R. Feinberg et al. / Evolution and Human Behavior xx (2008) xxx-xxx



B Spectrograms of a masculinized (left) and feminized (right) voice 5000 4000 1000 1000 1500 2000 2500 3000 3500 4000 4500

Fig. 1. Masculinized and feminized faces (A) and spectrograms of masculinized and feminized voices (B). Harmonic spacing (distance between the thin horizontal lines) is equal to the fundamental frequency (pitch) of the voice. Thus the voice on the left side of (B) has a lower pitch than the voice on the right side of (B). Note that the formant frequencies (dark bands on the spectrogram) and time (x-axis) do not change when pitch has been manipulated.

2.3. Procedure

273

274

275

276

277

278

279

280

281

282

283

284

285

286

287

288

Voices and faces were presented in separate blocks in random order. Masculine and feminine stimuli were presented in a forced-choice paradigm: Voices were presented side by side and participants chose how much they preferred either voice or face by selecting one of the ratings above the stimulus preferred. Faces were presented in an identical fashion. For voices, both voices were not played simultaneously, but rather, participants pushed play buttons on-screen to hear each voice individually. This method of forced-choice voice presentation has been used in other Internet-based studies of voice attractiveness (Feinberg et al., in press). All orders of stimuli presentation and the side that stimuli were presented on were fully randomized.

Subsets of female raters self-reported whether or not they are currently using hormonal contraceptives or have used hormonal contraceptives within the last 3 months prior to testing (Feinberg, Jones, Law-Smith, et al., 2006; Jones, 289 Perrett, et al., 2005; Welling et al., in press). Participants also 290 reported whether or not they were currently in a romantic 291 relationship (Little et al., 2002). One hundred twelve women 292 reported using hormonal contraceptives.

3. Results 294

For analyses, we calculated the number of trials on 295 which each participant chose the more masculine voice 296 (vocal masculinity preference) and the more masculine face 297 (facial masculinity preference). Poisson-based generalized 298 linear models with log-link functions were used to analyze 299 these data. Using the number of masculine faces or voices 300 chosen (as opposed to rating scale data) controls for the 301 possibility that correlations between facial and vocal 302 masculinity preferences may occur as a result of some 303

4

D.R. Feinberg et al. / Evolution and Human Behavior xx (2008) xxx-xxx

participants being more willing to use the scale end points than other participants.

3.1. Generalized preferences

304 305

306

307

308

309

310

311

312

313

314

315

316

317

318

320

322

323

324

325

326

327

328

329

330

331

332

333

334

335

337

338

339

341

342

343

344

345

346

347

Q2 319

We utilized a generalized linear model to test for general associations among vocal and facial masculinity preferences [dv=facial masculinity preference; factors: sex of rater (male, female); covariates: vocal masculinity preference, age of rater]. The test model was significantly different than the intercept-only model (both $\chi^2_5>141.864$, p<.0001). Analysis of deviance evaluated goodness of fit (both $D_{1754}=1765.204$, D/df=1.006). Vocal masculinity preferences significantly predicted facial masculinity preferences [$\beta=.005$, S.E.=0.024, 0.0001<confidence interval (CI)<0.01; $\chi^2_1=5.194$, p=.023]. No other effects or interactions were significant (all $\chi^2_1<1.114$, p>.291).

A separate generalized linear model [dv=vocal masculinity preference; factor: sex of rater (male, female); covariates: facial masculinity preference and age of rater was significantly different than the intercept-only model $(\chi^2_5=184.621, p<.0001)$. Analysis of deviance evaluated goodness of fit (both D_{1754} =3361.775, D/df=1.917). Facial masculinity preferences significantly predicted vocal masculinity preferences (β =.312, S.E.=0.084, 0.139 < CI < 0.485, $\chi^2_{5} = 12.444$, p < .001). Additionally, women had stronger vocal masculinity preferences in men's voices than men did (β =.825, S.E.=0.1733, 0.485 < CI < 1.165, $\chi^2_5 = 22.669$, p < .001). Facial masculinity preferences predicted vocal masculinity preferences more strongly among men than women ($\beta=-.123$, S.E.=0.0416, -0.204<CI<-0.041, χ^2_{5} =8.669, p=.003). No other effects or interactions were significant (all χ^2 ₁<3.291, all p>.07, which is the nonsignificant main effect of age on vocal masculinity preferences).

One-sample t tests revealed that, for both men and women, vocal and facial masculinity preferences were significantly above 50% (i.e., chance). Table 2 displays these statistics. For both male and female raters, vocal masculinity preferences were positively and significantly correlated with facial masculinity preferences (women: r_{1213} =.246, p<.0001; men: r_{547} =.366, p<.0001). Fisher's r-to-z test revealed a significantly higher correlation between vocal and facial masculinity preferences among men than women (Z=2.57, p=.010).

t2.1 Table 2 t2.2 Generalized face and voice masculinity preferences

Sex of rater	Modality of masculinity preference	T value	Mean % of masculine voices chosen	S.D.	df	p value
Male	Voice	14.52	65.9	25.9	546	<.0001
	Face	12.13	65.1	29.6	546	<.0001
Female	Voice	28.56	69.3	23.6	1212	<.0001
	Face	9.67	58.0	28.6	1212	<.0001

Hormonal contraceptives and masculinity preferences				
Using hormonal	% Masculine stimuli ch	nosen t3.3		
contraceptives	Face	Voice t3.4		

Using hormonal	% Masculine stir	nuli chosen t3.5
contraceptives	Face	Voice t3.4
No	58.33	70.39 t3.5
Yes	54.88	68.21 t3.6

3.2. Potential influencing factors

We created two generalized linear models for women's $_{357}$ ratings (dv's=facial or vocal masculinity preference; hormo- $_{358}$ nal contraceptive use, relationship status; covariates: vocal/ $_{359}$ facial masculinity preference, age of rater). Both models $_{360}$ were significantly different than the intercept-only model $_{361}$ (both $_{\chi}^2$) $_{8}$ >17.01, $_{p}$ <03). Analysis of deviance examined $_{362}$ goodness of fit (both $_{D312}$ <308, $_{D}$ / $_{df}$ <0.99).

We observed an interaction between hormonal contra- 364 ceptive use and the predictive strength of facial mascu- 365 linity preferences on vocal masculinity preferences 366 (β =.005, S.E.=0.024, 0.0001<CI<0.01. χ^2 1=4.277, 367 p=.039) and vice versa (β =.141, S.E.=0.0529, 368 0.38<CI<0.245. χ^2 =7.148, p=.008). In both cases, 369 predictions were stronger among women not using 370 hormonal contraceptives. We also observed a significant 371 main effect of hormonal contraceptive use on facial 372 masculinity preferences (β =-.556, S.E.=0.227, 373 -1.002<CI<-0.110. χ^2 1=5.976, p=.014). Women using 374 hormonal contraceptives had weaker masculinity prefer- 375 ences than women not using hormonal contraceptives. No 376 other effects or interactions were significant (all 377 χ^2 1=1.117, all p >.278).

To further investigate the role of hormonal contraceptives 379 on masculinity preferences, we analyzed the relationship 380 between women's facial and vocal masculinity preferences 381 separately for those women using hormonal contraceptives 382 and those not using hormonal contraceptives. Only those 383 women not using hormonal contraceptives exhibited corre- 384 lated preferences for facial and vocal masculinity (not using 385 hormonal contraceptives: r_{307} =.337, p<.0001; using hormo- 386 nal contraceptives: r_{112} =.112, p=.22). Fisher's r to z test 387 revealed that the positive correlation between facial and 388 vocal masculinity preferences was significantly stronger 389 among women not using hormonal contraceptives than 390 among women using hormonal contraceptives (z=2.134, 391 p=.033). Further analysis revealed that there was no 392 difference in the strength of the relationship between vocal 393 and facial masculinity preferences among women not using 394 hormonal contraceptives and men (z=-0.462, p=.644). 395 Table 3 highlights mean masculinity preferences of women 396 using and not using hormonal contraceptives. 397

3.3. Additional analyses

We repeated our analyses, substituting rating scale data 399 for the forced-choice data analyzed thus far. Rating scale 400 responses were coded using 0 (feminine face or voice rated 401

398

402

404

405

406

407

408

409

410

411

412

413

414

415

416

417

418

419

420

421

422

423

424

425

426

427 428

429

430

431

432

433

434

435

436

437

438

439

440

441

442

443

444

445

446 447

448

449

450

451

452

453

454

much more attractive) to 7 (masculine face or voice rated much more attractive), and the average rated masculinity preference calculated separately for the voice and face preference tests for each participant. Normal-based identity models of 8-point scale data revealed no qualitative differences between the findings for 8-point scale data and forced-choice data.

We also repeated our analyses of forced-choice (percent masculine voices or faces chosen) and 8-point scale data using analysis of covariance (ANCOVA). Findings from these ANCOVA analyses showed no qualitative differences from those of our custom generalized linear models.

4. Discussion

We found that preferences for men's facial and vocal masculinity were positively correlated among both male and female judges. These results are consistent with findings that men with attractive faces also tend to have attractive voices (Saxton et al., 2006). The collective results of these two studies lend support to the theory that women's preferences for vocal and facial masculinity are consistent, most likely because men's faces (Penton-Voak & Chen, 2004) and voices (Brukert et al., 2006; Dabbs & Mallinger, 1999) advertise common information about the senders' testosterone levels. Thus, we suggest that not only do men's faces and voices transmit common information about the underlying quality of the sender (Saxton et al., 2006), but also that perceivers use this cross-modal information in a way that may better inform their mate-choice decisions.

When analyzing general preferences, it appears that women showed a weaker relationship between facial and vocal masculinity preferences than men did. This pattern of results, however, occurred because only women not using hormonal contraceptives exhibited correlated preferences for vocal and facial masculinity. Thus, hormonal contraceptive use appears to mask the relationship between preferences for vocal and facial masculinity. Indeed, there was no significant difference in correlation strength between facial and vocal masculinity preferences among women not using hormonal contraceptives and men. Although it is likely that women's attractiveness ratings of masculinity in voices are matechoice relevant, as they appear only to correlate with facial masculinity preferences after puberty (Saxton et al., 2006), and menstrual cycle shifts in women's preferences for masculinity in voices are specific to men's but not women's voices (Feinberg et al., 2006), some researchers have suggested that men's attractiveness ratings of other men are an index of dominance (Penton-Voak et al., 2003). Future research should investigate the motivations that underpin same-sex attractiveness ratings of faces and voices.

Our findings highlight the importance of investigating preferences for male masculinity while taking into account possible sources of individual differences in preferences such as menstrual cycle phase (Feinberg, Jones, Law-Smith, et al., 2006; Penton-Voak et al., 1999; Puts, 2005), age (Little

et al., 2001; Saxton et al., 2006), and relationship context 456 (Little et al., 2002; Puts, 2005). In the current study, age 457 predicted the strength of women's preferences for vocal 458 masculinity but not the strength of their preferences for facial 459 masculinity (although a near-significant result was 460 observed). Age, however, is still a potential influencing 461 factor for cross-modal masculinity preferences, as age has 462 been found to correlate positively with women's facial 463 masculinity preferences in other studies in a manner 464 consistent with the results of this study (Little et al., 2001). 465 Additionally, menstrual cycle, self-rated attractiveness, and 466 relationship context may contribute to the collective findings 467 reported here.

We found that women not using oral contraceptives had 469 stronger facial and vocal masculinity preferences than 470 women using oral contraceptives. Since progesterone is a 471 major component of most hormonal contraceptives, this 472 finding complements those showing that raised progester- 473 one during the menstrual cycle is associated with increased 474 preferences for feminine faces (Jones et al., 2005; Welling 475 et al., in press) and voices (Puts, 2005). While Feinberg, 476 Jones, Law-Smith, et al. (2006) demonstrated that these 477 associations may be stronger among women with high trait 478 estrogen levels, Welling et al. (in press) recently found that 479 these associations may only emerge in women with 480 relatively high levels of estrogen during the late follicular 481 phase of the cycle (i.e., women with high "trait" estrogen). 482 Johnston et al. (2001) also found evidence for more 483 feminine women (as scored by a questionnaire) exhibit 484 larger menstrual cycle shifts in facial masculinity prefer- 485 ences than masculine women do. Future research should 486 be conducted to further explore these individual differ- 487 ences in the magnitude of cyclic shifts in women's 488 masculinity preference.

We also found that use of hormonal contraceptives was 490 associated with a lack of correlated cross-modal masculinity 491 preferences. This finding is consistent with that of Cornwell 492 et al. (2004) who found that correlated preferences for 493 opposite-sex putative pheromones and facial masculinity 494 were also found among women not using hormonal contra- 495 ceptives but were not found among women using hormonal 496 contraceptives. We exercise caution in interpreting this as 497 hormonal contraceptive use causally disrupting preferences, 498 as we cannot be sure that there were no other factors 499 associated with masculinity preferences that differed 500 between the two groups. For example, Little et al. (2002) 501 reported that their oral-contraceptive-using group attested to 502 having had more previous sexual partners than those not 503 using oral contraceptives.

By focusing our analytic lens on the *perceivers* rather 505 than the *senders*, we have found that preferences for facial 506 and vocal masculinity vary consistently between individuals 507 in a manner suggesting that preferences in the different 508 modalities are yoked. Furthermore, our finding is consistent 509 with data showing concordant preferences between visual 510 and olfactory preferences: individuals' preferences for 511

ARTICLE IN PRESS

D.R. Feinberg et al. / Evolution and Human Behavior xx (2008) xxx-xxx

masculine male faces are positively related to their preferences for male-typical putative pheromones (Cornwell et al., 2004). Thus, it is likely that the human body produces multiple ornaments that are cues to the same underlying quality and that these are used in conjunction by perceivers to assess the overall quality, dominance, or both of the individual in question.

Our findings provide evidence that humans have evolved to use multiple cues of the same mate quality, as has been found in many species (Candolin, 2003; Møller & Pomiankowski, 1993). Other work on humans has determined that men also send multiple correlated cues of mate quality, such as symmetry and masculinity (Gangestad & Thornhill, 2003) and symmetry and visible skin condition (Jones et al., 2004), potentially producing a better overall assessment of generalized mate quality (Johnstone, 1995, 1996). Thus it is likely that humans have evolved different ways of sending and receiving multiple mate-quality cues. Indeed, many seemingly disparate cues display common information about a single trait (Candolin, 2003) or the qualities of multiple traits (Johnstone, 1995, 1996). Both theories need not be mutually exclusive, and can be used in conjunction to provide a clearer picture of the individual's potential fitness.

We encourage future research to examine the extent to which multiple cues of the same qualities are integrated in forming mate preferences, and how individual differences in preferences may mediate or moderate these relationships. Indeed, more work needs to be done to determine if people sending disparate cues of mate quality are treated differently than those sending concordant mate-quality cues.

Acknowledgments

Anthony Little is supported by a Royal Society University Research Fellowship.

References

512

513

514

516

517

518

519

520

521

522

523

524

525

527

529

530

531

533

534

535

536

537

538

539

540

541

542

543

544

545

546

549

550 551

553

554

555 556

557

558

559

560

561 562

563

564 565

566

O4 552

Q3 526

- Abitbol, J., Abitbol, P., & Abitbol, B. (1999). Sex hormones and the female 547 548 voice. Journal of Voice, 13, 424-446.
 - Alonso, L. C., & Rosenfield, R. L. (2002). Oestrogens and puberty. Best Practice & Research Clinical Endocrinology & Metabolism, 16, 13-30.
 - Apicella, C., Feinberg, D., & Marlowe, F. (in press). Voice pitch predicts reproductive success in male hunter-gatherers. Biology Letters.
 - Archer, J. (1999). Risk-taking, fear, dominance, and testosterone. Behavioral and Brain Sciences, 22, 214-215.
 - Archer, J., Birring, S. S., & Wu, F. C. W. (1998). The association between testosterone and aggression among young men: Empirical findings and a meta-analysis. Aggressive Behavior, 24, 411-420.
 - Boersma, P., & Weenink, D. (2007). Praat. http://www.praat.org: SummerInstituteofLinguistics.
 - Book, A. S., Starzyk, K. B., & Quinsey, V. L. (2001). The relationship between testosterone and aggression: A meta-analysis. Aggression and Violent Behavior, 6, 579-599.
 - Booth, A., Johnson, D. R., & Granger, D. A. (1999). Testosterone and men's health. Journal of Behavioral Medicine, 22, 1-19.
 - Brukert, L., Lienard, J., Lacroix, A., Kreutzer, M., & Leboucher, G. (2006). Women use voice parameters to assess men's characteristics. Proceed-

- ings of the Royal Society of London, Series B-Biological Sciences, 273, 567
- Campbell, R., Benson, P. J., Wallace, S. B., Doesbergh, S., & Coleman, M. 569 (1999). More about brows: How poses that change brow position affect 570 perceptions of gender. Perception, 28, 489-504.
- Candolin, U. (2003). The use of multiple cues in mate choice. Biological 572 Reviews, 78, 575-595.
- Collins, S., & Missing, C. (2003). Vocal and visual attractiveness are related 574 in women. Animal Behaviour, 5, 997-1004.
- Collins, S. A. (2000). Men's voices and women's choices. Animal 576 Behaviour, 60, 773-780.
- Cornwell, R. E., Boothroyd, L., Burt, D. M., Feinberg, D. R., Jones, B. C., 578 Little, A. C., et al. (2004). Concordant preferences for opposite-sex 579 signals? Human pheromones and facial characteristics. Proceedings of 580 the Royal Society of London, Series B-Biological Sciences, 271, 581 635 - 640.
- Dabbs, J. M., & Mallinger, A. (1999). High testosterone levels predict low 583 voice pitch among men. Personality and Individual Differences, 27, 584
- DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., 586 Penton-Voak, I. S., et al. (2006). Correlated preferences for facial 587 masculinity and ideal or actual partner's masculinity. Proceedings of the 588 Royal Society of London, Series B, 273, 1355-1360.
- Fan, J., Dai, W., Liu, F., & Wu, J. (2005). Visual perception of male body 590 attractiveness. Proceedings of the Royal Society B-Biological Sciences, 591
- Fan, J., Liu, F., Wu, J., & Dai, W. (2004). Visual perception of female 593 physical attractiveness. Proceedings of the Royal Society of London 594 Series B—Biological Sciences, 271, 347-352.
- Feinberg, D. R., DeBruine, L. M., Jones, B. C., & Perrett, D. I. (in press). 596 The role of femininity and averageness in aesthetic judgements of 597 women's voices. Perception.
- Feinberg, D. R., Jones, B. C., DeBruine, L. M., Law Smith, M. J., 599 Cornwell, R. E., Hiller, S. G., et al. (2006). Maintenance of vocal 600 sexual dimorphism: Adaptive selection against androgyny. 18th 601 Human Behavior and Evolution Society (HBES) Conference. Phila- 602 delphia, PA, USA; 2006.
- Feinberg, D. R., Jones, B. C., Law-Smith, M. J., Moore, F. R., 604 DeBruine, L. M., & Cornwell, R. E., et al. (2006). Menstrual cycle, 605 trait estrogen level, and masculinity preferences in the human voice. 606 Hormones and Behavior, 49, 215-222.
- Feinberg, D. R., Jones, B. C., DeBruine, L. M., Moore, F. R., Law 608 Smith, M. J., & Cornwell, R. E., et al. (2005). The voice and face of 609 woman: One ornament that signals quality? Evolution and Human 610 Behavior, 26, 398-408.
- Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M., & Perrett, D. I. 612 (2005). Manipulations of fundamental and formant frequencies influence 613 the attractiveness of human male voices. Animal Behaviour, 69, 614
- Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M., & Perrett, D. I. 616 (2004). Manipulations of fundamental frequency and formant dispersion 617 influence attractiveness of male voices: Female preferences for 618 testosterone dependent traits in male voices. Fifth International 619 Conference on the Evolution of Language. Leipsig, Germany.
- Fitch, W. T., & Fritz, J. B. (2006). Rhesus macaques spontaneously perceive 621 formants in conspecific vocalizations. Journal of the Acoustical Society 622 of America, 120, 2132-2141.
- Folstad, I., & Karter, A. (1992). Parasites, bright males, and the 624 immunocompetence handicap. American Naturalist, 139, 603-623.
- Frost, P. (1994). Preference for darker faces in photographs at different 626 phases of the menstrual-cycle—Preliminary assessment of evidence for 627 a hormonal relationship. Perceptual and Motor Skills, 79, 507-514.
- Gangestad, S. W., & Thornhill, R. (2003). Facial masculinity and fluctuating 629 asymmetry. Evolution and Human Behavior, 24, 231–241.
- Ghazanfar, A. A., Turesson, H. K., Maier, J. X., van Dinther, R., Patterson, 631 R., & Logothetis, N. K. (2007). Vocal-tract resonances as indexical cues 632 in rhesus monkeys. Current Biology, 17, 425-430.

644

645

646

650

651

656

657

O6 658

659

660 661

662

663 664

665

666

667

668

669

670

671

676

677

678

679

680

681 682

683

688

689 690

691

692

693

694

- Gonzalez-Bono, E., Salvador, A., Serrano, M. A., & Ricarte, J. (1999).
 Testosterone, cortisol, and mood in a sports team competition. *Hormones and Behavior*, 35, 55–62.
- Hughes, S. M., Dispenza, F., & Gallup, G. G. (2004). Ratings of voice
 attractiveness predict sexual behavior and body configuration. *Evolution* and Human Behavior, 25, 295–304.
- Hughes, S. M., Harrison, M. A., & Gallup, G. G. (2002). The sound of
 symmetry—Voice as a marker of developmental instability. *Evolution and Human Behavior*, 23, 173–180.
 - Jasienska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breast and narrow waist indicate high reproductive potential in women. Proceedings of the Royal Society of London, Series B—Biological Sciences, 271, 1213–1217.
- Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001).
 Male facial attractiveness: Evidence for a hormone-mediated adaptive design. Evolution and Human Behavior, 22, 251–267.
 - Johnstone, R. A. (1995). Honest advertisement of multiple qualities using multiple signals. *Journal of Theoretical Biology*, 177, 87–94.
- Johnstone, R. A. (1996). Multiple displays in animal communication:
 Backup signals' and 'multiple messages'. Philosophical Transactions of the Royal Society of London, Series B—Biological Sciences, 351, 329–338.
 - Jones, B., DeBruine, L., Little, A., Conway, C., Welling, L., & Smith, F. (in press). Sensation seeking and men's face preferences. *Evolution and Human Behavior*.
 - Jones, B. C., Little, A. C., Boothroyd, L., DeBruine, L. M., Feinberg, D. R., Law Smith, M. J., et al. (2005). Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Hormones* and Behavior, 48, 283–290.
 - Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L., Cornwell, R. E., Feinberg, D. R., et al. (2005). Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings* of the Royal Society B—Biological Sciences, 272, 347–354.
 - Kraut, R., Olson, J., Banaji, M., Bruckman, A., Cohen, J., & Couper, M. (2004). Psychological research online—Report of board of scientific affairs advisory group on the conduct of research on the Internet. *American Psychologist*, 59, 105–117.
- Law-Smith, M. J., Perrett, D. I., Jones, B. C., Cornwell, R. E., Moore, F. R.,
 Feinberg, D. R., et al. (2006). Facial appearance is a cue to oestrogen
 levels in women. Proceedings of the Royal Society B—Biological
 Sciences, 273, 135–140.
 - Little, A. C., Burt, D. M., Penton-Voak, I. S., & Perrett, D. I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London, Series B—Biological Sciences*, 268, 39–44.
 - Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society London B*, 269, 1095–1100.
- Maynard-Smith, J. (1976). Evolution and the theory of games. Cambridge:
 Cambridge University Press.
- Møller, A. P., & Pomiankowski, A. (1993). Why have birds got multiple
 sexual ornaments? *Behavioral Ecology and Sociobiology*, 32, 167–176.
 - O'Connor, D. B., Archer, J., & Wu, F. C. W. (2004). Effects of testosterone on mood, aggression, and sexual behavior in young men: A doubleblind, placebo-controlled, cross-over study. *Journal of Clinical Endocrinology and Metabolism*, 89, 2837–2845.
 - Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior*, 25, 229–241.
- Penton-Voak, I. S., Jacobson, A., & Trivers, R. (2004). Populational differences in attractiveness judgements of male and female faces:
 Comparing British and Jamaican samples. Evolution and Human Behavior, 25, 355–370.

- Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P., 699
 & Perrett, D. I. (2003). Female condition influences preferences for 700
 sexual dimorphism in faces of male humans (*Homo sapiens*). *Journal of* 701
 Comparative Psychology, 117, 264–271.
- Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces 703 changes cyclically: Further evidence. Evolution and Human Behavior, 704 21, 39–48.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., 706 Murray, L. K., et al. (1999). Menstrual cycle alters face preference. 707 Nature, 399, 741–742.
- Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, 709
 D., et al. (1998). Effects of sexual dimorphism on facial attractiveness. 710
 Nature, 394, 884–887.
- Puts, D. A. (2005). Mating context and menstrual phase affect women's 712 preferences for male voice pitch. Evolution and Human Behavior, 26, 713 388–397.
- Puts, D. A., Gaulin, S. J. C., & Verdolini, K. (2006). Dominance and the 715 evolution of sexual dimorphism in human voice pitch. *Evolution and* 716 *Human Behavior*, 27, 283–296.
- Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., & 718
 Clutton-Brock, T. (2005). Red deer stags use formants as assessment 719
 cues during intrasexual agonistic interactions. Proceedings of the Royal 720
 Society B—Biological Sciences, 272, 941–947.
- Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual* 722 *Review of Psychology*, 57, 199–226.
- Rhodes, G., Hickford, C., & Jeffery, L. (2000). Sex-typicality and 724 attractiveness: Are supermale and superfemale faces super-attractive? 725
 British Journal of Psychology, 91, 125–140.
- Roney, J. R., Hanson, K. N., Durante, K. M., & Maestripieri, D. (2006). 727
 Reading men's faces: women's mate attractiveness judgments track 728
 men's testosterone and interest in infants. *Proceedings of the Royal* 729
 Society B—Biological Sciences, 273, 2169–2175.
- Rowe, R., Maughan, B., Worthman, C. M., Costello, E. J., & Angold, A. 731
 (2004). Testosterone, antisocial behavior, and social dominance in boys: 732
 Pubertal development and biosocial interaction. *Biological Psychiatry*, 733
 55, 546–552.
- Saxton, T. K., Caryl, P. G., & Roberts, S. C. (2006). Vocal and facial 735 attractiveness judgments of children, adolescents and adults: The 736 ontogeny of mate choice. *Ethology*, 112, 1179–1185.
- Scarbrough, P. S., & Johnston, V. S. (2005). Individual differences in 738 women's facial preferences as a function of digit ratio and mental 739 rotation ability. Evolution and Human Behavior, 26, 509–526.
- Studer, L., Aylwin, A., & Reddon, J. (2005). Testosterone, sexual offense 741 recidivism, and treatment effect among adult male sex offenders. Sexual 742 Abuse—A Journal of Research and Treatment, 17, 171–181.
 743
- Swaddle, J. P., & Reierson, G. W. (2002). Testosterone increases perceived 744 dominance but not attractiveness in human males. Proceedings of the 745 Royal Society of London Series B—Biological Sciences, 269, 746 2285–2289.
- Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in* 748 *Cognitive Sciences*, 3, 452–460.
- Thornhill, R., & Grammer, K. (1999). The body and face of woman: One 750 ornament that signals quality? *Evolution and Human Behavior*, 20, 751 105–120.
- Tremblay, R. E., Schaal, B., Boulerice, B., Arseneault, L., Soussignan, R. 753
 G. & Paquette, D., et al (1998). Testosterone, physical aggression, 754
 dominance, and physical development in early adolescence. *Interna-* 755
 tional Journal of Behavioral Development, 22, 753–777.
- Welling, L. L. M., Jones, B. C., DeBruine, L. M., Conway, C. A. L. S., M. J., 757
 Little, A. C., Feinberg, D. R., et al. Raised salivary testosterone in 758
 women is associated with increased attraction to masculine faces. Hor-759
 mones and Behavior, 52, 156–161 [Epub 2007 Apr 24].
- Wilson, M., & Daly, M. (2004). Do pretty women inspire men to discount the 761 future? Proceedings of the Royal Society of London Series B—Biological 762 Sciences 271, S177–S179.

763 764