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Symmetrical women have higher potential fertility

Grazyna Jasienska[a,b,*], Susan F. Lipson[c], Peter T. Ellison[c], Inger Thune[d,e], Anna Ziomkiewicz[a]

[a]*Department of Epidemiology and Population Studies, Jagiellonian University, Collegium Medicum, 31-531 Krakow, Poland*
[b]*Radcliffe Institute for Advanced Study, Harvard University, Cambridge, MA 02138, USA*
[c]*Department of Anthropology, Harvard University, Cambridge, MA 02138, USA*
[d]*Institute of Community Medicine, University of Tromso, Tromso, Norway*
[e]*Ulleval University Hospital, Oslo, Norway*

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Abstract

Fluctuating asymmetry (FA) is believed to reflect developmental stability and thus may serve as a marker of the biologic quality of individuals. To test the hypothesis that degree of FA is related to a woman's potential fertility, we measured finger length together with levels of estradiol in saliva samples collected daily for an entire menstrual cycle in 171 Polish urban and rural women. We show that women who are more symmetrical, as assessed by the degree of inequality in the fourth-digit length of their right and left hands, have 13% higher average levels of estradiol over the menstrual cycle than less symmetrical women (19.4 and 17.1 pmol/l, respectively; p=.0001). Among urban women, mid-cycle levels of estradiol were 28% higher in the symmetrical group than in the asymmetrical group. Because higher hormone levels in women may lead to a substantial rise in the probability of conception, low FA may therefore be associated with increased fertility.

Keywords: Fluctuating asymmetry; Health; Hormones; Menstrual cycle; Premenopausal women

* Corresponding author. Radcliffe Institute for Advanced Study, Harvard University, 34 Concord Ave., Cambridge, MA 02138, USA. Tel.: +1 617 495 8182; fax: +1 617 495 8136.
E-mail address: jasienska@post.harvard.edu (G. Jasienska).

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1. Introduction

Evolutionary psychology suggests that human traits that are considered attractive function as reliable markers of the biologic condition and reproductive potential of individuals (Grammer, Fink, Møller, & Thornhill, 2003; Symons, 1995) Women, at least in Western societies, are considered attractive when they have relatively narrow waists, large breasts, and symmetrical features (Henss, 2000; Singh, 1993). We have recently documented that waist-to-hip ratio and breast size are indeed indicators of reproductive potential in women because they are related to the levels of reproductive hormones (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004).

In humans, individuals of both sexes who are more symmetrical are considered more attractive (Gangestad, Thornhill, & Yeo, 1994; Grammer et al., 2003; Grammer & Thornhill, 1994; Thornhill & Gangestad, 1994, but see Kowner, 1996; Noor & Evans, 2003; Swaddle & Cuthill, 1995). The degree of asymmetry may be an important indicator of developmental stability and a biomarker of fitness (Jones et al., 2001). Random deviation from the perfect symmetry expected in bilateral structures of bilaterally symmetrical organisms is referred to as *fluctuating asymmetry* (FA) (Møller & Swaddle, 1997). FA may result from the influences of genetic and environmental stressors operating during fetal development (Møller & Swaddle, 1997). It has been linked to some aspects of human health (Manning, 1995; Manning, Koukourakis, & Brodie, 1997; Shackelford & Larsen, 1997; Waynforth, 1998), although other studies failed to find significant associations (Hume & Montgomerie, 2001; Milne et al., 2003; Rhodes et al., 2001; Tomkinson & Olds, 2000).

Very few studies show that the degree of FA correlates with reproductive potential. In men, more symmetrical individuals have higher sperm number per ejaculate, greater sperm speed and migration ability (Manning, Scutt, & Lewis-Jones, 1998), and higher sperm motility (Soler et al., 2003). In women, studies have indicated a relationship between breast symmetry and fertility-related traits. Women with higher breast symmetry have a higher number of offspring (Møller, Soler, & Thornhill, 1995)—a finding confirmed by another study that, in addition, documented an earlier age at first birth for more symmetrical women (Manning, Scutt, Whitehouse, & Leinster, 1997). However, both the higher number of children and lower age at first birth may be caused indirectly by the increased attractiveness of symmetrical women. Attractive women may be able to attract more partners and choose those with better socioeconomic status, which, in turn, may lead to a higher number of children in such unions. Similarly, earlier age at first birth in more attractive women may result from an earlier age at marriage, which is a strong predictor of first reproductive event (Wood, 1994). Therefore, the above data do not provide conclusive evidence of a causal biologic link between FA and fertility. To prove that such a link really exists, one needs to show a relationship between asymmetry and a woman's physiological reproductive potential. Such potential can be assessed by measurements of ovarian steroid hormones, which are indicators of the probability of conception and successful pregnancy (Baird et al., 1997; Baird et al., 1999; Gorkemli, Ak, Akyurek, Aktan, & Duman, 2004; Lipson & Ellison, 1996; Lukaszuk, Liss, Lukaszuk, & Maj, 2005; Sharara & McClamrock, 1999).

We hypothesize that in women, FA will be related to reproductive potential. More specifically, we expect that more symmetrical women would have higher levels of estradiol, which are predictors and determinants of successful pregnancy.

2. Materials and methods

2.1. Subjects

Subjects for the study were 133 urban and 50 rural women from Poland. Women were recruited for the study by advertisements and were selected for participation if they met the following criteria: age between 24 and 36 years, regular menstrual cycles and no fertility problem, no gynecologic and/or chronic disorder (i.e., diabetes, hypo/hyperthyroidism), not taking any hormonal medication or using hormonal contraception, and not being pregnant or lactating for at least 6 months before recruitment.

2.2. Anthropometric measurements

Measurements of body weight, height, percentage of body fat (by bioimpedance), and finger lengths were made by a trained anthropologist and were taken randomly with respect to the phase of the menstrual cycle. A detailed description of measurements was published elsewhere (Jasienska et al., 2004). A general questionnaire (partly administered by an interviewer and partly self-reported) was used to collect information on education; reproductive history; and past use of hormonal medication, tobacco, and alcohol. Data on birth weight and birth length were obtained from subjects' personal records. The second and fourth digits of each hand were measured to the nearest millimeter with a caliper; measurements were made on the ventral surface of the hand from the basal crease of the digit to the tip. Finger length measurements were not obtained for three women with missing digits or hand injuries. The lengths of the fourth right and fourth left fingers were compared for each woman, and the hormone levels were compared in analyses of variance (ANOVAs) based on dividing the subjects into two groups (i.e., symmetrical and asymmetrical women). If the fourth left and fourth right fingers differed in length by 0 or 1 mm, the woman was classified as symmetrical; if the fingers differed by 2 mm or greater (i.e., the observed difference in finger lengths was more pronounced than that resulting from measurement error), the woman was classified as asymmetrical. Complex structure of the hormonal data (i.e., the dependent variable being an entire hormonal profile of the menstrual cycle for each woman rather than a single measurement, as was typical of most earlier studies) led to the choice of ANOVA rather than regression analyses on individual subjects.

2.3. Hormonal collection and analysis

Women collected saliva samples for an entire menstrual cycle. Saliva samples from 20 days (reverse cycle Days −5 to −24) of each cycle were analyzed for the concentration of

Table 1
Anthropometric, reproductive, and lifestyle characteristics of groups of symmetrical and asymmetrical women

	Symmetrical women (n = 123[a]) [mean (S.D.)]	Asymmetrical women (n = 48[a]) [mean (S.D.)]	p
Age (years)	29.5 (3.29)	29.5 (3.37)	.99
Age at menarche (years)	13.4 (1.42)	13.3 (1.11)	.73
Education (years)	15.6 (3.27)	15.7 (3.03)	.88
Birth weight (g)	3303 (629.6)	3254 (590.0)	.65
Birth length (cm)	53.6 (3.46)	53.6 (4.46)	.97
Body weight (kg)	61.6 (10.57)	60.6 (8.31)	.52
Body height (cm)	162.8 (6.53)	165.1 (5.41)	.02
BMI (kg/m^2)	23.3 (3.82)	22.2 (2.73)	.07
Body fat (%)	27.8 (7.52)	25.8 (6.35)	.14
Breast-to-underbreast ratio	1.17 (0.043)	1.17 (0.039)	.42
Waist-to-hip ratio	0.72 (0.049)	0.72 (0.044)	.96
Absolute difference between fourth fingers (mm)	0.58 (0.495)	2.67 (1.191)	.0001
Length of menstrual cycle (days)	28.7 (3.6)	28.2 (3.66)	.32
Age at first birth (years)	23.2 (3.01)	23.0 (3.33)	.71
No. of children	0.9 (1.17)	0.8 (1.17)	.63
Physical activity (MET-h/day)	8.8 (3.02)	8.6 (2.63)	.72
Smoking (cigarettes/day)	1.95 (4.81)	1.90 (4.66)	.96
Alcohol consumption (U/day)	1.7 (1.64)	1.7 (1.52)	.97

p values derived from two-sided t tests.
[a] Numbers in groups may vary due to missing values.

17-b-estradiol using an I-125-based radioimmunoassay kit (No. 39100, Diagnostic Systems Laboratories, Webster, TX, USA) with published (Jasienska et al., 2004) modifications to the manufacturer's protocol. Prior to statistical analyses, cycles were aligned based on identification of the day of the mid-cycle estradiol drop (Day 0), which provides a reasonable estimate of the day of ovulation (Lipson & Ellison, 1996). Estradiol values from 18 consecutive days of aligned cycles were used in analyses. Because the day of the mid-cycle estradiol drop could not be reliably identified for nine subjects, they were excluded from the analyses, together with three subjects missing finger length data. Data on 171 women (124 urban and 47 rural) were used in the analyses.

2.4. Statistical analysis

We tested differences in anthropometric, lifestyle, and reproductive variables between symmetrical and asymmetrical women by two-sided t tests (Table 1). The mean lengths of the fourth fingers of the right and left hands were not significantly different [68.6 and 68.7 mm, respectively; paired t test, $t(170)=1.0$, $p=.32$]. In addition, the variance in the length of the right fourth finger was not significantly different from the variance in the length of the left fourth finger ($p>.25$). In contrast, average lengths of the second fingers of the right and left hands were significantly different [68.1 and 67.5 mm, respectively; paired t test, $t(170)=4.3$,

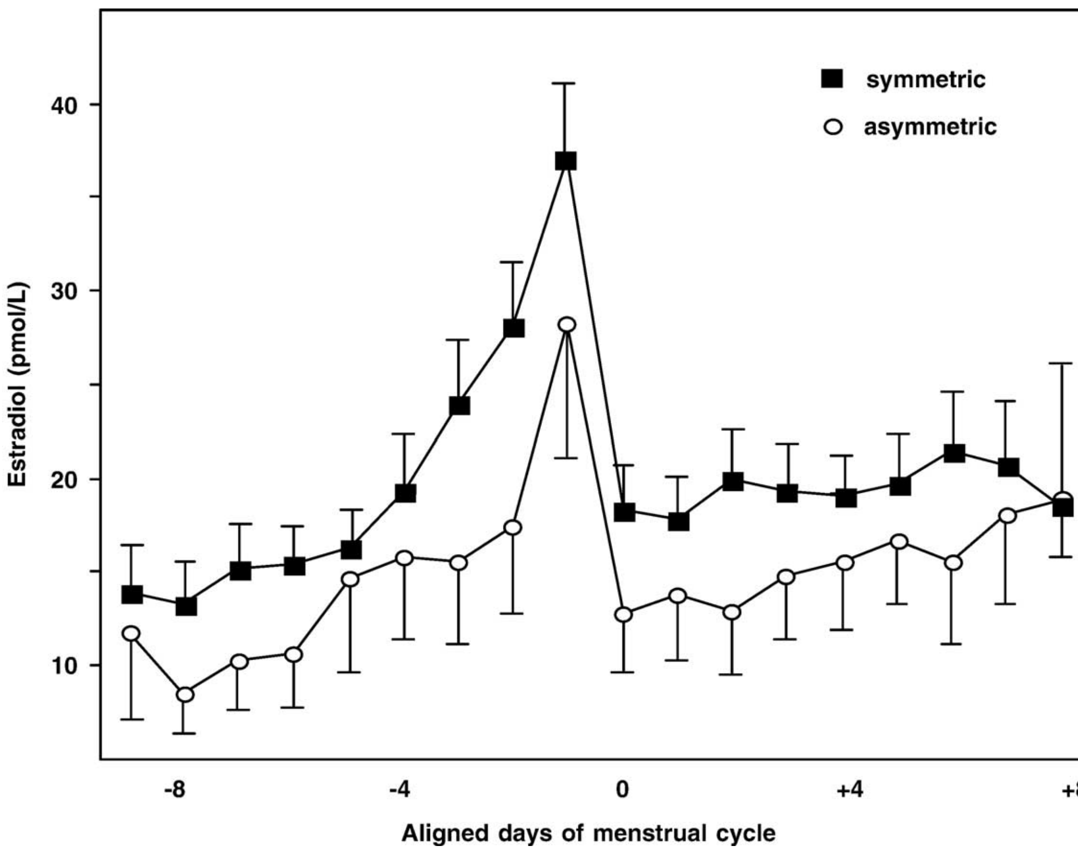

Fig. 1. Mean (with 95% confidence intervals) profiles of estradiol for symmetrical and asymmetrical urban women.

$p<.0001$]; consequently, because this indicated a directional asymmetry, measurements of the length of the second finger were not used in analyses. FA of the fourth finger had a symmetrical distribution, with low skewness (0.354, $p>.05$), but a significant leptokurtosis (kurtosis=3.508, $p<.001$). Leptokurtosis seems to be a common feature of the distribution of FA (Gangestad & Thornhill, 1999) and is suggested to be a result of early loss of highly asymmetrical individuals (Martin, Manning, & Dowrick, 1999).

Differences between the groups of symmetrical and asymmetrical women in estradiol levels for aligned cycle Days −9 to +8 were analyzed by two-way ANOVA. Classification as symmetrical and asymmetrical was used as one factor and day of the menstrual cycle was used as the second factor (with 18 levels). Because the symmetry groups showed statistically significant differences in height and differences in body mass index (BMI) that were approaching statistical significance, we performed additional analyses to test the effects of these potential confounders: a three-way ANOVA with height (divided into tertiles) as the additional factor and a three-way ANOVA with BMI (divided into tertiles) as the third factor.

We also tested differences between symmetrical and asymmetrical women in mid-cycle estradiol levels (aligned cycle Days −3 to +1) by two-way ANOVA. The mid-cycle phase,

Table 2
Mean estradiol levels (from aligned cycle Days −9 to +8) in groups of symmetrical and asymmetrical women in tertiles of BMI

	Symmetrical women		Asymmetrical women		
	Estradiol (pmol/l) [mean (S.D.)]	*n*	Mean estradiol (pmol/l) [mean (S.D.)]	*n*	*p*
Low BMI	18.4 (13.02)	36	16.3 (9.4)	19	.022
Moderate BMI	20.8 (15.72)	46	18.2 (10.73)	21	.003
High BMI	18.7 (14.47)	41	16.1 (9.61)	8	.045

which directly precedes ovulation, represents the part of the menstrual cycle with the highest estradiol levels.

In an attempt to eliminate possible confounding factors, all analyses were repeated with the sample restricted to include only urban women, as rural women have been shown to experience changes in reproductive hormones due to lifestyle influences, especially intense physical activity (Jasienska & Ellison, 1998, 2004; Jasienska, Ziomkiewicz, Thune, Lipson, & Ellison, in press).

3. Results

Symmetrical women had 13% higher mean estradiol levels than asymmetrical women [19.4 and 17.1 pmol/l, respectively; $F(1, 2805)=17.24$, $p=.0001$]. The difference was even more pronounced when this analysis was restricted to urban women. Symmetrical urban women had 21% higher mean estradiol levels than asymmetrical urban women [20.4 and 16.9 pmol/l, respectively; $F(1, 2023)=27.91$, $p=.0001$] (Fig. 1).

Symmetrical women had 21% higher mean mid-cycle estradiol levels than asymmetrical women [24.4 and 20.2 pmol/l, respectively; $F(1, 807)=12.98$, $p=.0003$]. In an analysis restricted to urban women, the difference in mean mid-cycle estradiol levels between symmetrical and asymmetrical women was even more pronounced, with levels in symmetrical women 28% higher than those in asymmetrical women [25.9 and 20.2 pmol/l, respectively; $F(1, 585)=16.14$, $p=.0001$].

Symmetrical and asymmetrical women differed in body height and BMI; the difference was significant for height and approached significance for BMI. There was no significant difference in other factors that could be potential confounders (Table 1). The differences in estradiol levels between symmetrical and asymmetrical women remained statistically significant [$F(1, 2733)=17.76$, $p=.0001$] in a three-way ANOVA with height tertiles as the third factor. Height tertiles did not differ significantly in estradiol levels [$F(2, 2733)=1.98$, $p=.14$]. Similarly, the results of a three-way ANOVA with BMI tertiles as the third factor showed that the differences in estradiol levels between symmetrical and asymmetrical women remained statistically significant after adjusting for the BMI [$F(1, 2733)=16.29$, $p=.0001$] (Table 2). BMI also showed a significant relationship with estradiol levels [$F(2, 2733)=7.79$,

p=.0004]. The interaction between symmetry and tertiles of BMI was not statistically significant [$F(1, 2733)=0.07$, p=.93].

4. Discussion

We have shown that a measurement of symmetry in women is related to levels of estradiol during the menstrual cycle. Women characterized as more symmetrical had higher levels of estradiol than less symmetrical women (Fig. 1). Estradiol produced during the menstrual cycle is crucial for successful conception, and levels of estradiol are important indicators of a woman's ability to conceive (Baird et al., 1997; Baird et al., 1999; Gorkemli et al., 2004; Lipson & Ellison, 1996; Lukaszuk et al., 2005; Sharara & McClamrock, 1999). In women from the United States, the average estradiol levels in a menstrual cycle were associated with the probability of conception of 12%, whereas a 37% rise in estradiol levels led to an increase of probability of conception to approximately 35% (Lipson & Ellison, 1996). In our study, mean mid-cycle estradiol levels in symmetrical urban women were almost 30% higher than those in asymmetrical women from the same population. Such difference in hormone levels suggests a substantial increase in the probability of conception for symmetrical women. We have recently shown that levels of estradiol in reproductive age women are related to their size at birth (Jasienska, Ziomkiewicz, Lipson, Thune, & Ellison, 2006), indicating that developmental conditions influence future fecundity. This finding may suggest a link between FA, which is also believed to arise due to developmental stressors, and estradiol levels in women.

Although we used a simple univariate indicator of symmetry (and this study would benefit from the use of more comprehensive multivariate measure of symmetry) in our study, we succeeded in measuring estradiol in samples collected daily for one entire menstrual cycle. Due to large intracycle variations in daily estradiol levels, such frequent sampling is necessary for precise assessment of individual hormonal levels (Jasienska, 2002). In addition, levels of estradiol measured in saliva, in contrast to serum measurements, represent the unbound—and therefore biologically active—fraction of that hormone (Ellison, 1988). We were also able to control for a wide array of factors that may potentially influence levels of ovarian hormones in women. Results of this study indicate that FA is related to levels of estradiol, even after controlling for potential confounders.

In this study, more symmetrical women differed from less symmetrical women in the mean levels of estradiol, which are related to the probability of conception (i.e., in their reproductive potential) but not in reproductive history traits. Age at menarche, age at first birth, and number of children were similar for both groups of women (Table 1). However, in modern family planning societies, a relationship between physiological reproductive potential and reproductive success may no longer exist. Age at menarche depends on nutritional status both in utero (Adair, 2001; Romundstad et al., 2003) and during childhood development (Ellison, 1982; Ellison, 1990; Vermeulen, 1993). In modern societies, age at first birth and number of children are mainly consequences of family planning. Although the women in our study did not use hormone-based contraception for at least 6 months prior to their participation, they might have used hormone-based contraception and other methods of family planning during the years before our study began. In addition, our study was not designed to investigate differences in reproductive success in relation to FA because the women in our study were relatively young and most likely their family size was not yet complete. In general, in modern societies, age at first birth and completed family size may depend more on behavioral than on physiological determinants, rendering a relationship between FA and these reproductive characteristics no longer detectable (but see Manning, Scutt, et al., 1997; Møller et al., 1995).

Because FA is hypothesized to be a biomarker of an individual's fitness, several investigations have searched for a relationship between symmetry and health, with mixed results (Al-Eisa, Egan, & Wassersug, 2004; Henderson & Anglin, 2003; Manning, Koukourakis, et al., 1997; Martin et al., 1999; Milne et al., 2003; see also recent reviews: Grammer, Fink, Møller, & Manning, 2005; Weeden & Sabini, 2005). Our study shows that more symmetrical women of reproductive age have higher levels of estrogen. Based on these findings, one may hypothesize that the relationship between symmetry and health may be different for premenopausal and postmenopausal women.

In women, many aspects of health are estrogen dependent, such as cardiovascular health, osteoporosis, depression, and reproductive cancers (Barrett-Conor & Bush, 1991; Jasienska, 2002; Jasienska & Thune, 2001a, 2001b; Jasienska, Thune, & Ellison, 2000; Key & Pike, 1988; Nguyen et al., 1995; Pike, Spicer, Dahmoush, & Press, 1993). Therefore, in women of reproductive age (premenopausal), those with higher levels of estrogens may also be in better health, because estrogen at normal physiological levels acts as an immunostimulant (Jacobson & Ansari, 2004; Kovacs, Messingham, & Gregory, 2002). However, women who had high levels of estrogens during their reproductive years may suffer detrimental health effects in their postmenopausal years, as high lifetime levels of reproductive hormones are related to an increased risk of breast cancer and other hormone-dependent cancers (Jasienska & Thune, 2001a, 2001b; Jasienska et al., 2000; Key & Pike, 1988; Pike et al., 1993). In contrast, due to lower estrogen levels in menstrual cycles, asymmetrical women may have more health problems and reduced fecundity prior to menopause than more symmetrical women but may benefit from a lower risk of hormone-dependent cancers in the postmenopausal period. Results of our research suggest that in studies on the relationship between symmetry and health in women, predictions should be made contingent upon a woman's menopausal status.

Other authors have suggested that the human preference for more symmetrical individuals evolved to facilitate the choice of partners with greater developmental stability. The results of this study suggest that, in women, symmetry is related to higher levels of estradiol and, thus, higher potential fertility. As a consequence, compared with men who do not use symmetry as a signal of women's potential fertility, men attracted to more symmetrical women may achieve higher reproductive success.

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References

Adair, L. S. (2001). Size at birth predicts age at menarche. *Pediatrics*, *107*, e59.

Al-Eisa, E., Egan, D., & Wassersug, R. (2004). Fluctuating asymmetry and low back pain. *Evolution and Human Behavior*, *25*, 31–37.

Baird, D. D., Weinberg, C. R., Zhou, H. B., Kamel, F., McConnaughey, D. R., Kesner, J. S., & Wilcox, A. J. (1999). Preimplantation urinary hormone profiles and the probability of conception in healthy women. *Fertility and Sterility*, *71*, 40–49.

Baird, D. D., Wilcox, A. J., Weinberg, C. R., Kamel, F., McConnaughey, D. R., Musey, P. I., & Collins, D. C. (1997). Preimplantation hormonal differences between the conception and non-conception menstrual cycles of 32 normal women. *Human Reproduction*, *12*, 2607–2613.

Barrett-Conor, E., & Bush, T. L. (1991). Estrogen and coronary heart disease in women. *Journal of the American Medical Association*, *265*, 1861–1867.

Ellison, P. T. (1982). Skeletal growth, fatness and menarcheal age: A comparison of two hypotheses. *Human Biology*, *54*, 269–281.

Ellison, P. T. (1988). Human salivary steroids: Methodological issues and applications in physical anthropology. *Yearbook of Physical Anthropology*, *31*, 115–142.

Ellison, P. T. (1990). Human ovarian function and reproductive ecology—new hypotheses. *American Anthropologist*, *92*, 933–952.

Gangestad, S. W., & Thornhill, R. (1999). Individual differences in developmental precision and fluctuating asymmetry: A model and its implications. *Journal of Evolutionary Biology*, *12*, 402–416.

Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, *15*, 73–85.

Grammer, K., Fink, B., Møller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: Sexual selection and the biology of beauty. *Biological Reviews*, *78*, 385–407.

Grammer, K., Fink, B., Møller, A. P., & Manning, J. T. (2005). Physical attractiveness and health: Comment on Weeden and Sabini (2005). *Psychological Bulletin*, *131*, 658–661.

Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, *108*, 233–243.

Gorkemli, H., Ak, D., Akyurek, C., Aktan, M., & Duman, S. (2004). Comparison of pregnancy outcomes of progesterone or progesterone plus estradiol for luteal phase support in ICSI–ET cycles. *Gynecologic and Obstetric Investigation*, *58*, 140–144.

Henderson, J. J. A., & Anglin, J. M. (2003). Facial attractiveness predicts longevity. *Evolution and Human Behavior*, *24*, 351–356.

Henss, R. (2000). Waist-to-hip ratio and female attractiveness. Evidence from photographic stimuli and methodological considerations. *Personality and Individual Differences*, *28*, 501–513.

Hume, D. K., & Montgomerie, R. (2001). Facial attractiveness signals different aspects of "quality" in women and men. *Evolution and Human Behavior*, *22*, 93–112.

Jacobson, J. D., & Ansari, M. A. (2004). Immunomodulatory actions of gonadal steroids may be mediated by gonadotropin-releasing hormone. *Endocrinology*, *145*, 330–336.

Jasienska, G. (2002). Are sex steroids suitable as biomarkers of breast cancer risk? Variation and repeatability of estimates. *International Journal of Cancer*, (Suppl 13), 129.

Jasienska, G., & Ellison, P. T. (1998). Physical work causes suppression of ovarian function in women. *Proceedings of the Royal Society of London B*, *265*, 1847–1851.

Jasienska, G., & Ellison, P. T. (2004). Energetic factors and seasonal changes in ovarian function in women from rural Poland. *American Journal of Human Biology*, *16*, 563–580.

Jasienska, G., & Thune, I. (2001a). Lifestyle, hormones, and risk of breast cancer. *British Medical Journal*, *322*, 586–587.

Jasienska, G., & Thune, I. (2001b). Lifestyle, progesterone and breast cancer. *British Medical Journal*, *323*, 1002.

Jasienska, G., Thune, I., & Ellison, P. T. (2000). Energetic factors, ovarian steroids and the risk of breast cancer. *European Journal of Cancer Prevention*, *9*, 231–239.

Jasienska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings of the Royal Society of London B, 271*, 1213–1217.

Jasienska, G., Ziomkiewicz, A., Lipson, S. F., Thune, I., & Ellison, P. T. (2006). High ponderal index at birth predicts high estradiol levels in adult women. *American Journal of Human Biology*, *18*, 133–140.

Jasienska G., Ziomkiewicz, A., Thune I., Lipson, S. F., Ellison, P. T. (in press). Habitual physical activity and estradiol levels in women of reproductive age. *European Journal of Cancer Prevention*.

Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Facial symmetry and judgments of apparent health—Support for a "good genes" explanation of the attractiveness–symmetry relationship. *Evolution and Human Behavior*, *22*, 417–429.

Key, T. J. A., & Pike, M. C. (1988). The role of oestrogens and progestogens in the epidemiology and prevention of breast cancer. *European Journal of Clinical Oncology*, *24*, 29–43.

Kowner, R. (1996). Facial asymmetry and attractiveness judgment in developmental perspective. *Journal of Experimental Psychology-Human Perception and Performance*, *22*, 662–675.

Kovacs, E. J., Messingham, K. A. N., & Gregory, M. S. (2002). Estrogen regulation of immune responses after injury. *Molecular and Cellular Endocrinology*, *193*, 129–135.

Lipson, S. F., & Ellison, P. T. (1996). Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Human Reproduction*, *11*, 2090–2096.

Lukaszuk, K., Liss, J., Lukaszuk, M., & Maj, B. (2005). Optimization of estradiol supplementation during the luteal phase improves the pregnancy rate in women undergoing in vitro fertilization–embryo transfer cycles. *Fertility and Sterility*, *83*, 1372–1376.

Manning, J. T. (1995). Fluctuating asymmetry and body weight in men and women—implications for sexual selection. *Ethology and Sociobiology*, *16*, 145–153.

Manning, J. T., Koukourakis, K., & Brodie, D. A. (1997). Fluctuating asymmetry, metabolic rate and sexual selection in human males. *Evolution and Human Behavior*, *18*, 15–21.

Manning, J. T., Scutt, D., & Lewis-Jones, D. I. (1998). Developmental stability, ejaculate size, and sperm quality in men. *Evolution and Human Behavior*, *19*, 273–282.

Manning, J. T., Scutt, D., Whitehouse, G. H., & Leinster, S. J. (1997). Breast asymmetry and phenotypic quality in women. *Evolution and Human Behavior*, *18*, 223–236.

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., Soler, M., & Thornhill, R. (1995). Breast asymmetry, sexual selection, and human reproductive success. *Ethology and Sociobiology*, *16*, 207–219.

Møller, A. P., & Swaddle, J. P. (1997). *Asymmetry, developmental stability, and evolution*. Oxford, London: Oxford University Press.

Nguyen, T. V., Jones, G., Sambrook, P. N., White, C. P., Kelly, P. J., & Eisman, J. A. (1995). Effects of estrogen exposure and reproductive factors on bone mineral density and osteoporotic fractures. *Journal of Clinical Endocrinology and Metabolism*, *80*, 2709–2714.

Noor, F., & Evans, D. C. (2003). The effect of facial symmetry on perceptions of personality and attractiveness. *Journal of Research in Personality*, *37*, 339–347.

Pike, M. C., Spicer, D. V., Dahmoush, L., & Press, M. F. (1993). Estrogens, progestogens, normal breast cell proliferation, and breast cancer risk. *Epidemiologic Reviews*, *15*, 17–35.

Rhodes, G., Zebrowitz, L. A., Clark, A., Kalick, S. M., Hightower, A., & McKay, R. (2001). Do facial averageness and symmetry signal health? *Evolution and Human Behavior*, *22*, 31–46.

Romundstad, P. R., Vatten, L. J., Nilsen, T. I. L., Holmen, T. L., Hsieh, C. C., Trichopoulos, D., & Stuver, S. O. (2003). Birth size in relation to age at menarche and adolescent body size: Implications for breast cancer risk. *International Journal of Cancer*, *105*, 400–403.

Shackelford, T. K., & Larsen, R. J. (1997). Facial asymmetry as an indicator of psychological, emotional, and physiological distress. *Journal of Personality and Social Psychology*, *72*, 456–466.

Sharara, F. I., & McClamrock, H. D. (1999). Ratio of oestradiol concentration on the day of human chorionic gonadotrophin administration to mid-luteal oestradiol concentration is predictive of in-vitro fertilization outcome. *Human Reproduction*, *14*, 2777–2782.

Singh, D. (1993). Body shape and women's attractiveness—the critical role of waist-to-hip ratio. *Human nature—an interdisciplinary biosocial perspective*, *4*, 297–321.

Soler, C., Nunez, M., Gutierrez, R., Nunez, J., Medina, P., Sancho, M., Alvarez, J., & Nunez, A. (2003). Facial attractiveness in men provides clues to semen quality. *Evolution and Human Behavior*, *24*, 199–207.

Swaddle, J. P., & Cuthill, I. C. (1995). Asymmetry and human facial attractiveness—symmetry may not always be beautiful. *Proceedings of the Royal Society of London B, 261*, 111–116.

Symons, D. (1995). Beauty is in the adaptation of the beholder: The evolutionary psychology of human female sexual attractiveness. In P. R. Abramson, & S. D. Pikerton (Eds.), *Sexual nature, sexual culture* (pp. 80–118). Chicago: University of Chicago Press.

Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual behavior. *Psychological Science*, *5*, 297–302.

Tomkinson, G., & Olds, T. (2000). Physiological correlates of bilateral symmetry in humans. *International Journal of Sports Medicine*, *21*, 545–550.

Vermeulen, A. (1993). Environment, human reproduction, menopause, and andropause. *Environmental Health Perspectives*, *2*, 91–100.

Waynforth, D. (1998). Fluctuating asymmetry and human male life-history traits in rural Belize. *Proceedings of the Royal Society of London B, 265*, 1497–1501.

Weeden, J., & Sabini, J. (2005). Physical attractiveness and health in Western societies: A review. *Psychological Bulletin*, *131*, 635–663.

Wood, J.W (1994). *Dynamics of human reproduction: Biology, biometry, demography*. New York: Aldine de Gruyter.