

Fluctuating asymmetry and preferences for sex-typical bodily characteristics

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Body size and shape seem to have been sexually selected in a variety of species, including humans, but little is known about what attractive bodies signal about underlying genotypic or phenotypic quality. A widely used indicator of phenotypic quality in evolutionary analyses is degree of symmetry (i.e., fluctuating asymmetry, FA) because it is a marker of developmental stability, which is defined as an organism's ability to develop toward an adaptive end-point despite perturbations during its ontogeny. Here we sought to establish whether attractive bodies signal low FA to observers, and, if so, which aspects of attractive bodies are most predictive of lower FA. We used a 3D optical body scanner to measure FA and to isolate size and shape characteristics in a sample of 77 individuals (40 males and 37 females). From the 3D body scan data, 360° videos were created that separated body shape from other aspects of visual appearance (e.g., skin color and facial features). These videos then were presented to 87 evaluators for attractiveness ratings. We found strong negative correlations between FA and bodily attractiveness in both sexes. Further, sex-typical body size and shape characteristics were rated as attractive and correlated negatively with FA. Finally, geometric morphometric analysis of joint configurations revealed that sex-typical joint configurations were associated with both perceived attractiveness and lower FA for male but not for female bodies. In sum, body size and shape seem to show evidence of sexual selection and indicate important information about the phenotypic quality of individuals.

3D morphometrics | body shape | developmental stability | sexual dimorphism | sexual selection

In humans, as in other species, sex differences in size and shape are attributed to divergent effects of morphology on the survival or reproductive success of each sex (1–10). For human females, smaller waist relative to hips (WHR), larger breasts, and longer legs relative to height have been attributed to fecundity selection and are perceived as attractive by males (8, 11, 12). In human males, greater height, larger size, and shorter legs relative to height are believed to have arisen through sexual selection by enhancing success in male–male rivalry (6, 7) and by being more attractive to females (6, 12). In addition, pronounced secondary sex characteristics may be preferred because they are signals of a pathogen-resistant genotype (13). However, recent theoretical models suggest that high-quality signalers may be more resistant, equally resistant, or less resistant to pathogens, depending on life history trade-offs between reproductive effort, survival, and fecundity (14, 15). For example, high-quality males that produce costly signals may compromise their future survival but nonetheless be more fit than their low-quality competitors.

If sex-typicality of body size and shape are attractive to the opposite sex because they indicate phenotypic quality, then these conspicuous sex-specific signals are expected to correlate negatively with FA. FA correlates inversely with buffering capacity against developmental stress across diverse taxa (9, 10, 16, 17). Higher FA is associated with increased morbidity and mortality, decreased fecundity, and other variables linked to natural and sexual selection (9, 10). Higher FA also is associated with poorer locomotory trait design and performance in several species,

including humans (18–23). Finally, it has been reported that bodily FA is inversely associated with attractiveness based on a person's odor (24), voice (25), facial appearance (26), and dance (27). Based on these theoretical considerations and empirical findings, we hypothesized that sex-typical bodily characteristics function as a signal of underlying developmental stability and therefore predicted that these characteristics would correlate negatively with FA in bodily features in general.

It should be noted that findings are mixed, and there is debate regarding the study of FA and sexual selection. For example, the strength of the negative relationship between FA and variables linked to sexual selection may be overestimated because of small sample size and publication bias (28). However, a study that tested directly for publication bias (29) did not find a significant difference in effect sizes (adjusted for sample size) between published and unpublished studies. Another report shows that the effect sizes in the study of FA are within the range of other fields in ecology and evolutionary biology (30). Considering the strong theoretical rationale for expecting bodily characteristics to function as reliable signals of quality, it is notable that no published study has demonstrated significant relationships between human body attractiveness, or shape-based secondary sex characteristics, and FA. In fact, 2 previously published attempts to correlate human bodily FA and attractiveness were unsuccessful (31, 32). One difficulty with demonstrating such relationships is that evaluations of body attractiveness potentially are influenced by cues unrelated to body shape, such as clothing, hair, skin color, facial appearance, or viewing angle. Additional difficulties are that subtle FAs are difficult to measure precisely, and composite measures of FA are more likely to reflect underlying developmental stability when more bilateral traits are included in the composite (33). We solved these problems by using a 3D optical scanner (34, 35) to extract precise body measurements for a large number of traits and to create controlled 360° video stimuli (Fig. 1A) that were stripped of visual information extraneous to body shape. Twenty-four bilateral traits were used to calculate the composite relative FA based on the neck, shoulder, breast, underarm, bicep, forearm, elbow, wrist, thigh, knee, calf, ankle, and foot. These traits were included because they revealed true FA rather than other types of asymmetries and exhibited high repeatabilities (see *Methods*). Scanner-produced body models of 40 males and 37 females [supporting information (SI) Movies S1 and S2] were presented to opposite-sex raters for evaluation on a 100-mm attractiveness scale. Thirty-seven males evaluated the female bodies, and 50 females evaluated the male bodies.

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Table 1. Zero-order correlations between relative fluctuating asymmetry, shape characteristics, and attractiveness by sex

	FA	Volume	WHR	WCR*	Bust size	Shoulder breadth	Leg slenderness	Height	Attractiveness
FA		-0.38 [†]	-0.47 [†]	-0.46 [†]	0.19	-0.30 [†]	0.44 [†]	-0.46 [†]	-0.37 [†]
Volume	0.29 [†]		0.50 [†]	0.52 [†]	-0.29 [†]	0.79 [†]	-0.26 [†]	0.56 [†]	-0.15
WHR	0.37 [†]	0.15		0.74 [†]	-0.42 [†]	0.39 [†]	0.57 [†]	-0.21	-0.65 [†]
WCR*	-0.41 [†]	0.37 [†]	0.32		-0.23	0.29	0.42 [†]	0.02	-0.63
Bust size	-0.25	0.05	-0.04	0.30 [†]		-0.03	-0.10	-0.24 [†]	0.10
Shoulder breadth	0.24	0.03	0.24	-0.15	-0.17		-0.17	0.45 [†]	0.25 [†]
Leg slenderness	-0.61 [†]	-0.44 [†]	0.00	0.33	-0.03	-0.42 [†]		0.25	-0.26 [†]
Height	0.32 [†]	0.59 [†]	-0.29	0.32	-0.03	-0.19	-0.08		0.44 [†]
Attractiveness	-0.57 [†]	-0.24	-0.55 [†]	-0.46 [†]	0.11	0.15	0.52 [†]	0.30 [†]	

Male-only correlations are above the diagonal.

*WCR was calculated differently for women than for men. In women, the bust to under-bust ratio divided by waist circumference was used, whereas for men the chest circumference was divided by the waist. Using the same composite measure of WCR for women as for men reduces the correlation to $-0.28, P = 0.04$ in women. If the female-specific measure (i.e., bust to under-bust ratio) is used, the correlation between FA and breast-to-waist ratio reverses for males ($r = 0.36, P = 0.002$).

[†] $P < 0.05$.

^{††} $P < 0.01$.

Guided by the hypothesis that sex-typicality signals developmental stability, we predicted that sex-typical bodily attractiveness would correlate negatively with FA. To test this hypothesis mediational regression analyses were performed. The first model tested whether FA correlated negatively with bodily attractiveness, independent of the sex-typicality of bodily characteristics. Attractiveness ratings of the 360° video stimuli were regressed upon the body masculinity component, FA, and these predictors' interaction terms with sex. The overall model was significant ($R^2 = 0.56, F_{5, 72} = 15.55, P < 0.0001$; Table S1). Specifically, above and beyond the expected positive effect of sex-typicality on attractiveness evaluations, FA accounted for significant unique variance as a negative predictor of bodily attractiveness in both sexes (partial $R^2 = 0.29, b = -0.46, t = -5.10, P < 0.001$, Fig. 1B). Furthermore independent of the negative effect of FA on attractiveness evaluations, more masculine bodies predicted higher attractiveness ratings in males (partial $R^2 = 0.24, b = 0.53, P < 0.001$), and more feminine bodies predicted higher attractiveness ratings in females (partial $R^2 = 0.27, b = -0.55, t = -4.33, P < 0.001$). In the second model we tested whether low FA predicted sex-typicality in bodily characteristics. Specifically, body masculinity was regressed on FA, sex, and the interaction terms between the 2. The overall regression model was significant: ($R^2 = 0.46, F_{3, 74} = 34.77, P < 0.0001$; Table S2). Specifically, lower FA predicted body masculinity in men (partial $R^2 = 0.25, b = -0.63, t = -5.33, P < 0.001$) and body femininity in women (partial $R^2 = 0.22, b = 0.27, t = 3.12, P < 0.001$). Thus the effect of FA on body attractiveness is partly but not fully mediated through sex-typicality of shape and size.

Geometric morphometric techniques were used to visualize sexually dimorphic dimensions of variation in body shape. PCA

of Procrustes-registered joint locations was used to identify dimensions of variation in their configuration. Compared with the PC of body masculinity used in the previous analyses, this assessment of landmark joint configuration is less dependent on hip and breast fat distribution. Because female bodily attractiveness is largely associated with fat distribution (8, 11, 30), we expected that joint configuration would be a better indicator of attractiveness and phenotypic quality in males than in females. The locations (x-y-z coordinates) of 18 landmarks were estimated using NX12 scanning software and the [TC]² body scanner. The 18 landmarks consisted of 8 pairs of bilateral joints (wrist, elbow, shoulder, acromioclavicular, sternoclavicular, ankle, knee, and hip), and 2 mid-line joints (sacroiliac joint and the C7/T1 intervertebral disk). A discriminant function based on sexually dimorphic principal components of variation in joint configuration discriminated (Wilk's $\lambda = 0.38; P < 0.0001$) between sexes with 87.6% accuracy, correctly classifying 84.9% of males and 90.6% of females. (The four most important PCs are illustrated and described in Fig. 1 C and D and in Fig. S1 A and B.) Higher scores on the discriminant function indicated greater joint configuration masculinity. The body masculinity component used in the previous regression model was orthogonal to sex-typical joint configuration among females (female $r = -0.07, P = 0.61$), suggesting that the joint configuration measure is robust to variation in fat distribution, a female-specific fecundity cue. In contrast, among males the body masculinity component used in the previous analysis was correlated positively with the sex-typical joint configuration score (male $r = 0.30, P < 0.01$), possibly because of shared variation in male-specific non-soft tissue traits (e.g., height, shoulder breadth).

Is sex-typical joint configuration attractive? To explore this possibility, attractiveness ratings were regressed on sex, torso volume, FA, joint configuration masculinity, and the sex interaction terms of the latter two predictor variables. The overall model was significant ($R^2 = 0.46, F_{6, 71} = 9.24, P < 0.0001$; Table S3). Specifically, above and beyond the independent negative effect of FA on attractiveness in both sexes (partial $R^2 = 0.29, b = -0.49, t = -5.13, P < 0.001$), masculine joint configurations predicted male (partial $R^2 = 0.14, b = 0.66, t = 3.27, P < 0.01$) but not female attractiveness (partial $R^2 = 0.02, b = -0.29, t = -1.13, P = 0.27$). Torso volume had a significant negative effect on attractiveness in this model (partial $R^2 = 0.07, b = -0.22, t = -2.15, P < 0.05$). Finally, to test whether FA was associated with joint configuration masculinity, joint configuration masculinity was regressed on sex, torso volume, FA, and the sex interaction terms of the latter two predictor variables. Once again the overall model was significant ($R^2 = 0.67, F_{4, 73} = 32.99, P < 0.001$;

Table 2. Mean and standard deviations of sexually dimorphic bodily characteristics

Trait	Male		Female		t value
	Mean	SD	Mean	SD	
Height (cm)	176.76	7.41	163.75	6.27	7.80*
Volume	2.56	0.62	2.23	0.60	3.15*
Shoulder breadth (cm)	44.20	3.50	38.40	2.70	6.91*
WHR	0.86	0.08	0.76	0.06	8.35*
Bust-to-under bust ratio (bust size)	1.08	0.03	1.17	0.05	12.19*
Leg slenderness	0.04	0.01	0.05	0.01	3.24*

* $P < 0.01$

Table 3. Mean signed fluctuating asymmetry (SFA), kurtosis, repeatabilities, and mean relative fluctuating asymmetry (RFA) for 24 traits measured

Trait	SFA (SD)	Kurtosis	Repeatability	RFA (SD)
Ankle girth	-1.52 (7.91)	1.24*	0.73*	0.006 (0.005)
Arm length	0.82 (14.06)	0.51	0.80*	0.002 (0.001)
Breast	1.73 (11.47)	3.83*	0.86*	0.036 (0.041)
Calf girth	0.75 (5.83)	0.86†	0.98*	0.013 (0.011)
Calf length	2.18 (14.44)	2.20*	0.98*	0.027 (0.028)
Elbow girth	-1.95 (9.61)	2.93*	0.86*	0.032 (0.026)
Foot girth	1.86 (5.12)	0.50	0.97*	0.032 (0.007)
Foot length	-1.52 (7.18)	0.59	0.97*	0.027 (0.007)
Forearm girth	1.82 (12.55)	1.66*	0.95*	0.043 (0.022)
Knee length	-0.99 (4.56)	0.89†	0.85	0.006 (0.009)
Leg length	0.10 (2.33)	4.53*	0.84*	0.002 (0.001)
Lower knee girth	0.82 (4.66)	0.07	0.94*	0.012 (0.011)
Mid-thigh girth	-1.19 (8.23)	0.63	0.89*	0.017 (0.019)
Minimum leg girth	0.56 (3.68)	1.03*	0.96*	0.014 (0.010)
Neck length	-0.13 (4.37)	4.68*	0.77*	0.002 (0.002)
Shoulder girth	2.09 (10.93)	1.32*	0.77*	0.027 (0.014)
Shoulder length	1.09 (15.48)	1.07*	0.82*	0.010 (0.007)
Thigh length	0.86 (4.84)	0.54	0.73*	0.012 (0.010)
Underarm girth	0.99 (15.48)	1.17*	0.76*	0.045 (0.040)
Underarm length	2.06 (12.49)	0.34	0.89	0.021 (0.014)
Upper arm girth	-1.01 (5.91)	0.47	0.91*	0.020 (0.010)
Upper knee girth	0.86 (4.90)	0.72	0.89*	0.011 (0.008)
Upper thigh girth	-1.88 (9.32)	0.47	0.83*	0.013 (0.010)
Wrist girth	0.73 (4.32)	4.53*	0.78*	0.021 (0.015)

* $P < 0.01$.† $P < 0.05$.

Table S4). Sex predicted joint configuration masculinity in this model (partial $R^2 = 0.61$, $b = -0.83$, $t = -10.10$, $P < 0.001$). Interestingly, lower FA in men predicted greater joint configuration masculinity (partial $R^2 = 0.11$, $b = -0.30$, $t = -2.21$, $P < 0.05$). Torso volume was not a significant predictor of the degree of joint configuration masculinity (partial $R^2 = 0.00$, $b = 0.03$, $t = 0.34$, $P = 0.73$), further suggesting that this measure of sexually dimorphic joint configuration is robust to variation in soft tissue distribution. There was no significant relation between female FA and the degree of joint configuration femininity (partial $R^2 = 0.02$, $b = -0.10$, $t = 1.22$, $P = 0.22$). The lack of association between FA and female-typical joint configuration may be caused by the removal of an important cue to female fecundity, soft-tissue distribution (8, 11).

Here, we show that bodily FA correlates negatively with bodily attractiveness and with sex-typicality of body shape. Our 360° video stimuli removed potential inherent biases unrelated to body shape, such as clothing, hair, skin color, facial appearance, and viewing angle. Further, because our composite measure of FA included more bilateral traits than previous studies (31, 32) and removed a potential source of measurement error (i.e., a human measurer), it may be a more accurate reflection of underlying developmental stability. Effect sizes are within the range of previous reports (34, 35) using the [TC]² 3D body scanner, thus lending further credibility to the usefulness of this technology for future studies.

Findings are consistent with previous reports that bodily FA is negatively associated with sex-typical facial structure (36, 37) and that relative leg length correlates differently with attractiveness across the sexes (12). Body size and shape are important not only for aesthetic preferences but also have significant functional consequences (18–23). For example relative leg length (38) and pelvis configuration (23) influence mobility in humans and thus could account in part for the previous associations found between human FA and locomotory performance

(22, 27). Fisher (39) hypothesized that many secondary sexual characters are arbitrary traits, whereas Zahavi (40) suggested that some traits become secondary sexual characteristics because they have important functional consequences. In a Jamaican sample, both sexes had higher FA in upper-body traits than in lower-body traits, perhaps because of the importance of lower body symmetry for locomotion (41). In the current sample we have replicated this effect, that is, in both sexes there is higher FA in upper-body traits ($M = 0.025$, $SD = 0.013$) than in lower-body traits ($M = 0.015$, $SD = 0.009$): [$t(76) = 2.30$, $P < 0.05$]. FA in bilateral traits that primarily serve a locomotory function could become a relatively stronger target of sexual selection than traits that do not primarily serve a locomotory function. Future studies should investigate this possibility.

In summary, our results indicate that FA—an important cross-species measure of developmental stability—is strongly negatively associated with human bodily attractiveness and with sex-typical bodily characteristics. In both sexes, an attractive body may be an indicator of underlying genotypic quality, hormonal and health status (including freedom from parasites), competitive ability, reproductive potential, or some combination of these factors.

Methods

Fluctuating Asymmetry. After acquiring informed consent, we collected measurements for 77 subjects (40 males, mean age = 20.90 ± 3.03 years; 37 females, mean age = 20.50 ± 2.36 years) with the [TC]² body scanner, a 24-camera optical imaging system with submillimeter accuracy (according to the manufacturer) that has been used in previous studies of human bodily attractiveness (34, 35). Participants entered the body scanner and were instructed to place their feet on the standardized floor markings and to hold the handlebars to keep their arms stationary during the scanning process. To establish repeatability and reduce measurement error, each trait was scanned twice and averaged. Asymmetry measurements were reliable indicators of between-subject differences (as opposed to measurement error). Signed FA (R-L) repeatabilities ranged from 0.73 to 0.98 (Table 3). We selected traits for analysis only when the signed asymmetries reflected true FA (42) rather than

Table 4. First 9 principal components of landmark configuration variation showing eigenvalues of the covariance matrix, variance explained, and the results of step-wise discriminant analysis

Principal component	Eigen value*	Percentage individual variance	Percentage cumulative variance	Discriminant function analysis results			
				Wilks' λ	Standardized discriminant coefficient	Structure coefficient (loading)	Significance
1	0.00143	35.70	35.70	0.922	0.551	0.228	$P < 0.00001$
2	0.00055	13.70	49.40	0.797	0.828	0.396	$P < 0.00001$
3	0.00035	8.79	58.20	0.972	-0.339	-0.133	$P < 0.05$
4	0.00034	8.38	66.60	0.720	0.924	0.490	$P < 0.00001$
5	0.00026	6.37	73.00				
6	0.00018	4.53	77.50	0.970	0.351	0.138	$P < 0.01$
7	0.00011	2.67	80.20				
8	0.00010	2.55	82.70				
9	0.00008	1.98	84.70				

Standardized discriminant function coefficients indicate the partial contribution of each variable to the discriminant function. Structure coefficients indicate the simple correlation between each variable and the discriminant score.

*Eigenvalues in this table may appear small because they are eigenvalues of the covariance matrix. Eigenvalues of the covariance matrix are used in the geometric morphometric analysis because the variables (Procrustes-registered landmark coordinates) have a common measurement scale. Sum of all eigenvalues equals the trace of the covariance matrix.

directional asymmetry or antisymmetry (i.e., all SFAs had positive leptokurtosis and 1-sample t tests showed that they did not depart significantly from a mean of 0). The [TC]² body scanner extracts hundreds of left-right measures, some of which are relevant only as clothing measurements (e.g., inseam measures) and so were excluded *a priori*. Composite fluctuating asymmetry was calculated by subtracting the average size of the left side of the trait from the right ($R - L$), correcting for trait size (i.e., dividing absolute unsigned asymmetry by average trait size, $R+L/2$), and then summing absolute values. Thus to calculate composite relative FA we used the formula $\sum (R - L / \text{Mean Trait Size})$. Mean intertrait FA correlations ranged from 0.01 to 0.77 (mean intertrait $r = 0.14$), and Cronbach's alpha equaled 0.67, suggesting that the 24-trait composite captured a large proportion of shared variation in what may be best characterized as "developmental instability." To calculate WHR, the narrowest waist circumference was divided by the widest hip circumference. Leg slenderness was calculated by dividing thigh height relative to overall height by the narrowest thigh girth.

Landmark Analyses. Approximate joint locations were generated by NX12 scanner software [TC]² using the H-ANIM standard. To eliminate non-shape variation in landmark data, the raw coordinates of the landmarks were registered using Generalized Procrustes analysis before the PCA of their configuration. Generalized Procrustes analysis is a best-fit procedure that removes scale, rotational, and translational differences between shapes (43–45). The Generalized Procrustes analysis was carried out using Morphologika (46). To identify dimensions of variation in landmark configuration, Morphologika then was used to conduct PCA on the Procrustes-registered landmark data in the tangent plane to Kendall's shape space (47). A Kaiser-Guttman criterion was used to select PCs for inclusion in subsequent analysis (i.e., PCs with eigenvalues greater than the average eigenvalue were retained). This led to the retention of the first 9 PCs, which together accounted for 84.7% of the variance in landmark configuration. Step-wise discriminant

analysis (SPSS 13) was used to establish which of the 9 principal components of landmark configuration variation (see Fig. 1 A and B and Fig. S1 A and B) were best able to discriminate between the bodies of male ($n = 73$) and female ($n = 64$) participants. (For this analysis we supplemented our sample with existing body scan samples provided by [TC]².) The resulting discriminant function incorporated PC1 to PC4 and PC6 (Table 4) and was a powerful discriminator (Wilks' $\lambda = 0.38$; $df = 5$; $\chi^2 = 127.6$, $P < 0.00001$), yielding correct sex classifications for 87.6% of participants based on their landmark configurations alone. (For illustration and description of the 4 most important PCs that contributed to the discriminant function, see Fig. 1 A and B and Fig. S1 A and B.) Discriminant function scores therefore were used as an index of 3D landmark configuration masculinity, with high scores indicating a more masculine joint configuration, and low scores indicating a more feminine joint configuration.

Evaluations. For all body scan stimuli, heads were removed from the images, and bodies were colored gray and rendered into 360° video using 3ds Max software (Autodesk Media and Entertainment). Bodies were projected onto a 2-m screen, one at a time in random order, for viewing by 87 evaluators (37 males, mean age = 21.27 ± 2.10 years; 50 females, mean age = 19.80 ± 1.98 years) who had given informed consent. Attractiveness ratings were made by placing a vertical mark on a 100-mm scale ranging from "unattractive" to "attractive." Marks were measured to the nearest millimeter by an assistant who was blinded with respect to FA and hypotheses. Ratings were averaged across evaluators because of high agreement (Cronbach's alphas > 0.82).

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