

**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 a priori 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).