The face of female dominance: Women with dominant faces have lower cortisol

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ABSTRACT

The human face displays a wealth of information, including information about dominance and fecundity. Dominance and fecundity are also associated with lower concentrations of the stress hormone cortisol, suggesting that cortisol may negatively predict facial dominance and attractiveness. We digitally photographed 61 women's faces, had these images rated by men and women for dominance, attractiveness, and femininity, and explored relationships between these perceptions and women's salivary cortisol concentrations. In a first study, we found that women with more dominant-appearing, but not more attractive, faces had lower cortisol levels. These associations were not due to age, ethnicity, time since waking, testosterone, or its interaction with cortisol. In a second study, composite images of women with low cortisol were perceived as more dominant than those of women with high cortisol significantly more often than chance by two samples of viewers, with a similar but non-significant trend in a third sample. However, data on perceptions of attractiveness were mixed; low-cortisol images were viewed as more attractive by two samples of US viewers and as less attractive by a sample of Mexican viewers. Our results suggest that having a more dominant-appearing face may be associated with lower stress and hence lower cortisol in women, and provide further evidence regarding the information content of the human face.

Introduction

Human faces provide rich information about such salient attributes as aggressive potential (Carré and McCormick, 2008; Pound et al., 2009), mate quality (Little et al., 2011; Puts et al., 2012), and fecundity (Puts et al., 2013; Roberts et al., 2004; Wheatley et al., 2014). Consequently, facial appearance influences perceptions of dominance and attractiveness. In fact, attractiveness and dominance as judged by an individual's acquaintances can be predicted above chance from independent observers' ratings of facial photographs (Doll et al., 2014).

In group-living animals, dominance status may promote individual fitness, but the benefits and the mechanisms by which males and females achieve dominance may be quite different. Males frequently achieve dominance by direct agonistic encounters with conspecifics, or through displaying traits that reflect the fighting ability of the bearer.

Dominance directly influences male reproductive success by increasing the number and/or quality of their mates (Clutton-Brock, 2007). By contrast, dominance in females generally increases fitness indirectly by increasing access to non-sexual or ecological resources, such food and reduced harassment from subordinate females or even from males when searching for mate (Tobias et al., 2012). The social control and predictability that female dominance affords may result in lower psychological stress (Sapolsky, 1992). This has led to the prediction that dominance will be associated with reduced synthesis of cortisol, the primary hormone involved in mobilizing energy reserves in response to stressful situations (Nelson, 2005). A negative relationship between dominance and cortisol has indeed been reported for a variety of animal taxa, including primates (Muller and Wrangham, 2004; Sapolsky, 1992).

Following from this, if facial appearance influences perceptions of dominance, then dominant-appearing faces may be linked to lower cortisol concentrations. There is also reason to expect that females with low cortisol might be more attractive to males (Rantala et al., 2013), as cortisol may lower fertility (Csemiczky et al., 2000; Nepomnaschy et al., 2006). If facial appearance provides information about women's fecundity, then attractive faces may be linked to lower cortisol concentrations. Prior research has found that cortisol negatively predicted

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attractiveness and moderated associations of testosterone with attractiveness and perceived dominance in men's faces (Moore et al., 2011a, 2011b; Rantala et al., 2012). To our knowledge, only one study has investigated the relationship between women's cortisol levels and facial attractiveness, reporting a negative association (Rantala et al., 2013), and none has investigated the relationship between women's cortisol and facial dominance. We therefore examined whether women's salivary cortisol levels predict assessments of their facial dominance and attractiveness and whether cortisol may predict average differences in facial appearance across individuals that influence these perceptions. Because cortisol may interact with testosterone in predicting both dominance (Mehta and Josephs, 2010) and facial attractiveness (Moore et al., 2011b; Rantala et al., 2012), we also explored relationships with women's testosterone levels.

Study 1

Methods

Participants

Sixty-one female undergraduate students (mean age = 19.2 ± 1.4, range = 18–24) from a large, northeastern United States university participated in this study. Reported ethnicities were 43 Caucasian, 8 Asian, 4 African-American, 3 Hispanic, and 3 "Other". All participants reported not having used the contraceptive pill in the last 90 days. Participants were recruited through the psychology department subject pool and received either course credit or US$10. Experiments were undertaken with the understanding and written consent of each subject, with the approval of the appropriate local ethics committee, and in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki).

Photographs

Participants were photographed from a distance of 2 m using a 12-megapixel Olympus E-300 camera with a mounted flash at a resolution of 1200 × 1000 pixels in uncompressed TIFF format. Participants removed all earrings, glasses, and facial jewelry, and used a headband if any hair was obstructing their facial features. Participants sat upright in a chair, maintaining a neutral expression with mouth closed. Facial photographs were each landmarked with 25 x,y-coordinates using the software program ImageJ (Schneider et al., 2012). To measure facial masculinity, we standardized and summed four sexually dimorphic facial measures: lower face height/total face height, face width/lower face height, eye width, and cheekbone prominence (Penton-Voak et al., 2001).

Hormone assays

To ensure that the participants were not taking supplements that might affect hormone concentrations, each participant was asked about her most recent caffeine consumption, current medication, and tobacco use. Participants rinsed their mouths with water before providing two saliva samples of 1–2 mL each via passive drool. The samples were collected near the beginning and end of each participant's laboratory session (mean time between samples = 32.0 ± 10.3 min). From each sample, .5 mL of saliva was aliquoted into a third tube to better capture average hormone levels across the time of participation, rather than peaks or troughs in pulsatile secretion patterns. The combined sample was shaken and then frozen at −20 °C until analysis by the Johns Hopkins Center for Interdisciplinary Salivary Bioscience Research (Baltimore, MD) using Salimetrics® kits.

Due to insufficient volume, cortisol could not be measured for 13 samples, and testosterone could not be measured for two samples, leaving 48 cortisol samples and 59 testosterone samples assayed. Samples were analyzed in duplicate via enzyme immunoassay. Duplicates correlated highly for both cortisol ($r_{48} = 1.00$, $p < 0.0001$) and testosterone ($r_{59} = 0.98$, $p < 0.0001$) and were consequently averaged. For cortisol assays, sensitivity is <0.003 μg/dL, and average intra-assay coefficient of variation is 3.5%. For testosterone assays, sensitivity is <1.0 pg/mL, and average intra-assay coefficient of variation is 4.6%.

Facial scores

Ninety-seven male (mean age = 19.5 ± 1.4) and 124 female (mean age = 18.7 ± 0.9) raters were recruited through the psychology department subject pool. We randomly assigned the facial photographs of female participants into one of four stimulus sets. Two sets had 15 stimulus faces, and the other two had 16 stimulus faces. Raters were unfamiliar with the individuals who provided stimulus faces, and each rater was randomly assigned to rate one stimulus set. All participants rated faces using 7-point Likert scales for attractiveness (1 = very unattractive, 7 = very attractive), femininity (1 = not very feminine, 7 = very feminine), and dominant-looking (1 = not very dominant, 7 = very dominant). Reliability was assessed with intra-class correlation (one-way random average measures, Shrout & Fleiss, 1979). Because some faces were rated by a slightly larger number of raters, we randomly sampled those ratings (without replacement) so that all faces had an equal number of ratings. Reliability was good for men's ratings [attractiveness: ICC (1.16) = 0.86; femininity: ICC (1.18) = 0.75; dominance: ICC (1.18) = 0.80] and for women's ratings [attractiveness: ICC (1.26) = 0.91; femininity: ICC (1.26) = 0.85; dominance: ICC (1.26) = 0.85].

Data treatment

We performed a principal component analysis (PCA) on ratings of women's facial attractiveness, femininity, and dominance using varimax rotation. The PCA resulted in two components with eigenvalues > 1 (see also Table 1). Female- and male-rated attractiveness and femininity loaded heavily and positively (factor loadings > 0.87) onto PC1, and female- and male-rated dominance loaded heavily and positively (factor loadings > 0.83) onto PC2. These components were saved as the variables "Facial Attractiveness PC" and "Facial Dominance PC", respectively.

Analysis of variance revealed no effect of ethnicity on Facial Attractiveness PC ($F_{3,54} = 0.48$, $p = 0.697$). However, there was a significant effect of ethnicity on Facial Dominance PC ($F_{3,54} = 10.52$, $p < 0.0001$): women reporting Asian ethnicity had significantly less dominant-appearing faces than all other groups (t-tests: all $p < 0.02$). With women reporting Asian ethnicity removed, there was no longer a significant effect of ethnicity ($F_{2,47} = 2.06$, $p = 0.139$). Consequently, ethnicity was dichotomized as Asian = 1, non-Asian = 0.

Thereafter, we performed two multiple regression analyses using Facial Attractiveness PC and Facial Dominance PC as dependent variables and age, time since walking, ethnicity, cortisol and testosterone as predictors. In order to identify violation of homogeneity and/or non-normality in the multiple regression models, we visually inspected the model residuals using a residuals-vs.-fitted-values plot and a normal "Q–Q" plot (Crawley, 2007; Zuur et al., 2009). No heterogeneity was detected in either model. Cortisol and testosterone values were natural log-transformed to correct skewness and hence normality. In addition, we checked for the presence of influential observations in each multiple regression model by measuring the Cook's distance of each observation (values > 1 are considered influential; Cook and Weisberg, 1982).

Table 1
Zero-order correlations between ratings of attractiveness, femininity, and dominance (collapsed across sex of rater).

	Femininity	Dominance
Attractiveness	.91***	.61***
Femininity		.46***

*** $p < .001$.

However, we detected no outliers. Analyses were performed in R (R Core Development Team 2009, version 2.10.0) and in SPSS (IBM Inc, version 20).

Results

The regression model predicting Facial Attractiveness PC was not statistically significant, nor was any predictor (Table 2). However, the multiple regression model predicting Facial Dominance PC showed that Asian ethnicity (described above) and cortisol were significant negative predictors, but age, time since waking, testosterone, and testosterone × cortisol were not significant predictors (Table 2). In multiple regression models, all variance inflation factors were <1.4, indicating that these results are unlikely to be confounded by multicolinearity among predictor variables. To confirm that the particular combination of control variables was not responsible for the observed relationships, we also examined zero-order correlations between cortisol on the one hand and Facial Dominance PC and Facial Attractiveness PC on the other (Table 3). Again, cortisol significantly negatively predicted Facial Dominance PC, but not Facial Attractiveness PC (Fig. 1). Facial Dominance PC remained significantly correlated with cortisol after excluding individuals reporting Asian ($r_{42} = -0.39$, $p < 0.01$) or non-White ($r_{33} = -0.36$, $p = 0.042$) ethnicity.

As an alternative to using principal components to characterize facial perceptions, we also produced composite variables by standardizing and summing facial attractiveness and femininity ratings to produce the variable "Combined Facial Attractiveness", and by standardizing and summing ratings of facial dominance to produce the variable "Combined Facial Dominance". In multiple regression models with independent variables identical to those reported above, Asian ethnicity ($\beta = -0.48$, $t = -3.87$, $p < 0.001$) and cortisol ($\beta = -0.38$, $t = -2.78$, $p = 0.008$) again predicted perceptions of facial dominance (Model: $F_{6,41} = 4.95$, $R^2 = 0.42$, $p < 0.001$), but not perceptions of facial attractiveness (Model: $F_{6,41} = 1.44$, $R^2 = 0.17$, $p = 0.225$).

Because previous research reported an association between women's facial attractiveness and cortisol (Rantala et al., 2013), we explored whether this previous finding might have reflected an association of facial attractiveness with perceived facial dominance. Combined Facial Dominance and Combined Facial Attractiveness scores (not PCs) were indeed significantly positively correlated in our data ($r_{61} = 0.54$, $p < 0.0001$, Table 3). Further, varimax rotation produces orthogonal components; hence, our Facial Attractiveness PC effectively controlled statistically for dominance, and our Facial Dominance PC effectively controlled statistically for attractiveness. Consequently, we examined relationships between cortisol and facial attractiveness and dominance composite variables. However, while Combined Facial Dominance significantly correlated with cortisol, Combined Facial

Table 3
Zero-order correlations between log-cortisol, log-testosterone, and raw scores of male- and female-rated facial attractiveness, dominance, and femininity.

	Testosterone	Attract PC	Attract comp	Dom PC	Dom comp
Cortisol	.35*	−.01	−.10	−.37**	−.36*
Testosterone		.13	.06	−.18	−.11
Attract PC			.96***	.00	.30*
Attract comp				.27*	.54***
Dom PC					.95***

* $p < .05$.
** $p < .01$.
*** $p < .001$.

Attractiveness did not (Table 3). Moreover, when we ran a multiple regression model with Combined Facial Attractiveness and Combined Facial Dominance entered as predictors of cortisol, perceived facial dominance was a significant predictor ($\beta = -0.41$, $t = -2.57$, $p = 0.013$), but facial attractiveness was not ($\beta = 0.11$, $t = 0.72$, $p = 0.473$, Model: $F_{2,49} = 3.62$, $R^2 = 0.13$, $p = 0.034$). Statistical significance of these results did not change if we controlled for age, Asian ethnicity, time since waking, testosterone, or the interaction of cortisol with testosterone.

Facial masculinity measured from landmarks marginally significantly predicted Facial Attractiveness PC ($r_{45} = -0.27$, $p = 0.078$) and Combined Facial Attractiveness ($r_{45} = -0.26$, $p = 0.089$), but not Facial Dominance PC ($r_{45} = -0.01$, $p = 0.947$), Combined Facial Dominance ($r_{45} = -0.09$, $p = 0.563$), or cortisol ($r_{33} = -0.18$, $p = 0.317$).
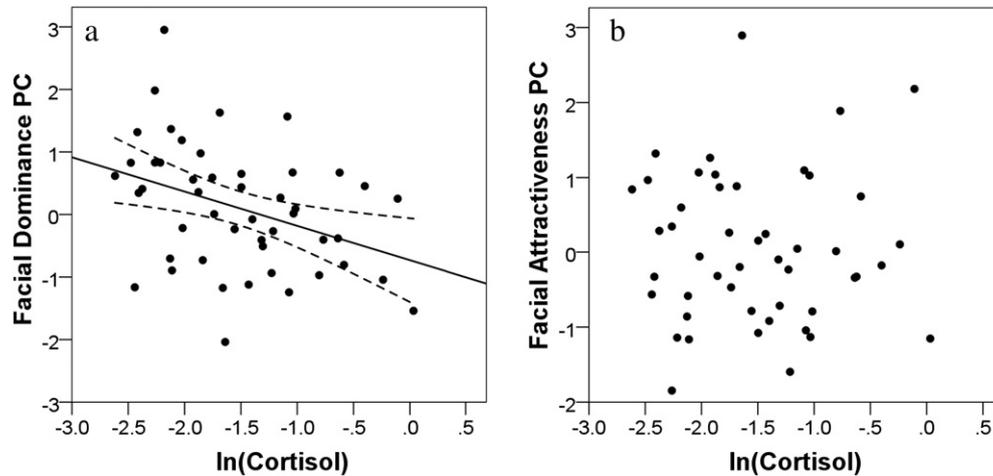
Study 2

It is possible that cortisol may predict average differences in facial appearance across individuals, such as directional variation in the size or proportions of facial features, and that these differences influence the perception of dominance and/or attractiveness. We explored this possibility by producing composite images (using Psychomorph software) of 10 women with the lowest cortisol levels and 10 women with the highest cortisol levels obtained from Study 1, and then we had these images compared for perceived dominance and attractiveness.

We controlled the possible confounding effect of ethnicity (e.g. Blair, Judd, Sadler and Jenkins, 2002) in two ways. First, we created a pair of composite images by balancing Asian ethnicity, because Asian women differed in rated perceived dominance from women reporting other ethnicities (Study 1). To do so, we replaced the image of the woman with the 8th highest cortisol (Asian ethnicity) with that of the woman with the 11th highest cortisol (White ethnicity) so that the high-cortisol and low-cortisol composite images (Fig. 2) were each composed of one Asian and nine non-Asian images. Second, we produced another pair of composite images (Fig. 3) from the images of the 10 women with the highest and the 10 women with the lowest cortisol levels who reported only White ethnicity.

We then asked 200 men (mean age = 21.5 ± 4.6) and 200 women (mean age = 21.0 ± 4.6) from the same large, northeastern US university which composite face appeared more attractive and more dominant (100 men and 100 women judged each pair with question order counterbalanced across participants). Respondents were approached in public areas of the campus and shown the images side by side (counterbalanced for order) on a Nexus 7 tablet.

Because the perception of dominance and attractiveness may vary among cultures, we sampled a second culture to judge the appearance of dominance and attractiveness in the composite images previously created. These data were collected from 100 men (mean age = 23.5 ± 4.6) and 100 women (mean age = 22.0 ± 7.6) at the National Autonomous University of Mexico (UNAM) campus. For this sample, we used only the second pair of composites created with only White

Table 2
Multiple regression models predicting facial attractiveness PC (principal component onto which ratings of attractiveness and femininity loaded heavily) and facial dominance PC (principal component onto which dominance ratings loaded heavily).

		$F_{6,41}$	R^2	β	t	p
Attractiveness	Model	.97	.12			0.458
	Age			−.17	−1.10	0.276
	Ethnicity			−.00	−.02	0.987
	Time since waking			−.19	−1.23	0.230
	Cortisol			−.15	−.89	0.380
	Testosterone			.20	1.27	0.212
	Cortisol × testosterone			.18	1.19	0.241
Dominance	Model	4.96	.42			**<0.001**
	Age			−.07	−.54	0.589
	Ethnicity			−.50	−4.04	**<0.001**
	Time since waking			−.07	−.54	0.592
	Cortisol			−.35	−2.54	**0.015**
	Testosterone			.04	.32	0.752
	Cortisol × testosterone			.10	.81	0.423

Note: Statistically significant results are in bold.

Fig. 1. Cortisol levels were negatively related to (a) facial dominance PC (principal component onto which female- and male-rated dominance loaded heavily), but not to (b) facial attractiveness PC (principal component onto which female- and male-rated attractiveness and femininity loaded heavily). In panel (a), least-squares regression line with 95% CI is plotted.

ethnicity, asking participants which was more attractive (*atractivo*) and which was more dominant (*dominante*).

Data were analyzed by fitting generalized linear models (GLMs) of the binomial family (with logit link function) for each response variable (perceived dominance and attractiveness), controlling for respondents' gender, age and ethnicity (for US sample), as well as question order and image position.

For the first set of composites (Fig. 2), US respondents tended to perceive the low-cortisol face as more dominant (71%) and more attractive (63%). These proportions were significantly greater than chance ($\chi^2 = 35.3, p < 0.0001$ and $\chi^2 = 12.5, p < 0.0001$, respectively), and no control variable significantly influenced the respondents' answers for perceived dominance (Resid. Dev. = 231.6, *d.f.* = 191, $p = 0.320$, see ESM 1a) or attractiveness (Resid. Dev. = 257.3, *d.f.* = 191, $p = 0.495$, see ESM 1b). For the second pair of composites (Fig. 3), US respondents again tended to choose the low-cortisol composite as more dominant, but this was not significantly different from chance (53%, $\chi^2 = 0.72, p = 0.396$). The low-cortisol image was again judged to be more attractive more frequently than chance (71%, $\chi^2 = 35.28, p < 00.0001$; Fig 3b). Again, no control variable significantly influenced the respondents' answers for perceived dominance (Resid. Dev. = 270.7, *d.f.* = 191, $p = 0.661$, see ESM 2a) or attractiveness (Resid. Dev. = 227.2, *d.f.* = 191, $p = 0.092$, see ESM 2b).

When the second (White only) pair of composite images was judged by Mexican respondents, the participants tended to perceive the low-cortisol face as more dominant (62%, $\chi^2 = 11.52, p < 0.001$; Fig. 3b).

The respondents' answers were not influenced by any control variables (Resid. Dev. = 263.2, *d.f.* = 195, $p = 0.656$, see ESM 3a). However, Mexican respondents tended to perceive the low-cortisol face as less attractive (31%, $\chi^2 = 27.38, p < 0.001$), with significant effects (GLM: Resid. Dev. = 234.4, *d.f.* = 195, $p = 0.005$, see ESM 3b) of image position ($z = -2.43, p = 0.014$) and question order ($z = 3.01, p = 0.002$). Specifically, when the first question was "who looks more attractive", the low-cortisol face was chosen by 41% of the participants ($\chi^2 = 3.24, p = 0.072$), but when this question was asked second, only 22% chose the low-cortisol face ($\chi^2 = 31.36, p < 0.001$). Similarly, when the low-cortisol face was shown on the left, it was judged to be more attractive 24% of the time ($\chi^2 = 27.04, p < 0.001$), but when it was shown on the right, it was chosen 39% of the time ($\chi^2 = 4.84, p = 0.030$).

Discussion

In group-living animals, including Old World primates, subordinate females suffer more threats and avoid others more frequently than do dominant females (Harcourt, 1987). These agonistic pressures increase subordinates' stress levels, leading to an increase in the synthesis of cortisol (Kirby et al., 2009; Nepomnaschy et al., 2006). Our results suggest that a similar relationship may exist in human females; we found that women with lower cortisol levels had more dominant-appearing faces. This relationship was independent of age, ethnicity, time since waking, testosterone, and the interaction of testosterone with cortisol. We also found that low-cortisol composite images were perceived as
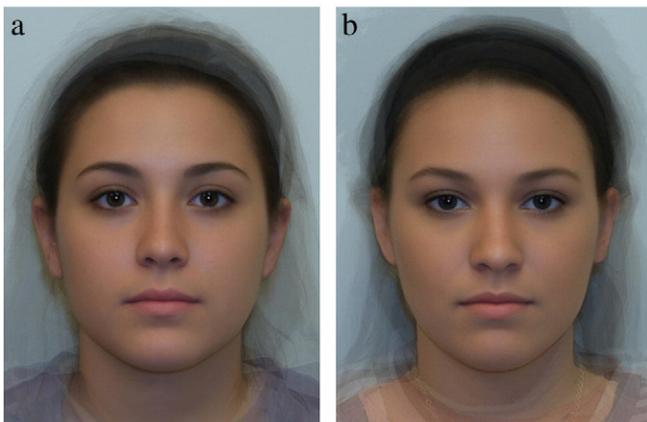
Fig. 2. Composite images balanced by Asian ethnicity of (a) the 10 women with the highest and (b) the 10 women with the lowest cortisol levels.
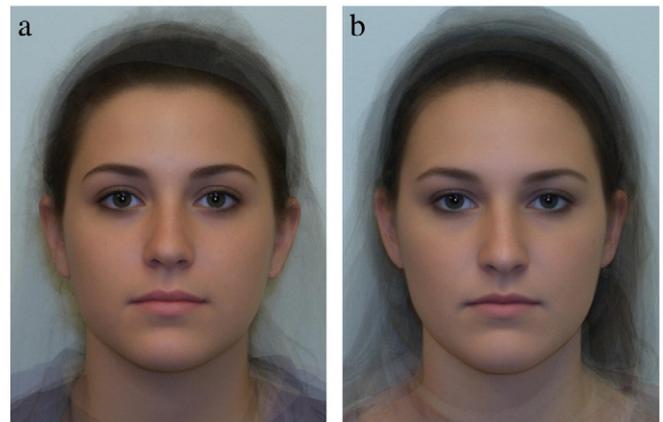
Fig. 3. Composite images of the 10 self-identified White women with (a) the highest and (b) the lowest cortisol levels.

being more dominant than high-cortisol composites by samples of US and Mexican participants, with a third (US) sample showing a non-significant tendency in this direction. Women with dominant-looking faces may receive greater deference, leading to reduced psychological and/or physical stress and reduced cortisol levels. Although Edwards and Casto (2013) found no relationship between cortisol and social status in college athletes, the high status afforded varsity athletes may have reduced variance in status, weakening any relationship with cortisol.

Not only might facial (and other) dominance decrease women's stress and cortisol levels, but the relationship between facial appearance and cortisol could also trace to earlier in development. Developmental stress could influence both facial morphology (Gangestad and Thornhill, 2003) and hypothalamic–pituitary–adrenal axis function, including cortisol production (Nepomnaschy and Flinn, 2009). If so, then developmental stress—perhaps especially psychosocial stress—might be expected to influence attractiveness as well, and cortisol should also predict facial attractiveness. Previous studies have shown that family stressors such as father absence and poor parental care during early childhood may induce higher cortisol levels in adulthood (Flinn and England, 1997) and have long-term negative effects on women's facial attractiveness (Boothroyd and Perrett, 2006). Indeed, Rantala et al. (2013) found a negative association between women's cortisol and facial attractiveness.

We found that composite variables for perceived dominance and attractiveness were highly correlated in our zero-order correlations, and that more dominant-looking faces were also considered more attractive by two of the three samples in our forced choice study (Study 2). However, our results also suggest that any influence of developmental stress on attractiveness is substantially smaller than the influence on perceived dominance: Cortisol did not predict our attractiveness PC in Study 1, where attractiveness was differentiated from perceived dominance via varimax rotation, which produces orthogonal components. Moreover, when both Combined Facial Dominance and Combined Facial Attractiveness composite variables were entered into a multiple regression model to predict cortisol concentrations, perceived dominance was a significant predictor, and attractiveness was not. Despite these results, it remains possible that developmental stress affects both perceived facial dominance and facial attractiveness, but that the effect of stress (as indicated by cortisol concentrations) on attractiveness is subsumed by the influence of stress on dominance. While this remains a possibility worth further exploration, we found only a very modest ($r = -0.10$) and statistically non-significant negative relationship between cortisol and our Combined Facial Attractiveness variable.

Finally, we found no systematic relationship between cortisol and perceptions of attractiveness in our composite images. Although the low-cortisol composite image was perceived as being more attractive by both samples of US participants, the opposite was found among Mexican participants. Because Mexican participants chose the low-cortisol face (which they perceived to be more dominant) as more attractive significantly less often when they first judged dominance than when they first judged attractiveness, this suggests that choosing a face as dominant made it subsequently less attractive. One interpretation of the discrepancy between the US and Mexican results is that dominant women are viewed less favorably in Mexico than in the US. Another possibility is that the terms "dominant" and "*dominante*" were interpreted differently by US and Mexican participants, respectively.

As cortisol does not exhibit regular changes over the ovulatory cycle (Kudielka and Kirschbaum, 2003), these relationships are unlikely to reflect differences across women in cycle phase. Moreover, inspection of our first pair of composite images (Fig. 2) suggests that high- and low-cortisol women differed in such facial characteristics as the ratio of width to height that are unlikely to change appreciably over the short term (e.g., monthly or daily). However, such differences were less clear in the composite created from images of women reporting only

White ethnicity (Fig. 3). We also found no relationship between cortisol and facial masculinity across the original images.

Cortisol levels measured at the same time of day are stable across several weeks (Liening et al., 2010), suggesting that our hormone measures tapped into individual differences in basal cortisol levels. However, cortisol levels fluctuate over the day and in response to environmental factors; thus our data cannot distinguish definitively between whether perceived facial dominance is associated with individual differences in women's baseline cortisol levels, or with the magnitude of any cortisol response that they experienced related to their laboratory visit. Indeed, dominance might be expected to predict lower values on both measures of cortisol, and future research should explore these possibilities.

Through producing high- and low-cortisol composite images, we explored whether there exist average differences in facial appearance associated with cortisol levels. However, it should be emphasized that even if cortisol and facial appearance are related, as indicated by perceptions of unmanipulated images in our data and those of others (Moore et al., 2011a, 2011b; Rantala et al., 2012, 2013), is not necessarily the case that the perceptual facial correlates of cortisol will be apparent in composite images. This is because correlates that are not directional in their expression will average out across faces. For example, if cortisol were associated with increased facial fluctuating asymmetry (for a review of research on fluctuating asymmetry, see, e.g., Van Dongen and Gangestad, 2011), then there would be no relationship between high- vs. low-cortisol composites and facial asymmetry, because leftward and rightward asymmetries would average out in the composite images. A similar situation would apply for other non-directional deviations from average face shape, and for uneven skin color. Our results from the composite images thus suggest that there may indeed be some directional differences between high- and low-cortisol faces that influence attractiveness and dominance, such as differences in the shape of individual features. Future research should employ more precise measures of face shape, such as spatially-dense 3D geometric morphometrics (Claes et al., 2012, 2014) in order to elucidate the facial features associated with women's cortisol concentrations.

Previous studies have shown that women's facial masculinity is negatively related to attractiveness and positively to perceptions of dominance (Perrett et al., 1998). Although we found marginally significant negative relationships between facial masculinity measured from landmarks and attractiveness, relationships with perceptions of dominance did not approach significance. The lack of relationships with dominance may reflect our use of unmanipulated faces as stimuli rather than face images in which masculinity has been manipulated using computer software, as in previous studies (e.g., Perrett et al., 1998; Watkins et al., 2012). It is also possible that the relationship between women's facial masculinity and dominance would have been stronger in our data if we had specified that the participants assess physical dominance, as facial masculinity as been found to increase perceptions of physical dominance but decrease perceptions of social dominance among women (Watkins et al., 2012).

Although this was not the focus of the present research, we were also unable to replicate our previous finding (Wheatley et al., 2014) of a negative association between women's testosterone levels and facial attractiveness. This discrepancy may reflect differences in sample characteristics (e.g., all participants taking hormonal contraception in Wheatley et al. vs. no participants taking hormonal contraception in the present research), the larger sample size ($n = 189$) in Wheatley et al., or other methodological differences (e.g., collecting hormonal data and face images at two time points for each participant in Wheatley et al.).

We also found no relationship between testosterone and perceived facial dominance, either in zero-order correlations or after controlling for cortisol and its interaction with testosterone. Several prior human studies have linked indices of dominance to testosterone levels, though others have not (reviewed in Mehta and Josephs, 2010). Recent work

(Mehta and Josephs, 2010) suggests that it is important to measure and control for cortisol and cortisol × testosterone as we did when investigating relationships between testosterone and dominance. A potentially crucial difference is that previous studies collected behavioral measures of dominance, whereas we investigated a morphological correlate of dominance perceptions.

Finally, although we are aware that perceived dominance in women's faces may not be linked to real social dominance, we cannot rule out this possibility, especially because previous studies in men have shown that perceived dominance in men's faces is correlated with measures of men's overall dominance, including men's self-rated dominance, assessments made by their acquaintances, and eventual military rank (Doll et al., 2014; Mueller and Mazur, 1996, 1997). Nevertheless, in contrast with the large number of studies about dominance in men, with important recent exceptions (e.g., Edwards and Casto, 2013; Mehta and Josephs, 2010), relationships between cortisol, dominance, and attractiveness are understudied in women. Therefore, it will be important to explore whether women's cortisol relates to their dominance measured by other means, such as assessments made by familiar peers. Future research should also clarify the specific facial features that are associated with women's cortisol levels and that influence perceptions of women's dominance.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yhbeh.2015.03.006.

References

Blair, I.V., Judd, C.M., Sadler, M.S., Jenkins, C., 2002. The role of Afrocentric features in person perception: judging by features and categories. J. Pers. Soc. Psychol. 83, 5–25.

Boothroyd, L.G., Perrett, D.I., 2006. Facial and bodily correlates of family background. Proc. Biol. Sci. 273, 2375–2380.

Carré, J.M., McCormick, C.M., 2008. In your face: facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. Proc. R. Soc. B Biol. Sci. 275, 2651–2656.

Claes, P., Walters, M., Shriver, M.D., Puts, D., Gibson, G., Clement, J., et al., 2012. Sexual dimorphism in multiple aspects of 3D facial symmetry and asymmetry defined by spatially dense geometric morphometrics. J. Anat. 221, 97–114.

Claes, P., Liberton, D.K., Daniels, K., Rosana, K.M., Quillen, E.E., Pearson, L.N., et al., 2014. Modeling 3D facial shape from DNA. PLoS Genet. 10, e1004224.

Clutton-Brock, T., 2007. Sexual selection in males and females. Science 318, 1882–1885.

Cook, R.D., Weisberg, S., 1982. Residuals and Influence in Regression. Chapman and Hall, New York.

Crawley, M.J., 2007. The R Book. Wiley.

Csemiczky, G., Landgren, B.M., Collins, A., 2000. The influence of stress and state anxiety on the outcome of IVF-treatment: psychological and endocrinological assessment of Swedish women entering IVF-treatment. Acta Obstet. Gynecol. Scand. 79, 113–118.

Doll, L.M., Hill, A.K., Cárdenas, R.A., Welling, L.L.M., Wheatley, J.R., Puts, D.A., 2014. How well do men's faces and voices index mate quality and dominance? Hum. Nat. 25, 200–212.

Edwards, D.A., Casto, K.V., 2013. Women's intercollegiate athletic competition: cortisol, testosterone, and the dual-hormone hypothesis as it relates to status among teammates. Horm. Behav. 64, 153–160.

Flinn, M.V., England, B.G., 1997. Social economics of childhood glucocorticoid stress response and health. Am. J. Phys. Anthropol. 102, 33–53.

Gangestad, S.W., Thornhill, R., 2003. Facial masculinity and fluctuating asymmetry. Evol. Hum. Behav. 24, 231–241.

Harcourt, A.H., 1987. Dominance and fertility among female primates. J. Zool. 213, 471–487.

Kirby, E.D., Geraghty, A.C., Ubuka, T., Bentley, G.E., Kaufer, D., 2009. Stress increases putative gonadotropin inhibitory hormone and decreases luteinizing hormone in male rats. Proc. Natl. Acad. Sci. U. S. A. 106, 11324–11329.

Kudielka, B.M., Kirschbaum, C., 2003. Awakening cortisol responses are influenced by health status and awakening time but not by menstrual cycle phase. Psychoneuroendocrinology 28, 35–47.

Liening, S.H., Stanton, S.J., Saini, E.K., Schultheiss, O.C., 2010. Salivary testosterone, cortisol, and progesterone: two-week stability, interhormone correlations, and effects of time of day, menstrual cycle, and oral contraceptive use on steroid hormone levels. Physiol. Behav. 99, 8–16.

Little, A.C., DeBruine, L.M., 2011. Facial attractiveness: evolutionary based research. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366, 1638–1659.

Mehta, P.H., Josephs, R.A., 2010. Testosterone and cortisol jointly regulate dominance: evidence for a dual-hormone hypothesis. Horm. Behav. 58, 898–906.

Moore, F.R., Al Dujaili, E.A., Cornwell, R.E., Smith, M.J., Lawson, J.F., Sharp, M., et al., 2011a. Cues to sex- and stress-hormones in the human male face: functions of glucocorticoids in the immunocompetence handicap hypothesis. Horm. Behav. 60, 269–274.

Moore, F.R., Cornwell, R.E., Smith, M.J., Al Dujaili, E.A., Sharp, M., Perrett, D.I., 2011b. Evidence for the stress-linked immunocompetence handicap hypothesis in human male faces. Proc. R. Soc. B Biol. Sci. 278, 774–780.

Mueller, U., Mazur, A., 1996. Facial dominance of West Point cadets as a predictor of later rank. Soc. Forces 74, 823–850.

Mueller, U., Mazur, A., 1997. Facial dominance in Homo sapiens as honest signaling of male quality. Behav. Ecol. 8, 569–579.

Muller, M., Wrangham, R., 2004. Dominance, cortisol and stress in wild chimpanzees (Pan troglodytes schweinfurthii). Behav. Ecol. Sociobiol. 55, 332–340.

Nelson, R.J., 2005. An Introduction to Behavioral Endocrinology. 3rd ed. Sinauer Associates, Sunderland, MA.

Nepomnaschy, P.A., Flinn, M.V., 2009. Early life influences on the ontogeny of the neuroendocrine stress response in the human child. In: Ellison, P.T., Gray, P.B. (Eds.), Endocrinology of Social Relationships. Harvard University Press, Cambridge, MA, pp. 364–382.

Nepomnaschy, P.A., Welch, K.B., McConnell, D.S., Low, B.S., Strassmann, B.I., England, B.G., 2006. Cortisol levels and very early pregnancy loss in humans. Proc. Natl. Acad. Sci. U. S. A. 103, 3938–3942.

Penton-Voak, I.S., Jones, B.C., Little, A.C., Baker, S., Tiddeman, B., Burt, D.M., et al., 2001. Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. Proc. Biol. Sci. 268, 1617–1623.

Perrett, D.I., Lee, K.J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D.M., et al., 1998. Effects of sexual dimorphism on facial attractiveness. Nature 394, 884–887.

Pound, N., Penton-Voak, I.S., Surridge, A.K., 2009. Testosterone responses to competition in men are related to facial masculinity. Proc. R. Soc. B Biol. Sci. 276, 153–159.

Puts, D.A., Jones, B.C., DeBruine, L.M., 2012. Sexual selection on human faces and voices. J. Sex Res. 49, 227–243.

Puts, D.A., Bailey, D.H., Cárdenas, R.A., Burriss, R.P., Welling, L.L., Wheatley, J.R., et al., 2013. Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. Horm. Behav. 63, 13–19.

Rantala, M.J., Moore, F.R., Skrinda, I., Krama, T., Kivleniece, I., Kecko, S., et al., 2012. Evidence for the stress-linked immunocompetence handicap hypothesis in humans. Nat. Commun. 3, 694–698.

Rantala, M.J., Coetzee, V., Moore, F.R., Skrinda, I., Kecko, S., Krama, T., et al., 2013. Facial attractiveness is related to women's cortisol and body fat, but not with immune responsiveness. Biol. Lett. 9.

R Core Development Team, M.J., 2009. R: A language and environment for statistical computing, v. 2.10.0. R Foundation for Statistical Computing. Vienna, Austria URL http://www.R-project.org/.

Roberts, S.C., Havlicek, J., Flegr, J., Hruskova, M., Little, A.C., Jones, B.C., et al., 2004. Female facial attractiveness increases during the fertile phase of the menstrual cycle. Proc. Biol. Sci. 271 (Suppl. 5), S270–S272.

Sapolsky, R.M., 1992. Cortisol concentrations and the social significance of rank instability among wild baboons. Psychoneuroendocrinology 17, 701–709.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675.

Shrout, P.E., Fleiss, J.L., 1979. Intraclass correlations: uses in assessing rater reliability. Psychol. Bull. 86, 420–428.

Tobias, J.A., Montgomerie, R., Lyon, B.E., 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. Philos. Trans. R. Soc. Lond. B Biol. Sci. 367, 2274–2293.

Van Dongen, S., Gangestad, S.W., 2011. Human fluctuating asymmetry in relation to health and quality: a meta-analysis. Evol. Hum. Behav. 32, 380–398.

Watkins, C.D., Quist, M.C., Smith, F.G., DeBruine, L.M., Jones, B.C., 2012. Individual differences in women's perceptions of other women's dominance. Eur. J. Personal. 26, 79–86.

Wheatley, J.R., Apicella, C.A., Burriss, R.P., Cárdenas, R.A., Bailey, D.H., Welling, L.L.M., et al., 2014. Women's faces and voices are cues to reproductive potential in industrial and forager societies. Evol. Hum. Behav. 35, 264–271.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer.