

Cross-cultural variation in women's preferences for cues to sex- and stress-hormones in the male face

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Women in the UK prefer the faces of men with low levels of the stress hormone cortisol, and the relationship is moderated by the sex hormone testosterone. In a Latvian sample, however, women's preferences were not affected by cortisol, and the interaction with testosterone differed from that of the UK. To further explore cross-cultural variation in preferences for facial cues to sex- and stress-hormones, we tested the preferences of women from 13 countries for facial composites constructed to differ in combinations of the hormones. We found significant relationships between a measure of societal development (the United Nations human development index 2011) and preferences for cues to testosterone in the face, and the interaction between preferences for cues to testosterone and cortisol. We also found a significant relationship between preferences for cues to testosterone and a societal-level measure of parasite stress. We conclude that societal-level ecological factors influence the relative value of traits revealed by combinations of sex- and stress-hormones.

Keywords: stress-linked immunocompetence handicap, cortisol, testosterone, face, attractiveness, masculinity

1. Introduction

In the immunocompetence handicap hypothesis, the honesty of secondary sexual traits as indicators of immunocompetence is maintained via testosterone, which stimulates trait expression while suppressing the immune system [1]. Recently, the glucocorticoid stress hormones have been implicated in the model [2–4] owing to their effects on the immune system [5] and secondary sexual traits [6,7]. We found that women from the UK preferred the faces of men with low levels of the glucocorticoid cortisol, and that preferences for cues to testosterone were strongest for the faces of men with high cortisol [8,9]. We proposed that this interaction could stem from the superior ability of high-testosterone men to cope with detrimental effects of

stress [9]. In a similar study from a Latvian population, however, we did not find a relationship between cortisol and facial attractiveness, and found women to prefer the faces of men with high testosterone [10]. Furthermore, the interaction between the hormones was such that preferences for cues to testosterone were strongest for the faces of men with low cortisol. Identifying the nature of relationships between combinations of sex- and stress-hormones and secondary sexual traits is necessary in order to model roles of stress in sexual selection. Therefore, it is valuable to analyse systematic variation in female preferences for cues to the hormones in order to infer relevant selection pressures.

It is possible that divergent results from the UK and Latvia stem from societal-level differences in preferences, or from methodological differences between studies. DeBruine et al. [11] report a relationship between the parasite load of nations and women's preferences for testosterone-dependent facial characteristics, such that women in countries with a high parasite load expressed stronger preferences for facial masculinity. Furthermore, studies of the roles of testosterone and glucocorticoid stress hormones in the sexual signalling of non-human species show systematic variation in their combined effects with environmental harshness. The direction of a relationship between stress and plumage coloration in the red bishop (*Euplectes orix*), for example, was contingent upon rainfall and, in turn, stress moderated a relationship between testosterone and plumage [12]. Alternatively, it is possible that the difference in results arises from a difference in the methodology: in the UK sample, we measured preferences for composite male faces constructed to differ in cues to combinations of the hormones, whereas in the Latvian sample, we tested relationships across the faces of individual men, rather than morphed stimuli. To test whether societal-level or methodological differences account for unstable relationships between testosterone, cortisol and facial attractiveness, we tested preferences of women for the composite faces constructed in our previous research [8,9] from countries that differed on a broad measure of societal development (human development index (HDI); [13]) as well as more specific measures (resource inequality and pathogen stress).

2. Material and methods

(a) Participants

A total of 2842 women (mean age: 26.51 (s.d. $\frac{1}{4}$ 8.36)) were recruited via an online data collection forum advertised across eight countries (reaching participants from 12 nations) and a data collection session in rural Cameroon (owing to limited internet access in this population). Table 1 shows the sample profile.

(b) Face preferences

Two sets of four composite images from the faces of Caucasian males who differed in combinations of testosterone (T) and cortisol (C) (high T high C; high T low C; low T high C; low T low C; [8,9]) were displayed in random order for participants to rate for attractiveness (1 $\frac{1}{4}$ not at all attractive, 7 $\frac{1}{4}$ extremely attractive). For full details of stimuli construction see [8,9]. Mean preferences for combinations of testosterone and cortisol were computed from preferences for both stimulus sets. Mean preference for the composite faces with cues to high testosterone was calculated as the mean of preferences for the high T high C and high T low C composites (high T preference), and mean preference for those faces with cues to low testosterone was calculated as the mean of preferences for the low T high C and low T low C faces (low T preference). The mean low T preference was subtracted from the mean high T preference to produce a testosterone-preference score (high values indicate a preference for high-testosterone composites). Similar calculations were conducted to compute preferences for high- and low-cortisol faces.

(c) Human development index

2011-HDI scores were extracted for the 13 countries [13]. This is a composite score from 0 to 1

Table 1. Numbers of participants recruited from each of 13 countries, with ethnicity profiles and human development index (HDI; 2011), Gini and pathogen stress scores.

country	n	Gini (year)	pathogen stress	HDI	ethnicity (%)			
					Caucasian	Black African	Asian	other
UK	152	34 (2005)	-3.49	0.86	95	0	3	2
US	262	45 (2007)	-1.74	0.91	84	1	4	10
Finland	1545	26.8 (2008)	-3.62	0.88	99	0	1	0
Latvia	76	35.2 (2010)	-2.34	0.81	96	0	0	4
Russia	39	42 (2010)	0.09	0.76	82	0	8	10
Poland	58	34.2 (2008)	-3.06	0.81	98	0	0	2
South Africa	16	65 (2005)	2.81	0.62	81	6	13	0
Estonia	391	31.3 (2010)	-2.37	0.84	98	0	0	2
Japan	11	37.6 (2008)	-2.23	0.9	0	0	100	0
Mexico	83	51.7 (2008)	1.8	0.77	6	0	0	94
Sweden	86	23 (2005)	-3.31	0.9	94	0	3	3
Namibia	88	70.7 (2003)	2.55	0.63	93	1	0	6
Cameroon	30	44.6 (2001)	5.27	0.48	0	100	0	0

Table 2. β -values for bivariate relationships between HDI and preferences for cues to high T and C, and the interaction term of the two, in male faces.

	preference for cues to high over low T	preference for cues to high over low C	T \times C interaction term
	adj. $R^2 = 0.69, F_{1,12} = 27.84^{**}$	adj. $R^2 = 0.2, F_{1,12} = 3.9$	adj. $R^2 = 0.25, F_{1,12} = 4.93^*$
HDI	-0.85*	-0.51	0.56*

** $p < 0.001$ and * $p < 0.05$.

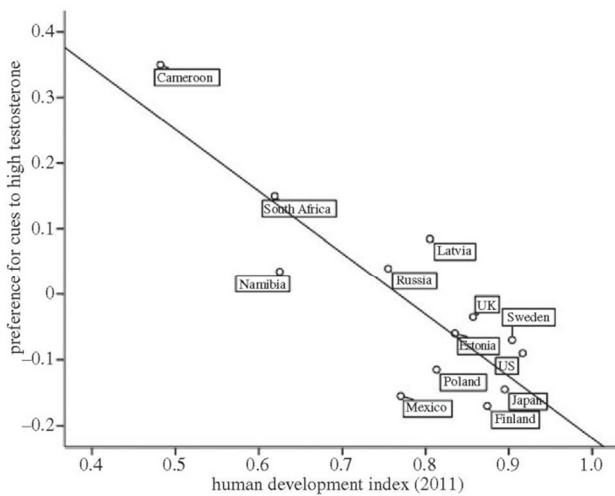


Figure 1. Negative relationship between national human development index score and women's preference for cues to high testosterone in the male face.

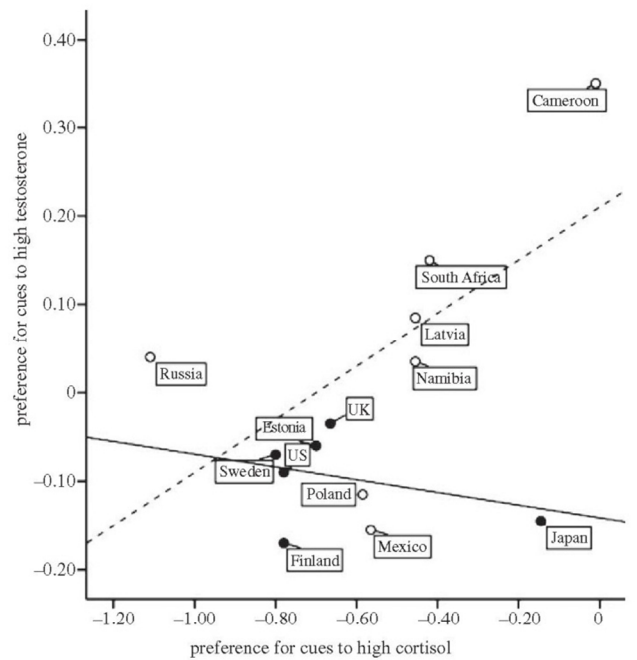


Figure 2. Relationships between women's preferences for cues to high testosterone and cues to high cortisol in the male face, which is negative in countries with a high human development index (HDI) score (bold line and shaded data points) and positive in those with a low score (broken line and empty data points). To demonstrate the significant relationship between HDI score and the interaction between preferences for cues to testosterone and cortisol, countries have been split by median HDI.

(1/4 highest standard of living) calculated from measures of life expectancy, literacy and education, and is used to categorize countries by standard of living. HDI ranged from 0.482 (low) to 0.91 (very high).

(d) Gini coefficient

These statistical scores representing income disparity across households in a population (0 = perfect equality) were extracted for the 13 countries (https://www.cia.gov/library/publications/the-world-factbook/fields/print_2172.html). The most recent available scores were selected for each nation (table 1) and ranged from some of the lowest in the world (e.g. Sweden) to some of the highest (i.e. Namibia) (https://www.cia.gov/library/publications/the-world-factbook/fields/print_2172.html).

(e) Pathogen stress

We used Fincher & Thornhills' [14] measure of combined parasite stress, comprising summed scores of societal-level infectious disease load and non-zoonotic parasite prevalence.

3. Results

The distribution of variables did not differ from normality (Kolmogorov-Smirnov, all $p > 0.3$). We first conducted three standard linear regression models (independent variable: HDI; dependent variables: (i) preference for cues to high over low T; (ii) preference for cues to high over low C; and (iii) the interaction term of preferences for cues to testosterone and cortisol (calculated as the product of the centred testosterone- and cortisol-preference scores). For full results see table 2.

There were significant bivariate relationships between HDI and preference for facial cues to testosterone (figure 1) and between HDI and the testosterone x cortisol interaction term. Both significant relationships were linear and addition of sample size for each society did not influence results (addition of HDI, HDI and number of participants in each sample to the models did not result in significant R change). The HDI score for Cameroon was below the mean — 2s.d. When the HDI score for Cameroon was removed from analyses, significant bivariate relationships remained ($p < 0.03$).

Figure 2 shows the relationship between the testosterone x cortisol interaction term and HDI. While participants in all 13 countries preferred faces of males with low cortisol, the strength of this preference was dependent upon that for cues to testosterone. Participants in low HDI countries (i.e. below the median HDI for the 13 countries) who preferred cues to high testosterone also preferred cues to high cortisol, whereas those in high HDI countries who preferred cues to high testosterone preferred cues to low cortisol.

We added the Gini and combined parasite stress scores to the models as predictor variables. HDI was removed owing to low tolerance to collinearity (0.14). There was a significant bivariate relationship between pathogen stress and preferences for facial cues to testosterone (adj. $R = 0.51$, $\Delta^2_{12} = 7.22$, $p = 0.011$; pathogen stress: $\beta = 1.06$, $p = 0.008$; Gini: $\beta = -0.44$, $p = 0.2$). Models were non-significant for preferences for facial cues to cortisol (adj. $R = 0.1$, $\Delta^2_{12} = 1.66$, $p = 0.238$) and the T x C interaction term (adj. $R = 0.11$, $F_{2,12} = 1.77$, $p = 0.22$).

4. Discussion

We sought to identify any societal-level variation in women's preferences for cues to combinations of testosterone and cortisol in composite male facial stimuli. Consistent with previous research was an inverse relationship between preferences for cues to testosterone and a societal-level measure of development. We found no evidence for societal-level variation in preferences for facial cues to cortisol, with consistent preferences for cues to low cortisol across societies. Importantly, the relationship between HDI and the interaction between preferences for cues to testosterone and cortisol demonstrated that women's preferences for combinations of the

hormones varied across societies in accordance with standard of living.

The relationships between both HDI and pathogen stress and preferences for facial cues to testosterone are consistent with DeBruine et al. [11], who found an inverse relationship between pathogen stress and the strength of women's preferences for male facial masculinity (see also [15]). Women's preferences for high-testosterone men are adjusted facultatively in response to the demands of the current environment. While there was variation in the extent to which women in our 13 societies expressed preferences for low-cortisol faces, in no instance did women prefer high-cortisol faces. This further supports our conclusion that women seek to avoid cues to stress in a potential mate [8,9].

The relationship between HDI and the interaction between preferences for testosterone and cortisol demonstrates that preferences for combinations of the hormones vary with societal-level demands. The pattern of the relationship is such that an inverse relationship between preferences for cues to high levels of testosterone and cortisol is strongest in high HDI. The results of the current study suggest that divergent findings from UK and Latvian samples reported in our previous work [8–10] may stem from societal-level differences in relative preferences for cues to sex- and stress-hormones. Figure 2 shows that women in the Latvian sample expressed stronger preferences for cues to testosterone and cortisol than did women in the UK. Perhaps, combinations of the hormones signal different traits or qualities (e.g. health or dominance), which are weighted differently in mate preferences by women in different societies. Our inclusion of more specific measures of societal ecology (i.e. resource inequality and pathogen stress) did not yield significant relationships with preferences for cues to combinations of the hormones. It will be interesting, however, to test the preferences of women across a larger sample of societies worldwide. Furthermore, our samples were largely limited to Caucasian women, and all participants rated Caucasian men's faces. It will be more ; ecologically valid to construct facial stimuli, and to recruit participants, of different ethnicities. Finally, while our results suggest that the unstable relationships between testosterone, cortisol and attractiveness reported previously are due, at least in part, to cross-cultural variation in preferences, in order to completely rule out the effect of stimuli type, it will be necessary to conduct similar cross-cultural work on preferences for the faces of individual men, and to test preferences for facial stimuli matched for ethnicity .

In conclusion, the results of the current study support previous findings that women's preferences for cues to testosterone in men's faces vary with societal-level measures of development and pathogen load. Furthermore, our results indicate that women's preferences for cues to combinations of sex- and stress-hormones are similarly dependent upon societal development, and suggest that future work should seek to identify the traits signalled by cues to combinations of these hormones.

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References

1. Folstad I, Karter AJ. 1992 Parasites, bright males and the immunocompetence handicap. *Am. Nat.* 139, 603 –622. (doi:10.1086/285346)
2. Buchanan KL. 2000 Stress and the evolution of condition dependent signals. *Trends Ecol. Evol.* 15, 156 – 160. (doi:10.1016/S0169-5347(99)01812-1)
3. Evans MR, Goldsmith AR, Norris SRA. 2000 The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behav. Ecol. Sociobiol.* 47, 156–163. (doi:10.1007/s002650050006)
4. Møller AP. 1995 Hormones, handicaps and bright birds. *Trends Ecol. Evol.* 10, 121. (doi:10.1016/ S0169-5347(00)89008-4)
5. Martin LB. 2009 Stress and immunity in wild vertebrates: timing is everything. *Gen. Comp. Endocrinol.* 163, 70 –76. (doi:10.1016/j.ygcen. 2009.03.008)

6. Bortolotti GR, Mougoet F, Martinez-Padilla J, Webster LMI, Piertney SB. 2009 Physiological stress mediates the honesty of social signals. *PLoS ONE* 4, e4983. (doi:10.1371/journal.pone.0004983) Roberts ML, Buchanan KL, Bennett ATD, Evans MR. 2007 Mate choice in zebra finches: does corticosterone play a role? *Anim. Behav.* 74, 921 – 929. (doi:10.1016/j.anbehav.2006.12.021)
7. Moore FR, Cornwell RE, Law Smith MJ, Al Dujaili E, Sharp M, Perrett DI. 2011 A test of the stress-linked immunocompetence handicap hypothesis in human male faces. *Proc. R. Soc. B* 278, 774– 780. (doi:10.1098/rspb.2010.1678)
8. Moore FR, Al Dujaili EAS, Cornwell RE, Law Smith MJ, Lawson JF, Sharp M, Perrett DI. 2011 Cues to sex- and stress-hormones in the human male face: functions of glucocorticoids in the immunocompetence handicap hypothesis. *Horm. Behav.* 60, 269 – 274. (doi:10.1016/j.yhbeh.2011.05.010)
9. Rantala MJ, Moore FR, Krama T, Kivleniece I, Skrinda I, Kecko S, Krams I. 2012 Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nat. Commun.* 3, 694. (doi:10.1038/ncomms1696)
10. DeBruine LM, Little AC, Jones BC. 2012 Extending parasite-stress theory to variation in human mate preferences (Commentary on Fincher and Thornhill). *Behav. Brain Sci.* 35, 26-27. (Doi:10.1017/S0140525X11000987)
12. Edler AV, Friedl TWP. 2010 Individual quality and carotenoid-based plumage ornaments in male red bishops (*Euplectes orix*): plumage is not all that counts. *Biol. J. Linn. Soc.* 99, 384 – 397. (doi:10.1111/j.1095-8312.2009.01354.x)
13. United Nations Development Plan. 2011 Human development report 2011. Sustainability and equity: towards a better future for all. London, UK; New York, NY: Palgrave Macmillan.
14. Fincher CL, Thornhill R. 2012 Parasite-stress promotes in-group assortative sociality: the cases of strong family ties and heightened religiosity. *Behav. Brain Sci.* 35, 61 –119. (doi:10.1017/S0140525 X11000021)
15. Brooks R, Scott IM, Maklakov AA, Kasumovic MM, Clark AP, Penton-Voak IS. 2011 National income inequality predicts women’s preferences for masculinized faces better than health does. *Proc. R. Soc. B* 278, 810 –812. (doi:10.1098/rspb.2010.0964)