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1 Lack of correlation between fluctuating asymmetry and morphological masculinity/femininity in
2 primate skulls

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8

9 **Abstract**

10

11 As both degree of masculinity/femininity in sexually dimorphic organisms and developmental
12 instability are put forward as indicators of individual quality, they are expected to correlate
13 positively. However, the results in the literature are equivocal. One reason may be that most research
14 has been performed in populations exposed to relatively low levels of parasitism. This paper studies
15 associations between the degree of masculinity/femininity and the fluctuating asymmetry (a measure
16 of developmental instability) of skulls of three primate species (baboon (*Papio anubis*), eastern
17 lowland gorilla (*Gorilla beringei graueri*) and chimpanzee (*Pan troglodytes*)) collected in the wild.
18 The exposure to infection and parasites is likely to be higher in these animals compared to captive
19 primates and humans, therefore likely to increase the levels of association. While the degree of
20 individual masculinity/femininity and levels of fluctuating asymmetry were quantified accurately, I
21 found no evidence of an association between them. My results thus are in line with the conclusion of
22 a recent meta-analysis, that there is little evidence for associations between masculinity/femininity
23 and developmental instability.

24

25 **Introduction**

26 Small directionally random bodily and facial deviations from perfect symmetry or from directional
27 asymmetry (i.e., consistent asymmetries in a particular direction), termed fluctuating asymmetry (
28 FA), are commonly used markers of developmental instability (DI), the inability of a developing
29 organism to buffer its development against random perturbations (Klingenberg, 2003). DI may
30 increase with stress (like malnutrition, inbreeding depression or exposure to toxic compounds) and
31 may inversely relate to individual quality (Palmer and Strobeck, 1986, Polak, 2003). The underlying
32 idea about the use of FA as a measure of DI is that both sides represent independent replicates of the
33 same developmental event under identical conditions. Differences between sides then must reflect
34 minor developmental errors (Palmer and Strobeck, 1986, Klingenberg, 2003). Initially, the concept
35 of DI was applied at the population level to detect sources of environmental or genetic stress
36 (Leamy, 1984). Later, the concept was also studied at the individual level (e.g., Møller, 1992),
37 assuming a genetic basis of DI (Møller and Thornhill, 1997). However, Møller and Thornhill (1997)
38 received a lot of criticism (e.g., Houle, 1997, Palmer and Strobeck, 1997) and the debate about the
39 genetic basis of DI is still unresolved (e.g., Van Dongen & Forstmeier, 2013). Furthermore, the
40 association between DI and individual fitness or health also varies a lot between studies (e.g., Van
41 Dongen & Gangestad, 2011). In a recent meta-analysis of the human literature, a robust association
42 between DI and measures of health and quality (e.g., reproductive success indicators, attractiveness)
43 was found, but also a large amount of unexplained variation across studies emerged (Van Dongen &
44 Gangestad, 2011). In addition, signatures of publication bias were found through negative
45 associations between effect sizes and sample sizes reducing the estimated average strength of
46 association from 0.18 to 0.10 (Van Dongen & Gangestad, 2011). Consequently, generalizations of
47 observed patterns require great care. This also seems to be the case for some specific areas of FA
48 research including the association between FA and attractiveness (Van Dongen, 2011, 2012), casting

49 doubt on the general link between DI and individual quality (as measured by for example, health,
50 survival probability or reproductive success).

51 One area of research on the link between DI and individual quality that has received a reasonable
52 amount of attention in the recent literature are associations between FA and levels of morphological
53 masculinity or femininity in human body and faces, as the latter may also reflect individual quality
54 (Van Dongen, 2012). Sexual selection, resulting in sometimes very obvious morphological and
55 behavioral differences between males and females, has intrigued biologists at least since the work by
56 Darwin during the mid nineteenth century (Darwin, 1859)). A central theme in the evolution of sexual
57 dimorphism is to understand which selective forces act on males and females that differ in their
58 levels of masculinity and femininity, respectively (Fairbairn & Blanckenhorn, 2007). One approach
59 to study this research question is to estimate covariances between stress and levels of
60 masculinity/femininity. One such measure of stress – applied in this study – is developmental
61 instability, as estimated by FA.

62 Sexual dimorphism occurs when at the species level, males and females differ in particular features
63 as a result of sexual selection. Besides the evolution of an average (morphological) difference
64 between males and females, sexual selection also causes within-sex variation in these traits
65 (Fairbairn & Blanckenhorn, 2007). Some males will be more masculine than others, while some
66 females will be more feminine than others. More masculine or feminine features are (assumed to be)
67 associated with higher testosterone or estrogen levels respectively (Verdonck et al., 1999; Little et
68 al., 2008; Lefevre et al., 2014), which in turn may act as immunosuppressant (Kanda et al., 1996;
69 Perrett et al., 1998). It has therefore been argued that larger secondary sexual characteristics should
70 be related to a healthier immune system because only healthy individuals can afford the high sex
71 hormone handicap (Zahavi, 1975; Gangestad & Thornhill, 2003; Little et al., 2008). This hypothesis
72 fits the ‘good genes’ hypothesis, where individuals bearing genes that result in a more efficient
73 immune system are also able to resist developmental perturbations during growth (Perrett et al.,

74 1998; Gangestad & Thornhill, 2003; Little et al., 2008). However, because of trade-offs between
75 investment in reproductive traits and somatic investment (e.g., immune defenses), high quality
76 individuals may, under intense sexual selection, be ‘forced’ to invest in reproduction to such a large
77 degree that they actually have worse health and poorer survival prospects than individuals of low
78 quality (Getty, 2002; Kokko et al., 2002). Thus, if both symmetry and masculinity/femininity reflect
79 or signal quality, both should be positively correlated where high quality males can grow symmetric
80 and masculine and high quality females can grow symmetric and feminine (Little, et al., 2008;
81 Brown, et al., 2008; Gangestad & Thornhill, 2003). However, if sexual selection drives high quality
82 individuals to display extreme masculine/feminine features, these may come at the expense of health
83 herewith potentially modifying the association between masculinity/femininity and FA. In extreme
84 cases, one would predict a negative association between symmetry and masculinity in males, and a
85 negative one between symmetry and femininity in females. Recently, Puts (2010) argued that
86 androgen-dependent masculine traits may be produced in proportion to inherited
87 immunocompetence, so that good-gene males end up little healthier than average. The regulation of
88 androgen levels and the response to them may thus have evolved as a means of producing sexually
89 selected traits in proportion to a male’s ability to safely bare them. If so, little or no relationship
90 between masculinity/femininity and FA is expected. This last hypothesis can be seen as a
91 combination of the two previous ones, which of course are not mutually exclusive and can operate
92 within a single population. The direction and degree of association between FA and
93 masculinity/femininity could thus be interpreted as a measure of the strength of sexual selection and
94 associated investments in reproductive traits.

95 The association between FA and measures of masculinity/femininity has been studied several times
96 (see Van Dongen, 2009, 2012 and Van Dongen & Gangestad, 2011 for recent reviews;). At least
97 some studies have shown higher symmetry in more masculine males and more or feminine females
98 respectively (Little et al., 2008; Brown et al., 2008; Gangestad & Thornhill, 2003). A similar result

99 was reported for macaques Little et al., 2008). Others found much less convincing results (Koehler et
100 al., 2004). In a review of this literature using meta-analysis techniques, estimates of average effect
101 sizes were close to zero (Van Dongen 2012). The same conclusion was reached for associations
102 between FA and digit ratios (Van Dongen 2009). Nevertheless, Van Dongen (2012) also noted that
103 strong and robust conclusions could not be reached at present. Firstly, between-study variability in
104 outcomes results in relatively wide confidence intervals (Van Dongen & Gangestad, 2011). In
105 addition, the link between FA and DI is inherently weak (because a variance is estimated using only
106 2 datapoints), leading to even wider confidence intervals, such that weak to moderate associations
107 between DI and masculinity/femininity cannot be excluded on the basis of the current studies
108 available. Furthermore, most research in humans is conducted in our Western society, where the
109 occurrence of infections and parasitism are relatively weak (although allergies and auto-immune
110 diseases may be higher), which could mask the immunosuppressant effects of sex hormones, and
111 thus the expected associations with FA. Exceptions are the work on Hadza and free ranging rhesus
112 macaques (Little et al., 2008).

113 The aim of this paper is to contribute to this literature by studying the association between individual
114 masculinity/femininity and FA in skulls of primates captured in the wild. I obtained 3D landmark
115 data from the skulls of 121 primates with different degrees of sexual dimorphism and different
116 mating systems (namely baboon (*Papio anubis*), eastern lowland gorilla (*Gorilla beringei graueri*)
117 and chimpanzee (*Pan troglodytes*)). In a first step of the analyses, I studied sexual dimorphism and
118 obtained estimates of masculinity/femininity at the individual level in skull size and shape. Next, I
119 obtained estimates of individual shape FA and tested the hypothesis that it was correlated with the
120 masculinity/femininity estimates. Patterns were also compared between the three species as their
121 levels of sexual dimorphism differ as well. Baboons live in groups composed of several males and
122 females and success in male-male competition increases male reproductive success (Smuts, 1987;
123 Bergman et al., 2003). Gorillas mainly live in a unimale, multifemale system, where the dominant

124 silverback male protects the group from external threats and tries to prevent females to mate with
125 other lone silverback males (Robbins et al., 2001; Yamagiwa et al., 2003). Chimpanzees have a
126 polygynandrous mating system where both males and females mate with several potential mates
127 (Newton-Fisher, 2014). Gorillas and baboons show much stronger sexual dimorphism compared to
128 chimpanzees (Cobb & O'Higgins, 2007). I predict to observe stronger correlations in this study
129 compared to previously published ones, because 3D shape analyses are performed providing more
130 accurate estimates of masculinity/femininity and asymmetry, and because animals were captured in
131 the wild and most likely suffered a higher exposure to infection and parasitism. In addition, given the
132 stronger sexual selection in baboons and gorillas (also compared to humans), the strongest
133 associations are predicted in these species.

134

135 **Methods**

136 I obtained permission from the Museum of Africa in Tervuren Belgium to access the collections and
137 perform measurements. All the specimens used were collected in the wild in east central Africa and
138 were donated to the museum as part of their permanent collection. All measurements were performed
139 at the Museum by one specifically trained technician. All available skulls were examined and
140 discarded if they showed damaged and/or wear that prohibited identifying all landmarks. I also
141 discarded skulls from juvenile animals (if third molars were not yet present and/or if canines were
142 not fully erupted and/or if sutures were not closed) or when the sex was unknown (often the case for
143 juvenile specimens). In total, 121 were considered of sufficient quality to allow accurate
144 measurement: 50 eastern lowland gorillas (*Gorilla beringei graueri*; 22 males and 28 females; all
145 collected in the Republic of Congo; collection years ranged between 1910 and 1986), 46 olive
146 baboons (*Papio anubis*; 11 males and 35 females; all collected in the Republic of Congo; collection
147 years ranged between 1911 and 1996) and 25 chimpanzees (*Pan troglodytes schweinfurthii* (N=25);
148 12 males and 13 females; mainly collected in the Republic of Congo (N=22), one individual

149 collected in Tanzania, one collected in Burundi and one of unknown origin; collection years ranged
150 between 1896 and 1977). On each skull, a set of 20 3D landmarks (Fig.1) were placed twice on
151 separate days using a microscribe GX2. Geometric morphometric analysis was performed in
152 MorphoJ (version 1.02d) (Klingenberg, 2011). After Procrustes fit, a Procrustes ANOVA was
153 performed to determine the variation due to real FA, measurement error and to test for directional
154 asymmetry (DA) for each species separately.

155 The degree of sexual dimorphism in each species was tested and explored in two ways. First, skull
156 size was estimated as the natural logarithm of centroid size (to assure approximate normality) and
157 compared between males and females in the three species using t-tests. The degree of sexual
158 dimorphism was expressed as a percentage of difference in size between males and females relative
159 to the mean skull size across males and females. Next, a canonical variate analysis was performed to
160 study shape sexual dimorphism in the skull and significance was tested using permutation on the
161 Procrustes distance. Individual scores of both centroid size and the canonical variate of shape sexual
162 dimorphism were then used as measure of masculinity/femininity. Their associations with
163 developmental instability were studied using individual shape FA expressed as a Procrustes distance
164 between sides of the Procrustes alignment after correcting for DA as measure of individual DI,
165 herewith assuming an isotropic model. This choice appeared reasonable as results using the
166 Mahalanobis distance were very similar (details not shown). After standardisation of the masculinity
167 scores by species and sex, an ANCOVA model was set up with skull shape FA as the dependent
168 variable. Individual masculinity scores (either centroid size or shape) were treated as continuous
169 covariates, and interactions with sex and species were also added. Sex and species were also added
170 as main effects to ensure that different intercepts could be estimated in this model. However, since
171 the FA values were standardised by sex and species, the significance of these main effects was not
172 tested. Indeed, in this analysis, the focus is on the association between FA and
173 masculinity/femininity and how this differs between males and females and between species. These

174 differences in associations can be investigated and tested by the two-way and three-way interactions.
175 The t-tests and ANCOVA analyses were performed in R (version 2.10). This approach, using 3D
176 landmark data and obtaining both 3D size and shape estimates of individual masculinity/femininity
177 and 3D shape fluctuating asymmetry is novel to this area of research.

178 **Results**

179 *Directional asymmetry, real fluctuating asymmetry and measurement error:*

180 For each species the mean square of the individual-side interaction was statistically significant and
181 the mean square was larger than the residual variation (gorilla: $MS_{ind*side} = 19.2E-5$, $MS_{error} = 0.9E-5$,
182 $F_{1176,5300} = 4.23$, $p < 0.0001$; baboon: $MS_{ind*side} = 3.3E-5$, $MS_{error} = 1.2E-5$, $F_{1080,4876} = 2.77$, $p < 0.0001$
183 ; chimpanzee: $MS_{ind*side} = 4.1E-5$, $MS_{error} = 3.1E-5$, $F_{696,3180} = 1.31$, $p < 0.0001$). Each species showed
184 significant directional asymmetry (gorilla: $F_{24,1176} = 4.88$, $p < 0.0001$; baboon: $F_{24,1080} = 2.17$,
185 $p = 0.001$; chimpanzee: $F_{24,696} = 1.96$, $p = 0.004$) (Fig. 2).

186

187 *Sexual dimorphism in size and shape:*

188 Skull centroid sizes differed significantly between males and females in each species. Size
189 dimorphism was highest in gorilla (log centroid size: male = 15.1 (SE = 0.007); female = 14.9 (SE =
190 0.005); dimorphism = 1.34%; $t_{48} = 21.9$, $p < 0.0001$), slightly smaller in baboons (log centroid size:
191 male = 14.8 (SE = 0.02); female = 14.6 (SE = 0.01); dimorphism = 1.15%; $t_{44} = 5.6$, $p < 0.0001$), and
192 smallest is chimpanzees (log centroid size: male = 14.74 (SE = 0.01); female = 14.67 (SE = 0.01);
193 dimorphism = 0.41%; $t_{23} = 3.42$, $p < 0.001$). Shape sexual dimorphism was statistically significant in
194 each species (permutation test, all $p < 0.0001$). Dimorphism was highest in baboons (Procrustes
195 distance = 0.07), slightly smaller in gorillas (Procrustes distance = 0.065) and smallest in
196 chimpanzees (Procrustes distance = 0.04) (see Fig.3 for shape differences). No significant
197 associations were found between skull centroid size and individual masculinity/femininity in males
198 and females from the three species (gorilla: males: $r = -0.11$, $N = 28$, $p = 0.58$; females: $r = -0.25$, $N = 22$,

199 $p=0.25$; baboon: males: $r=0.15$, $N=35$, $p=0.24$; females: $r=0.13$, $N=11$, $p=0.70$; chimpanzee: males:
200 $r=-0.45$, $N=12$, $p=0.12$; females: $r=-0.12$, $N=13$, $p=0.69$) indicating the absence of an allometric
201 association between size and sexual dimorphism.

202
203 *Associations between masculinity/femininity and fluctuating asymmetry:*

204 None of the interactions nor the individual masculinity/femininity were statistically significant (all
205 $p>0.2$) (Table 1, Figure 4). Across the three species, the correlation coefficients between FA and
206 masculinity/femininity equaled 0.03 ($N=75$, $p=0.83$) for males and -0.11 ($N=46$, $p=0.46$) for females
207 for centroid size masculinity/femininity; and 0.06 ($N=75$, $p=0.58$) for males and 0.04 ($N=46$, $p=0.81$)
208 for females for shape dimorphism. Correlation coefficients of these associations for males and
209 females of each species separately were not statistically significant (Table 2).

210 211 **Discussion**

212 In contrast to initial predictions, I did not find an association between individual developmental
213 instability and measures of individual masculinity/femininity. While relative strong associations
214 were predicted because I studied specimens captured in the wild and because in baboons and gorillas,
215 sexual selection and dimorphism is strong, this was not supported in this study. Nevertheless, the
216 magnitude of skull shape dimorphism was comparable to that reported by Cobb and O'Higgins
217 (2007). Different predictions can be made about the association between individual
218 masculinity/femininity and developmental instability (see introduction). A recent meta-analysis
219 found no strong evidence for either a positive or negative association between DI and
220 masculinity/femininity, which appears in line with the idea that individuals would trade inherited
221 immunocompetence for sexual competitiveness (Van Dongen 2012). The overall association in the
222 meta-analysis was nearly zero (Puts, 2010; Van Dongen 2012), which is also supported by this study.

223 Thus, no evidence was found that developmental instability and masculinity/femininity are
224 correlated, either positively or negatively, supporting Puts' (2010) view.

225 In the context of null results, it is important to note that levels of individual asymmetry only weakly
226 reflect variation in developmental instability if one or few traits are studied (e.g., Gangestad &
227 Thornhill, 1999; Van Dongen 2012). The reason for this is that when using asymmetry as a measure
228 of DI, one attempts to estimate a variance using only two data points. Therefore, individual
229 asymmetry can only estimate population level FA and the underlying level of DI very crudely. For
230 linear measurements and independently developing traits, it is possible to transform correlation
231 coefficients of associations between asymmetry and a factor of interest into correlation coefficients
232 between DI and those factors. Such transformations are available either for single or multiple traits
233 (Gangestad and Thornhill, 1999). However, no such transformation is available for landmark data. If
234 I assume that the observed correlation coefficients are underestimates by a factor between 2 and 4
235 (see e.g., Gangestad & Thornhill, 1999), the 95% confidence interval of the association between
236 masculinity/femininity and DI could be as wide as between roughly -0.3 and 0.4. The implication
237 thus clearly is that in spite of a moderate sample size (see e.g., Gangestad & Thornhill, 1999; Van
238 Dongen, 2012) of 121 and the use of landmark data, this study – albeit contributing to the evidence
239 of a lack of association between DI and masculinity/femininity – in itself only allows to conclude
240 that associations are unlikely to be above 0.4, and not to make any robust conclusions about the
241 existence of such associations. Nevertheless, it is thus crucial to report all results, either positive or
242 negative, to avoid problems of publication bias when performing meta-analyses. Fortunately, this
243 area of research, i.e., the study of the link between developmental instability and
244 masculinity/femininity, does not seem to suffer from selective reporting (Van Dongen 2012).

245

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247 constructive comments helping to improve this manuscript.

248

249

250 **References**

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362 Zahavi A (1975) Mate selection: a selection for a handicap. *Journal of Theoretical Biology* 53, 205-
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364 Table 1: Tests of significance of the linear model with skull shape fluctuating asymmetry as
365 dependent variable, and masculinity/femininity (scaled size and shape) as continuous explanatory
366 variable and interactions with species and sex as fixed factors. The factors species and sex, albeit
367 added to the model to allow for different intercepts for the different regression lines, were not tested
368 as main effects because the asymmetry and masculinity/femininity values were standardised by both
369 species (gorilla, baboon and chimpanzee) and sex.

370

371 source	centroid size	shape
372 masculinity/femininity	$F_{1,116} = 1.69$	$F_{1,116} = 0.12$
373 masculinity/femininity*species	$F_{1,114} = 0.42$	$F_{1,114} = 0.39$
374 masculinity/femininity*sex	$F_{1,113} = 0.19$	$F_{1,113} = 0.74$
375 sex*species	$F_{2,111} = 0.83$	$F_{2,111} = 0.78$
376 masculinity/femininity*sex*species	$F_{2,109} = 0.09$	$F_{2,109} = 0.77$

377

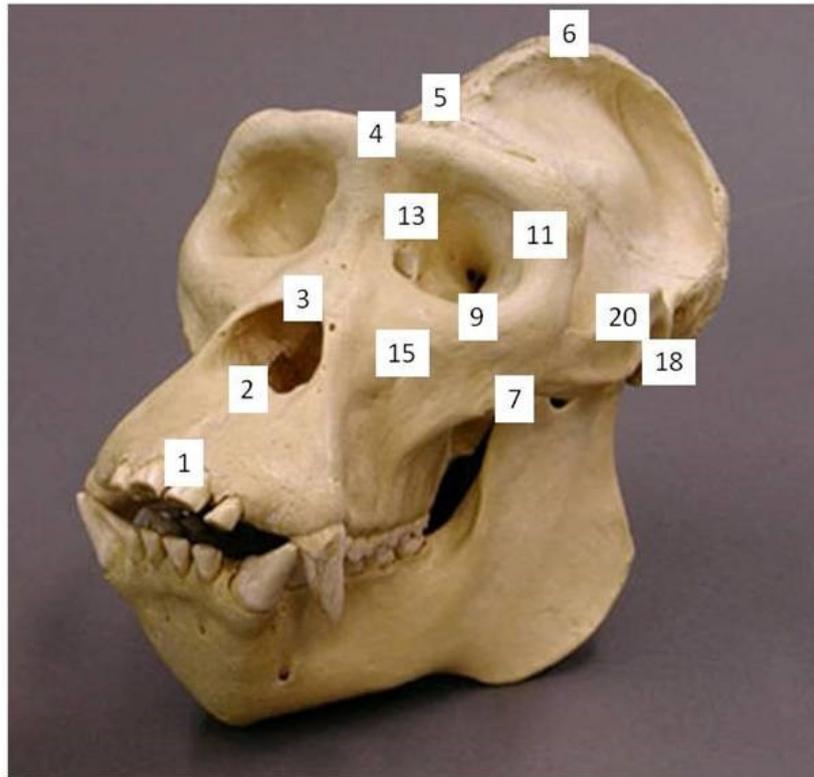
378

379 Table 2: Correlation coefficients and p-values of the association between asymmetry and masculinity
380 for males and females in the three species studied (gorilla, baboon and chimpanzee).

381	Species	sex	shape FA vs. size masculinity	shape FA vs. size masculinity
382	Baboon	male (N=35)	0.29 (p=0.09)	0.27 (p=0.12)
383		female (N=11)	0.14 (p=0.68)	-0.17 (p=0.62)
384	Chimpanzee	male (N=12)	0.22 (p=0.49)	-0.08 (p=0.81)
385		female (N=13)	-0.00 (p=0.99)	0.08 (p=0.79)
386	Gorilla	male (N=28)	0.07 (p=0.73)	0.08 (p=0.68)
387		female (N=22)	0.03 (p=0.90)	-0.20 (p=0.37)

388

389 Figure 1: Overview of landmarks put on the skulls of 3 species of primates. 1: intradentale superior;
390 2: premaxillare; 3: nasale; 4: nasion; 5: bregma; 6: lambda; 7/8: zygomaxillare; 9/10: zygo-orbitale ;
391 11/12: fronto-malare; 13/14: fronto-lacrimale; 15/16: foramen infraorbitale; 17/18: zygomaxillare
392 inferior; 19/20: zygomaxillare superior.
393

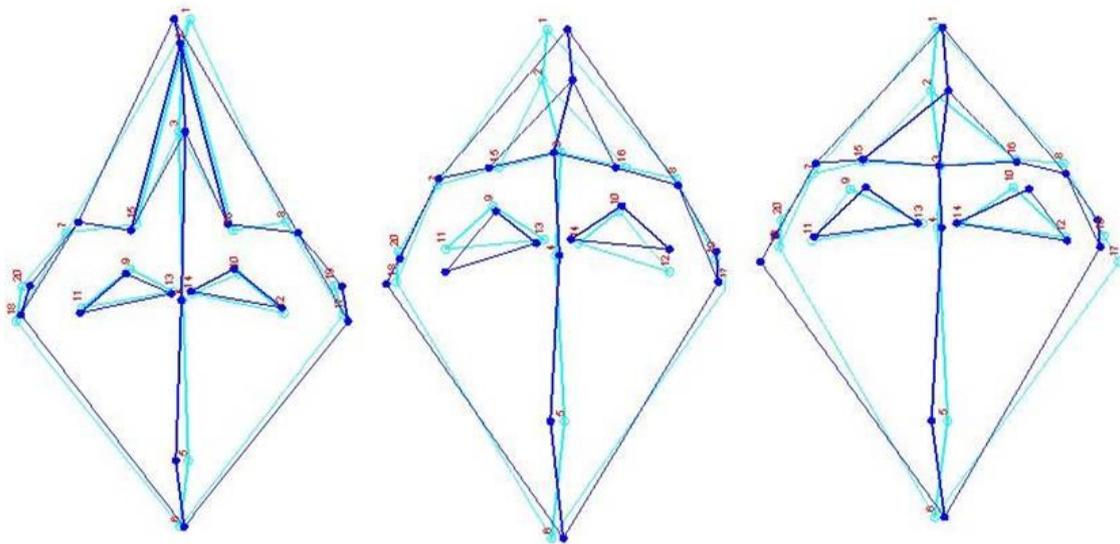


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397 Figure 2: Directional asymmetry in the skulls of baboon (left), gorilla (middle) and chimpanzee
398 (right) shown as a wireframe graph. The dark blue outline provides the average degree of directional
399 asymmetry in each species. Readers should look at the online version of the paper for better plots.

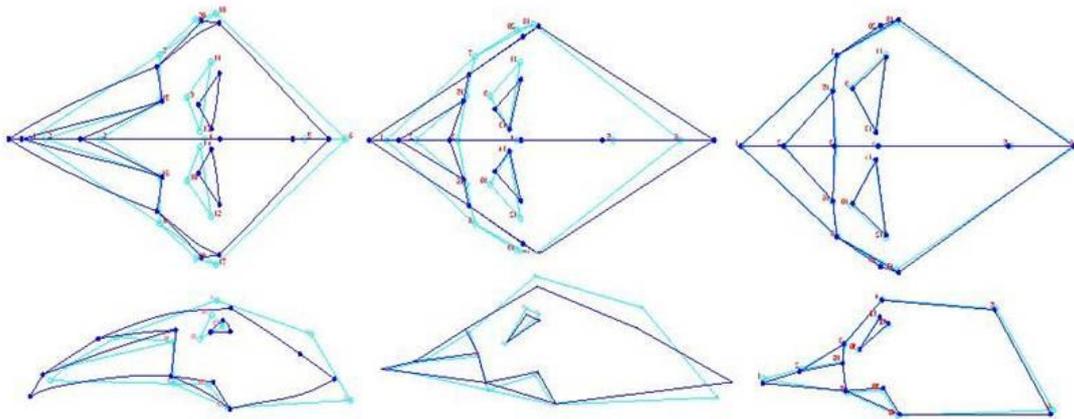
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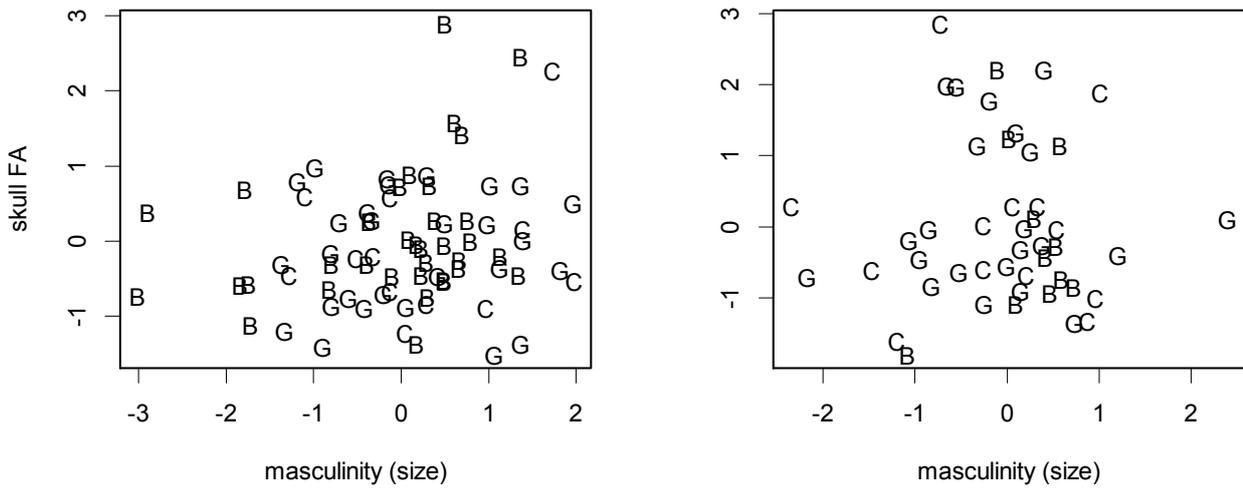
402

403 Figure 3. Graphical display of sexual dimorphism in baboon (left), gorilla (middle) and chimpanzee
404 (right). The top row displays the shape dimorphism viewed from the top of the skull, while the
405 bottom row provides a lateral view. Dark lines correspond to female skulls, the light blue to 1
406 standard deviation shape variation in sexual dimorphism in the masculine direction. Readers should
407 look at the online version of the paper for better plots.

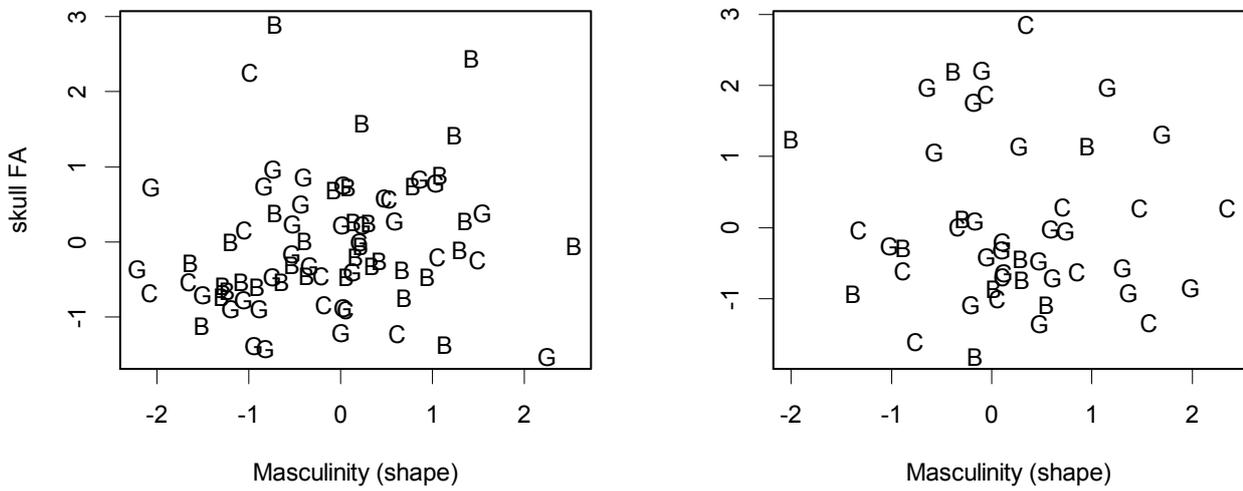


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410 Figure 4. Association between skull shape fluctuating asymmetry (FA) and masculinity (scaled size
411 (top graphs) and shape (bottom graphs) masculinity) in male (right) and female (left) primates
412 (B=baboon, G=Gorilla, C=Chimpanzee).



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