



Digit ratio (2D:4D) predicts facial, but not voice or body odour, attractiveness in men

Journal:	Proceedings B
Manuscript ID:	RSPB-2011-0544.R1
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Ferdenzi, Camille; University of Geneva, Swiss Center for Affective Sciences Lemaître, Jean-François; Université Lyon 1, Unité Mixte de Recherche 5558, Biométrie et Biologie Evolutive Leongómez, Juan; University of Stirling, Psychology Roberts, S.; University of Stirling, Psychology
Subject:	Behaviour < BIOLOGY, Evolution < BIOLOGY
Keywords:	Mate Choice, Finger Ratio, Testosterone, Face Symmetry, Masculinity
Proceedings B category:	Behavioural Ecology



Digit ratio	predicts	face	attractiveness
Digitiano	predicio.	Juce	and activeness

1	
2	
3	
4	
5	Digit ratio (2D:4D) predicts facial, but not voice or body odour,
6	attractiveness in men
7	
8	
9	
10	Camille Ferdenzi ¹ , Jean-François Lemaître ² , Juan David Leongómez ³
11	and S. Craig Roberts ³
12	
13	¹ Swiss Centre for Affective Sciences, University of Geneva, 7 rue des Battoirs, 1205
14	Geneva, Switzerland. camille.ferdenzi@unige.ch
15	² Unité Mixte de Recherche 5558, Biométrie et Biologie Evolutive, Université Lyon 1, 43
16	Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France. jean-
17	francois.lemaitre@univ-lyon1.fr
18	³ University of Stirling, Stirling FK9 4LA, Scotland, United Kingdom.
19	j.d.leongomezpena@stir.ac.uk and craig.roberts@stir.ac.uk
20	

21	
22	
23	Abstract
24	
25	There is growing evidence that human second-to-fourth digit ratio, or 2D:4D, is related
26	to facial features involved in attractiveness, certainly mediated by <i>in utero</i> hormonal effects.
27	The present study extends the investigation to other phenotypic, hormone-related,
28	determinants of human attractiveness: voice and body odour. Pictures of faces with a neutral
29	expression, recordings of voices pronouncing vowels, and axillary odour samples captured on
30	cotton pads worn for 24 hours, were provided by 49 adult male donors. These stimuli were
31	rated on attractiveness and masculinity scales by two groups of 49 and 35 females,
32	approximately half of these in each sample using hormonal contraception. Multivariate
33	regression analyses showed that males' lower (more masculine) right 2D:4D ratio and lower
34	right minus left 2D:4D (Dr-l) were associated with a more attractive, and in some cases more
35	symmetrical, but not more masculine face. However, 2D:4D and Dr-l did not predict voice
36	and body odour masculinity or attractiveness. The results were interpreted in terms of
37	differential effects of prenatal and circulating testosterone, male facial shape being
38	supposedly more dependent on foetal levels (reflected by 2D:4D ratio), whereas body odour
39	and vocal characteristics could be more dependent on variation in adult circulating
40	testosterone levels.
41	
42	
43	Keywords: Mate choice; Finger Ratio; Testosterone; Face Symmetry; Masculinity.
44	

45 **1. INTRODUCTION**

46

The relative length of the second (index) and fourth (ring) fingers, or 2D:4D ratio, is 47 48 sexually dimorphic in several species, with lower 2D:4D ratios for males than females in 49 mammals [1,2], while in birds it appears to be the reverse [3]. Although the precise genetic mechanism explaining this sexual dimorphism is still unclear, there is compelling evidence 50 51 that *in utero* foetal testosterone and foetal estrogen influence 2D:4D ratio in humans [1,4-6]. 52 For example, males suffering from congenital adrenal hyperplasia (CAH), an enzymatic deficiency that entails excessive levels of androgens during the foetal period, have 53 54 particularly low 2D:4D ratio [7]. More generally, men exposed to high levels of prenatal 55 androgens develop low 2D:4D ratio [4,7].

56

57 Androgens such as testosterone are also involved in the development and maintenance of 58 secondary sexual characters and thereby in mate choice [8,9]. Because maintaining a high level of testosterone is costly for males [e.g., 10,11], those that display enhanced sexual 59 60 characters without suffering too much from immunosuppression are considered as high quality males [12]. Therefore, women should ultimately increase their reproductive success 61 62 by choosing mates displaying testosterone-dependent sexual traits [12,13]. In humans, men 63 with higher levels of circulating testosterone have voices with lower fundamental frequency [14] and more masculine faces [15,16], two traits that are preferred by women when they 64 65 become sexually mature (see [17] for voices, and [18] for faces).

66

67 Since the growth of the 4th finger is dependent on the level of prenatal androgen, and 68 since some authors have hypothesized a positive correlation between prenatal and adult 69 testosterone levels [1,19], 2D:4D ratios might correlate negatively with some other

70 testosterone-dependent traits [1]. If these traits such as voices and faces are sexually selected, 71 then measures of 2D:4D should be a good predictor of men's attractiveness. To date, investigations of these putative relationships are scarce and remain principally focused on 72 73 face and body masculinity of men (e.g. [20]) since this trait is testosterone-dependent [16] 74 and preferred by women in a mate choice context [18]. Moreover, results from these studies 75 are conflicting. For example, Neave et al. [20] found a negative correlation between 2D:4D ratios of the left and right hand and the female perception of male facial dominance and 76 masculinity but Koehler et al. [21] failed to repeat these results and found no relationship 77 78 between 2D:4D and body and face masculinity. Furthermore, some authors found a link 79 between 2D:4D and attractiveness [22-24], whereas others did not [20]. 80

To date, studies testing relationships between 2D:4D ratios and sexually selected traits are only focused on men's bodies and faces although there is evidence that women use multiple testosterone-dependent cues to select mates, such as voice [25] and body odour [26,27]. As for faces [15], voice frequency and thus attractiveness are related to the level of salivary testosterone [14]. Similarly, androgen level is likely to influence body odour since steroid compounds of axillary odour such as androstadienone are more present in males [28] and are products of testosterone transformation by underarm bacteria [29,30].

88

In this study, for the first time, we investigated in three sensory modalities involved in human mate choice (voice, body odour and face) whether second-to-fourth digit ratio of left and right hands, and digit ratio difference between the two hands (Dr-l, also related to prenatal testosterone sensitivity [31,32]), can predict men masculinity and attractiveness. We predicted that 2D:4D ratio and Dr-l would be negatively correlated with face, voice and odour masculinity and attractiveness, as evaluated by females. As voice frequency and face

Submitted to Proceedings of the Royal Society B

Digit ratio predicts face attractiveness

95 symmetry influence women preference for men (deeper voices are preferred [33]; more
96 symmetrical faces are more attractive [34,35]), we also measured these two factors and linked
97 them to 2D:4D ratios. Finally, we controlled for the use of hormonal contraceptives by the
98 female raters, since this could alter women preference for various male features such as body
99 odour, face and voice [36,37].

- 101
- 102 **2. METHODS**

103

104 (a) *Participants*

Participants were 49 Caucasian male donors aged between 18 and 33 years old (Mean \pm SD = 22.3 \pm 4.0 yrs), recruited among students of the University of Liverpool. From these, we obtained 2D:4D measures, a voice sample and a facial photograph. Axillary odour samples were collected for 28 of them who were non-smokers, as is standard in odour rating research because of the influence of smoking on body odour quality [38,39].

110 Male axillary odour samples were evaluated by 49 Caucasian female students of the University of Liverpool, aged between 19 and 34 years old (Mean \pm SD = 21.8 \pm 3.2 yrs). Of 111 112 these, 26 reported taking hormone-based contraception (hereafter named 'pill users') and 23 113 were not (hereafter named 'non-pill users'). Each odour sample was rated fresh by nine to ten 114 women during one of five rating sessions at the University of Liverpool, between November 115 2007 and February 2008. Men's faces were judged by 27 of these women (Mean \pm SD = 21.8 ± 3.4 yrs, 14 'pill users', 13 'non-pill users'). Due to experimental constraints, the voices 116 were evaluated later (November and December 2010) by a separate group of female students 117 of the University of Stirling (n = 35, Mean \pm SD = 20.1 \pm 3.5, range: 18 to 34 vrs, 20 'pill 118 119 users', 15 'non-pill users', Caucasian). Although both groups of raters were similar in terms

120	of age, culture (British) and occupation (students), we controlled for consistency of their
121	evaluations. Hence, we asked the voice raters to rate the men's faces, previously rated by the
122	Liverpool group. Rating of both groups were highly consistent for face short-term
123	attractiveness (Intra-class Correlation Coefficient: ICC = 0.944 , $p < 0.001$), long-term
124	attractiveness (ICC = 0.942, $p < 0.001$), masculinity (ICC = 0.923, $p < 0.001$) and symmetry
125	(ICC = 0.889, $p < 0.001$). Therefore, both groups were considered as equivalent. All
126	participants gave their written informed consent, and the study was approved by the
127	Committee on Research Ethics of the University of Liverpool and of the University of
128	Stirling.

129

130 **(b)** *Voice samples*

Participants' voice was recorded on a digital recorder (M-Audio Microtrack 24/96) with 131 132 a cardioid condenser microphone (Technica ATR55 Telemike Shotgun), in a quiet room at about 15 cm from the microphone. Participants were required to recite two sentences of the 133 rainbow passage [40] and the monophthong vowels "eh", "ee", "ah", "oh" and "oo". This 134 135 sequence was then repeated once. Female ratings and measure of voice frequency were 136 performed on the second repetition (when participants are more relaxed) and on the three vowels in middle ("ee", "ah", "oh"; see Supplementary Material 1) to limit intonation 137 138 variations. Voice frequency F_0 was measured with Praat 4.6 (www.praat.org). Voice attractiveness and masculinity ratings were collected on 1-to-7 scales with E-Prime Software 139 140 (2.0, Psychology Software Tools), after equalizing the samples in intensity (in Matlab 7.10) 141 and length (2 sec, in Praat).

142

143 (c) Axillary odour samples

144 Axillary odour samples were collected on cotton pads (9.5 x 6.5 cm, Boots UK Ltd) 145 fastened onto both axillae for 24 hours. Participants were instructed to refrain from eating 146 strong food, drinking alcohol, smoking, doing sport and having sexual intercourse, 2 days before and during odour collection. They were also required to shower with a non-perfumed 147 148 soap before fastening the pads, and not to use any scented products such as perfume or 149 deodorant. Samples were presented fresh to female raters a few hours (range: 2-8 hours) after 150 pads were removed from the armpits. Odour samples were placed in glass flasks, presented in 151 a random order to the raters, and evaluated for attractiveness and masculinity on 9-point 152 scales. The variable used in this study was the average ratings of the right and left side. For 153 more details about the procedure of odour collection and rating, see [38].

154

155 (d) Face samples

156 Full face pictures of the male participants were taken in standardized conditions of light with a Canon Powershot camera. Participants were asked to have a neutral expression and to 157 158 look at the camera without any vertical or horizontal tilt of the head. Distance to the camera 159 was constant and participants wore a dark gown. Images were resampled to 400x480 pixels 160 with resolution 72 dpi. Using Psychomorph 8.4 (Perrett & Tiddeman, University of St 161 Andrews, UK), faces were normalized according to pupils and mouth position, and face 162 symmetry was computed using 7 bilateral points (pupils, outermost and innermost eye 163 corners, leftmost and rightmost points of the nose, mouth corners, cheekbones and jaws; 164 Supplementary Material 2). The asymmetry index was the sum of the vertical and horizontal asymmetry indices. Vertical and horizontal asymmetries were respectively the sum of 165 166 differences in vertical and horizontal locations of each of the seven facial features (see details in [41]). Placement of the points and computation of the asymmetry index were performed 167

168twice, and averaged since the two asymmetry indices were highly consistent (ICC = 0.876,169p < 0.001). Men's faces were presented in random order with a java applet. Female170participants were asked to rate the faces for short-term attractiveness (i.e., considering the171person as a dinner date or holiday romance), long-term attractiveness (i.e., considering the172person as a long-term partner), masculinity and symmetry of the faces on 1-to-7 scales. They173were asked to skip the ratings of the men they knew.

- 174
- 175 (e) *Measures of 2D:4D*

The length of index and ring fingers of the male participants was measured to the nearest 176 177 0.1 mm using Vernier callipers, directly on fingers (more reliable than indirect measures 178 performed on a photocopy of the hands [42]). Measurement was taken from the most 179 proximal ventral crease of the digit to the tip of the finger. To limit measurement errors, the 180 procedure was repeated three times, and as the measures were highly correlated (ICC = 0.986, p < 0.001) they were averaged. The index-to-ring ratio (2D:4D) for the left and 181 182 right hand separately were then computed, as well as the difference between right and left 183 2D:4D (Dr-l).

184

185 (f) Data analysis

All variables had normal distributions (assessed by Kolmogorov-Smirnov tests) and parametric statistics were thus used. In addition, no extreme values were to be removed before performing analyzes. Tests were two-tailed and were conducted using Statistica 9.0 and SPSS 18.0. The link between 2D:4D and visual, auditory, and olfactory stimuli was investigated using multivariate simple regressions, with face, voice, and odour characteristics (masculinity, attractiveness, etc.) as dependent variables and 2D:4D as predictor. The difference between 'pill users' and 'non-pill users' was tested with paired *t*-tests and the

193	relation between masculinity, attractiveness and other dimensions was assessed with Pearson
194	correlation coefficients.
195	
196	
197	3. RESULTS
198	
199	(a) <i>Voice</i>
200	First, correlations between male voice frequency and both rated attractiveness and rated
201	masculinity were significantly negative ($r = -0.69$ and $r = -0.63$, respectively, $n = 48$,
202	p < 0.001). Attractiveness and masculinity correlated positively ($r = 0.77$, $n = 48$, $p < 0.001$).
203	'Pill users' gave slightly higher attractiveness ratings than the 'non-pill users' ($t_{47} = 2.14$,
204	$p = 0.038$), but the two groups did not differ on the masculinity ratings ($t_{47} = 0.95$, $p = 0.35$)
205	(Supplementary Material 3).
206	Multivariate simple regressions were performed to determine whether 2D:4D ratio of
207	right hand, 2D:4D of left hand, and difference between right and left 2D:4D (Dr-l), were
208	significant predictors of voice frequency, and rated attractiveness and masculinity. Voice
209	frequency and voice attractiveness were predicted neither by the right 2D:4D ratio, Dr-l (table
210	1) nor left 2D:4D (Supplementary Material 4). Voice masculinity was predicted only by left
211	hand 2D:4D when 'non-pill users' were taken into account (Supplementary Material 4).
212	
213	(b) Body odour
214	The correlation between masculinity and attractiveness of males' body odours was
215	significantly negative ($r = -0.54$, $n = 28$, $p = 0.003$). Average ratings of the 'pill users' and
216	'non-pill users' did not differ (attractiveness: $t_{27} = 0.44$, $p = 0.66$; masculinity: $t_{27} = 0.01$
217	p = 0.99; Supplementary Material 3).

218	As for voice ratings, multivariate simple regressions were performed to determine
219	whether 2D:4D ratio of right and left hand were significant predictors of body odour
220	attractiveness and masculinity. There were significant effects for 2D:4D of the right hand
221	only. Although masculinity was not predicted by 2D:4D (right, left, Dr-l), attractiveness was
222	(by right 2D:4D) when only 'non-pill users' were taken into account (table 1, Supplementary
223	Material 4).

- 224
- 225 (c) Face

First, masculinity was correlated neither with attractiveness (short-term attractiveness:

227 r = 0.15, p = 0.30; long-term attractiveness: 0.24, p = 0.10; n = 47) nor with face symmetry

(perceived by females: r = 0.20, p = 0.17; measured in Psychomorph: r = 0.05, p = 0.73;

229 n = 47). Long-term and short-term attractiveness were highly correlated (r = 0.96, n = 47,

230 p < 0.001), and symmetry rated and perceived were correlated too (r = 0.39, n = 47,

231 p < 0.01). Attractiveness was correlated with perceived face symmetry (short-term

attractiveness: r = 0.67, p < 0.001; long-term attractiveness: 0.66, p < 0.001; n = 47), but not

or only marginally with measured face symmetry (short-term attractiveness: r = -0.22,

234 p = 0.14; and long-term attractiveness: r = -0.28, p = 0.06; n = 47). Contrary to odours, mean

face ratings of the 'pill users' and 'non-pill users' significantly differed. Compared to 'pill

users', 'non-pill users' gave higher attractiveness (short-term: $t_{46} = 1.99$, p = 0.052; long-

237 term: $t_{27} = 6.06$, p < 0.001), higher masculinity ($t_{27} = 4.59$, p < 0.001) and higher symmetry

238 ratings ($t_{27} = 8.03$, p < 0.001) (Supplementary Material 3).

As for voice and odour ratings, multivariate simple regressions were performed to determine whether right 2D:4D, left 2D:4D, and Dr-l were significant predictors of face attractiveness and masculinity. There were significant effects for 2D:4D of the right hand and for the right-left difference Dr-l (table 1). Long-term and short-term attractiveness were

Submitted to Proceedings of the Royal Society B

Digit ratio predicts face attractiveness

significantly predicted by right 2D:4D and by Dr-l. Perceived symmetry was predicted by
right 2D:4D only, and face masculinity was not predicted by any of the 2D:4D variables.
These results remained unchanged when 'pill users' and 'non-pill users' are analyzed
separately.

247

248 4. DISCUSSION

249

250 In this study, we tested whether second-to-fourth digit ratio (2D:4D) of left hand, right hand and right minus left hand Dr-l, can predict men masculinity and attractiveness for three 251 252 sensory modalities involved in human mate choice: voice, body odour and face. Our main 253 finding is that right hand 2D:4D and Dr-l are significant predictors of attractiveness but not masculinity of male faces, whether they are considered as short-term or long-term potential 254 255 partners. Right hand 2D:4D also predicts perceived facial symmetry. The link between 256 2D:4D and facial attractiveness is consistent with previous studies investigating either selfevaluated attractiveness [22,23] or men's attractiveness rated by women [22,24]. This 257 258 illustrates a female preference for low 2D:4D men, possibly driven by the fact that these have 259 more symmetrical faces. Such a preference might have evolved because it increases females' reproductive success by gaining benefits from partners who are physically more robust [1] 260 261 and who have more fertile ejaculates [43,44]. 262 Our results differ from other studies that found significant relationship between 263 dominant/masculine personality traits and 2D:4D [45], and from a study by Neave et al. [20]

who report a similar negative association between 2D:4D ratio (of both hands) and

265 masculinity, but not attractiveness. However, ours and Neave *et al.*'s results are not

266 necessarily contradictory. Indeed, men who are able to pay costs of high levels of testosterone

267 (see [12]), will consequently develop masculine phenotypes [15]. At the same time,

268	symmetric faces are likely to be found in individuals who have a better developmental
269	stability [13], which reflects a better resistance to parasites and poor environmental
270	conditions [46]. Therefore, some particularly good quality males should express
271	simultaneously masculine and symmetric faces. Thus, one could expect 2D:4D to predict
272	both face masculinity and symmetry, and the fact that only one of these predictions were
273	found in our and Neave et al.'s study might be an effect of sampling or of differences in
274	2D:4D measurement procedure. These effects are likely to be subtle since other studies
275	failed, as we did, to find a link between 2D:4D ratio and masculinity features [21].
276	Replication of our findings, the direction of which contradicts another study on 2D:4D
277	and facial symmetry [47], would thus be worthwhile. Furthermore, future research will be
278	necessary to better understand the relationship between prenatal androgen exposure and adult
279	face attractiveness. Our study cannot directly address the mechanism underlying this
280	relationship, and the present results provide no evidence that prenatal testosterone is the
281	causal factor of both low 2D:4D and high attractiveness (via face symmetry). Indeed, it may
282	be possible that the causal factor that explains the relationship between 2D:4D and
283	attractiveness is situated at another level. For example, a high level of parental attractiveness,
284	because it reflects genetic quality, might provide the foetus both with 'good genes' (high
285	level of testosterone) and a healthy prenatal environment allowing high developmental
286	stability.

287

The significant link between male facial attributes and 2D:4D ratio we found was observed for the right hand only, which has a more male-like ratio than the left hand (right: M = 0.97, SD = 0.03; left: M = 0.98, SD = 0.02; $t_{48} = 3.57, p < 0.001$). This result supports the assumption of Tanner (1990, cited in [1]), according to which "sexually dimorphic traits tend to be expressed in the male form more strongly on the right side of the body". This side-

Page 13 of 21

Submitted to Proceedings of the Royal Society B

Digit ratio predicts face attractiveness

related difference is also supported by Manning *et al.* [43], who found stronger association between testosterone levels and 2D:4D ratios on the right hand compared to the left hand, as well as by other authors [4]. The authors hypothesize a stronger action of androgens on the digits of the right hand (see [48] for a meta-analysis).

297

298 Surprisingly, we found a positive relationship between 2D:4D ratios of men and the 299 evaluation of their body odour attractiveness and voice masculinity by the 'non-pill users'. 300 This result is contrary to our predictions and deserves further investigation, especially taking into account the impact of cycle stage on this kind of evaluations. In this respect, we found 301 302 that spontaneously ovulating women gave higher facial attractiveness, masculinity and 303 symmetry ratings than 'pill users', which is concordant with previous studies showing that fertile women prefer less feminized [49] and more symmetrical male faces ([50] but see 304 305 [51]). However, this result was not confirmed in the second group of females who evaluated the faces, which might be due to the proportion of women being in their fertile phase during 306 data collection, a factor that we did not control. 307

308

309 The fact that 2D:4D does not reliably predict voice and body odour attractiveness or 310 masculinity is not due to the fact that different groups of females rated faces and voices. 311 Indeed, not only both groups were highly correlated, but we also performed the regressions of table 1 and Supplementary Material 4 again with the data of the 'voice raters' group and the 312 313 results were replicated (the only difference being a lower level of significance for the effects 314 in pill users, detail of the results not presented here). Rather, this absence of relationship between 2D:4D ratio and vocal and olfactory traits might stem from the fact that voice and 315 316 body odour are by nature more variable than facial shape and more related to current 317 circulating levels of testosterone in the adult individual (but see [52]). Consistent with this

318 hypothesis, Evans et al. [14] found that voice frequency is related to the level of circulating 319 testosterone but not to the indicator of prenatal testosterone level 2D:4D (see also [53,54]), 320 whereas the reverse was found for faces ([20], but see [15]). All together, these results raise 321 the question of the relative dissociation between organisational and activational effects of 322 testosterone [8], organisational effects being irreversible and occurring during sensitive 323 periods of early development, and activational ones being impermanent and occurring in 324 adulthood. Foetal testosterone might serve to organize certain features of the face like bones 325 (jaws and cheek bones) that will subsequently be activated during puberty and remain 326 relatively stable thereafter. On the contrary, voice is produced by the larynx that is made of 327 muscles and cartilage, and body odour consists in the degradation of products of the 328 metabolism by skin bacteria: both of them are likely to change at anytime under the influence of circulating hormones. Indeed, voice quality significantly changes with therapeutic 329 330 administration of testosterone (e.g. [55]) or more subtly with normal daily variations of testosterone concentration [14], and some major compounds of axillary odours are by-331 products of androgen substances [29]. 332 333 334 335 **5. CONCLUSION** 336

Our study suggests that both right hand 2D:4D and right-minus-left 2D:4D (Dr-l) are good predictors of facial attractiveness in men, but not of their voice or body odour attractiveness. We showed, for the first time, that this effect might be supported by the link between 2D:4D and face symmetry, one indicator of male quality. Physical features closely linked to foetal levels of testosterone, such as face shape, are more likely to be correlated with second-to-fourth digit ratios than traits believed to be directly controlled by circulating

Page 15 of 21

Submitted to Proceedings of the Royal Society B

Digit ratio predicts face attractiveness

343	level of testosterone later in life history (voice and body odour). We advocate that more
344	research is needed to investigate the action of both early and adult testosterone levels on the
345	development of sexually dimorphic traits involved in human attractiveness, including those
346	we have examined here. The present study suggests that masculine and attractive features of
347	voice and body odour might not be shaped in utero but later during life history: the timing
348	(and even the existence, for body odour) of an action of testosterone on these two modalities
349	remain to be elucidated in the future.

350

351

352 Acknowledgments

353 The authors wish to thank the participants, Kirsty Elliott and Marta Vondrova for their

help in data collection, Rob Burriss, Hannah Rowland and Tamsin Saxton for technical

advice, and Bernard Tiddeman and David Perrett for use of the Psychomorph software. One

anonymous reviewer and Markus Rantala are also thanked for their constructive comments

357 on the manuscript. This research was supported by Fyssen Foundation, Paris.

358

359

360 **REFERENCES**

- 361 1. Manning, J. T. 2002 *Digit ratio: A pointer to fertility, behavior, and health.* New
 362 Brunswick, NJ: Rutgers University Press.
- 363

2. Nelson, E. & Shultz, S. 2010 Finger length ratios (2D:4D) in anthropoids implicate
reduced prenatal androgens in social bonding. *Am. J. Phys. Anthropol.* 141, 395-405.
(doi:10.1002/ajpa.21157).

367

368 3. Burley, N. T. & Foster, V. S. 2004 Digit ratio varies with sex, egg order and strength of 369 mate preference in zebra finches. *Proc. R. Soc. B* **271**, 239-244.

370 (doi:10.1098/rspb.2003.2562).

371

4. Lutchmaya, S., Baron-Cohen, S., Raggatt, P., Knickmeyer, R. & Manning, J. T. 2004 2nd to 4th digit ratios, fetal testosterone and estradiol. *Early Hum. Dev.* **77**, 23-28.

374 375	(doi:10.1016/j.earlhumdev.2003.12.002).
376	5. Breedlove, S. M. 2010 Minireview: Organizational hypothesis: instances of the fingerpost.
3//	<i>Endocrinology</i> 151 , 4116-4122. (doi:10.1210/en.2010-0041).
3/8	
3/9	6. van Honk, J., Schutter, D. J., Bos, P. A., Kruijt, A., Lentjes, E. G. & Baron-Conen, S. In
380	press. Testosterone administration impairs cognitive empathy in women depending on
381	second-to-fourth digit ratio. $PNAS$. (doi:10.10/3/pnas.1011891108).
382 292	7 Olten A. Kalvanov M. & Varia N 2002 The ratio of second and faveth disit langths
202 201	7. Oktell, A., Kalyoncu, M. & Yallş, N. 2002 The fatto of second- and fourth-digit lengths
204 205	and congenitar adrenar hyperprasia due to 21 -invariance denotency. <i>Early Tum. Dev.</i> 70, 47.54 (doi:10.1016/S0378.2782(02)00073.7)
385	47-54. (doi.10.1010/30378-3782(02)00075-7).
387	8 Nerve N 2008 Hormones and Rehaviour: A Psychological Approach Combridge:
388	Cambridge University Press
389	Camorage Oniversity (1655.
390	9 Andersson M B 1994 Servel Selection Princeton NI: Princeton University Press
391	<i>y</i> . Andersson, W. D. 1994 Sexual Selection. I findeton, W. Thineeton Oniversity (1655).
392	10 Reed W L Clark M E Parker P G Raouf S A Arguedas N Monk D S Snaidr
393	E. Nolan, V. & Ketterson, E. D. 2006 Physiological effects on demography: a long-term
394	experimental study of testosterone's effects on fitness. Am. Nat. 167, 667-683.
395	(doi:10.1086/503054).
396	
397	11. Mills, S. C., Grapputo, A., Jokinen, I., Koskela, E., Mappes, T. & Poikonen, T. 2010
398	Fitness trade-offs mediated by immunosuppression costs in a small mammal. <i>Evolution</i> 64,
399	166-179. (doi:10.1111/j.1558-5646.2009.00820.x).
400	
401	12. Folstad, I. & Karter, A. J. 1992 Parasites, bright males, and the immunocompetence
402	handicap. Am. Nat. 139, 603-622. (doi:10.1086/281919).
403	
404	13. Thornhill, R. & Gangestad, S. W. 1999 The scent of symmetry: a human sex pheromone
405	that signals fitness? Evol. Hum. Behav. 20, 175-201. (doi:10.1016/S1090-5138(99)00005-7).
406	
407	14. Evans, S., Neave, N., Wakelin, D. & Hamilton, C. 2008 The relationship between
408	testosterone and vocal frequencies in human males. <i>Physiol. Behav.</i> 93 , 783-788.
409	(doi:10.1016/j.physbeh.2007.11.033).
410	
411	15. Penton-Voak, I. S. & Chen, J. Y. 2004 High salivary testosterone is linked to masculine
412	male facial appearance in humans. Evol. Hum. Behav. 25, 229-241.
413	(doi:10.1016/j.evoinumbenav.2004.04.003).
414	16 Decend NJ Denten Marla I. C. & Comilar A. K. 2000 Testestances recorded to
415	10. Pound, N., Penton-Voak, I. S. & Surridge, A. K. 2009 Testosterone responses to
410	(doi:10.1008/remb.2008.0000)
41/ /10	(doi.10.1098/isp0.2008.0990).
410 /10	17 Saxton T.K. Debruine I. M. Jones B.C. Little A.C. & Roberts S.C. 2000 Face and
420	voice attractiveness judgments change during adolescence Fuel Hum Rohav 30 308-408
421	(doi:10.1016/i evolhumbehav 2009.06.004)
422	(uor.10.1010/j.070/mumoenu7.2007.00.00+).
423	18. Little, A. C., Saxton, T. K., Roberts, S. C., Jones, B. C., Debruine, L. M., Vukovic, J.,

424 425 426 427	Perrett, D. I., Feinberg, D. R. & Chenore, T. 2010 Women's preferences for masculinity in male faces are highest during reproductive age range and lower around puberty and post-menopause. <i>Psychoneuroendocrinology</i> 35 , 912-920. (doi:10.1016/j.psyneuen.2009.12.006).
428 429 430 431	19. Jamison, S. C., Meier, R. J. & Campbell, B. C. 1993 Dermatoglyphic asymmetry and testosterone levels in normal males. <i>Am. J. Phys. Anthropol.</i> 90 , 185-198. (doi:10.1002/ajpa.1330900205).
432 433 434 435	20. Neave, N., Laing, S., Fink, B. & Manning, J. T. 2003 Second to fourth digit ratio, testosterone and perceived male dominance. <i>Proc. R. Soc. B</i> 270 , 2167-2172. (doi:10.1098/rspb.2003.2502).
436 437 438 439	21. Koehler, N., Simmons, L. W. & Rhodes, G. 2004 How well does second-to-fourth-digit ratio in hands correlate with other indications of masculinity in males? <i>Proc. R. Soc. B</i> 271 , S296-298. (doi:10.1098/rsbl.2004.0163).
440 441 442 443	22. Bogaert, A. F., Fawcett, C. C. & Jamieson, L. K. 2009 Attractiveness, body size, masculine sex roles and 2D:4D ratios in men. <i>Pers. Indiv. Differ.</i> 47 , 273-278. (doi:10.1016/j.paid.2009.03.011).
444 445 446 447	23. Manning, J. T. & Quinton, S. 2007 Association of digit ratio (2D:4D) with self-reported attractiveness in men and women: evidence from the BBC internet survey. <i>J. Individ. Diff.</i> 28 , 73-77. (doi:10.1027/1614-0001.28.2.73).
448 449 450 451	24. Roney, J. R. & Maestripieri, D. 2004 Relative digit lengths predict men's behavior and attractiveness during social interactions with women. <i>Hum. Nature</i> 15 , 271-282. (doi:10.1007/s12110-004-1009-5).
452 453 454	25. Collins, S. 2000 Men's voices and women's choices. <i>Anim. Behav.</i> 60 , 773-780. (doi:10.1006/anbe.2000.1523).
455 456 457 458 459	26. Havlicek, J., Saxton, T. K., Roberts, S. C., Jozifkova, E., Lhota, S., Valentova, J. & Flegr, J. 2008 He sees, she smells? Male and female reports of sensory reliance in mate choice and non-mate choice contexts. <i>Pers. Indiv. Differ.</i> 45 , 565-570. (doi:doi:10.1016/j.paid.2008.06.019).
460 461 462	27. Wedekind, C., Seebeck, T., Bettens, F. & Paepke, A. J. 1995 MHC-dependent mate preferences in humans. <i>Proc. R. Soc. B</i> 260, 245-249. (doi:10.1098/rspb.1995.0087).
463 464 465 466	28. Bird, S. & Gower, D. B. 1981 The validation and use of a radioimmunoassay for 5 alpha- androst-16-en-3-one in human axillary collections. <i>J. Steroid Biochem.</i> 14 , 213-219. (doi:10.1016/0022-4731(81)90176-X).
467 468 469 470	29. Rennie, P. J., Holland, K. T., Mallet, A. I., Watkins, W. J. & Gower, D. B. 1989 Testosterone metabolism by human axillary bacteria. <i>Biochem. Soc. Trans.</i> 17 , 1017-1018. (doi:10.1042/bst0171017).
471 472 473	30. Havlicek, J., Murray, A. K., Saxton, T. K. & Roberts, S. C. 2010 Current issues in the study of androstenes in human chemosignalling. <i>Vitam. Horm.</i> 83 , 47-81. (doi:10.1016/S0083-6729(10)83003-1).

 31. Manning, J. T., Bundred, P. E., Newton, D. J. & Flanagan, B. F. 2003 The second to fourth digit ratio and variation in the androgen receptor gene. <i>Evol. Hum. Behav.</i> 24, 399-405. (doi:10.1016/S1090-5138(03)00052-7). 32. Hurd, P. L., Vaillancourt, K. L. & Dinsdale, N. L. In press. Aggression, digit ratio and variation in androgen receptor and monoamine oxidase A genes in men. <i>Behav. Genet.</i> (doi:10.1007/s10519-010-9404-7). 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated dour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjp017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 Sh. Wanng, S. L., Burderder, D. S. Reffer, D. S. Comp. Barborn in Section 105 (doi:10.1016/S1090-5138(03)00052-7). 32. Hurd, P. L., Vaillancourt, K. L. & Dinsdale, N. L. In press. Aggression, digit ratio and variation in nadrogen receptor and monoamine oxidase A genes in men. <i>Behav. Genet.</i> (doi:10.1007/s10519-010-9404-7). 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav. 69</i>, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol. 108</i>, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav. 20</i>, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol. 25</i>, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B 275</i>, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses 34</i>, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses 31</i>, 747-752. (doi:10.1093/chemse/bjp017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 Iduit 10.1016/S1090-5138(03)00052-7). 32. Hurd, P. L., Vaillancourt, K. L. & Dinsdale, N. L. In press. Aggression, digit ratio and variation in androgen receptor and monoamine oxidase A genes in men. <i>Behav. Genet.</i> (doi:10.1007/s10519-010-9404-7). 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 (doi:10.1016/S1050-5156(05)0032-7). 32. Hurd, P. L., Vaillancourt, K. L. & Dinsdale, N. L. In press. Aggression, digit ratio and variation in androgen receptor and monoamine oxidase A genes in men. <i>Behav. Genet.</i> (doi:10.1007/s10519-010-9404-7). 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 32. Hurd, P. L., Vaillancourt, K. L. & Dinsdale, N. L. In press. Aggression, digit ratio and variation in androgen receptor and monoamine oxidase A genes in men. <i>Behav. Genet.</i> (doi:10.1007/s10519-010-9404-7). 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 479 32. Hult, P. L., Valnaheduri, K. L. & Dinsdale, N. L. in piess. Aggression, digit failo and variation in androgen receptor and monoamine oxidase A genes in men. <i>Behav. Genet.</i> (doi:10.1007/s10519-010-9404-7). 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjj037). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 Variation in androgen receptor and monoamine oxidase A genes in men. <i>Bendy. Genet.</i> (doi:10.1007/s10519-010-9404-7). 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 (doi:10.100//s10519-010-9404-7). 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 33. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 J. Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M. & Perrett, D. I. 2005 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). J. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). S. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). A. Avergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). T. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). S. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 male voices. <i>Anim. Behav.</i> 69, 561-568. (doi:10.1016/j.anbehav.2004.06.012). 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 34. Grammer, K. & Thornhill, R. 1994 Human (Homo sapiens) facial attractiveness and sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 sexual selection: the role of symmetry and averageness. <i>J. Comp. Psychol.</i> 108, 233-242. (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjp1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook.</i> New York: Harper & Row.
 (doi:10.1037/0735-7036.108.3.233). 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjp017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 490 491 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 495 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 497 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook.</i> New York: Harper & Row.
 35. Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A. & Edwards, R. 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjp1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 1999 Symmetry and human facial attractiveness. <i>Evol. Hum. Behav.</i> 20, 295-307. (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 (doi:10.1016/S1090-5138(99)00014-8). 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook.</i> New York: Harper & Row.
 36. Alvergne, A. & Lummaa, V. 2010 Does the contraceptive pill alter mate choice in humans? <i>Trends Ecol. Evol.</i> 25, 171-179. (doi:10.1016/j.tree.2009.08.003). 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 b): Hivergine, H. & Bahmaa, V. 2010 Does the confidee prive pin area mater mater mater in the second of the pin area mater mater mater in the second of the pin area mater mater in the second of the pin area mater mater in the second of the pin area mater mater in the second of the pin area mater mater in the second of the pin area mater mater in the second of the pin area mater mater in the pin area mater mater
 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 37. Roberts, S. C., Gosling, L. M., Carter, V. & Petrie, M. 2008 MHC-correlated odour preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook.</i> New York: Harper & Row.
 499 preferences in humans and the use of oral contraceptives. <i>Proc. R. Soc. B</i> 275, 2715-2722. 500 (doi:10.1098/rspb.2008.0825). 501 502 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related 503 perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 504 505 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor 506 attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 507 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 (doi:10.1098/rspb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 (doi:10.1098/15pb.2008.0825). 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 301 38. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axillary odor: are there side-related perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 502 58. Ferdenzi, C., Schaal, B. & Roberts, S. C. 2009 Human axinary odor: are there side-related 503 perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 504 505 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor 506 attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). 507 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 503 perceptual differences? <i>Chem. Senses</i> 34, 565-571. (doi:10.1093/chemse/bjp037). 504 505 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 507 508 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bj1017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 39. Havlicek, J. & Lenochova, P. 2006 The effect of meat consumption on body odor attractiveness. <i>Chem. Senses</i> 31, 747-752. (doi:10.1093/chemse/bjl017). 40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i>. New York: Harper & Row.
 attractiveness. Chem. Senses 31, 747-752. (doi:10.1093/chemse/bj1017). 40. Fairbanks, G. 1960 Voice and Articulation Drillbook. New York: Harper & Row.
 40. Fairbanks, G. 1960 Voice and Articulation Drillbook. New York: Harper & Row.
40. Fairbanks, G. 1960 <i>Voice and Articulation Drillbook</i> . New York: Harper & Row.
509
510 41. Scheib, J. E., Gangestad, S. W. & Thornhill, R. 1999 Facial attractiveness, symmetry and
511 cues of good genes. <i>Proc. R. Soc. B</i> 266 , 1913-1917. (doi:10.1098/rspb.1999.0866).
512
513 42. Manning, J. T., Baron-Cohen, S., Wheelwright, S. & Fink, B. 2010 Is digit ratio (2D:4D)
514 related to systemizing and empathizing? Evidence from direct finger measurements reported
515 in the BBC internet survey. Pers. Indiv. Differ. 48, 767-771.
516 (doi:10.1016/j.paid.2010.01.030).
517
518 43. Manning, J. T., Scutt, D., Wilson, J. & Lewis-Jones, D. I. 1998 The ratio of 2nd to 4th
519 digit length: a predictor of sperm numbers and concentrations of testosterone luteinizing
520 hormone and oestrogen <i>Hum. Reprod.</i> 13 3000-3004 (doi:10.1093/humren/13.11.3000)
520 hormone and oestrogen. <i>Hum. Reprod.</i> 13 , 3000-3004. (doi:10.1093/humrep/13.11.3000). 521
 bormone and oestrogen. <i>Hum. Reprod.</i> 13, 3000-3004. (doi:10.1093/humrep/13.11.3000). 44. Auger, J. & Eustache, F. In press Second to fourth digit ratios male genital development

524 525	Androl. (doi:10.1111/j.1365-2605.2010.01124.x).
525 526 527	45. Manning, J. T. & Fink, B. 2008 Digit ratio (2D:4D), dominance, reproductive success, asymmetry, and sociosexuality in the BBC Internet Study. <i>Am. J. Hum. Biol.</i> 20 , 451-461.
528 529	(doi:10.1002/ajhb.20767).
530 531	46. Rhodes, G. 2006 The evolutionary psychology of facial beauty. <i>Annu. Rev. Psychol.</i> 57 , 199-226. (doi:10.1146/annurev.psych.57.102904.190208).
532 533	47. Fink, B., Manning, J. T., Neave, N. & Grammer, K. 2004 Second to fourth digit ratio and
534 535	facial asymmetry. <i>Evol. Hum. Benav.</i> 25, 125-132. (doi:10.1016/S1090-5138(03)00084-9).
536 537 538	48. Hönekopp, J. & Watson, S. 2010 Meta-analysis of digit ratio 2D:4D shows greater sex difference in the right hand. <i>Am. J. Hum. Biol.</i> 22 , 619-630. (doi:10.1002/ajhb.21054).
539 540 541	49. Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. 1999 Menstrual cycle alters face preference. <i>Nature</i> 399 , 741-742. (doi:10.1038/21557).
542 543 544	50. Little, A. C., Jones, B. C., Burt, D. M. & Perrett, D. I. 2007 Preferences for symmetry in faces change across the menstrual cycle. <i>Biol. Psychol.</i> 76 , 209-216.
545 546	(doi:10.1016/j.biopsycho.2007.08.003).
547 548 549 550	51. Peters, M., Simmons, L. W. & Rhodes, G. 2009 Preferences across the menstrual cycle for masculinity and symmetry in photographs of male faces and bodies. <i>PLoS ONE</i> 4 , e4138. (doi:10.1371/journal.pone.0004138).
551 552 553 554	52. Rantala, M. J., Eriksson, C. J. P., Vainikka, A. & Kortet, R. 2006 Male steroid hormones and female preference for male body odor. <i>Evol. Hum. Behav.</i> 27 , 259-269. (doi:10.1016/j.evolhumbehav.2005.11.002).
555 556 557 558	53. Hughes, S. M., Harrison, M. A. & Gallup, G. G. 2002 The sound of symmetry: voice as a marker of developmental instability. <i>Evol. Hum. Behav.</i> 23 , 173-180. (doi:10.1016/S1090-5138(01)00099-X).
559 560 561 562	54. Puts, D. A., Gaulin, S. J. C., Sporter, R. J. & McBurney, D. H. 2004 Sex hormones and finger length. What does 2D:4D indicate? <i>Evol. Hum. Behav.</i> 25, 182-199. (doi:10.1016/j.evolhumbehav.2004.03.005).
562 563 564 565	55. Akcam, T., Bolu, E., Merati, A. L., Durmus, C., Gerek, M. & Ozkaptan, Y. 2004 Voice changes after androgen therapy for hypogonadotrophic hypogonadism. <i>Laryngoscope</i> 114 , 1587-1591. (doi:10.1097/00005537-200409000-00016).

566 **TABLE CAPTION**

567

- Table 1 Link between digit ratio (2D:4D) of the right hand and right hand minus left hand 568
- 569 2D:4D (Dr-l), and voice, odour and face characteristics of 49 men, determined by a simple
- linear regression (voice pitch, R^2) and multivariate linear regressions (other measures, β). df: 570
- degrees of freedom; *: p < 0.05; **: p < 0.01. A negative β value indicates an inverse 571
- 572 relationship between 2D:4D ratio and the dependent variable. Results for left 2D:4D are
- 573 presented in Supplementary Material 4.

nd th.

			Right 2D:4D				Right minus Left 2D:4D (Dr-l)			
Modality	Raters	Dimension	Wilks 	R^2/β	F(df)	Р	Wilks 	R^2/β	F(df)	Р
Voice	n/a	Frequency		0.02	(1,46) 0.88	0.353		0.01	(1,46) 0.00	0.949
	Total	Attractiveness Masculinity	0.96	0.19 0.17	(1,46) 1.78 (1,46) 1.43	0.198 0.237	0.98	0.05 -0.04	(1,46) 0.10 (1,46) 0.09	0.749 0.771
	'Pill users'	Attractiveness Masculinity	0.97	0.18 0.16	(1,46) 1.58 (1,46) 1.16	0.215 0.287	1.00	0.01 -0.02	(1,46) 0.01 (1,46) 0.02	0.924 0.881
	'Non-pill users'	Attractiveness Masculinity	0.95	0.20 0.19	(1,46) 1.82 (1,46) 1.77	0.183 0.190	0.96	0.09 -0.07	(1,46) 0.37 (1,46) 0.24	0.547 0.625
Odour	Total	Attractiveness Masculinity	0.89	0.25 -0.32	(1,26) 1.78 (1,26) 2.98	0.193 0.096	0.93	0.09 -0.27	(1,26) 0.24 (1,26) 2.00	0.632 0.169
	'Pill users'	Attractiveness Masculinity	0.90	0.05 -0.31	(1,26) 0.06 (1,26) 2.81	0.811 0.105	0.99	-0.04 -0.06	(1,26) 0.05 (1,26) 0.11	0.831 0.745
	'Non-pill users'	Attractiveness Masculinity	0.85	0.38 -0.10	(1,26) 4.38 (1,26) 0.25	0.046 * 0.618	0.86	0.36 -0.23	(1,26) 3.96 (1,26) 1.45	0.057 0.239
Face	Total	Attractiveness ST ^a Attractiveness LT ^b Symmetry perceived Asymmetry measured Masculinity	0.76 *	-0.42 -0.43 -0.41 0.29 -0.20	$\begin{array}{c} (1,45) \ 9.59 \\ (1,45) \ 10.49 \\ (1,45) \ 9.17 \\ (1,45) \ 4.05 \\ (1,45) \ 1.79 \end{array}$	0.003 ** 0.002 ** 0.004 ** 0.050 0.187	0.86	-0.33 -0.35 -0.25 0.20 -0.02	(1,45) 5.51 (1,45) 6.48 (1,45) 3.07 (1,45) 1.78 (1,45) 0.02	0.023 * 0.014 * 0.086 0.188 0.903
	'Pill users'	Attractiveness ST Attractiveness LT Symmetry perceived Masculinity	0.79 *	-0.41 -0.41 -0.40 -0.21	(1,45) 8.86 (1,45) 9.26 (1,45) 8.45 (1,45) 2.17	0.005 ** 0.004 ** 0.006 ** 0.148	0.81	-0.30 -0.38 -0.25 -0.01	(1,45) 4.61 (1,45) 7.66 (1,45) 3.00 (1,45) 0.01	0.037 * 0.008 ** 0.090 0.921
	'Non-pill users'	Attractiveness ST Attractiveness LT Symmetry perceived Masculinity	0.78 *	-0.41 -0.44 -0.38 -0.19	(1,45) 8.83 (1,45) 10.89 (1,45) 7.51 (1,45) 1.71	0.005 ** 0.002 ** 0.009 ** 0.198	0.88	-0.34 -0.32 -0.23 -0.05	(1,45) 5.94 (1,45) 5.16 (1,45) 2.47 (1,45) 0.11	0.019 * 0.028 * 0.123 0.737

^a ST: for a Short-Term partner; ^b LT: for a Long-Term partner