UNIVERSITY OF CALIFORNIA

Santa Barbara

Hormonal and Morphological Predictors of Women's Body Attractiveness

A Thesis submitted in partial satisfaction of the

requirements for the degree Master of Arts

in Psychology

by

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June 2016

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ABSTRACT

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Does women's body attractiveness predict indices of reproductive capacity? Prior research has provided evidence that large breast size and low waist-to-hip ratio (WHR) are positively associated with women's estrogen and progesterone concentrations, but no previous studies appear to have directly tested whether ratings of women's body attractiveness are predicted by higher concentrations of ovarian hormones measured across broad regions of the menstrual cycle. Here, we collected daily saliva samples across 1-2 menstrual cycles from a sample of young women; assayed the samples for estradiol, progesterone, and testosterone; obtained anthropometric measurements of the women's bodies; and also obtained attractiveness ratings of the women's bodies from photographs of them taken in standardized clothing with faces obscured. Contrary to previous research, mean hormone concentrations were uncorrelated with breast size and WHR. Body mass index (BMI) was a very strong negative predictor of body attractiveness ratings, similar to previous findings. Zero-order associations between women's mean hormone concentrations and mean attractiveness ratings were not significant; however, after controlling for BMI, attractiveness ratings were independently and positively associated with both estradiol and testosterone concentrations. Discussion focuses on the implications of these findings for whether attractiveness assessment mechanisms are specialized for the detection of cues of differential fecundity in young women's bodies.

I. Introduction

Evolutionary approaches to understanding human physical attractiveness posit that preference mechanisms ought to be designed to hone in on cues of qualities in others that predicted reproductive success over evolutionary history (e.g., Gangestad & Scheyd, 2005; Symons, 1995). It is well established that cues of health and genetic quality, such as fluctuating asymmetry, are important inputs to psychological mechanisms assessing female physical attractiveness (e.g., Brown et al., 2008; Jones et al., 2001; Thornhill & Gangestad, 1993); less is known regarding the potential importance of fertility cues in judgments of female physical attractiveness. Given the extreme energetic investment required to produce human offspring, the many competing energetic demands in ancestral environments likely gave rise to substantial natural variation in female fertility, both between-women and within-women, over time (Ellison, 2001). As such, we might expect cognitive mechanisms underlying male mating psychology to be particularly attuned to cues of fertility in women.

Present fertility may be appropriately indexed by women's concentrations of ovarian hormones across the menstrual cycle, given that levels of estradiol and progesterone are positively associated with the probability of conception within a cycle (Baird et al., 1999; Lipson & Ellison, 1996; Stewart, Overstreet, Nakajima, & Lasley, 1993; Venners et al., 2006). Late follicular estradiol has been shown to be associated with female facial attractiveness (Law Smith et al., 2006; see also Puts et al., 2013), and the mean of two estradiol measurements taken from the follicular and luteal phases was observed to be associated with ratings of combined facial and body attractiveness (Durante & Li, 2009). However, little is known regarding the relationship between ovarian hormones and women's body attractiveness alone. Given that sex hormones are largely responsible for the deposition of fat during development and the resulting body shapes of women (e.g., Bjorntorp, 1991), and men typically place principal importance on body attractiveness in short-term mating contexts where conception-risk ought to be the chief consideration (Confer, Perilloux, & Buss, 2010; Jonason, Raulston, & Rotolo, 2012), we might expect body attractiveness to have a particularly strong association with ovarian hormone levels.

A recent study investigated the relationship between female body shape and sex hormone levels across broad regions of the menstrual cycle in a group of Polish women (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). Salivary estradiol and progesterone were negatively associated with waist-to-hip ratio (WHR) and positively associated with breast size, such that women with small waists and large breasts exhibited a hormonal profile most compatible with fecundity. These findings provide preliminary evidence for the notion that perceptual mechanisms assessing female attractiveness hone in on non-arbitrary indicators of fecundity, but a better test is whether attractiveness ratings themselves are predicted by hormone concentrations.

Rilling, Kaufman, Smith, Patel, & Worthman (2009) obtained ratings of body attractiveness but found no significant relationship between these ratings and a single estradiol measurement that did not control for cycle day. Without controlling for cycle day, it is difficult to interpret their results: women's hormone levels fluctuate greatly over the menstrual cycle.

A woman's fertility varies not only during the menstrual cycle, but between them. Lactation, energetic stress, illness and age all lower fertility, creating lower estradiol levels over the entire cycle (Ellison, 2001). Features that index overall levels of estradiol and progesterone may, therefore, be differentially weighted by adaptations in men that were designed for assessing and responding sexually to women. Yet no study to date has measured ovarian hormones across broad regions of the menstrual cycle, to test whether women's' body attractiveness is predicted by their present fertility.

In the present research, we collected daily saliva samples across 1-2 menstrual cycles from naturally-cycling women and assayed them for estradiol, progesterone, and testosterone. These women were photographed from the front, back, and profile view. We constructed arrays of these photos for each woman with faces blocked, and had them rated by independent judges for physical attractiveness. Based on the premise that perceptual mechanisms for assessing female physical attractiveness ought to hone in on cues of fecundity in female bodies, we hypothesized that sex hormone (estradiol and progesterone) concentrations would positively predict attractiveness ratings. We also expected to replicate Jasienska et al.'s (2004) finding that that sex hormone concentrations are positively associated with low WHR and large breasts. Last, based on recurrent findings in the extant literature on female physical attractiveness, we hypothesized that lower WHR and BMI measures would predict higher attractiveness ratings (e.g., Rilling et al., 2009; Singh & Singh, 2011; Streeter & McBurney, 2003; Tovee & Cornelissen, 2001).

II. Methods

A. Body Stimuli

1. Stimulus Participants

Body photographs were obtained from a sample of women who participated in a larger study on the relationship between ovarian hormones and sexual psychology and behavior within natural menstrual cycles (see Roney & Simmons, 2013). Women participants provided daily saliva samples each morning (to control for diurnal variation in hormones; see Bao et al., 2003) across 1-2 menstrual cycles. Although 52 total women participated in the study, saliva samples were not sent for assay for women with many missing samples, and hormone data were ultimately obtained for 43 women; 41 of these women provided consent for use of their photographs in research. Of those women, 33 were judged to have experienced at least one ovulatory menstrual cycle (see below). These 33 women comprise the final stimulus sample (Mean age ± SD = 18.85 ± 1.28 years). Nineteen of the women self-identified as White, seven as Asian, five as Hispanic, and two as mixed ethnicity; none of the hormone variables, body dimensions, or attractiveness ratings differed significantly across ethnic categories.

2. Anthropometry

Participants attended four laboratory sessions per menstrual cycle; anthropometric measurements were obtained in one of the sessions from the first cycle. Weight, muscle mass, body fat, visceral fat, and water percentage were measured using a Tanita electrical impedance scale (Tanita BC-573), and height was self-reported via questionnaire. All measures were taken by individuals who were blind to the attractiveness ratings.

The values for height and weight were used to calculate body mass index (BMI). Women research assistants used measuring tapes to measure breast size (the widest circumference at the level of the chest) and underbreast circumference; following Jasienska et al. (2004), the ratio of these two values was employed as a measure of relative breast size. Bras were not removed before measurement, which may have introduced measurement error, although the average relative breast size in our sample (Mean breast size ± SD = 1.15 ± 0.04) was very similar to that reported by Jasienska et al. (2004; Mean breast size ± SD = 1.16 ±

0.04). WHR was initially measured using measuring tapes but a number of values appeared implausible when compared to the photographs, suggesting that our research assistants identified waists in inconsistent ways. We therefore attempted to obtain reliable measurements of WHR from the women's photographs using a technique for photo measurements that was validated against more standardized direct body measurements (Steve Gaulin, personal communication, September 2012): the waist was defined as the narrowest point on the torso below the breasts, and the hips were defined as the widest point below the waist. Two research assistants independently measured these using Adobe Photoshop Elements 3.0, and computed the ratio of the two; these measurements were highly reliable ($r = 0.97$) and the means of the two ratios were used for data analyses.

3. Hormone measures

Morning saliva samples were first stored in women's home freezers and then delivered weekly to our research lab, after which they were stored at -80 C until shipping for assay (for full details of the collection procedure, see Roney & Simmons, 2013). We initially estimated the day of ovulation as 15 days prior to the end of each cycle, and sent for assay all samples in a nine-day window centered on the estimated day of ovulation, as well as samples from alternating days outside of this window. Samples were shipped on dry ice to the Endocrine Core Laboratory at the California Regional Primate Research Center, Davis, CA, where they were assayed for concentrations of estradiol, testosterone, and progesterone. Full details of the assay procedures can be found in Roney & Simmons (2013); intra- and inter-assay CVs were below 10 percent for each of the hormones.

Hormone data were used to re-estimate the day of ovulation based on the mid-cycle estradiol drop, following the procedures described in Jasienska et al. (2004) and Lipson &

Ellison (1996) . Following Jasienska et al. (2004), we computed cycle mean estradiol as the mean estradiol concentration for the 18 cycle days centered on the estimated day of ovulation (days -8 to +9 relative to ovulation as day zero), whereas cycle mean progesterone was computed as the average concentration of progesterone in the final 14 days of the cycle. Although Jasienska et al. did not measure testosterone, we computed cycle mean testosterone the same way as cycle mean estradiol (i.e., an average of the 18 cycle days centered on ovulation), given similarities in the secretion patterns of these hormones. Because identification of the day of ovulation was not possible in anovulatory cycles, we restricted data analyses to ovulatory cycles in order to ensure that similar cycle regions were being compared across women. Following Ellison et al. (1987), we defined a cycle as anovulatory when it did not achieve a maximum progesterone value of at least 300 pmol/L.

Among the 41 women with both photo consent and hormone data, eight did not experience an ovulatory cycle based on the above criterion. Among the remaining women, 18 had hormone data for two ovulatory cycles, 10 women participated in both cycles only one of which was judged ovulatory, and five women participated in a single cycle that was judged ovulatory. Thus, the final sample included hormone data from two cycles for 18 women and from one cycle for 15 women. Subject mean hormone concentrations were computed from a single cycle mean (as defined above) for the 15 women with one ovulatory cycle and as the average of the two cycle means for the 18 women with two ovulatory cycles. (A consequence of this procedure is that some women had more reliable mean hormone values than others due to the larger number of sample days. However, a set of mixed regression models that treated daily hormone concentrations as dependent variables and body dimensions and attractiveness ratings as higher level predictor variables – and thereby weighted women with more hormone data more heavily due to the more reliable estimates of their hormone concentrations – produced identical statistical conclusions to those presented below using subject mean hormone values). Data analyses tested associations between these subject mean hormone values and both body shape dimensions and mean body attractiveness ratings.

4. Stimulus photos

During the third laboratory session of the first cycle (typically within the luteal phase), each woman was photographed in standardized dress comprised of grey gym shorts and a blue tank top shirt. Photos were taken with a digital camera at a standard distance in a windowless room with artificial lighting. For each woman, photos were taken from front-facing, back-facing, and side-facing perspectives; these three photos were placed together onto a single stimulus array for each woman, with an opaque mask blocking the head area in each photo. An example stimulus array appears in Fig. 1.

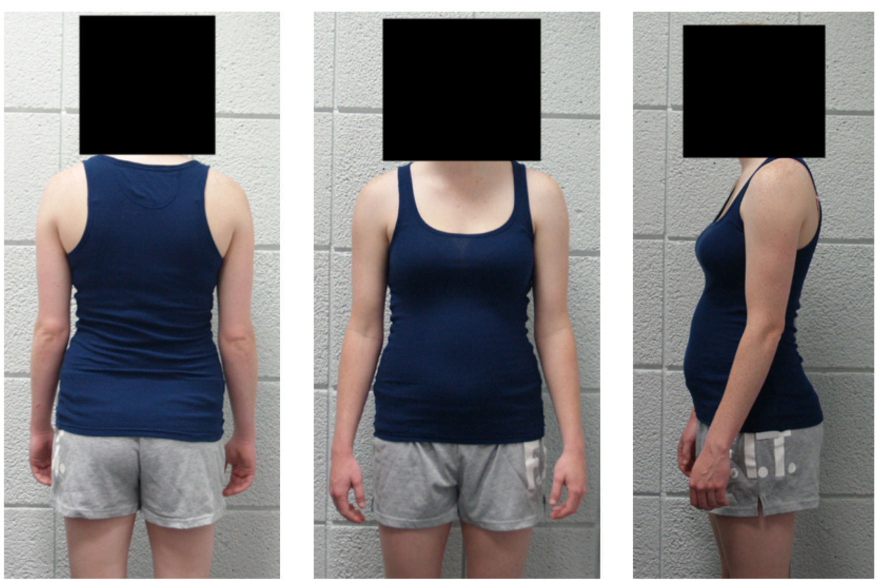

Figure 1. Sample stimulus photo.

B. *Stimulus Ratings*

1. Rating Participants

Raters were UCSB students who participated in exchange for partial course credit. The primary 39 raters were 23 men (Mean age ± SD = 19.17 ± 1.50 years) and 16 women (Mean age ± SD = 18.81 ± 1.22 years), but an additional batch of 19 raters comprised of 11 women (Mean age ± SD = 19.64 ± 0.67 years) and 8 men (Mean age ± SD= 19.38 ± 1.30 years) was recruited in order to obtain ratings for five stimulus photos that were previously omitted due to a clerical error. Participants provided written, informed consent for their participation, and all procedures were approved by the UCSB Institutional Review Board.

2. Rating Procedures

Raters viewed the stimulus photos one at a time on a computer and were asked: "How physically attractive do you find this woman, relative to other women of the same age?" (1-7 scale). After rating all of the stimuli for general attractiveness, participants read the following: "We will now be focusing on the woman's attractiveness as a LONG-TERM [SHORT-TERM] mate," and ratings of either long- or short-term attractiveness followed on the same scale, with the order of these two rating dimensions counterbalanced across raters. The order of photo presentation was randomized within each rating dimension.

There was high between-rater agreement for each of the three rating dimensions (all ICCs > 0.90); thus, ratings were aggregated across raters to give each woman a mean rating for each rating dimension. The three rating dimensions also had high reliability ($\alpha = 0.99$ for the mean ratings) and were therefore averaged to create a composite attractiveness variable that was used in subsequent data analyses. Male and female raters were in high agreement regarding their perceptions of the women's attractiveness (ICC = 0.92 for the composite mean attractiveness ratings). In addition, for all of the correlations between composite attractiveness ratings and other variables presented in the Results, there were no significant differences between correlations computed using only male raters and those computed using only female raters (Fisher's *z*-test; all *p*s > 0.40). The average attractiveness rating was just below the midpoint of scale (composite attractiveness mean = 3.92, S.D. = 1.05).

3. Data analyses

Pearson correlation, partial correlation, and multiple regression were employed to test relationships between women's mean hormone concentrations (as defined in 2.1.3), body dimensions, and rated attractiveness. Following Jasienska et al. (2004), we also constructed categorical body dimension groups (top vs. bottom quartile) for WHR and for breast size, as well as combinations of above and below average WHR with above and below average breast sizes). *t*-tests and one-way ANOVAs were used to test whether such groups differed in mean hormone concentrations. Bias-corrected, nonparametric bootstrapping procedures (see Preacher & Hayes, 2008) were employed as tests of whether specific body dimensions statistically mediated relationships between hormone concentrations and attractiveness ratings. This analysis essentially tests whether a third variable is related to both the hormones and attractiveness ratings such that its addition to the model significantly diminishes the direct effect of hormones on attractiveness ratings; mediation is established if the 95% confidence interval for the unstandardized indirect effect does not include zero.

Measured variables more than three standard deviations from their respective means were excluded to avoid undue influence of outliers; one subject mean testosterone concentration and one BMI value were thus excluded (effect sizes for significant effects were generally larger with the outliers included). After outlier removal, all mean hormone and body dimension variables were approximately normally distributed by visual inspection and the Shapiro-Wilk test.

III. Results

A. Hormones

Excluding the one woman whose mean testosterone concentration was an outlier, the 32 women in the sample provided 798 saliva samples from the middle 18 days of their respective cycles out of 900 eligible cycle days (89% compliance rate). After selection of saliva samples from alternating days outside of the nine-day window surrounding the initial estimate of mid-cycle, measured hormone concentrations were available for 565 and 577 of these days for estradiol and testosterone, respectively (insufficient remaining quantity of saliva for assay accounted for the difference given that testosterone was assayed first). With respect to the final 14 days of the cycle, 631 saliva samples were collected out of 700 eligible cycle days (90% compliance rate); progesterone assay values were obtained for 388 of these days.

B. Hormones and Body Dimensions

Table 1 presents correlations between mean hormone concentrations, body dimensions, and body attractiveness ratings. Contrary to previous findings (Jasienska et al, 2004), there were null zero-order correlations between body dimensions and hormones; neither WHR nor breast size was significantly associated with mean estradiol, progesterone, or testosterone.

Table 1
Zero-order correlations between mean hormone concentrations[a], body dimensions, and mean body attractiveness ratings.

	Attractiveness	Estradiol	Testosterone	Progesterone	WHR	Breast size
Estradiol	0.23					
Testosterone	0.14	0.16				
Progesterone	- 0.21	0.15	0.01			
WHR	- 0.45*	0	- 0.07	0.23		
Breast size	- 0.14	- 0.01	0.24	- 0.16	- 0.14	
BMI	- 0.80***	0	0.13	0.22	0.55**	0.19

[a] Estradiol and testosterone concentrations represent subject means for 18 days surrounding ovulation; progesterone concentrations represent subject means for the last 14 days of the cycle.
***$p < 0.001$
**$p < 0.01$
*$p < 0.05$

A series of one-way ANOVAs were conducted to investigate differences in mean estradiol, progesterone, and testosterone across four body shape categories defined by Jasienska et al. (2004): narrow waist, large breasts; narrow waist, small breasts; broad waist, large breasts; broad waist, small breasts. "Narrow" and "broad" waists represent women below or above the mean WHR, respectively, whereas "small" and "large" breasts represent women below or above the mean breast size. There were no significant differences in any of the hormones across the four body shape groups (all *p*s > .46). Likewise, a series of t-tests investigating differences in mean estradiol, progesterone, and testosterone between top and bottom quartiles of breast size and WHR revealed no significant differences in hormone concentrations between these groups for either body shape. Jasienska et al. (2004) also tested associations between body dimensions and hormone concentrations within narrower ranges of cycle days (e.g., estradiol concentrations on the day of ovulation); we again found only null results when we tested the same correlations presented in Table 1 within these narrower cycle day windows.

C. Predictors of Body Attractiveness Ratings

1. Morphological Predictors

Consistent with previous research, body attractiveness was significantly associated with lower WHR and lower BMI (see Table 1). A multiple regression with WHR and BMI entered together as predictors of body attractiveness ratings revealed a strong independent effect of BMI ($\beta = -0.79$, $p < 0.001$) and a null effect of WHR ($\beta = -0.02$, $p = 0.87$). BMI accounted for approximately 64% of the variance in women's body attractiveness.

2. Hormonal Predictors

As can be seen from Table 1, there were no significant zero-order correlations between subject mean hormone concentrations and body attractiveness ratings, although power limitations may have prevented detection of a small association between estradiol and attractiveness ($r = 0.23$). The large association between BMI and attractiveness may have obscured the influence of smaller predictor variables, however, and we therefore tested whether hormone concentrations were correlated with attractiveness ratings after controlling for the influence of BMI. Table 2 demonstrates that subject mean estradiol and testosterone both exhibited significant partial correlations with body attractiveness ratings after controlling for BMI. Progesterone was not a significant independent predictor of the body attractiveness residuals from BMI, and neither WHR nor breast size had residual variance from BMI that was significantly associated with any hormone.

Table 2
Partial correlations between hormones, body dimensions, and body attractiveness ratings after controlling for BMI.

	Attractiveness	WHR	Breast size
Estradiol	0.39*	0	- 0.01
Testosterone	0.42*	- 0.17	0.22
Progesterone	- 0.06	0.14	- 0.21

*$p < 0.05$

A multiple regression analysis testing the partial effects of BMI, testosterone, and estradiol revealed independent effects of BMI (β = -0.83, $p < 0.001$), mean estradiol (β = 0.20, $p = 0.055$), and mean testosterone (β = 0.22, $p = 0.04$); the two hormones jointly explained an additional 10% of the variance in body attractiveness beyond that explained by BMI alone (change in R^2 F (2, 27) = 5.24, $p = 0.01$).

Given that the estradiol and testosterone measurements represented subject means for 18 days surrounding ovulation, it is possible that their associations with body attractiveness could have been driven by effects in a narrow region of the cycle. To assess this, Fig. 2 plots hormone concentrations against day of the cycle (aligned on the estimated day of ovulation as day zero) with separate curves for women who were above and below the mean residual attractiveness rating after controlling for BMI. It can be seen that estradiol was consistently higher across the entire cycle among women who were rated more attractive than predicted by their BMI alone (Fig. 2A); this pattern was less consistent for testosterone, but still visible across broad regions of the cycle (Fig. 2B). In contrast, the curves were very similar across the entire cycle for progesterone (Fig. 2C).

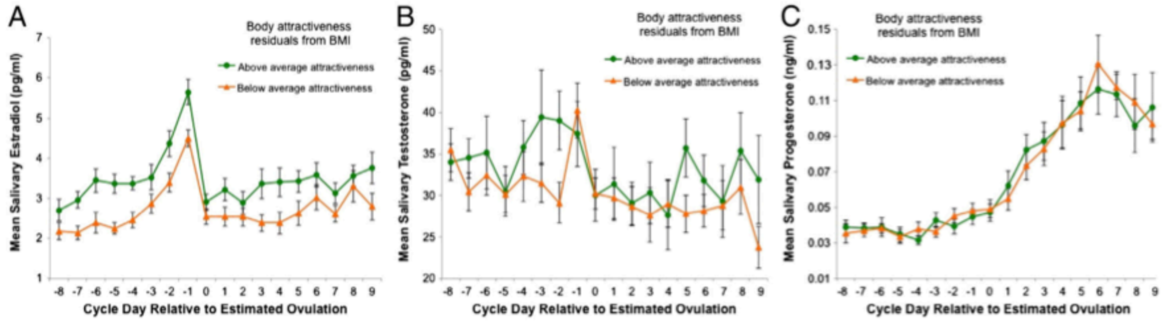

Figure 2. Mean salivary estradiol (A), testosterone (B), and progesterone (C) concentrations aligned against estimated day of cycle (day 0 represents the estimated day of ovulation) separated by women who were above and below average, respectively, for the residuals of attractiveness ratings regressed onto BMI. Error bars represent SE.

The patterns depicted in Fig. 2 suggest that, after controlling for BMI, other observable cues in women's bodies contribute to attractiveness judgments and predict concentrations of estradiol and testosterone. In an exploratory attempt to identify such cues, we employed nonparametric bootstrapping methods to first test whether scale measures of women's muscle mass, visceral fat, body fat, or water percentage were significant mediators between either estradiol or testosterone and women's body attractiveness, controlling for BMI. None of these variables significantly mediated the relationship between either of the hormones and attractiveness ratings, whether the mediators were tested separately or jointly (all CIs for the indirect effects included zero).

Based on the subjective impression that women with higher residual attractiveness ratings had waists that angled inward more sharply from their upper torsos, we also computed a ratio of shoulder width (measured from front-facing photos) to waist width and tested it as a mediator of the hormone effects. This shoulder-to-waist (SWR) ratio was in fact a significant mediator between residual variance in women's body attractiveness from BMI and both their estradiol (Indirect Effect = 0.118, SE = 0.080, 95% CI = 0.016 - 0.417) and testosterone (Indirect Effect = 0.018, SE = 0.01, 95% CI = 0.004 – 0.051) concentrations, with larger SWR associated with both higher hormone concentrations and greater attractiveness. Neither shoulder width nor waist width on its own was a significant mediator of the relationship between hormone concentrations and residual attractiveness ratings (all CIs included 0).

IV. Discussion

A. Hormones, Body Dimensions, and Body Attractiveness

The present research is the first to demonstrate a direct link between women's body attractiveness and ovarian hormone concentrations across broad regions of the menstrual cycle. There were no significant zero-order correlations between women's hormone concentrations and ratings of their attractiveness. After controlling for women's BMI, however, women's concentrations of estradiol and testosterone were significantly positively associated with the body attractiveness ratings. As can be seen from Figure 5, this relationship held across the entire menstrual cycle and was not driven by effects during a specific region of the cycle. This finding thus provides evidence for the notion that preference mechanisms in men may in fact hone in on cues of fertility in young women's bodies, and speaks against traditional views in the social sciences that physical attractiveness is culturally arbitrary, though interpretive questions are raised by the necessity of holding BMI constant in order to demonstrate robust relationships between hormones and attractiveness.

Given previous research demonstrating higher estradiol and progesterone among women with lower WHR and larger breast size (Jasienska et al., 2004), WHR and breast size were expected to mediate any relationship between body attractiveness and hormone concentrations. However, there was no evidence of this in our study. Neither breast size nor WHR were associated with subject mean concentrations of estradiol, progesterone, or testosterone; nor did they predict any hormone after controlling for variability in these body shapes due to BMI.

Differences in study samples or measurement techniques may help account for inconsistencies between our results and those of Jasienska et al. (2004). Whereas Jasienska et al. (2004) investigated over a hundred Polish women (mean age = 29 years), our sample was overall younger (mean age = 18 years), more ethnically heterogeneous, and much smaller. Menstrual cycles are notably less stable in young women (Metcalf & Mackenzie, 1980) and may vary across cultural groups (Vitzthum, 2009), although ethnicity was not associated with any variables examined in the present study and data were analyzed only from cycles that were confirmed to be ovulatory. We measured WHR from photographs as opposed to direct body measurements like Jasienska et al. (2004), although it should be noted that the correlations between WHR and attractiveness in our sample were very similar to those reported elsewhere (compare Table 1 to findings in Corneliseen, Hancock, Kiviniemi, George, & Tovee, 2009; Faries & Bartholomew, 2012), which suggests that our measurements were consistent with others in this literature. Although our sample size was not large, low power is unlikely to explain the null relationships between hormones, WHR, and breast size given that correlations here did not even trend in the direction predicted by Jasienska et al. (2004) (see Table 1). Furthermore, despite our smaller sample, we still discovered a robust relationship between estradiol, testosterone, and residual variance in body attractiveness not accounted for by BMI.

The lack of relationships between hormone concentrations and either WHR or breast size suggested that at least one other physical cue was mediating the relationship between estradiol, testosterone, and body attractiveness residuals from BMI. Although we could not identify the physical cue of estradiol in women's bodies, exploratory post-hoc analyses revealed shoulder-to-waist ratio (SWR) as a statistical mediator of the effects of both estradiol and testosterone on body attractiveness ratings. These results should be interpreted with caution, however, given both the number of potential mediators tested and the fact that we had no way of testing whether observers actually used this ratio as a perceptual cue that contributed to their attractiveness judgments.

SWR might correlate inversely with android fat depositions (i.e. fat in the abdomen and upper torso) because such fat will cause the waist to spread out toward the width of the shoulders and thus reduce the ratio. It is known that abdominal fat is not perfectly captured by either WHR or BMI (Wells, 2010), and SWR could be a better index of this feature.

Abdominal girth typically increases with pregnancy, parity (Lassek & Gaulin, 2008), age (Wells, 2010), and in the presence of intestinal parasites. The amount of abdominal fat is also inversely related to the availability of essential fatty acids necessary for fetal and infant neurodevelopment (Lassek & Gaulin, 2008). Thus, relative abdominal girth may provide important information about women's reproductive potential, and may correlate negatively with women's body attractiveness. Prior research has demonstrated negative associations between women's body attractiveness and measures of waist girth such as abdominal depth and waist circumference (e.g., Faries & Bartholomew, 2012; Rilling et al., 2009). Studies with eye trackers have also shown that perceivers are more likely to fixate first on (Dixson, Grimshaw, Linklater, & Dixson, 2011) and fixate more overall on (Cornelissen, Hancock, Kiviemi, George, & Tovee, 2009) the abdominal compared to hip or pelvic regions when assessing body attractiveness. To test whether android fat deposits are used as a perceptual cue when assessing women's body attractiveness, ideally, this fat would be measured more directly via tools such as dual-energy X-ray absorptiometry scans (see Faries & Bartholomew, 2012; Sowers, Beebe, McConnell, Randolph, & Jannausch, 2001). Future research that combined such measurements with hormone assays would allow for more precise tests of which body dimensions may account for relationships between hormones and body attractiveness.

B. The Importance of BMI

In this study, BMI was the single most important predictor of women's body attractiveness, such that the bodies of women with low BMI received much higher attractiveness ratings than the bodies of women with high BMI. Neither WHR nor breast size predicted attractiveness independent of BMI, which supports previous research suggesting that BMI is a stronger predictor of body attractiveness than is WHR (e.g. Tovee & Cornelissen, 2001). However, our sample was comprised of women within a very restricted range of WHR; all subjects were young and ovulating, exhibiting WHRs from .62 - .79. If WHR is used to guide broad first pass assessments of a woman's fertile state, then WHR might more strongly predict the body attractiveness of women sampled from across the entire age spectrum; within young women of reproductive age, other cues of health or fertility such as body weight might have relatively stronger effects on attractiveness (Aaron Blackwell, personal communication, May 2013).

However, why was it necessary to control for BMI in order to see clear relationships between ovarian hormone concentrations and body attractiveness ratings? If specialized preference mechanisms track cues of fecundity as indexed by hormone concentrations, then we might expect positive zero-order correlations between hormones and attractiveness without having to control for other variables. We offer two conjectures regarding this issue.

1. BMI and Fitness

First, BMI may predict other fitness-relevant traits aside from fecundity that are also relevant to attractiveness judgments. Higher BMI is strongly predictive of a wide array of health problems in industrialized countries (e.g., Calle, Rodriquez, Walker-Thurmond, & Thun, 2003; Gilmore, 1999; Manson et al., 1995; Willett et al., 1995). Although many of those health problems may not have been relevant to reproductive success in ancestral environments, higher BMI has also been associated with greater fluctuating asymmetry (Hume & Montgomerie, 2001; Losken, Fishman, Denson, Moyer, & Carlson, 2005; Manning, 1995; Milne et al., 2003) and higher rates of inflammation (e.g. Festa et al., 2001; Panagiotakos, Pitsavos, Yannakoulia, Chrysohoou, & Stefanadis, 2005; Trayhurn & Wood, 2005), suggesting that greater BMI may predict greater developmental instability and reduced immunocompetence, both of which likely entailed fitness costs to mates independent of their effects on fecundity. These inverse associations of BMI with health and developmental stability – at least in industrialized nations – may lead cues of high BMI to become associated with poor health, thus partly explaining the negative effect of BMI on attractiveness. In addition, BMI is on average positively correlated with age in the United States (Brown, Kaye, & Folsom, 1992; Fryar, Gu, & Ogden, 2012; Lassek & Gaulin, 2006), such that high BMI may become associated with declining reproductive value and thereby reduced attractiveness via that association, even among young women see Wells, 2010). These associations of BMI with health and age appear to be reversed under conditions of food shortage. For example, women's BMI is known to decline with age in many subsistence societies (see Jeliffe & Maddocks, 1964; Little, Leslie, & Campbell, 1992; Shell-Duncan & Yung, 2004; Tracer, 1991). Moreover, BMI positively indexes health in societies where the range of BMI is overall lower; see Hosegood & Campbell, 2003; Pierce et al., 2010). Therefore, preference mechanisms that track cues of health and reproductive value may produce opposite associations between BMI and attractiveness in regions of food surplus compared to regions with chronic nutritional stress (see Swami & Tovee, 2007; Wells, 2010).

In sum, BMI here could act as a cue of health and age that has such large effects on attractiveness ratings that it swamps the smaller effects on attractiveness of cues associated with ovarian hormone production; once BMI is held constant, however, cues of hormone concentrations emerge as significant predictors of attractiveness. On this account, specialized perceptual mechanisms do in fact track cues of fertility, but these cues have smaller effects on attractiveness than do cues associated with BMI.

2. SHBG and Free Hormones

Second, correlations between attractiveness ratings and salivary measures of hormone concentrations may be partially obscured by associations between BMI and sex hormone binding globulin (SHBG). SHBG binds to both estradiol and testosterone and higher SHBG concentrations reduce the free, bioavailable concentrations of these hormones that are measured in salivary assays (Ellison, 1988). Higher BMI very strongly and consistently predicts lower SHBG (e.g., Bruning, Bonfrer, Hart, et al., 1992; Dorgan et al., 1995; Thomas et al., 1997; Turcato et al., 1997; Tworoger et al., 2006; for a review, see Morisset, Blouin, & Tchernof, 2008), and experimentally induced weight loss can produce doubling of SHBG concentrations in as little as two weeks, with associated drops in free but not total hormone concentrations) (e.g., Kiddy et al., 1989; Kiddy et al., 1992; Turcateo et al., 1997; for a review, see Morisset et al., 2008). These patterns suggest that higher BMI is likely to be associated with artificially inflated measures of salivary, free hormones relative to the total ovarian hormone production; consistent with this, in a large study of premenopausal women, lower BMI was predicted higher total estradiol, but was uncorrelated with free estradiol (Tworoger et al., 2006). This in turn implies that when two women have the same free hormone concentrations but differ in BMI, the woman with lower BMI is likely to have greater ovarian hormone production since a greater fraction of her hormones will be bound to SHBG. Likewise, when two women have the same BMI but differ in free hormone concentrations, the woman with greater free hormone concentrations should have higher ovarian production since the effect of BMI on SHBG will be held constant. As such, if perceivers' attractiveness judgments specifically track cues of ovarian hormone production, then lower BMI should predict attractiveness when free hormones are held constant, and free hormones should predict attractiveness when BMI is held constant. That is exactly the pattern produced by our regression models. In short, controlling for BMI may increase the size of correlations between free hormone concentrations and attractiveness ratings by removing the variability in measured hormone concentrations that is associated with binding proteins and is thus potentially unrelated to fecundity. This idea could be tested more directly in future research that used blood samples in order to test associations between body attractiveness and both total and free hormone concentrations. We might expect total estradiol to be a better predictor of both ovarian production and body attractiveness than free estradiol, and the proportion of unbound to bound estradiol might vary predictably based on the women's BMI.

3. Further Thoughts on BMI

As a quick aside, a question that remains unanswered in this literature is why BMI may index health or reproductive value differently under different environmental conditions. A preference for low BMI is pervasive in high SES and Western societies (Swami et al., 2010; Rilling et al., 2009; Singh & Singh, 2001; Streeter & McBurney, 2003; Tovee & Cornelissen, 2001), but relatively high BMI tends to be preferred in low SES and non-Western societies (Anderson, Crawford, Nadeau, & Lindberg, 1991; Swami & Tovee, 2007; Marlowe & Wetsman, 2001; Yu & Shephard, 1999). Given that fat stores have several important metabolic and immunological functions (Wells, 2010), buffer the effects of environmental energetic constraints on female reproductive function (Ellison, 2001), and are metabolized during pregnancy and lactation (Rebuffe-Scrive et al., 1985; Norgan, 1997), *prima facie*, high BMI in women seems more adaptive than low BMI. Why, then, is there a preference for low BMI in high SES societies?

From a functional perspective, a preference for low BMI might make sense if there were some cost to storing, metabolizing, or carrying fat that exceeded its benefits under certain ecological conditions; perhaps, in environments where resources are consistently abundant, the benefits of extra energy availability diminish greatly, rendering fat storage a maladaptive strategy. Some experimental research with non-human animals manipulating diet energy has shown that fat storage increases under conditions of long-term dietary scarcity but decreases with multigenerational exposure to high-energy diets, suggesting that there may indeed be a cost to storing fat (Warbrick-Smith, Behmer, Lee, Raubenheimer, & Simpson, 2006).

Future research with humans could address this question in several ways. First, if individuals in better condition overall or with greater genetic fitness calibrate their fat storage adaptively to environmental energy availability, we might expect the women with high BMI in low SES societies to have the greatest ovarian production because they are in the best overall condition, and likewise for the women with low BMI in high SES societies. This could be tested directly by measuring total and free hormones, as well as conception rates for women in two societies where preferences for women's BMI differ, as in the populations reported by Swami and Tovee (2007). A second study could measure fluctuating asymmetry in high and low BMI women in low SES societies; research has shown that women with high BMI in high SES societies have higher fluctuating asymmetry (Hume & Montgomerie, 2001; Losken, Fishman, Denson, Moyer, & Carlson, 2005; Manning, 1995; Milne et al., 2003), but it could be the case that women in low SES societies show the opposite pattern—low BMI with high fluctuating asymmetry. This is expected if fat storage strategies represent an adaptive calibration to environmental energy availability, and individuals with high genetic quality can both withstand environmental perturbations during development and calibrate their fat storage to environmental energy availability better than individuals with lower genetic quality. Third, although the cues that trigger environmental energy availability have not been established, it might be the case that the children of mothers who experienced extreme dietary energy scarcity during pregnancy are more likely to have high BMI if they grow up in high-energy environments than the children of mothers who did not experience energy scarcity during pregnancy. Longitudinal studies that investigated the health of children born to holocaust survivors might shed light on this prediction.

C. Independent Effects of Testosterone on Attractiveness

The positive effect of testosterone on attractiveness after controlling for BMI was surprising given evidence that elevated testosterone in women may promote visceral fat deposition (e.g., Evans, Hoffman, Kalkhoff, & Kissebah, 1983; Sowers et al., 2001) and be associated with reduced fecundity (e.g., Okon, Laird, Tuckerman, & Li, 1998; Steinberger, Smith, Tcholakian, & Rodriguez-Rigau, 1979). Many of the negative effects of testosterone on reproductive functioning are associated with obesity (Clark et al., 1995; Kiddy et al., 1992; Pasquali, Casimirri, & Vicennati, 1997) and associated reductions in SHBG (see above), however. Thus, controlling for BMI may more uniquely capture follicle-derived sources of testosterone that could, in principle, be associated with higher fecundity. Testosterone acts as a precursor to estradiol produced by the dominant follicle, for instance, and peri-ovulatory peaks in estradiol are typically accompanied by concomitant peaks in testosterone (e.g., Abraham, 1974; Campbell & Ellison, 1992; Roney & Simmons, 2013) such that larger dominant follicles that produce higher estradiol in more fertile cycles may likewise produce higher testosterone. As such, the combination of estradiol and testosterone concentrations may better predict dominant follicle production within ovulatory cycle than does the concentration of either hormone alone, thus potentially explaining the independent effects of the two hormones on attractiveness ratings. In addition, although testosterone does seem to be related to abdominal fat deposition in women, it could be the case that the body shapes that young women exhibit are more related to androgens and estrogens during puberty than current circulating levels of free testosterone and estradiol. These thoughts are all speculation, of course, and the unexpected association of attractiveness with testosterone concentrations warrants replication before assigning much confidence to the robustness of this finding.

D. Limitations and Conclusions

Potential limitations of the present research, besides the small, young, and somewhat heterogeneous study sample, are the incomplete hormone data and body measures. Due to financial constraints, we were not able to obtain hormone measurements for every day outside of the 9-day window surrounding a woman's estimated ovulation. We also did not have access to the equipment necessary for gathering comprehensive body shape information, such as dual-energy X-ray absorptiometry scans (see Faries & Bartholomew, 2012; Sowers, Beebe, McConnell, Randolph, & Jannausch, 2001).

However, to our knowledge, the present study is the first to demonstrate a relationship between women's body attractiveness and concentrations of ovarian hormones measured across broad regions of the menstrual cycle. Both estradiol and testosterone independently predicted body attractiveness ratings after controlling for the effects of BMI, which suggests that preference mechanisms may indeed track cues of fecundity in young women's bodies. The evidence for specialized attractiveness assessment mechanisms could be substantially strengthened via cross-cultural demonstrated of relationships between hormones and attractiveness across diverse ecological and social conditions, however, and tests of such relationships therefore represent an important direction for future research. Future studies should also focus on elucidating the physical cue(s) mediating the relationships between hormones and body attractiveness, including testing replication of the SWR effect.

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