Signals of Genetic Quality and Maternal Investment Capacity: The Dynamic Effects of Fluctuating Asymmetry and Waist-to-Hip Ratio on Men's Ratings of Women's Attractiveness

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Abstract

Fluctuating asymmetry (FA) and waist-to-hip ratio (WHR) are frequently studied physical attractiveness variables in social and evolutionary psychology. FA represents deviations in bilateral symmetry—differences between left and right body parts. WHR is the ratio of the smallest part of the waist to the largest part of the hips. Although FA and WHR are important mate preference criteria, research has not examined their joint influence on attraction. Thus, 140 heterosexual male undergraduates ranked—and 118 rated—the attractiveness of 10 photographs of rear-facing nude women. Women's FA and WHR were negatively related to attractiveness separately, after controlling for each other and after controlling for body mass index (BMI). An FA \times WHR interaction emerged, such that men's preferences for lower WHRs increased as FA decreased, even after controlling for BMI. FA and WHR affected attractiveness in ways consistent with the information they carry and its likely effects on offspring quality.

Keywords

attractiveness, body mass index, evolutionary psychology, fluctuating asymmetry, waist-to-hip ratio

What makes a human body attractive? What aspects of bodily attractiveness are important, and how do different attributes interact in shaping overall attractiveness? When men evaluate women as potential mates, do they value a symmetrical figure or a curvaceous one more? Do women's symmetry and curvaceousness have an interactive effect on men's ratings of attractiveness? And do men's mate preferences hold when controlling for women's body mass? Social, health, cognitive, developmental, and evolutionary psychologists have sought to answer such questions about physical attractiveness in humans (e.g., Langlois & Roggman, 1990; Weeden & Sabini, 2005). Traditionally, social psychologists have been more interested in the interpersonal aspects of attraction (e.g., propinquity, familiarity, similarity) than in physical cues that may signal mate quality. Evolutionarily psychologists, however, believe that attractiveness is in the adaptations of the beholder (Rhodes, 2006; Sugiyama, 2005; Symons, 1995); organisms evolve to see any reliable markers of fitness as attractive (Andersson, 1994). On this view, different phenotypic traits may signal different components of reproductive fitness. Two such potential markers of fitness are fluctuating asymmetry (FA) and waist-to-hip ratio (WHR), yet no research has jointly examined both traits to assess their relative importance to attractiveness or the extent to which they interact.

Fluctuating Asymmetry

FA is defined as deviations in bilateral symmetry—measured differences between left and right body parts. Most organisms

are genetically programmed to develop identically on the right and the left. Thus, deviation from perfect bilateral symmetry is believed to reflect the degree to which an individual's genotype is unsuccessful at buffering it from the developmental assaults of parasites, pathogens, and other environmental stressors (Møller, 1992b; Thornhill & Gangestad, 1993; Van Valen, 1962). As predicted by this view, FA is negatively correlated with several measures of fitness, including health, longevity, mental health, cognitive performance, genetic heterozygosity, fecundity, growth, and survival, and it is positively correlated with parasite load, depression, and other health risks (Kowner, 2001; Manning, Scutt, Whitehouse, & Leinster, 1997; Martin, Manning, & Dowrick, 1999; Milne et al., 2003; Møller, 1997, 1999; Møller & Thornhill, 1997; Qazi, Wilson, & Abrahams, 2004; Scutt, Manning, Whitehouse, Leinster, & Massey, 1997; Thornhill & Møller, 1997). Low FA is thus a candidate phenotypic marker of genotypic quality (for reviews, see Møller & Swaddle, 1997; Møller & Thornhill, 1997; Van Dongen, 2006).

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If low FA serves as a cue to a well-buffered, fit genotype, then good-genes sexual selection theory predicts that it should be attractive in mate-choice contexts. Both animal (Møller, 1992a; Swaddle & Cuthill, 1994) and human (Thornhill & Gangestad, 1994; Tovée, Tasker, & Benson, 2000) studies support this prediction, and the effect is seen with both facial and bodily stimuli (Brown et al., 2008; Gangestad, Thornhill, & Yeo, 1994; Grammar & Thornhill, 1994; Perrett et al., 1999; Scheib, Gangestad, & Thornhill, 1999; Singh, 1995). Moreover, evidence suggests that the benefit of low FA is not merely aesthetic: Males (at least) can translate it into reproductive opportunities. For example, low-FA men experience more extrapair copulations and more lifetime sex partners than their less symmetrical counterparts (Gangestad & Thornhill, 1997; Thornhill & Gangestad, 1994).

Waist-to-Hip Ratio

WHR is a measured ratio of the smallest part of the waist to the largest part of the hips. In women, lower WHRs are seen as more attractive (Braun & Bryan, 2006; Singh, 1993), and this preference tends to generalize across economic conditions (Webster, 2008) and across many cultures (Furnham, Moutafi, & Baguma, 2002). Values for WHR range from 0.65 to 0.80 for most Western women, and some studies suggest that a value somewhat less than 0.7 is optimally attractive (Sugiyama, 2005). Singh (1993) proposed that WHR is the best indicator of a woman's current reproductive capability, and as such men have an evolved mechanism for detecting this indicator and using it in judgments of women's attractiveness. WHR has been correlated with long-term health (Bjorntorp, 1988; Folsom et al., 1993), with fertility through its correlation with hormone regimes (Kaye, Folsom, Prineas, Potter, & Gapstur, 1990; Zaadstra et al., 1993), and, because it reflects the storage of neurodevelopmentally important fatty acids, with cognitive ability in both mothers and their offspring (Lassek & Gaulin, 2008). In line with these fitness effects, men rate women's figures with low WHRs as the most feminine, healthy, attractive, and desirable for both casual and long-term relationships (Furnham, McClelland, & Omer, 2003; Furnham, Tan, & McManus, 1997; Henss, 1991; Singh, 1993; Singh & Luis, 1994; Singh & Randall, 2007; Singh & Young, 1995; Streeter & McBurney, 2003; for an opposing view, see Yu & Shepard, 1998).

Body Mass Index

Body mass index (BMI) is a standard medical measure of a person's weight in proportion to the square of his or her height. BMI has also been advanced as an important dimension of female bodily attractiveness (e.g., Tovée & Cornelissen, 2001; Tovée, Maisey, Emery, & Cornelissen, 1999). Whether BMI or WHR is a more important dimension of attractiveness is an ongoing debate. Our choice of FA and WHR as competing dimensions of female attractiveness was motivated by our specific research objectives: We wanted to contrast a measure of maternal investment capacity to a measure of genetic quality. We thought it important to have traits representing the two major benefit types—genes and investment—that can be obtained from mates. A considerable literature supports our assumption that WHR indexes maternal investment capacity (e.g., Lassek & Gaulin, 2008) and that symmetry indexes genetic quality (e.g., Gangestad et al., 1994). Similar evidence regarding the genetic or investment signaling content of BMI is presently lacking. Nevertheless, to address the BMI–WHR debate, we control for BMI and the BMI \times WHR interaction in our analyses of WHR and FA.

The Present Research

Surprisingly, no studies have simultaneously examined the effects of FA and WHR on attractiveness, despite their natural co-occurrence. In addition, although much is known about the linear effects of FA and WHR on attractiveness, comparatively little is known about their dynamic, interactive effects or their relative importance. Jointly testing these effects is important to evolutionary theory because it can help resolve whether FA and WHR are equally important to men's views of female attractiveness and whether the effects of these two traits depend on one another. Given the theoretical and empirical literature reviewed above, we made five predictions:

- 1. FA and WHR will each be negatively related to attractiveness in separate regressions.
- 2. FA and WHR will each be negatively related to attractiveness after controlling for each other.
- 3. FA and WHR will each be negatively related to attractiveness after controlling for each other and BMI.
- FA and WHR will interact, such that the negative WHRattractiveness relationship will become even more negative as FA decreases.
- 5. The FA \times WHR interaction will remain significant after controlling for BMI and the BMI \times WHR interaction.

Method

Participants

Participants were 140 heterosexual male undergraduates (ages 18 to 26 years; M = 18.8, SD = 1.3).

Stimuli

The 10 stimuli were $8" \times 11"$ photographic-quality color prints of full-body, unclothed, young (ages 18 to 27 years; M = 22.1, SD = 2.7) Caucasian American women in a standard rear pose (Gomi, 1998), with heads cropped to avoid hair as a confound. Using a preexisting catalog of photographs of actual women (Gomi, 1998) was a substantial improvement over the line drawings used in many previous WHR studies (e.g., Singh, 1993; Tassinary & Hansen, 1998).

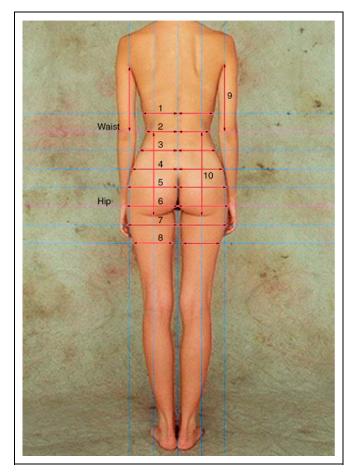


Figure 1. A reproduction of a sample stimulus overlaid here with the components of the fluctuating asymmetry (FA) index Note: The index was measured as the additive deviation of the left and right sides of seven horizontal lines measured from the vertical centerline of the image, plus the additive deviation of left and right thigh width at an eighth horizontal line, plus the additive deviation in height of two pairs of left and right vertical lines measured from a horizontal reference line to two bodily features. The formula used was $FA = \sum_i ((|L_i - R_i|) / ((L_i + R_i) / 2))$, where L and R represent the left and right measurements of traits i, 1 through 10.

FA and WHR of stimuli were measured in pixels using Adobe Photoshop 6.0. FA was defined as the summed deviations of the left and right sides of seven horizontal lines measured from the vertical centerline of the image, plus the summed deviation of left and right thigh width at an eighth horizontal line, plus the deviations in height of two pairs of left and right vertical lines measured from a horizontal reference line to two bodily landmarks (Figure 1). The placement of the horizontal lines was anchored by the waist and hip horizontals to evenly divide the distance between the waist and hip into quarters, with additional horizontal lines evenly placed above the waist (Line 1) and below the hip (Lines 7 and 8). WHR was calculated as the length of the horizontal line across the narrowest point at the waist divided by the length of the horizontal line across the widest point at the hips. BMI was calculated using the standard metric formula based on weight and height, kg/m^2 . The 10 stimulus photographs were chosen from 100 photographs (Gomi, 1998). Stimulus set inclusion was based

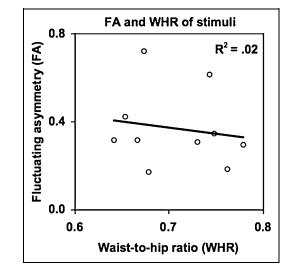


Figure 2. The relationship between fluctuating asymmetry (FA) and waist-to-hip ratio (WHR) among the 10 stimulus photographs selected for administration Note: These measures were not significantly correlated.

 Table I. Descriptive Statistics and Correlations for 10 Stimulus

 Photographs of Women

			Range		Correlations	
	М	SD	Min	Max	FA	WHR
Fluctuating asymmetry	0.37	0.17	0.17	0.72	_	.08ª
Waist-to-hip ratio	0.71	0.05	0.64	0.78	16	—
Body mass index	18.62	2.06	14.69	21.85	.55†	09

Note: FA = Fluctuating asymmetry. WHR = Waist-to-hip ratio.

a. FA-WHR correlation among a larger sample of 63 Gomi (1998) photographs. $^{\dagger}\,\rho$ = .10.

on discordance between FA and WHR (r = -.16, ns; Figure 2); however, this discordance was also present in a larger sample of 63 photographs (r = .08, ns; Table 1), suggesting that the 10 photographs we chose were largely representative of the overall Gomi (1998) sample.

Measures and Procedure

All 140 participants ranked $(1 = most \ attractive, \ 10 = least \ attractive)$ and 118 of these participants also rated $(1 = least \ attractive)$ and 118 of these participants also rated $(1 = least \ attractive$ to $7 = most \ attractive)$ 10 photographs on their "attractiveness as a partner." Rankings were inverted prior to analyses $(10 = most \ attractive, \ 1 = least \ attractive)$ to be in a direction consistent with the ratings. No time limit was imposed.

Data Analysis

Participants' responses produced a hierarchical data structure, with the 10 female stimuli representing repeated measures nested within male participants. As a result, we analyzed the data using a series of multilevel models via the Hierarchical Linear Modeling program (HLM 6; Raudenbush, Bryk, Cheong, & Congdon, 2004). In multilevel models, within- and between-participant variation can be modeled simultaneously at Levels 1 and 2, respectively (see Nezlek, 2001; Raudenbush & Bryk, 2002). For example, the Level 1 or within-participant model for testing FA and WHR as simultaneous predictors of attractiveness ratings was:

Attractiveness
$$\text{Rating}_{ij} = \pi_{0j} + \pi_{1j} (\text{FA} - \text{Mean FA})_{ij}$$

+ $\pi_{2j} (\text{WHR} - \text{Mean WHR})_{ij} + e_{ij}$.

In this model, Attractiveness Rating_{*ij*} represents the attractiveness rating given to the stimulus woman *i* by male participant *j*. The intercept π_{0j} represents the mean attractiveness rating for participant *j* when FA and WHR are at their mean. The coefficient π_{1j} (FA – Mean FA)_{*ij*} represents the mean-centered effect (or slope) of FA on attractiveness ratings controlling for WHR for participant *j*. Similarly, the coefficient π_{2j} (WHR – Mean WHR)_{*ij*} represents the mean-centered effect (or slope) of WHR on attractiveness ratings controlling for FA for participant *j*. Both FA and WHR were modeled as continuous measures. The error term e_{ij} represents the Level 1 or within-participant residual variance.

In multilevel models, coefficients from one level of analysis (within participant) can be modeled at another level of analysis (between participant). For the Level 1 model described above, the corresponding Level 2 model was:

$$\pi_{0j} = eta_{00} + r_{0j},$$
 $\pi_{1j} = eta_{10} + r_{1j},$
 $\pi_{2j} = eta_{20} + r_{2j}.$

In this model, the within-participant regression coefficients from Level 1 (i.e., π_{0i} , π_{1i} , and π_{2i}) were modeled at Level 2 as a function of their respective means or intercepts (i.e., β_{00} , β_{10} , and β_{20}). For example, β_{10} represents the betweenparticipant average of all participants' within-participant FA-attractiveness slopes, controlling for WHR. Similarly, β_{20} represents the between-participant average of all participants' within-participant WHR-attractiveness slopes, controlling for FA. The coefficients of interest here are β_{10} and β_{20} ; we want to know if each is significantly different from zero. In general linear modeling terms, this procedure is analogous to conducting a series of within-participant regressions, taking the resulting coefficients, and performing a one-sample t test on each type of coefficient to see whether they are different from zero on average. The error terms (i.e., r_{0i} , r_{1i} , and r_{2i}) represent the Level 2 or between-participant residual variance.

Results

Preliminary Analyses

Stimulus set descriptive statistics and correlations among FA, WHR, and BMI are shown in Table 1. None of these measures was significantly correlated; however, the FA–BMI correlation was substantial in magnitude (r = .55). Men's attractiveness rankings and ratings of the 10 stimulus women were highly correlated (r = .96) and produced similar results. All multilevel models produced normally distributed residuals and p values < .001 except where noted.¹

Fluctuating Asymmetry and Waist-to-Hip Ratio

In separate regressions, both FA and WHR were negatively related to attractiveness rankings and ratings (Prediction 1), and simultaneous regressions showed these negative effects to be independent (Prediction 2, Figure 3), even after controlling for BMI (Prediction 3, Table 2).

Fluctuating Asymmetry by Waist-to-Hip Ratio Interaction

A significant FA \times WHR interaction emerged for attractiveness rankings and rankings (Prediction 4, Table 2, Figure 4), such that the simple WHR-attractiveness slopes were more negative for low-FA (-1 SD) women (rankings: β_{20} = -40.61, t(139) = -22.00, pr = -.88; ratings: $\beta_{20} = -22.10$, t(117) = -21.83, pr = -.90) than for high-FA (+1 SD) women (rankings: $\beta_{20} = -26.67$, t(139) = -10.80, pr = -.68; ratings: $\beta_{20} = -12.48$, t(117) = -11.28, pr = -.72). The FA \times WHR interaction remained significant even after controlling for BMI and the BMI \times WHR interaction (Prediction 5) and actually grew stronger, suggesting a suppression effect (MacKinnon, Krull, & Lockwood, 2000). Although this last model might be slightly biased (see Yzerbyt, Muller, & Judd, 2004), it presents fewer problems than testing the full FA \times WHR \times BMI interaction model (e.g., multicollinearity), which would require eight predictors for only 10 data points per participant.

Discussion

Using realistic stimuli, our predictions were supported for men's rankings and ratings of women's attractiveness. FA and WHR were negatively related to women's attractiveness, both separately and when controlling for each other, which was a novel finding; this remained true even after controlling for BMI, which was also negatively related to attractiveness. FA and WHR were also dynamic, producing an interaction: The effect of WHR on attractiveness grew more negative as FA decreased.

On a theoretical level, mates offer two classes of attributes: genes and parental investment. Mate choice criteria are expected to track individual differences in the quality of one (or both) of these contributions. But the two classes of benefits can be expected to have differential impacts on offspring fitness—differential impacts that are somewhat counterintuitive.

Figure 3. Spaghetti plots from 118 within-person ordinary least squares (OLS) regressions predicting men's ratings of women's attractiveness as a function of women's (a) fluctuating asymmetry (FA) controlling for waist-to-hip ratio (WHR) and (b) WHR controlling for FA

Note: Thin gray lines represent individual participants' slopes; thick black lines represent relationships for the average participant. Although OLS estimates are shown here, restricted maximum likelihood estimation was used in all multilevel models. Higher numbers indicate greater attractiveness. Both FA and WHR were modeled as continuous predictors; the full range is shown for each measure. Spaghetti plots from 140 within-person OLS regressions predicting men's rankings of women's attractiveness produced similar results.

Although genes are commonly assumed to be definitively heritable, it should be remembered that, because of meiosis, each parent passes only half of his or her genes to any given offspring and that favorable parental gene combinations providing good environmental buffering will often not be transmitted as a unit. On the other hand, parental investment capacities are features of the established adult phenotype and can be assumed to affect each and every offspring in an undiluted way. For these reasons, markers of parental investment capacity are more fully indicative of a potential mate's contributions than are manifestations of his or her genetic quality.

Low FA is widely argued to reflect genetic quality via the reproductive benefits of pathogen resistance (Hamilton, 1980; Hamilton & Zuk, 1982). Our findings suggest that men value cues to pathogen resistance in women. Low WHR may signal maternal investment capacities, offering cues to fertility and stored resources to support offspring neurodevelopment (Lassek & Gaulin, 2008). The latter would be especially important in a lineage, such as our own, that experienced strong selection for brain expansion during its evolution. Thus, the high investment capacity signaled by low WHR may be comparatively more attractive than high levels of genetic quality signaled by low FA. Supporting this view, WHR consistently produced stronger effect sizes than FA on men's ratings and rankings of women's attractiveness. Regarding the BMI-WHR debate, both measures had a strong and nearly equal impact on men's ratings and rankings of women's attractiveness, with WHR explaining slightly more variance in attractiveness than BMI in nearly every model tested.

Limitations

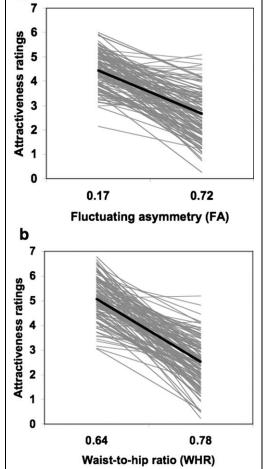
Our findings are limited in at least two ways. First, the size and characteristics of our stimulus set may limit the generalizability and ecological validity of our findings. Our stimulus sample size of 10 women was relatively small. This was done in part because rating-and especially ranking-all 100 Gomi (1998) photographs would have been cognitively taxing for participants and may have caused mental fatigue. Our stimulus set of women was Caucasian and young (ages 18 to 27 years) to match our mostly Caucasian and young male participant sample (ages 18 to 26 years). As women age, their FA, WHR, and BMI typically increase, and men's mating preferences based on these characteristics may change as they age. Thus, our findings may generalize only to young, Caucasian male participants rating young, Caucasian female targets.

Second, our findings may be limited by the FA measure we developed for this study. Our FA measure was novel because FA measures in prior studies have typically been based on facial or body metrics involving ear, foot, ankle, hand, wrist, and elbow breadth (cf. Gangestad et al., 1994). Nevertheless, because FA is defined as deviations in bilateral symmetrymeasured differences between left and right body parts-it should be reflected not only in ear, foot, ankle, hand, wrist, and elbow breadth but also in our 10 measures of back symmetry (Figure 1). Given this fact, we felt that our adaptation of prior FA measurement methods to preexisting photos of women's nude backs was reasonable, reliable, and valid.

Although our FA measure correlated with BMI (r = .55, p = .10), our participants seemed to respond to FA in that FA remained a significant negative predictor of attractiveness even after controlling for WHR, the FA \times WHR interaction, BMI, and the BMI \times WHR interaction. Thus, men appear to be noticing something in women uniquely associated with FA that was not accounted for by either WHR or BMI.

Implications

Men appear to value bodily cues in women relating to both genetic quality (FA) and maternal investment capacity (WHR),



	Rankings			Ratings		
Variable	Coef.	t	r or þr	Coef.	t	r or þi
Prediction 1: Separate regressions						
FA	-4.92	-11.06 [*]	68	-2.42	-13.70^{*}	78
WHR	-31.34	-26.47 [*]	91	-16.39	-20.93 [*]	89
BMI	-0.68	-19.37 [*]	85	-0.33	-21.07^{*}	89
Prediction 2: Simultaneous regression						
FA	-6.50	-17.36 [*]	83	-3.24	- 7.9 *	86
WHR	-34.93	-27.04 [*]	92	-18.18	-22.76 [*]	90
Prediction 3: Simultaneous regression,						
controlling for BMI						
FA	-2.24	-5.40 [*]	42	-1.13	-5.96 *	48
WHR	-35.13	-28.67 [*]	92	-18.28	-22.84 [*]	90
BMI	-0.65	-20.31 [*]	86	-0.32	-18.43*	86
Prediction 4: Testing the FA $ imes$ WHR interaction						
FA	-6.25	-16.58^{*}	81	-3.07	- 7.9 *	86
WHR	-33.64	-25.01 [*]	90	-17.29	-21.62 [*]	89
FA imes WHR interaction	41.00	4. 16 [*]	.33	28.32	6.91 [*]	.54
Prediction 5: Testing the FA $ imes$ WHR interaction,						
controlling for BMI and BMI \times WHR						
FA	-1.37	-3.18 [†]	26	-0.63	-3.23*	29
WHR	-32.66	-25.02*	90	-16.82	-21.14*	89
$FA \times WHR$ interaction	71.12	6.92*	.51	44.66	8.52*	.62
BMI	-0.73	-17.33 [*]	83	-0.36	-14.52^{*}	80
BMI $ imes$ WHR interaction	0.92	0.88	.07	0.24	0.40	.04

 Table 2. Men's Rankings and Ratings of Women's Attractiveness as Functions of Women's Fluctuating Asymmetry (FA), Waist-to-Hip Ratio (WHR), and Body Mass Index (BMI)

Note: pr = partial correlation. The unit of analysis was male participant (rankings: N = 140; ratings: n = 118).

 $^{\dagger} p = .002. \ ^{*} p < .001.$

with a preference for the latter. In addition, our findings suggest that men increasingly value maternal investment as genetic quality increases (an FA \times WHR interaction). Why might this be? Seeking evidence of good potential maternal investment in a future mate does little good if there is evidence that her genetic quality is poor. For example, a woman with especially high FA may be carrying genes that are suboptimal with respect to current parasite and pathogen challenges. If her high FA reflects this genetic suboptimality, then her capacity for maternal investment in (relatively low-quality) children may be moot. In other words, it is not surprising that cues to investment capacity and genetic quality interact in shaping men's judgments and that, in particular, men value cues to genetic quality (low FA) increase.

Furthermore, we suspect that the FA \times WHR interaction we observed may not necessarily be unique to these features. That is, this type of interaction may generalize to other dimensions of social judgment or person perception that may be relevant to mate preferences. For example, imagine a person attempting to select a mate from a pool of mates who vary in neuroticism (emotional stability) and intelligence (cognitive ability). A dynamic interactive model might best account for possible threshold effects, especially if the attractiveness of intelligence depends on emotional stability. For example, if a target person is especially neurotic, how intelligent he or she is may not matter; however, if he or she is at least moderately emotionally stable, intelligence may play a stronger role in attraction. Thus, we feel the FA \times WHR interaction may generalize to other mate preference characteristics. Specifically, if this model were correct, one might expect to see a similar interaction for other mating cues relating to genetic quality and maternal investment capacity. We also speculate, however, that this model may generalize even to other types of social judgment involved with person perception. Further research will be needed to explore these possibilities.

On a broader theoretical level, social psychology has made great strides in understanding the interpersonal antecedents (e.g., propinquity, familiarity, similarity) and consequences (e.g., the halo effect) of physical attractiveness, whereas evolutionary psychology asks why particular traits have positive or negative effects on attractiveness (e.g., "What fitness benefit might result from attending to a trait?"). In this sense, social and evolutionary psychology can be thought of as presenting complementary explanations of human attractiveness. The present findings advance social psychological theory on human attractiveness in at least two ways.

First, our results suggest that men attend to women's FA and WHR when evaluating their attractiveness. The effects of FA and WHR operate in a way that is consistent with the

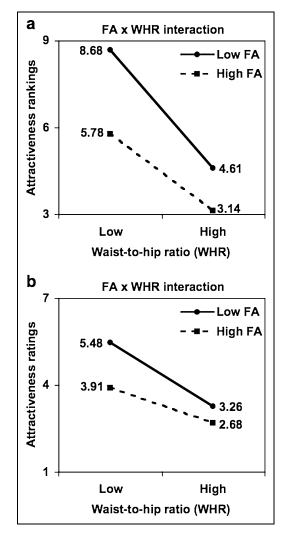


Figure 4. The fluctuating asymmetry (FA) \times waist-to-hip ratio (WHR) interaction for men's (a) rankings and (b) ratings of women's attractiveness

Note: Higher numbers indicate greater attractiveness. Both FA and WHR were modeled as continuous predictors; the terms *low* and *high* correspond to \pm I SD from the mean of their respective measures.

information they carry and its likely effects on offspring quality. Future research could strive to examine FA and WHR in concert with contextual and interpersonal variables relevant to attraction (e.g., propinquity, familiarity, similarity). We predict that such social variables will at least partially mediate the direct FA-attractiveness and WHR-attractiveness relationships.

Second, our findings suggest that social psychological theories of interpersonal attraction may need to be expanded to integrate some of the adaptive, biological cues that underlie what we label as *attractive*. Accumulating evidence suggests that humans possess several evolved mate-evaluation algorithms that function to track the abilities to conceive, produce, and nurture viable offspring and that the judgments that these algorithms generate are key aspects of interpersonal attraction. Of course, for these arguments to be correct, such judgments do not have to be conscious or even cognitively penetrable. It is hoped that the present study will help to foster an integrated evolutionary social psychology of human physical attraction.

Note

 Supplementary analyses, in which the 10 female targets were the unit of analysis instead of the 140 male participants, are available from the corresponding author and at http://tinyurl.com/faxwhr. These statistics were consistent with our main findings, suggesting that our results may generalize to female targets in addition to male raters.

Authors' Note

This research, based on Helen Perilloux's doctoral dissertation, was presented in posters at the 16th and 17th annual meetings of the Human Behavior and Evolution Society in Berlin, Germany (July 2004), and Austin, Texas (June 2005).

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Declaration of Conflict of Interest

The authors declared that they had no conflicts of interests with respect to their authorship or the publication of this article.

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References

- Andersson, M. (1994). Sexual selection. Princeton, NJ: Princeton University Press.
- Bjorntorp, P. (1988). The associations between obesity, adipose tissue distribution, and disease. *Acta Medica Scandinavica*, 723(Suppl.), 121-134.
- Braun, M., & Bryan, A. (2006). Female waist-to-hip and male waistto-shoulder ratios as determinants of romantic partner desirability. *Journal of Social and Personal Relationships*, 23, 805-819.
- Brown, W. M., Price, M. E., Kang, J., Pound, N., Zhao, Y., & Yu, H. (2008). Fluctuating asymmetry and preferences for sex-typical bodily characteristics. *Proceeding of the National Academy of Sciences of the United States of America*, 105, 12938-12943.
- Folsom, A. R., Kaye, S. A., Sellers, T. A., Hong, C. P., Cerhan, J. R., Potter, J. D., et al. (1993). Body fat distribution and 5-year risk of death in older women. *Journal of the American Medical Association*, 269, 483-487.
- Furnham, A., McClelland, A., & Omer, L. (2003). A cross-cultural comparison of ratings of perceived fecundity and sexual attractiveness as a function of body weight and waist-to-hip ratio. *Psychol*ogy, *Health, and Medicine*, 8, 219-230.
- Furnham, A., Moutafi, J., & Baguma, P. (2002). A cross-cultural study on the role of weight and waist-to-hip ratio on female attractiveness. *Personality and Individual Differences*, 32, 729-745.

- Furnham, A., Tan, T., & McManus, C. (1997). Waist-to-hip ratio and preferences for body shape: A replication and extension. *Personality and Individual Differences*, 22, 539-549.
- Gangestad, S. W., & Thornhill, R. (1997). The evolutionary psychology of extra-pair sex: The role of fluctuating asymmetry. *Evolution* and Human Behavior, 18, 69-88.
- Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, 15, 73-85.
- Gomi, A. (1998). Americans 1.0, Los Angeles 1994 [CD-ROM]. Bunkasha, Japan: Digitalogue.
- Grammar, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, 108, 233-242.
- Hamilton, W. D. (1980). Sex versus non-sex versus parasite. Oikos, 35, 282-290.
- Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites. *Science*, 218, 384-387.
- Henss, R. (1991). Perceiving age and attractiveness in facial photographs. *Journal of Applied Social Psychology*, 21, 933-946.
- Kaye, S. A., Folsom, A. R., Prineas, R. J., Potter, J. D., & Gapstur, S. M. (1990). The association of body fat distribution with lifestyle and reproductive factors in a population study of postmenopausal women. *International Journal of Obesity*, 14, 583-591.
- Kowner, R. (2001). Psychological perspective on human developmental stability and fluctuating asymmetry: Sources, applications and implications. *British Journal of Psychology*, 92, 447-469.
- Langlois, J. H., & Roggman, L. A. (1990). Attractive faces are only average. *Psychological Science*, 1, 115-121.
- Lassek, W. D., & Gaulin, S. J. C. (2008). Waist-hip ratio and cognitive ability: Is gluteofemoral fat a privileged store of neurodevelopmental resources? *Evolution and Human Behavior*, 29, 26-34.
- MacKinnon, D. P., Krull, J. L., & Lockwood, C. M. (2000). Equivalence of the mediation, confounding and suppression effect. *Prevention Science*, 1, 173-181.
- Manning, J. T., Scutt, D., Whitehouse, G. H., & Leinster, S. (1997). Breast asymmetry and phenotypic quality in women. *Evolution* and Human Behavior, 18, 1-13.
- Martin, S. M., Manning, J. T., & Dowrick, C. F. (1999). Fluctuating asymmetry, relative digit length, and depression in men. *Evolution* and Human Behavior, 20, 203-214.
- Milne, B. J., Belsky, J., Poulton, R., Thomson, W. M., Caspi, A., & Kieser, J. (2003). Fluctuating asymmetry and physical health among young adults. *Evolution and Human Behavior*, 24, 53-63.
- Møller, A. P. (1992a). Female swallow preference for symmetrical male sexual ornaments. *Nature*, 357, 238-240.
- Møller, A. P. (1992b). Parasites differentially increase the degree of fluctuating asymmetry in secondary sexual characteristics. *Journal* of Evolutionary Biology, 5, 691-699.
- Møller, A. P. (1997). Developmental stability and fitness: A review. *American Naturalist*, 149, 916-932.
- Møller, A. P. (1999). Asymmetry as a predictor of growth, fecundity, and survival. *Ecology Letters*, 2, 149-156.
- Møller, A. P., & Swaddle, J. P. (1997). Asymmetry, developmental stability, and evolution. New York: Oxford University Press.

- Møller, A. P., & Thornhill, R. (1997). A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology*, 10, 1-16.
- Nezlek, J. B. (2001). Multilevel random coefficient analyses of event and interval contingent data in social and personality psychology research. *Personality and Social Psychology Bulletin*, 27, 771-785.
- Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A., & Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, 20, 295-307.
- Qazi, R., Wilson, G. D., & Abrahams, S. (2004). Developmental instability is associated with neurocognitive performance in heterosexual and homosexual men, but not in women. *Behavioral Neuroscience*, 118, 243-247.
- Raudenbush, S. W., & Bryk, A. S. (2002). Hierarchical linear models: Applications and data analysis methods. (2nd ed.). Thousand Oaks, CA: Sage.
- Raudenbush, S. W., Bryk, A. S., Cheong, Y. F., & Congdon, R. T., Jr. (2004). HLM 6: Hierarchical linear and nonlinear modeling. Lincolnwood, IL: Scientific Software International.
- Rhodes, G. (2006). The evolutionary psychology of facial beauty. Annual Review of Psychology, 57, 199-236.
- Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry, and cues of good genes. *Proceedings of the Royal Society of London B*, 266, 1913-1917.
- Scutt, D., Manning, J., Whitehouse, G., Leinster, S., & Massey, C. (1997). The relationship between breast asymmetry, breast size and the occurrence of breast cancer. *British Journal of Radiology*, 70, 1017-1021.
- Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist-to-hip ratio. *Journal of Personality and Social Psychology*, 65, 293-307.
- Singh, D. (1995). Female health, attractiveness, and desirability for relationship: Role of breast asymmetry and waist-to-hip ratio. *Ethology and Sociobiology*, 16, 465-481.
- Singh, D., & Luis, S. (1994). Ethnic and gender consensus for the effect of WHR on judgment of women's attractiveness. *Human Nature*, 6, 51-65.
- Singh, D., & Randall, P. K. (2007). Beauty is in the eye of the plastic surgeon: Waist-hip ratio (WHR) and women's attractiveness. *Personality and Individual Differences*, 43, 483-507.
- Singh, D., & Young, R. (1995). Body weight, WHR, breasts and hips: Role in judgments of female attractiveness and desirability for relationships. *Ethology and Sociobiology*, 16, 483-507.
- Streeter, S. A., & McBurney, D. H. (2003). Waist-hip ratio and attractiveness: New evidence and a critique of "a critical test." *Evolution and Human Behavior*, 24, 88-98.
- Sugiyama, L. S. (2005). Physical attractiveness in adaptationist perspective. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 292-343). Hoboken, NJ: John Wiley.
- Swaddle, J. P., & Cuthill, I. C. (1994). Preference for symmetric males by female zebra finches. *Nature*, 367, 165-166.
- Symons, D. (1995). Beauty is in the adaptations of the beholder. In P. R. Abramson & S. D. Pinkerson (Eds.), *Sexual nature, sexual culture* (pp. 80-118). Chicago: University of Chicago Press.
- Tassinary, L. G., & Hansen, K. A. (1998). A critical test of the waistto-hip-ratio hypothesis of female physical attractiveness. *Psychological Science*, 9, 150-155.

- Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature*, *4*, 237-269.
- Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual behavior. *Psychological Science*, 5, 297-302.
- Thornhill, R., & Møller, A. P. (1997). Developmental stability, disease, and medicine. *Biological Reviews*, *72*, 497-548.
- Tovée, M., & Cornelissen, P. (2001). Female and male perception of female physical attractiveness in front-view and profile. *British Journal of Psychology*, 92, 391-402.
- Tovée, M. J., Maisey, D. S., Emery, J. L., & Cornelissen, P. L. (1999). Visual cues to female physical attractiveness. *Proceedings of the Royal Society of London B*, 266, 211-218.
- Tovée, M. J., Tasker, K., & Benson, P. J. (2000). Is symmetry a visual cue to attractiveness in the human female body? *Evolution and Human Behavior*, 21, 191-200.
- Van Dongen, S. (2006). Fluctuating asymmetry and developmental instability in evolutionary biology: Past, present and future. *Journal of Evolutionary Biology*, 19, 1727-1743.
- Van Valen, L. (1962). A study of fluctuating symmetry. *Evolution*, 16, 125-142.
- Webster, G. D. (2008). *Playboy* playmates, the Dow Jones, consumer sentiment, 9/11, and the Doomsday Clock: A critical examination of the environmental security hypothesis. *Journal of Social, Evolutionary, and Cultural Psychology*, 2, 23-41.
- Weeden, J., & Sabini, J. (2005). Physical attractiveness and health in Western societies: A review. *Psychological Bulletin*, 131, 635-653.

- Yu, D. W., & Shepard, G. H. (1998). Is beauty in the eye of the beholder? *Nature*, 396, 321-322.
- Yzerbyt, V., Muller, D., & Judd, C. M. (2004). Adjusting researchers' approach to adjustment: On the use of covariates when testing interactions. *Journal of Experimental Social Psychology*, 40, 424-431.
- Zaadstra, B. M., Seidell, J. C., Van Noord, P. A., te Velde, E. R., Habbema, J. D., Vrieswijk, B., et al. (1993). Fat and female fecundity: Prospective study of effect of body fat distribution on conception rates. *British Medical Journal*, 306, 484-487.

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