

Title:

SYMMETRY IS RELATED TO SEXUAL DIMORPHISM IN FACES: DATA
ACROSS CULTURE AND SPECIES

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1 **Summary**

2 **Background**

3 Many animals both display and assess multiple signals. Two prominently
4 studied traits are symmetry and sexual dimorphism, which, for many animals,
5 are proposed cues to heritable fitness benefits. These traits are associated
6 with other potential benefits, such as fertility. In humans, the face has been
7 extensively studied in terms of attractiveness. Faces have the potential to be
8 advertisements of mate quality and both symmetry and sexual dimorphism
9 have been linked to the attractiveness of human face shape.

10 **Methodology/Principal Findings**

11 Here we show that measurements of symmetry and sexual dimorphism from
12 faces are related in humans, both in Europeans and African hunter-gatherers,
13 and in a non-human primate. Using human judges, symmetry measurements
14 were also related to perceived sexual dimorphism. In all samples, symmetric
15 males had more masculine facial proportions and symmetric females had
16 more feminine facial proportions.

17 **Conclusions/Significance**

18 Our findings support the claim that sexual dimorphism and symmetry in faces
19 are signals advertising quality by providing evidence that there must be a
20 biological mechanism linking the two traits during development. Such data
21 also suggests that the signalling properties of faces are universal across
22 human populations and are potentially phylogenetically old in primates.

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25

26 Increasingly attention is being paid to the complexity of animal signalling [1].
27 Many animals display multiple traits and assess multiple signals. Multiple traits
28 may be signals of the same factor, and so serve to enhance the accuracy with
29 which receivers assess a single factor, or else signal different facets of an
30 individual's quality [2]. In terms of sexual selection, signalling traits can be
31 divided by their role in intrasexual (same-sex competition) and intersexual
32 (choices of the opposite-sex) selection. While faces are likely to play a role in
33 same-sex competition [3], it is the later form of sexual selection that has been
34 most prominently applied to research on human facial attractiveness.

35 Darwin [4] laid out the first notions of how evolution of traits by
36 preference could occur. Self-reinforcing, or "runaway", selection [5] may
37 explain certain traits. After a preference for any particular trait has arisen, for
38 example, a preference for long tails in a bird species, females begin to
39 reproduce with males in possession of long-tails to produce offspring with both
40 genes for long tails (in males) and genes for a preference for long tails (in
41 females). A feedback loop between genes for traits and preferences produce
42 stronger preferences and ever more elaborate expression of traits. The initial
43 preference could come from a sensory disposition evolved for another
44 purpose [6] and hence arbitrary. The idea that male or female morphology
45 may be attractive because it exploits an already existing preference in the
46 opposite-sex has been called the perceptual or sensory bias view [7].

47 In contrast to such views, indicator mechanisms of sexual selection
48 propose that certain traits are preferred because they are associated with

49 either phenotypic or genotypic quality [8] and therefore act as cues and hence
50 can be signals of quality. A key concept in indicator mechanisms is the notion
51 of handicaps. Individuals may find mates who carry a costly handicap more
52 attractive because the fact they have survived with the handicap is an
53 indicator of their genetic quality [9]. Many traits also require energy to produce
54 and so individuals must be in good condition to afford their production.
55 Handicaps can then be 'honest' – low quality individuals cannot 'fake' such
56 traits. Individuals who choose partners in possession of such traits will
57 produce more offspring than those who do not.

58 An important question is whether particular traits are driven by indicator
59 mechanisms or are driven by arbitrary preferences. Researchers have
60 suggested that different signals of the same quality should inter-correlate
61 [10,11], which would support indicator mechanisms in their evolution. For
62 example, in humans, the judged attractiveness of female bodies correlates
63 with facial attractiveness [11] and the pitch of female voices also positively
64 predicts facial attractiveness [12]. Both studies suggest that the three traits
65 measured are in part signalling one aspect of quality. Such a relationship
66 should come about because the underlying quality advertised by one trait will
67 also be reflected in other traits. If traits advertise discrete aspects of quality,
68 then there is no apriori reason to expect such traits to co-vary. Theories
69 suggesting that traits are being driven by perceptual bias or via arbitrary
70 runaway selection also do not predict co-variation.

71 Two important traits thought to relate to mate-quality in many animals
72 are symmetry and sexual dimorphism [13,14]. Fluctuating asymmetry (FA)
73 [15] is thought to reflect an individual's ability to maintain the stable

74 development of their morphology under the prevailing environmental
75 conditions. Fluctuating asymmetry is a useful measure as it subsumes a large
76 amount of individual variation in development, reflecting differences in genetic
77 (e.g., inbreeding, mutation, and homozygosity) and environmental (e.g.,
78 nutrient intake, parasite load) factors [16]. While the issue is controversial [17],
79 many studies do show links between symmetry and quality including factors
80 such as growth rate, fecundity, fertility and survivability [16,18,19] and one
81 study has shown that symmetry in both men and women is negatively related
82 to self-reported health problems [20]. Potentially, any link between symmetry
83 and quality, no matter how weak, may be sufficient to create a selection
84 pressure to choose symmetric mates. Symmetry in human faces has then
85 been suggested to be a cue to heritable fitness benefits [21,22] and studies of
86 real [23,24] and manipulated faces [22,25] show that symmetry is found
87 attractive. Facial symmetry is found attractive in different human cultures [26]
88 and in monkey species [27].

89 In some species sexually dimorphic traits advertise genetic quality [14].
90 Larger jawbones, more prominent cheekbones, and thinner cheeks are all
91 sexually dimorphic features in human faces characteristic of males [28,29].
92 Such masculine features are associated with higher testosterone in males [30]
93 while feminine features are associated with higher oestrogen in females [31].
94 Secondary sexual characteristics may be linked to parasite resistance
95 because the sex hormones which influence their growth, particularly
96 testosterone, lower immuno-competence [32]. Larger secondary sexual
97 characteristics should be related to a healthier immune system because only
98 healthy organisms can afford the high sex hormone handicap on the immune

99 system that is necessary to produce them [33]. There is evidence in humans
100 that testosterone acts as an immunosuppressant [34] but the data for women
101 is less clear (see discussion). Testosterone may have a greater impact on
102 immune function than oestrogen making sexually dimorphic features more
103 costly for males.

104 Perceived masculinity in human faces is positively correlated with
105 males' long-term health as assessed from medical records [35] and from self-
106 reports [20]. Sexual dimorphism may also be linked to other mechanisms of
107 quality advertising through links with testosterone, which influences behaviour
108 [36]. In women femininity may also be linked to fertility through an association
109 with oestrogen [31]. Sexual dimorphism in faces, another proposed marker of
110 genetic quality [21,29,37], also influences preferences. Males prefer feminised
111 female faces and females show increased preferences for masculinity in
112 contexts consistent with masculinity signalling some aspect of quality [38,39].

113 If symmetry and masculinity honestly indicate the quality of individuals,
114 high quality individuals should develop large sexual ornaments which have
115 little asymmetry. There is evidence for this within and across bird species
116 where larger ornaments, such as tails, tend to be more symmetrical than
117 smaller ornaments [13]. Associations between symmetry and trait size are
118 more consistent with indicator models than an arbitrary process [8,13]. If
119 quality was unrelated to size and symmetry we would expect the cost of
120 ornamentation to create developmental stress for their owners leading to
121 increased asymmetry in large ornaments. However, if only high quality
122 individuals are capable of bearing the handicap of growing large traits or
123 symmetric traits we would expect size and symmetry of traits to correlate.

124 If symmetry and sexual dimorphism in faces indicate quality then a
125 positive correlation between symmetry and sexual dimorphism would be
126 predicted. Evidence for associations between symmetry and sexual
127 dimorphism in men and women is equivocal, however [23,24,40,41], and as of
128 yet only city-based student samples have been examined.

129 Here we examined the relationship between measured facial symmetry
130 and facial sexual dimorphism in human population samples from Europe and
131 from an environment likely to reflect humans living under more evolutionary
132 relevant conditions (the Hadza of Tanzania, Africa) as well as in a non-human
133 primate (rhesus macaques, *Macaca mulatta*). We measured facial symmetry
134 and sexual dimorphism from landmark points and tested for relationships
135 between symmetry and sexually dimorphic proportions. We also tested if
136 composites of symmetrical faces within each sample were perceived as being
137 more sex-typical than composites of asymmetric faces.

138

139 **Methods**

140 **Photographs**

141 For the European images, male (177 individuals) and female (318 individuals)
142 participants had their photograph taken in the laboratory with a digital camera
143 under standardised lighting conditions. Participants were asked to pose with a
144 neutral expression and to look directly into the camera to produce front on
145 facial photographs. Participants were asked not to smile and to relax their face
146 during photographs. Neutral expressions (as posed by our participants) can
147 be seen in the average faces presented later. All individuals were less than 30
148 years old (ranging from 17-29, mean = 20.6, SD =2.2). Participants were UK

149 based university students who volunteered to take part in psychology studies
150 and were primarily UK residents. The photographs were taken at the
151 universities of Liverpool, Stirling, and St Andrews. Written consent was
152 obtained for all participants and the collection of photographs was approved
153 by relevant ethics committees at each institution.

154 The macaque and Hadza images could not be collected under
155 laboratory conditions. For the macaque images, a digital video camera was
156 used to capture images of adult males (105 individuals) and females (111
157 individuals) from the free-ranging population of rhesus macaques on Cayo
158 Santiago, Puerto Rico. Only full-face images with neutral expressions were
159 used, taken from video footage. All macaques had identifying tattoos, which
160 were noted during image acquisition by CW, ensuring that all individuals
161 included were unique. Images were collected from Cayo Santiago field
162 station, the Primate Ecology Section of the National Institutes of Health
163 Laboratory of Perinatal Physiology, which abides by US laws and practices in
164 the ethical treatment of animals.

165 For the Hadza images, male (67 individuals) and female (69
166 individuals) participants had their photograph taken with a digital camera
167 under variable outside lighting conditions. Participants were asked to pose
168 with a neutral expression and to look directly into the camera. Head tilt and
169 variation was evident for Hadza images and so images were selected by ACL
170 on the basis of having a young adult appearance, a neutral expression, and
171 they were looking directly the camera. Images were taken by FWM and the
172 full set represented the majority of Hadza. Perceived age was used to select
173 Hadza images and examining the composite images below show the average

174 perceived ages. Verbal consent was obtained for all participants and the
175 collection of photographs was approved by Harvard's ethics internal review
176 board. Written consent was not obtained due to constraints in the field and
177 posing for the photographs implies implicit consent.

178

179 **Measurements**

180 We estimated horizontal asymmetry from x-y co-ordinates of 6 bilateral points
181 following techniques used in previous studies [23,24,37] (see Figure 1).
182 Briefly, symmetry was calculated by taking left and right deviation from the
183 midline, calculated from inter-pupillary distance, for points and then summing
184 the absolute value of individual scores. These symmetry measurements have
185 been found to correlate with perceived measures of symmetry [24]. While
186 pictures were initially screened for head tilt there was still the potential for
187 outliers in facial asymmetry. For the full set, including all image types, mean
188 asymmetry ranged from 5.8 to 187.7 with a mean of 50.0 and a standard
189 deviation of 29.4. This suggested extreme values beyond two standard
190 deviations (109) and so we adopted a conservative criterion of 120 to remove
191 potential outliers. Any images with asymmetry scores higher than 120 were
192 then excluded from the analysis for all sets. This removed 27 images from the
193 original set of 874.

194 Sexual dimorphism measures were also taken from points marked on
195 facial features (Figure 1). The identification of these features has been found
196 to be reliable in previous studies [23,37]. Following earlier studies, faces were
197 standardised on interpupillary distance to eliminate variation in head distance
198 from the camera. This is of particular importance for the Hadza and macaque

199 images taken under non-standard conditions at varying camera distances.
200 Colour differences between the images are irrelevant for measurements as
201 they involve only shape information.

202 In total, four sexual dimorphism measurements were taken. These
203 were Cheekbone Prominence (ChP, D3/D6), Jaw Height/Lower Face Height
204 (JH/LFH, D9/D8), Lower Face Height/Face Height (LFH/FH, D7/D8), and Face
205 Width/Lower Face Height (FW/LFH, D3/D8). These were found to be sexually
206 dimorphic in the European sample here (see below) and in previous studies
207 [24]. JH/LFH is a new measure here.

208

209 *Descriptives and distributions of scores*

210 Descriptives for each variable split by image type and sex of image can be
211 seen in Table S1. Kolmogorov-Smirnoff tests were used to test for normality of
212 distribution (presented in Table S1). Significant deviation from normality was
213 seen notably for asymmetry in the European sample in both men and women.
214 This was the result of a skew towards low asymmetry for these measurements
215 from these image sets.

216

217 *Fluctuating asymmetry and directional asymmetry*

218 The six measures of asymmetry (D1 to D6) may display fluctuating
219 asymmetry, (FA, right minus left approx 0) or directional asymmetry (DA, right
220 minus left deviates from 0). We randomly selected 50 images from each
221 grouping (male/female x macaque/ European/Hadza) so that each image set
222 was equally represented in the following calculations. We calculated scores
223 for right-left for each trait and conducted 1-sample t-tests against 0 to test for

224 deviations. This revealed directional asymmetry for 4 traits. If traits exhibit DA
225 then some individual variation may be due to heritable variation rather than
226 being a measure of developmental stability [42]. We must then exercise some
227 caution in concluding that such measures reflect only developmental stability.
228 While the differences are significant, we do note that the proportions do not
229 indicate uniformity of direction (i.e., it is not true that, for example, the distance
230 from the inner eye to the midline is always greater on the right hand side of
231 the face) . We note also the large sample sizes here allow us to see small
232 effects and that there is a positive correlation between a composite score of
233 FA and a composite score of DA traits ($r = .174$, $p = .003$) indicating the
234 measures tap the same underlying factor. Most importantly, while 4 of the 6
235 traits demonstrate DA this does not mean that a significant proportion of the
236 measure is DA. Our measure represents FA+DA. For each face we computed
237 a second measure taking the difference from the average difference from the
238 mean for each trait. For this score the mean is exactly 0 and represents an
239 estimation of FA only, controlling for average genetic or other effects that
240 cause the trait to be directional in nature. The correlation between our original
241 measure and this second number for our sample is very high ($r = .96$, $p <$
242 $.001$, $r^2 = .92$) indicating that DA likely accounts for only 8% while FA
243 accounts for 92% of the variance in our original measures. This suggests our
244 measure largely reflects FA and not DA. See Table S2 for descriptive
245 statistics of asymmetry.

246

247 *Sexual dimorphism in measures*

248 Multivariate ANOVA's were carried out with sex of face as the fixed factor and
249 masculinity measures as the dependent variables. For Europeans this
250 revealed significant sexual dimorphism for all traits, with females scoring
251 higher for FW/LFH ($F_{1,493} = 57.2, p < .001$) and ChP ($F_{1,493} = 82.8, p < .001$)
252 and males scoring higher for JH/LFH ($F_{1,493} = 53.0, p < .001$) and LFH/FH
253 ($F_{1,493} = 45.6, p < .001$). For Hadza this revealed significant sexual
254 dimorphism for FW/LFH ($F_{1,134} = 26.7, p < .001$) and ChP ($F_{1,134} = 8.1, p =$
255 $.005$), with females scoring higher for both these traits but no significant
256 differences for JH/LFH ($F_{1,134} = 0.1, p = .75$) and LFH/FH ($F_{1,134} = 0.4, p =$
257 $.53$). For macaques this revealed significant or near significant sexual
258 dimorphism for all traits, with females scoring higher for ChP ($F_{1,214} = 4.7, p =$
259 $.031$) and males scoring higher for JH/LFH ($F_{1,214} = 9.3, p = .003$), LFH/FH
260 ($F_{1,214} = 141.5, p < .001$) and FW/LFH ($F_{1,214} = 3.5, p = .061$).

261

262 *Correlations between measures of masculinity and with symmetry*

263 Tables S3, S4, and S5 show the correlations between all of the variables for
264 each image set and for male and female images. The correlations with
265 asymmetry are equivalent to the results of the regression analysis as only a
266 single variable persists in each analysis.

267

268 **Making composite images**

269 The 15 highest and lowest asymmetry scores for males and females were
270 selected to make up the composites. For each set of 15 face images a single
271 composite face was produced. The composite faces were created using
272 specially designed software. Key locations (174 points) were manually marked

273 around the main features and the outline of each face. The average location
274 of each point in the 15 faces for each composite was then calculated. The
275 features of the individual faces were then morphed to the relevant average
276 shape before superimposing the images to produce a photographic quality
277 result. For more information on this technique see [43,44]. Composite images
278 can be seen in Figure 1.

279 As the Hadza and the macaque images differed in lighting conditions
280 we blended the shape and colour of the symmetric and asymmetric version
281 together for each pair and then applied only the resultant colour to each
282 original pair. This meant all images were standardised within pairs, so that
283 both images possessed the same basic colouration. Images were also
284 cropped to display only facial information.

285 An additional set of composite pairs were created for control purposes.
286 These were made using the same methods as above but consisted of 15
287 randomly selected images from the appropriate groups. While random these
288 images were labelled in the same manner (symmetric/asymmetric).

289

290 **Rating the composite images**

291 *Participants*

292 50 individuals (27 female, mean age 28.8, SD = 6.7) judged the
293 symmetric/asymmetric composites. 37 individuals judged the random
294 composites (23 female, mean age 28.3, SD = 10.7). All individuals were
295 volunteers responding to link on an electronic poster system and were UK
296 based university students.

297

298 *Procedure*

299 Participants were administered a short questionnaire assessing age and sex
300 before completing the face tests. The 6 pairs of symmetric and asymmetric
301 faces of each sex were presented in separate blocks. Male faces were rated
302 first, followed by female faces. Faces appeared on the screen side by side.
303 Both order and side of presentation were randomised. Participants were
304 asked to choose the face of the pair that they found most typical for that sex
305 (i.e., for male faces: “which face appears most typical of males”). This action
306 initiated the next face trial. A second set of participants completed the same
307 trials but using the random composites.

308

309 **Results**310 *Measurements: composite measures of sexual dimorphism*

311 In order for comparison amongst face type scores were standardised
312 separately by face-type so that the mean for each group was 0 with a
313 standard deviation of 1. An overall asymmetry score (sum of the absolute
314 values of deviation from midline for D1-D6) and an overall masculinity score
315 ($[(JH/LFH+LFH/FH)]-[ChP+ FW/LFH]$) were calculated.

316 A univariate ANCOVA was conducted with asymmetry as the
317 dependent variable, face-type (European/Hadza/Macaque) as a factor, and
318 average masculinity as covariate. For female faces this revealed masculinity
319 was not significantly related to asymmetry ($F_{1,452} = 2.10$, $p = .148$). Other
320 effects and interactions were not significant ($F_{2,452} < 2.44$, $p > .088$). For male
321 faces this revealed masculinity was significantly related to asymmetry ($F_{1,343} =$
322 12.09 , $p < .001$). Other effects and interactions were not significant ($F_{2,343} <$

323 1.23 , $p > .295$). Pearson product moment correlations between asymmetry
324 and masculinity revealed that there was no significant correlation for female
325 faces ($r = -0.48$, $p = .285$) and a significant negative correlation for males
326 faces ($r = -.203$, $p < .001$).

327 As a secondary analysis we conducted a discriminant analysis using
328 the four sexually dimorphic measures to discriminate sex of face separately
329 for each face-type. Groups differed based on classification: European (Wilks'
330 Lambda = .74, $X^2 = 148.98$, $DF = 4$, $p < .001$), Hadza (Wilks' Lambda = .78,
331 $X^2 = 33.11$, $DF = 4$, $p < .001$), and macaque (Wilks' Lambda = .96, $X^2 = 8.25$,
332 $DF = 4$, $p = .083$). Classification was correct/incorrect: female 346/152, male
333 238/111. A univariate ANOVA was conducted with asymmetry as the
334 dependent variable, and face-type (European/Hadza/Macaque), sex
335 (male/female), and classification (male/female) as factors. This revealed a
336 significant interaction between sex and classification ($F_{1,835} = 4.07$, $p = .044$).
337 The interaction reflected that faces that were misclassified according to facial
338 measures demonstrated greater asymmetry than faces that were classified as
339 sex typical (see Figure 2). A theoretically unrelated significant interaction
340 between face-type and classification was also found ($F_{1,835} = 4.37$, $p = .012$).
341 Other effects and interactions were not significant ($F_{1/2,343} < 1.22$, $p > .296$).

342

343 *Measurements: regression of sexually dimorphic traits by sex and face-type*

344 Overall asymmetry score was predicted using the four individual
345 measures of sexual dimorphism (see Methods) entered into a backwards
346 linear regression analysis ($p = .1$ criteria, only the final model is reported
347 here). Measures of sexual dimorphism were treated separately as correlations

348 between these traits were generally low. For full interrelationships between
349 measures of symmetry and sexual dimorphism see Tables S3, S4, and S5.

350 For European faces, the model was close to significant for females
351 ($F_{1,316} = 3.1, p = .080, R^2 = .01$) where the masculine trait LFH/FH was
352 positively related to asymmetry ($\beta = .10, p = .080$). The model for males was
353 significant ($F_{1,175} = 6.6, p = .011, R^2 = .04$) where the masculine trait JH/LFH
354 was negatively related to asymmetry ($\beta = -.19, p = .011$).

355 For Hadza faces, the model was not significant for females with no
356 significant predictors (all $p > .23$) but was significant for males ($F_{1,65} = 7.1, p =$
357 $.010, R^2 = .10$), where the masculine trait JH/LFH was negatively related to
358 asymmetry ($\beta = -.31, p = .010$).

359 For macaque faces, the model revealed a significant model for females
360 ($F_{1,109} = 4.6, p = .035, R^2 = .04$), where the masculine trait JH/LFH was
361 positively related to asymmetry ($\beta = .20, p = .035$). The model for males was
362 also significant ($F_{1,103} = 4.0, p = .047, R^2 = .04$), where the masculine trait
363 LFH/FH was negatively related to asymmetry ($\beta = -.19, p = .047$).

364 The results of this analysis are robust to corrections for multiple tests
365 (see Text S1, Table S6).

366

367 *Perception of composites*

368 Measured sexual dimorphism may not capture all aspects of this trait to which
369 humans are visually sensitive. To examine perception, composite images of
370 individuals with high and low facial asymmetry were created for males and
371 females of each population (see Methods, Figure 3). These image pairs were
372 shown to European human participants, who were asked out of the pair which

373 was more typical of their sex in appearance. Chi square tests were conducted
374 on the proportions showing that, for females, symmetric Hadza ($\chi^2 = 5.1, p =$
375 $.021$) and Europeans ($\chi^2 = 25.9, p < .001$) were selected as more typically
376 female than asymmetric Hadza and Europeans. Proportions were not
377 significantly different for female symmetric and asymmetric macaques ($\chi^2 =$
378 $0.7, p = .40$). For males, symmetric Hadza ($\chi^2 = 2.9, p = .088, p = .044$ one-
379 tailed as predicted from measurement data), macaques ($\chi^2 = 3.9, p = .048$),
380 and Europeans ($\chi^2 = 8.0, p = .005$) were selected as more typically male than
381 asymmetric Hadza, macaques, and Europeans. Proportions can be seen in
382 Figure 4. A binomial test revealed that the proportion of symmetric images
383 being chosen as most sexually dimorphic significantly differed from chance
384 (chosen = 6/6, chance 3/6, $p = .031$).

385 Comparing the overall scores to chance (50%) using one-sample t-
386 tests revealed that the choice of symmetric/asymmetric composites differed
387 from chance (mean=67%, SD=17%, $t_{49} = 7.01, p < .001$) while the random
388 composites did not (mean=47%, SD=17%, $t_{36} = 7.01, p = .337$). An
389 independent-samples t-test revealed a significant difference in choice
390 between symmetric/asymmetric and random composites ($t_{85} = 5.36, p < .001$).
391 Thus the overall pattern for the composites was that symmetric images were
392 seen as more sexually dimorphic in humans and male macaques using both
393 chance and a control set of images as criterion.

394

395 **Discussion**

396 Our results indicate that symmetry and sexually dimorphic traits are related in
397 male and female faces in humans, in a modern western society and in a

398 different society living under conditions better approximating human
399 evolutionary history, and across species, both in humans and a non-human
400 primate. We found symmetry was related to sexual dimorphism using physical
401 measurements of large numbers of faces and perceptual tests based on the
402 perceived sexual dimorphism of faces that were most and least symmetric in
403 our samples. We note that only European participants provided the ratings of
404 the composites and it is likely difficult for them with limited experience to judge
405 masculinity in Hadza and macaque faces. In fact this raises an interesting
406 point. The generally consistent judgement that symmetric individuals
407 appeared more sexually dimorphic across all face types from European
408 judges that there is some commonality in features that cross culture and
409 species.

410 We note that the measurements may not necessarily capture sexual
411 dimorphism fully (as suggested by the discriminant analysis) but that together
412 the patterns of the measurement and perceptual data supports the notion that
413 sexual dimorphism and symmetry in faces are linked. We also note that some
414 caution must be taken in interpretation as our symmetry measurements do not
415 all fully fulfil the criteria for fluctuating asymmetry, though appear to mainly
416 capture FA and not DA (see Methods). The DA in our measures might reflect
417 expressive habits, for example, natural smiles are asymmetric reflecting
418 hemispheric specialisation in the control of emotion [45]. We also note that the
419 different types of analysis reveal some differences in sex effects as sexual
420 dimorphism was not found to be related to symmetry using an additive
421 measure whereas a relationship emerged in the discriminant analysis. The
422 overall pattern, however, is that symmetry was related to some aspect of

423 dimorphism either via one aspect of measurement: overall additive or
424 discriminative measurements, individual trait measures, or perceptual
425 measures.

426 If sexual dimorphism and symmetry in faces advertise quality in both
427 males and females then only high quality males can grow symmetric and
428 masculine and high quality females can grow symmetric and feminine. Similar
429 arguments have been put forward to explain co-variation between trait size
430 and symmetry in birds [13]. This relationship then suggests that notions of
431 symmetry and sexual dimorphism signalling a single aspect of quality are true.
432 We also note, however, that the relationship is not absolute, leaving the
433 potential that both may also signal other separable qualities. Symmetry and
434 sexual dimorphism may then be seen as complementary signals of the same
435 quality, but may also signal other qualities independently. Previous studies
436 have shown negative associations between symmetry and trait size in the
437 secondary sexual traits of a variety of taxa, including birds and primates
438 [3,13]. The results here demonstrate that faces are involved in selection with
439 no obvious association with weaponry involved in intra-sexual selection, as
440 shown in previous studies of primate tooth dimorphism. Bare skin on faces in
441 primate species is common [46], further highlighting the potential role for
442 sexual selection acting on faces across the primate lineage.

443 Sexual dimorphism is facilitated by sex hormones [47]. Symmetry is
444 linked to developmental stability [16]. Symmetry and sexual dimorphism may
445 be linked by an underlying biological factor. For example, both may reflect
446 gene quality. If high quality genes are those that code, potentially, for efficient
447 immune systems, high metabolic efficiency, or even behavioural traits that

448 secure resources for an organism during development, then such genes may
449 also allow an organism to grow both symmetric and sexually dimorphic. By
450 measuring how well an organism can cope with genomic stress and
451 environmental perturbations, symmetry may be an honest signal of gene-
452 quality given that studies show that such stressors during development
453 increase asymmetry [48]. The link between sexual dimorphism and good-
454 genes advertisement has produced many more theories. Honest signalling in
455 this case might arise through an immuno-competence handicap mechanism
456 [49], whereby sex hormones represent a behavioural or immunological
457 handicap to the organism. Other mechanisms may also create honesty in
458 hormone mediated traits, for example via cortisol levels [50]. Theoretically,
459 honesty can also arise, when high-quality individuals achieve greater benefit
460 from an allocation to a trait than do low-quality individuals even when the
461 costs of the trait are equivalent [51]. Mate choice based on symmetry and
462 sexual dimorphism may then provide indirect benefits, acquiring good-genes
463 from partners that benefit offspring, or direct benefits, acquiring factors other
464 than good-genes from partners that benefit the choosing individual, such as
465 resources. Of course there are other potential benefits of sexual dimorphism
466 and symmetry, for example fertility [19,31]. Ultimately it may be unnecessary
467 to consider the relative weights of indirect and direct benefits as they are
468 difficult to tease apart. For example, males with good-genes for immunity may
469 also be most able to provide food or defend a large, high quality territory; thus
470 selection for good resources/behaviour may reflect selection for good-genes.
471 The current study shows that symmetry and sexual dimorphism are related in
472 both male and female faces across cultures and species. Examining the

473 regression models suggests that the relationship between symmetry and
474 sexual dimorphism is stronger for males than for females for both the
475 European and Hadza samples; Hadza males also retain symmetry with age
476 more than females do [52]. In the additive measures, symmetry was related to
477 dimorphism only for males, but the discriminant measure was related in
478 females. Our perceptual test may be biased in examining sex differences as it
479 is dependent on the number of images in the sample. For example, we may
480 see the largest effect in females in the European sample potentially because
481 we had the largest number of participants in this group, making the
482 composites more likely to represent the extremes of asymmetry. Following the
483 regression models then, we do see a more consistent effect in male faces.
484 The immuno-competence-handicap hypothesis was originally proposed for
485 males and there is reasonable evidence testosterone reduces immune
486 function [32]. Weaker relationships for symmetry and femininity in females
487 may stem from the fact that the relationship between oestrogen and immuno-
488 competence appears weaker than between testosterone and immuno-
489 competence. In humans, higher oestrogen is linked to development of cancers
490 [53], suggestive of a reduction in immune function, although animal studies
491 suggest that while suppressing cell-mediated immunity, oestrogen may
492 enhance humoral immunity [54]. As feminine facial traits differ less from
493 immature traits than do male traits [28], they are also potentially less costly to
494 produce. Taken together these findings suggest that feminine traits may be
495 less powerful signals of good-genes than masculine traits, although we note
496 there that here femininity in female faces is correlated with symmetry, another
497 proposed aspect of quality. Additionally, our data does not necessarily support

498 the idea that sexual dimorphism represents a single continuum in faces. We
499 generally found relatively weak correlations amongst dimorphism measures
500 (see Tables S3, S4, and S5). Here perhaps we have evidence that certain
501 face traits may be more involved in sexual selection than others.

502 While studies demonstrate that preferences can arise via experience
503 [55,56], as a by-product of pattern recognition in the visual system works
504 without either trait being related to quality, such reasoning does not predict co-
505 variation between traits in natural populations. It has also been suggested the
506 preference for symmetry of tails in bird species may in fact be due to
507 aerodynamics and not developmental stress [17]. While this would be
508 plausible for a species in which small deviations in symmetry may have large
509 effects, as is the case for flying, it is difficult to imagine such small deviations
510 in symmetry would impact on motor action in faces so much as to appear
511 unattractive. Such views imply that symmetry and sexual dimorphism
512 preferences are arbitrary and neither view proposes underlying mechanisms
513 that would influence the development of both.

514 In conclusion, our finding of sex specific co-variation with symmetry,
515 femininity for females, masculinity for males, indicates then that both sexual
516 dimorphism and symmetry likely are signals advertising quality. We have
517 shown such a relationship in diverse human cultures and in a monkey
518 species, which suggests that signalling properties of faces are universal
519 across human populations and that facial advertisements of quality may have
520 arisen relatively early in the phylogeny of primates.

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Figure Legends

Figure 1: Measurements for symmetry and sexual dimorphism. Symmetry was calculated by taking left and right deviation from the midline, calculated from inter-pupillary distance, for points D1-D6 and then summing the absolute value of individual scores. Sexual dimorphism was measured by measuring distance between specific points and calculating four ratios based on these distances: Cheekbone Prominence (ChP, D3/D6), Jaw Height/Lower Face Height (JH/LFH, D9/D8), Lower Face Height/Face Height (LFH/FH, D8/D7), and Face Width/Lower Face Height (FW/LFH, D3/D8). All images were normalised on inter-pupillary distance.

Figure 2: Asymmetry (\pm 1SE of mean) of faces classified as male or female in the discriminant analysis by sex of face. A significant interaction was found between sex of face and classification ($F_{1,835} = 4.07$, $p = .044$) indicating that those correctly classified to their own sex were more symmetric than those misclassified to the opposite-sex.

Figure 3: High and low symmetry composite faces for macaques, Hadza, and Europeans. All images are normalised on inter-pupillary distance to control relative image size, have been made perfectly symmetric, and each high/low pair possesses the average colour information of both. Perceptual differences are then dependent on shape differences between high and low symmetry faces that are independent of symmetry.

Figure 4: Proportion of individuals choosing high and low symmetry composite faces for macaques, Hadza, and Europeans as most sex-typical (i.e. masculine for males, feminine for females).