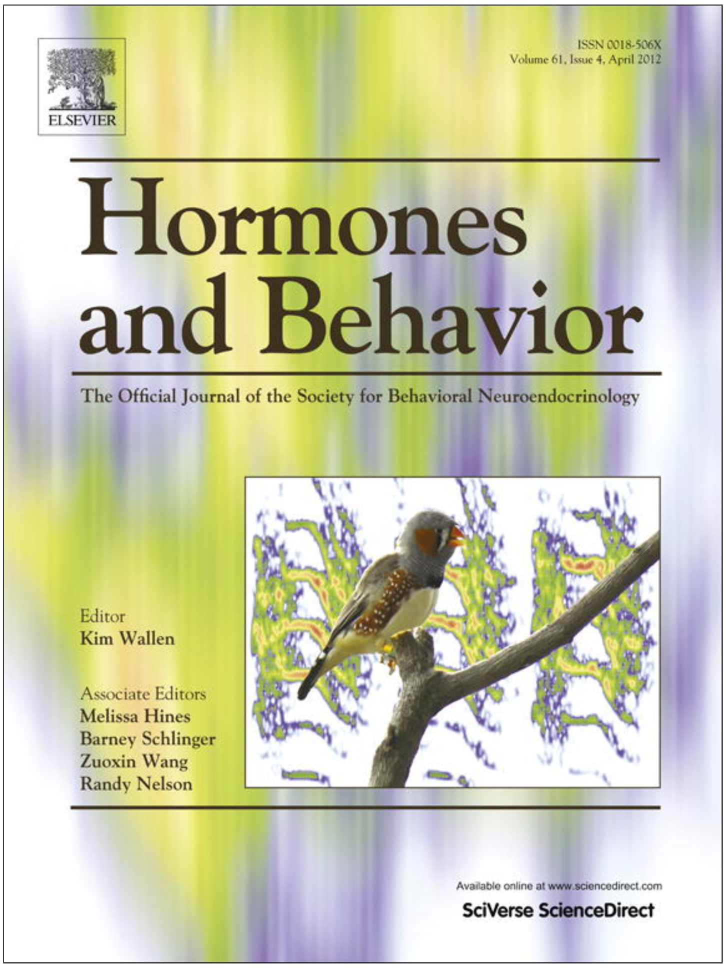
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Temperament and ovarian reproductive hormones in women: Evidence from a study during the entire menstrual cycle

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ABSTRACT

Personality and temperament were hypothesized to function as important factors affecting life history strategies. Recent research has demonstrated the association between temperamental traits and reproduction in humans, however, the underlying mechanisms are still poorly understood.

This study presents evidence for an association between temperamental traits and woman's fecundity, as indicated by levels of ovarian steroid hormones during the menstrual cycle. On a large sample of urban, reproductive age women (n = 108) we demonstrated that activity, endurance and emotional reactivity are associated with levels of estrogen and with a pattern of change of progesterone levels. Women high in activity, high in endurance and low in emotional reactivity had up to twice as high estradiol levels and more favorable progesterone profiles as women low in activity, low in endurance and high in emotional reactivity. The temperamental traits we measured highly overlap with extraversion, neuroticism and negative emotionality that were reported to correlate with reproductive success. Our findings thus suggest a possible explanation for these relationships, linking personality and women's reproductive success through a hormonal pathway.

Introduction

Recent advances in behavioral ecology suggest that personality is associated with life history strategies (Biro and Stamps, 2008; Nettle, 2006). Among others, personality and temperamental traits were demonstrated to predict characteristics directly related to reproductive success in men and women (Alvergne et al., 2010a; Jokela et al., 2009, 2010, 2011). Extraversion and sociability were shown to positively correlate with marital status, number of mates, age at birth of first or second child and total number of children, while neuroticism and emotionality were shown to correlate negatively with most of those characteristics (Jokela et al., 2009, 2010, 2011 but see Alvergne et al., 2010a). The same traits were also indicated as important mate choice criteria, with higher extraversion and sociability increasing while higher neuroticism decreasing the chances of being chosen as a mate (Buss et al., 1990; Figueredo et al., 2006; Simpson and Gangestad, 1992).

Most explanations of these findings refer to social and behavioral characteristics of personality trait beholders (Alvergne et al., 2010a; Jokela et al., 2009). However, variation in reproductive success among individuals that differ in personality or temperament might be also explained via pathways other than behavioral or social, especially for women. Success of conception, pregnancy and childbearing is largely dependent on the biological quality (Joffe et al., 2009), fecundity and resource availability (Ellison, 2003) of a future mother. Several studies demonstrated that reproductive outcomes in women are related to energetic status (reviewed in Abu-Saad and Fraser, 2010), which influences reproductive hormone levels (Jasienska et al., 2006c; Ziomkiewicz et al., 2008). Further, traits related to women's physical attractiveness have been demonstrated to predict women's fecundity and hormone levels (Jasienska et al., 2004; Jasienska et al., 2006b,; Law Smith et al., 2006 but see Geary, 2005; Weeden and Sabini, 2005 for a critical discussion of these results). Thus, it is possible that the observed relationship between reproductive success and personality might be explained by the relationship between these characteristics and women's fecundity.

Although relationships between temperament and fecundity have been demonstrated in animal studies (Blache and Bickell, 2011; von Borell et al., 2007) and studies on human males (Alvergne et al., 2010b;

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Giotakos et al., 2004), to our knowledge, this possibility has never been examined in human females.

To explore the relation between ovarian function and temperament, we rely on Strelau's Regulative Theory of Temperament (RTT) (Strelau, 1996, 2008). This biologically based, functional theory postulates that temperament should be understood as a constellation of energetic and temporal characteristics of behavior which help individuals in adapting to the environment (Strelau, 1996). Apart from being explicit about the function of temperament, RTT is also to some extent explicit about the physiological mechanisms underlying temperament. It proposes that differences in temperamental traits between individuals result from their specific level of reactivity to environmental stimulation, which is in turn determined by 'neurohormonal individuality' (Strelau, 1996), a specific configuration of biochemical and neurophysiological mechanisms.

Given these assumptions, we asked whether individual differences in temperament among women are associated with intra-individual variation in their ovarian hormone levels. We also argued that the observed relationship between reproductive success and personality and temperamental traits might be based on the relationship between these traits and women's fecundity. As neuroticism and extraversion had been demonstrated to predict reproductive success in women (Alvergne et al., 2010a, 2010b; Jokela et al., 2010), we hypothesized that temperamental traits correlated with these characteristics should be related to ovarian steroid levels.

Materials and methods

Study group

One hundred and fourteen women of reproductive age ($M=29.5$, $SD=3.57$) from the city of Wroclaw, South-Western Poland took part in the study. Women were recruited from the general city population by newspaper and television advertisement published early in the spring 2008 and 2009. They were included in the sample based on the following criteria: regular menstrual cycles from 24 to 36 days, not being pregnant or lactating for at least 3 months prior to the study, not using hormonal contraceptives, having good health, and in particular, not being diagnosed with any reproductive or endocrinological diseases. Participants collected daily, first morning urine samples for one entire menstrual cycle and filled in the temperament questionnaire. Urine samples were collected to plastic vials delivered together with the set of questionnaires. Immediately after taking, samples were marked with name and collection date, closed and stored in subjects' home freezers set to the lowest possible temperature until the end of the sampling period. After the end of the sampling period (last day of the menstrual cycle), research assistants collected samples from participants' homes and transported them on ice to the laboratory for analysis.

Anthropometrical measurements of body height, weight, fat content and waist, hips, breasts and under-breast circumferences were also taken. Additionally, once during the study period women completed a general questionnaire collecting information about their reproductive history, education, employment, marital status, number of children, smoking and alcohol drinking, and temperamental questionnaire. Each woman gave written consent for the participation in the project. Study protocol was approved by the appropriate committee of the Ministry of Science and Higher Education.

Temperament assessment

Temperament was assessed with the Formal Characteristics of Behavior — Temperament Inventory (FCB-TI) (Strelau and Zawadzki, 1995). This questionnaire measures six temperamental traits postulated by the Regulative Theory of Temperament: Briskness (BR), Perseveration (PE), Sensory Sensitivity (SS), Emotional Reactivity (ER), Activity (AC) and Endurance (EN). Although less in use than the popular NEO-FFI (Costa and McCrea, 1992) the FCB-TI is a highly reliable method of temperament assessment. Details for FCB-TI are presented in Supplementary materials.

Scores for the six temperamental traits were calculated following published procedure (Zawadzki and Strelau, 1995). Furthermore, participants' constellations of temperamental traits were assessed (Strelau, 2008; Zawadzki and Strelau, 1995) based on the scores of three traits describing energetic aspect of behavior: EN, AC and ER. Scores for these traits describe the ability of a person to process environmental stimulation. High ability to process stimulation individuals (HAPS) are those characterized by above median value of EN and AC and below median value of ER. Low ability to process stimulation individuals (LAPS) are those characterized by below median value of EN and AC and above median value of ER. Based on these three traits, there are eight possible groupings described in the literature (Strelau, 2008; Zawadzki and Strelau, 1995). The validity of identifying such trait configurations and, specifically, focusing on these two groups has been confirmed in empirical studies on temperament and response to stress. In these studies, out of the eight possible groupings, LAPS exhibited the highest reactivity and HAPS exhibited the lowest reactivity to chronic and traumatic stress, as evidenced by symptoms of job burnout and post-traumatic stress disorder (Strelau, 2008). Thus, the LAPS and HAPS groups represent the extremes of the continuum of reactivity to environmental stimulation. Based on the relations between traits postulated by RTT and Big Five models of personality, these two groups, LAPS and HAPS, would correspond, respectively to neurotic-introverted vs. emotionally stable-extraverted individuals in Big Five terminology (Strelau, 2008; Strelau and Zawadzki, 1995). Applying the above mentioned criteria resulted in 26 women identified as LAPS and 26 women identified as HAPS.

Hormonal analysis and data preparation

The urinary concentration of estrone glucuronide (E1G) and pregnanediol glucuronide (PdG) were analyzed using commercially available competitive enzyme immunoassay kits from Immunometrics Ltd. (London, UK) with protocol of analysis as described by the producer. The Estrone-3-Glucuronide EIA used an anti-Estrone-3-Glucuronide rabbit antibody and alkaline phosphatase labeled Estrone-3-Glucuronide. Pregnanediol-3a-Glucuronide EIA used an anti-Pregnanediol-3a-Glucuronide rabbit antibody and alkaline phosphatase labeled Pregnanediol-3a-Glucuronide. Intra- and interassay coefficients of variation were less than 8% for all assays. Eighteen daily samples for follicular and luteal E1G concentrations and fourteen daily samples for luteal PdG concentrations were analyzed for each women menstrual cycle.

E1G and PdG daily values data were corrected for differences in urine concentration using method by Miro et al. (2004). Missing E1G and PdG daily values were replaced using smoothed cubic splines (Brumback and Rice, 1998). This routine was performed only in cases where the number of missing daily values was less than three in a sequence. There was only one subject in the described sample for whom this condition was not fulfilled and this subject was removed from analyses.

Cycles were assigned as ovulatory when PdG daily values were at least three times higher when compared to the baseline and this increase in concentrations persisted for at least three days (Kassam et al., 1996). The day of ovulation was inferred from changes in E1G to PdG ratio during the cycle using the day of luteal transition algorithm (DLT), (Baird et al., 1991) with modification for low concentrations of PdG (Waller et al., 1998). Based on these methods, cycles of 108 out of 114 women were assigned as "ovulatory" and for those cycles the day of ovulation was estimated. Further, menstrual cycles were aligned on the estimated day of ovulation which was designated as "day 0". For E1G, days of follicular phase were given negative numbers and days of luteal phase positive numbers. The following indices of ovarian activity were calculated: E1G cycle (mean E1G for days from-9 to 8), E1G

Table 1
Correlations between mean levels of progesterone metabolites, log-transformed mean estradiol metabolites and temperamental traits. Correlations that are statistically significant are marked with an asterisk.

N = 108	ln E1G cycle	ln E1G follicular	ln E1G luteal	ln E1G midcycle	PdG cycle	PdG luteal	PdG midluteal
Briskness	0.01	−0.01	0.01	−0.01	−0.08	−0.04	−0.02
Perseveration	−0.07	−0.07	−0.09	−0.05	−0.07	−0.06	−0.08
Sensory sensitivity	0.12	0.14	0.10	0.12	0.17	0.18	0.14
Emotional reactivity	−0.18	−0.19	−0.19*	−0.13	0.09	0.05	−0.02
Endurance	0.20*	0.19*	0.28*	0.19*	−0.04	0.06	0.06
Activity	0.26**	0.26*	0.25**	0.25**	0.04	−0.03	−0.01

E1G — estrone glucuronide, PdG — pregnanediol glucuronide.
* $p<0.05$.
** $p<0.01$.

follicular (mean E1G for days from −9 to −1), E1G luteal (mean E1G for days from 0 to 8), E1G midcycle (mean E1G for days from −2 to 2). For PdG, last fourteen daily values were taken as the index of luteal activity and the following indices were calculated: PdG cycle (mean PdG from the entire cycle), PdG luteal (mean PdG from days −14 to −1), PdG midluteal (mean PdG from days from −9 to −5).

Statistical analysis

Natural logarithms were calculated for single values and mean indices of E1G during the cycle to assure normality of the distributions where necessary. Relationships between temperamental traits and ovarian metabolites were assessed using correlation analysis (Pearson correlation for AC, ER and Spearman correlation for BR, PE, SS and EN) and linear regression models with body fat percentage as the additional independent factor, as it was found to have a negative influence on levels of E1G.

Independent samples t-tests were used to assess the differences in anthropometrics and physical activity between LAPS and HAPS women. Moreover, analyses of variance and covariance were used to investigate differences in mean levels of E1G and PdG during the cycle and its phases between these two groups, with body fat as a covariant. Mixed model analysis of variance was used to assess the statistical significance of differences between the groups with respect to hormonal profiles during the entire cycle. The within-group effects of menstrual cycle day and the interaction effects of cycle day and temperamental group were modeled by linear and quadratic trends. Because of the lack of statistically significant relationship between hormonal indices and age, cycle length, height and physical activity these factors were omitted in the models.

Table 2
Results of regression analysis with Endurance, Activity and body fat as independent predictors of mean E1G level.

	Endurance			Activity		
N = 108	R^2	p	β	R^2	*p*	β
ln E1G cycle	0.11	<0.005		0.126	<0.001	
Temperamental trait		<0.05	0.18		<0.05	0.21
Body fat		<0.01	−0.30		<0.01	−0.27
ln E1G follicular	0.10	<0.005		0.118	<0.005	
Temperamental Trait		NS	0.17		<0.05	0.20
Body fat		<0.01	−0.29		<0.01	−0.27
ln E1G luteal	0.12	<0.005		0.119	<0.001	
Temperamental Trait		<0.05	0.19		<0.05	0.21
Body fat		<0.01	−0.30		<0.01	−0.27
ln E1G midcycle	0.12	<0.001		0.134	<0.001	
Temperamental trait		NS	0.17		<0.05	0.20
Body fat		<0.01	−0.30		<0.01	−0.30

E1G — estrone glucuronide.

Results

We found positive correlations between the levels of E1G during the menstrual cycle and the temperamental traits of endurance and activity, and a negative correlation between emotional reactivity and the levels of E1G during the luteal phase. In contrast, no significant correlations were found for any of the temperamental traits and mean levels of PdG (Table 1).

Results of the correlation analyses were further confirmed by the regression analysis where body fat was entered as an independent predictor to the model, in addition to the temperamental traits (Table 2). After entering body fat, endurance remained significantly positively related to the average E1G levels during the whole cycle ($\beta=0.18$, $p<0.05$) and during the luteal phase ($\beta=0.19$, $p<0.05$). Activity was significantly positively related to the average levels of E1G during the whole cycle ($\beta=0.213$, $p<0.05$), the midcycle ($\beta=0.20$, $p<0.05$), follicular phase ($\beta=0.20$, $p<0.05$) and luteal phase ($\beta=0.21$, $p<0.05$). All other tested relationships were statistically non-significant.

Additional evidence for the association between temperament and ovarian hormone levels comes from the comparisons between groups of women characterized by low and high ability to process stimulation. HAPS women had significantly higher levels of E1G during the whole cycle ($t(50)=-2.38$, $p<0.05$), the midcycle ($t(50)=-2.28$, $p<0.05$), follicular phase ($t(50)=-2.04$, $p<0.05$) and luteal phase ($t(50)=-2.64$, $p<0.02$). This difference remained significant after adjusting for body fat percentage in the analysis of covariance (for the average levels of E1G during the whole cycle, $F_{1,51}=5.05$, $p<0.05$, the midcycle, $F_{1,51}=4.55$, $p<0.05$, and the luteal phase $F_{1,51}=6.28$, $p<0.02$) (Table 3). The LAPS and HAPS groups did not differ significantly with respect to any of the measured anthropometric, demographic or life-style factors such as age, age of menarche, height, weight or physical activity.

In addition, a comparison of the E1G menstrual profiles by a mixed model analysis of variance showed significantly higher levels of E1G in HAPS women when compared to LAPS women (main effect of temperamental group: $F_{1,51}=5.06$, $p<0.05$). In terms of untransformed values of E1G, HAPS women had up to twice as high levels of E1G during the cycle as LAPS women (Fig. 1a). The same analysis for PdG profiles in the luteal phase revealed an interaction effect of temperamental group and day of luteal phase ($F_{13,676}=3.21$, $p<0.05$), which was approximated by a quadratic trend, as indicated by a within-subjects contrast

Table 3
Differences in log-transformed mean levels of E1G during the whole menstrual cycle, the follicular and the luteal phase between LAPS and HAPS women, adjusted for body fat.

	LAPS women N = 26		HAPS women N = 26			
	Mean	95% CI	Mean	95% CI	p	Cohen's d
ln E1G cycle	3.62	3.365–3.870	4.16	3.765–4.563	0.029	0.66
ln E1G follicular	3.58	3.308–3.851	4.05	3.660–4.449	0.062	0.57
ln E1G luteal	3.63	3.374–3.881	4.24	3.836–4.655	0.016	0.73
ln E1G midcycle	3.90	3.627–4.167	4.46	4.029–4.887	0.038	0.63

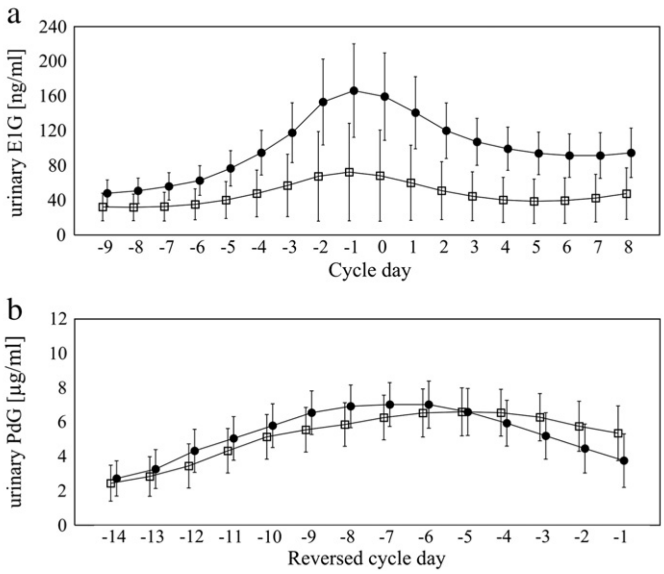

Fig. 1. Profiles (raw daily means with 95% confidence intervals) of estrone glucuronide (E1G) (a) and pregnanediol glucuronide (PdG) (b) during the menstrual cycle in women with high ability to process stimulation (HAPS, black dots) and women with low ability to process stimulation (LAPS, white squares).

($p<0.05$; the linear contrast was n.s.). The pattern of change of PdG concentrations during the luteal phase was different for the two temperament groups, with LAPS women having lower PdG levels in the middle of the luteal phase and higher PdG levels at the end of the luteal phase, as compared to the HAPS women (Fig. 1b).

Discussion

To our knowledge, this is the first study that clearly demonstrates the relationship between women's temperament and levels of ovarian reproductive hormones during the menstrual cycle. We have shown that estradiol levels are associated with the temperamental traits of endurance, activity and emotional reactivity. Moreover, we demonstrated that specific constellations of these traits predicted levels of ovarian hormones during the cycle. Women characterized by high activity, high endurance and low emotional reactivity (HAPS women) had up to twice as high levels of estradiol when compared to women with low activity, low endurance and high emotional reactivity (LAPS women). These women also had more favorable progesterone profiles. Taken together, our findings suggest that HAPS women have higher potential fertility than LAPS women.

Although no other study on temperament and ovarian hormones can be directly compared with our results, there is some indirect evidence to support our findings. Netter et al. (1998) investigated the relationship between behavioral adaptability to external requirements, personality and reproductive hormone levels in a small sample of healthy women of reproductive age. They found that women with low ability to adapt to external requirements had simultaneously lower levels of ovarian hormones during the cycle, lower extraversion and higher neuroticism than women with high ability to adapt to external requirements. As activity, endurance and emotional reactivity correlate highly with neuroticism and extraversion (Strelau and Zawadzki, 1995), these results are in agreement with our findings. However, it should be noted that Netter and colleagues did not demonstrate a direct link between personality traits and ovarian hormones, while in our results this association is clearly present.

Indirect evidence also comes from a study by Nepomnaschy et al. (2004). Given that the ability to process stimulation reflects reactivity to stressors (Strelau, 2008), our findings are in line with those of Nepomnaschy et al. (2004). They both point to the possibility that high stress experienced by a woman may lead to reproductive suppression. As high midluteal PdG concentrations are crucial for implantation (Wilcox et al., 1999), maintaining lower levels of midluteal PdG may be one way of preventing pregnancy in unfavorable psychosocial contexts.

Other confirmative evidence comes from studies on the genetic basis of temperament and personality. Firstly, it was demonstrated that personality traits depend on polymorphisms in genes for estrogen receptors and estrogen metabolism. In particular, neuroticism was related to a single nucleotide polymorphism or a dinucleotide repeated polymorphism in estrogen receptor 1 gene (ESR-1) (Miller et al., 2010). Women with higher neuroticism had at least one recessive allele in different loci of the ESR1 gene. The same polymorphism is related to the levels of estradiol during the menstrual cycle (Sowers et al., 2006), suggesting that lower level of estradiol is associated with higher neuroticism. Secondly, polymorphisms in genes CYP17 and CYP2C19, regulating activity of cytochrome P450, were found to be associated with several personality traits in Japanese women (Ishii et al., 2007). Cytochrome P450 is responsible for metabolizing testosterone, estradiol and progesterone. Several studies, including our own (Haiman et al., 2007; Jasienska et al., 2006a; Small et al., 2005), show that polymorphism in CYP17 and CYP19 is related to the levels of estradiol in women.

Thirdly, relevant evidence includes studies linking temperamental and personality traits with polymorphism in the 5-HTT serotonin transporter gene (Sen et al., 2004) and 5-HT_{2A} serotonin receptor binding (Frokjaer et al., 2008). Dragan and Oniszczenko (2006) for instance, reported a relationship between polymorphism in 5-HTT and temperamental traits of endurance and activity assessed with FCB-TI in Polish women. Women who had at least one recessive allele of the serotonin transporter gene scored significantly higher on endurance and activity than women with both dominant alleles of this gene. Frokjaer et al. (2008) demonstrated positive association between neuroticism and 5-HT_{2A} receptor binding in frontolimbic region of the human brain.

Serotoninergic system is highly and positively influenced by ovarian reproductive hormones (Lasiuk and Hegadoren, 2007). Studies demonstrated that estradiol can increase synthesis and decrease catabolism of serotonine in human brain (Osterlund, 2010). Moreover it down-regulates pre- and postsynaptic 5-HT_{1A} receptors and up-regulates postsynaptic 5-HT_{2A} receptors (Osterlund, 2010). Together with the aforementioned evidence on the relationship between serotoninergic system and temperament and personality this constitutes a viable explanation for the results observed in our study.

Given the correlational nature of our study, it is possible that the observed association between temperament and ovarian hormones might be explained by other, mediating factors. Indeed, animal studies point to the possibility that nutritional status and energy balance might influence this association. In particular, it was demonstrated that temperamental traits (boldness, activity, aggressiveness) were positively related to food intake and, in consequence, to nutritional status in animals (for review see Biro and Stamps, 2008). Nutritional status and energy balance were also found to influence ovarian steroid hormones in humans (Jasienska et al., 2006a, 2006b, 2006c; Ziomkiewicz et al., 2008). In the present study, we controlled nutritional status by measuring body fat content. Body fat was also included as a covariate in all analyses assessing the differences between temperamental groups with respect to ovarian steroid levels. Results of these analyses excluded the possibility that the association between temperament and reproductive hormone levels is mediated by body fat. However, less evident differences between the temperamental groups, e.g. in energy balance, might still contribute to the observed association.

Our findings shed light on the possible hormonal basis of the recently demonstrated relationship between personality traits and reproductive success in women. Studies by Jokela et al. (2009, 2011) in two industrial populations (contemporary Finns and Americans) showed a negative effect of emotionality and neuroticism, and a positive effect of extraversion on the probability of having children and on completed fertility in women. Although we did not measure emotionality (Buss and Plomin, 1984), neuroticism or extraversion (Costa and McCrea, 1992), the traits we assessed are closely related to these characteristics. In particular, Activity and Extraversion correlate positively ($r=0.63$), Emotional Reactivity and Neuroticism also correlate positively ($r=0.66$) and Endurance and Neuroticism correlate negatively ($r=-0.52$) (Strelau and Zawadzki, 1995; for other relevant correlations see Supplementary material). High correlations between these traits allow us to infer the possible hormonal link between personality traits measured by Jokela et al. (2009, 2011) and reproductive success in women. Lower activity and lower endurance (associated with higher neuroticism and lower extraversion) was in our sample related to lower levels of estradiol during the cycle and less favorable profiles of progesterone. In contrast, higher activity and higher endurance (associated with higher extraversion and lower neuroticism) was related to higher levels of ovarian hormones favoring conception and implantation. In both cases the strongest effect was observed when these traits were taken together with emotional reactivity. Our results suggest that high extraversion and low neuroticism in women can both be related to higher reproductive success via higher potential fertility indicated by high levels of reproductive hormones.

Maintaining high levels of ovarian hormones is costly and can be advertised in morphological traits as a signal of good biological quality, as was demonstrated by us (Jasienska et al., 2004, 2006b,) and others (Law Smith et al., 2006). The present study shows that ovarian hormone levels are also associated with behavioral characteristics, commonly assessed as temperament.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.yhbeh.2012.01.017.

References

Abu-Saad, K., Fraser, D., 2010. Maternal nutrition and birth outcomes. Epidemiol. Rev. 32, 5–25.
Alvergne, A., Jokela, M., Lummaa, V., 2010a. Personality and reproductive success in a high-fertility human population. Proc. Natl. Acad. Sci. U. S. A. 107, 11745–11750.
Alvergne, A., Jokela, M., Faurie, Ch., Lummaa, V., 2010b. Personality and testosterone in men from a high-fertility population. Pers. Individ. Dif. 49, 840–844.
Baird, D.D., Weinberg, C.R., Wilcox, A.J., McConnaughey, D.R., Musey, P.I., 1991. Using the ratio of urinary oestrogen and progesterone metabolites to estimate day of ovulation. Stat. Med. 10, 255–266.
Biro, P.A., Stamps, J.A., 2008. Are animal personality traits linked to life history productivity? Trends Ecol. Evol. 23, 361–368.
Blache, D., Bickell, S.L., 2011. External and internal modulators of sheep reproduction. Reprod. Biol. 11, 61–77.
Brumback, B.A., Rice, J.A., 1998. Smoothing spline models for the analysis of nested and crossed samples of curves. J. Am. Stat. Assoc. 93, 961–976.
Buss, A., Plomin, R., 1984. Temperament: Early Developing Personality Traits. Erlbaum, Hillsdale, NJ, pp. 1–185.
Buss, D.M., Abbott, M., Angleitner, A., et al., 1990. International preferences in selecting mates. J. Cross Cult. Psychol. 21, 5–47.
Costa, P.T., McCrea, R.R., 1992. Revised NEO Personality Inventory (NEO PI-R) and NEO Five-Factor Inventory (NEO-FFI). Psychological Assessment Resources, Odessa, FL, pp. 1–101.
Dragan, W.L., Oniszczenko, W., 2006. Association of a functional polymorphism in the serotonin transporter gene with personality traits in females in a Polish population. Neuropsychobiology 54, 45–50.
Ellison, P.T., 2003. Energetics and reproductive effort. Am. J. Hum. Biol. 15, 342–351.
Figueredo, A., Sefcek, J., Jones, D., 2006. The ideal romantic partner personality. Pers. Individ. Dif. 41, 431–441.
Frokjaer, V.G., Mortensen, E.L., Nielsen, F.A., Haugbol, S., Pinborg, L.H., Adams, K.H., Svarer, C., Hasselbalch, S.G., Holm, S., Paulson, O.B., Knudsen, G.M., 2008. Frontolimbic serotonin 2A receptor binding in healthy subjects is associated with personality risk factors for affective disorder. Biol. Psychiatry 15, 569–576.
Geary, D., 2005. Evolution of life-history trade-offs in mate attractiveness and health: comment on Weeden and Sabini (2005). Psychol. Bull. 131, 654–657.
Giotakos, O., Markianos, M., Vaidakis, N., Christodoulou, G.N., 2004. Sex hormones and biogenic amine turnover of sex offenders in relation to their temperament and character dimensions. Psychiatry Res. 127, 185–193.
Haiman, C.A., Dossus, L., Setiawan, V.W., Stram, D.O., Dunning, A.M., Thomas, G., Thun, M.J., Albanes, D., Altshuler, D., Ardanaz, E., Boeing, H., Buring, J., Burtt, N., Calle, E.E., Chanock, S., Clavel-Chapelon, F., Colditz, G.A., Cox, D.G., Feigelson, H.S., Hankinson, S.E., Hayes, R.B., Henderson, B.E., Hirschhorn, J.N., Hoover, R., Hunter, D.J., Kaaks, R., Kolonel, L.N., Le Marchand, L., Lenner, P., Lund, E., Panico, S., Peeters, P.H., Pike, M.C., Riboli, E., Tjonneland, A., Travis, R., Trichopoulos, D., Wacholder, S., Ziegler, R.G., 2007. Genetic variation at the CYP19A1 locus predicts circulating estrogen levels but not breast cancer risk in postmenopausal women. Cancer Res. 67, 1893–1897.
Ishii, G., Suzuki, A., Oshino, S., Shiraishi, H., Otani, K., 2007. CYP2C19 polymorphism affects personality traits of Japanese females. Neurosci. Lett. 411, 77–80.
Jasienska, G., Ziomkiewicz, A., Ellison, P.T., Lipson, S.F., Thune, I., 2004. Large breasts and narrow waists indicate high reproductive potential in women. Proc. Biol. Sci. 271, 1213–1217.
Jasienska, G., Kapiszewska, M., Ellison, P.T., Kalemba-Drozdz, M., Nenko, I., Thune, I., Ziomkiewicz, A., 2006a. CYP17 genotypes differ in salivary 17-beta estradiol levels: a study based on hormonal profiles from entire menstrual cycles. Cancer Epidemiol. Biomarkers Prev. 15, 2131–2135.
Jasienska, G., Lipson, S., Ellison, P., Thune, I., Ziomkiewicz, A., 2006b. Symmetrical women have higher potential fertility. Evol. Hum. Behav. 27, 390–400.
Jasienska, G., Ziomkiewicz, A., Thune, I., Lipson, S.F., Ellison, P.T., 2006c. Habitual physical activity and estradiol levels in women of reproductive age. Eur. J. Cancer Prev. 15, 439–445.
Joffe, M., Key, J., Best, N., Jensen, T.K., Keiding, N., 2009. The role of biological fertility in predicting family size. Hum. Reprod. 24, 1999–2006.
Jokela, M., Kivimaki, M., Elovainio, M., Keltikangas-Jarvinen, L., 2009. Personality and having children: a two-way relationship. J. Pers. Soc. Psychol. 96, 218–230.
Jokela, M., Hintsa, T., Hintsanen, M., Keltikangas-Jarvinen, L., 2010. Adult temperament and childbearing over the life course. Eur. J. Pers. 24, 151–166.
Jokela, M., Alvergne, A., Pollet, T.V., Lummaa, V., 2011. Reproductive behavior and personality traits of the Five Factor Model. Eur. J. Pers. 25, 487–500.
Kassam, A., Overstreet, J.W., Snow-Harter, C., de Sousa, M.J., Gold, E.B., Lasley, B.L., 1996. Identification of anovulation and transient luteal function using a urinary pregnanediol-3-glucuronide ratio algorithm. Environ. Health Perspect. 104, 408–413.
Lasiuk, G.C., Hegadoren, K.M., 2007. The effects of estradiol on central serotonergic systems and its relationship to mood in women. Biol. Res. Nurs. 9, 147–160.
Law Smith, M.J., Perrett, D.I., Jones, B.C., Cornwell, R.E., Moore, F.R., Feinberg, D.R., Boothroyd, L.G., Durrani, S.J., Stirrat, M.R., Whiten, S., Pitman, R.M., Hillier, S.G., 2006. Facial appearance is a cue to oestrogen levels in women. Proc. Biol. Sci. 273, 135–140.
Miller, A., Vo, H., Huo, L., Roca, C., Schmidt, P.J., Rubinow, D.R., 2010. Estrogen receptor alpha (ESR-1) associations with psychological traits in women with PMDD and controls. J. Psychiatr. Res. 44, 788–794.
Miro, F., Coley, J., Gani, M.M., Perry, P.W., Talbot, D., Aspinall, L.J., 2004. Comparison between creatinine and pregnanediol adjustments in the retrospective analysis of urinary hormone profiles during the human menstrual cycle. Clin. Chem. Lab. Med. 42, 1043–1050.
Nepomnaschy, P., Welch, K., McConnell, D., Strassmann, B.I., England, B.G., 2004. Stress and female reproductive function: a study of daily variations in cortisol, gonadotrophins, and gonadal steroids in a rural Mayan population. Am. J. Hum. Biol. 16, 523–532.
Netter, P., Hennig, J., Huwe, S., Daume, E., 1998. Disturbed behavioral adaptability as related to reproductive hormones and emotional states during the menstrual cycle. Eur. J. Pers. 12, 287–300.
Nettle, D., 2006. The evolution of personality variation in humans and other animals. Am. Psychol. 61, 622–631.
Osterlund, M.K., 2010. Underlying mechanisms mediating the antidepressant effects of estrogens. Biochim. Biophys. Acta 1800, 1136–1144.
Sen, S., Burmeister, M., Ghosh, D., 2004. Meta-analysis of the association between a serotonin transporter promoter polymorphism (5-HTTLPR) and anxiety-related personality traits. Am. J. Med. Genet. B Neuropsychiatr. Genet. 127B, 85–89.
Simpson, J.A., Gangestad, S.W., 1992. Sociosexuality and romantic partner choice. J. Pers. 60, 31–51.
Small, C.M., Marcus, M., Sherman, S.L., Sullivan, A.K., Manatunga, A.K., Feigelson, H.S., 2005. CYP17 genotype predicts serum hormone levels among pre-menopausal women. Hum. Reprod. 20, 2162–2167.
Sowers, M.R., Jannausch, M.L., McConnell, D.S., Kardia, S.R., Randolph, J.F., 2006. Endogenous estradiol and its association with estrogen receptor gene polymorphisms. Am. J. Med. 119, S16–S22.
Strelau, J., 1996. The regulative theory of temperament: current status. Pers. Individ. Dif. 20, 131–142.
Strelau, J., 2008. Temperament as a Regulator of Behavior: After Fifty Years of Research. Eliot Werner Publications, Clinton Corners, New York, pp. 144–148.
Strelau, J., Zawadzki, B., 1995. The Formal Characteristics of Behavior—Temperament Inventory (FCB-TI): Validity studies. Eur. J. Pers. 9, 207–229.
von Borell, E., Dobson, H., Prunier, A., 2007. Stress, behaviour and reproductive performance in female cattle and pigs. Horm. Behav. 52, 130–138.
Waller, K., Swan, S.H., Windham, G.C., Fenster, L., Elkin, E.P., Lasley, B.L., 1998. Use of urine biomarkers to evaluate menstrual function in healthy premenopausal women. Am. J. Epidemiol. 147, 1071–1080.
Weeden, J., Sabini, J., 2005. Physical attractiveness and health in Western societies: a review. Psychol. Bull. 131, 635–653.

Wilcox, A.J., Baird, D.D., Weinberg, C.R., 1999. Time of implantation of the conceptus and loss of pregnancy. N. Engl. J. Med. 340, 1796–1799.

Zawadzki, B., Strelau, J., 1995. Theoretical foundations, construction and psychometric properties of the Formal Characteristics of Behavior — Temperament Inventory (Podstawy teoretyczne, konstrukcja i własności psychometryczne inwentarza Formalna Charakterystyka Zachowania — Kwestionariusz Temperamentu). (in Polish) Stud. Psychol. 33, 49–96.

Ziomkiewicz, A., Ellison, P.T., Lipson, S.F., Thune, I., Jasienska, G., 2008. Body fat, energy balance and estradiol levels: a study based on hormonal profiles from complete menstrual cycles. Hum. Reprod. 23, 2555–2563.