Adiposity, compared to masculinity, serves as a more valid cue to immunocompetence in human mate choice

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Summary

According to the "good genes" hypothesis, females choose males based on traits that indicate the male's genetic quality in terms of disease resistance. The "immunocompetence handicap hypothesis (ICHH)" proposed that secondary sexual traits serve as indicators of male genetic quality because they indicate that males can contend with the immunosuppressive effects of testosterone. Masculinity is commonly assumed to serve as such a secondary sexual trait. Yet women do not consistently prefer masculine looking men, nor is masculinity consistently related to health across studies. Here we show that adiposity, but not masculinity, significantly mediates the relationship between a direct measure of immune response (Hepatitis B

antibody response) and attractiveness for both body and facial measurements. In addition, we show that circulating testosterone is more closely associated with adiposity than masculinity. These findings indicate that adiposity, compared to masculinity, serves as a more important cue to immunocompetence in female mate choice.

Key words: mate choice; good genes; immunocompetence handicap hypothesis; masculinity; adiposity; attractiveness

1. Introduction

Females choose males based on the direct benefits they can provide, such as resources, but also because of indirect benefits, such as "good genes" that are passed on to her offspring [1]. In a highly influential study, Hamilton and Zuk [2] found that birds with more striking plumage (males and females) and song (males only) had significantly fewer blood parasites than their less striking counterparts. Folstad and Karter [3] interpreted these condition dependent cues to be secondary sexual cues. They proposed that exaggerated secondary sexual cues in males indicate genetic quality by showing that the male can contend with the immunosuppressive effects of testosterone [3]. According to the ICHH, secondary sexual cues "enables females to assess the status of a potential partner's parasite burden and resistance" [3]. Thus, in order for females to use cues to immunocompetence in mate choice, a cue needs to be (a) sexually selected, and (b) significantly related to the immune response. More specifically, the cue should mediate the relationship between immune response and attractiveness.

Masculinity is generally considered to serve as a secondary sexual cue to immunocompetence in human mate choice [e.g. 4-7]. Nevertheless, studies testing the

relationship between masculinity and attractiveness have produced mixed results [for review see 6, 8]. Studies have varyingly found a preference for masculinity [e.g. 9-11], femininity [e.g. 12, 13] or no significant preference for sexual dimorphism [e.g. 4, 14, 15]. This inconsistency in masculinity preferences might be partly attributed to a trade-off between the benefits (e.g. genetic quality) and costs (e.g. negative personality attributes) associated with masculinity [12]. The relationship between masculinity and health measurements is also inconsistent across studies. Rhodes *et al.* [7] found a modest positive association between rated facial masculinity in young adolescent male faces and medically assessed health scores. Similarly, Thornhill and Gangestad [5] showed that men with a higher level of measured facial masculinity report a lower incidence of antibiotics use and respiratory diseases, but not stomach and intestinal infections, than less masculine men. In contrast, Lie *et al*. [14] did not find any significant relationship between facial masculinity and an indirect measure of innate immunity (diversity at the major histocompatability complex). To our knowledge, no previous study has tested the relationship between masculinity and a direct measure of immunity.

We propose that adiposity could serve as a valid cue to immunocompetence in humans because it significantly influences attractiveness [8, 16-20] and is highly associated with various health measures [20-27]. Several studies found that the Body Mass Index (BMI; weight scaled for height) significantly predicts male and female bodily attractiveness [for review see 8, 16, 18, 19]. The link between BMI and general health measures has also been well-established. Obese and overweight individuals are at increased risk of developing various diseases [e.g. 25-27]. More specifically, BMI plays a crucial role in immunity. On the one end of the spectrum, malnourished individuals, particularly those with protein-calorie malnutrition, are less

immunocompetent than normal weight individuals [22]. On the other, several studies show that obese individuals are also less immunocompetent than their non-obese counterparts [e.g. 21].

Rated facial adiposity, in turn, significantly predicts facial attractiveness and serves as a robust cue to health, since it is significantly related to both health judgements and actual measures of health (increased respiratory infections, antibiotics use and reduced cardiovascular health [20]. Adolescent facial adiposity judgements are associated with all-cause mortality (particularly heart disease mortality) and several medically assessed chronic conditions in a large longitudinal study (n = 3027 [24]). Adiposity is also highly heritable [28], thus a person with an optimal level of adiposity could potentially provide not only direct but also indirect benefits to a partner.

In a previous study utilising the current sample we found a significant positive association between a direct measure of immune response (antibody response to a Hepatitis B vaccine) and facial attractiveness [29]. To determine which facial or body cues underlie the relationship between immune response and attractiveness, we use mediational analysis, a subset of structural equation modelling [30]. The first aim of this study is to test whether masculinity and/or adiposity significantly mediate the relationship between immune response and attractiveness in both the face and body of human males. We selected female raters in the fertile phase of their menstrual cycle to rate the males for attractiveness because women in the fertile phase are considered to be more attentive to phenotypic cues indicating heritable quality [31, 32]. Second, we test whether masculinity (and adiposity) is significantly associated with circulating testosterone levels since a second basic assumption of the ICHH is that secondary sexual cues are positively associated with circulating testosterone levels [3]. Previous

work utilising the current sample showed a significant positive association between circulating testosterone and facial attractiveness [29].

The trade-off between the benefits and costs associated with masculinity could mask a relationship between masculinity and attractiveness. The third aim of the study is therefore to test whether the female raters show a consistent preference for sexual dimorphism or whether some women prefer more masculine looking men while other women prefer more feminine looking men.

2. Materials and methods

2.1 Participants.

Sixty-nine Caucasian males (mean age: 23.0, s.d. 3.9, range 19-31), a subsample of 74 males who agreed to have body photographs taken, were recruited from the University and Transportation College of Daugavpils, Latvia. Full colour facial and full body photographs were taken with a Nikon D50 digital camera under standardized conditions, with participants wearing standardized underwear. We measured each participant's percentage body fat (hereafter body adiposity; Omron Body Composition Monitor BF500), a more accurate measure of adiposity than BMI [33]. In addition, we assessed testosterone and anti-HBsAg (Hepatitis B antibody) levels from 10ml of venous blood collected ~30 minutes before, and 1 month after, a dose of hepatitis B vaccine (Engerix B, Glaxosmithkline) was administered. Blood samples were collected between 9am and 11am. Levels of anti-HBsAg were assessed using enzyme immunoassay (AxSYM®, Abbott Laboratories) and commercially available kits (AUSAB®, Abbott Laboratories). Testosterone levels were assessed using competitive chemoluminescent enzyme immunoassay with commercially available kits (Immulite®2000 Total Testosterone). For a full description of methods

see Rantala *et al.* [29]. Testosterone levels were consistent pre-and-post vaccination (Cronbach $\alpha = 0.90$) and were therefore averaged for each participant. No participant expressed anti-HBsAg prior to vaccination.

2.2. Image ratings.

Twenty-nine heterosexual Caucasian women reporting regular menstrual cycles and no use of hormonal contraception from the University of Daugavpils, Latvia (mean age: 20.0, s.d.1.9) rated the body and facial images for sexual attractiveness on an 11 point Likert scale (-5 = very unattractive, 0 = neutral and +5 = very attractive). The women were selected from a larger group of 94 women because they were in the fertile phase of their menstrual cycle. The fertile phase was calculated as the 5 days before ovulation and the day of ovulation itself [34]. Ovulation was assumed to occur 14 days before the onset of menses. The method is commonly used in evolutionary psychological studies [32].

The images were also rated for: body and facial masculinity by 20 heterosexual Finnish participants (10 male; mean age: 24.3, s.d. 4.3) on a 7 point Likert scale (1 = not masculine, 7 = very masculine) and facial adiposity by 14 heterosexual Latvian women (mean age: 23.6, s.d. 4.1) on an 11 point Likert scale (-5 = very underweight, 0 = normal weight, +5 = very overweight). Images were presented in random order and body images were presented with faces blurred. Inter-rater reliability was high for all ratings (all Cronbach $\alpha > 0.93$), thus were averaged across raters for all ratings.

2.3. Analyses.

Descriptive statistics for each measure are reported in Table S1. Body adiposity and all the averaged rating measures were normally distributed (skewness and kurtosis between ± 1.2), except Anti-HBsAg (skewness and kurtosis > 2) and facial attractiveness (kurtosis 1.7), so we performed a Box-Cox transformation and log transformation to normalise the distributions of the respective measures (skewness and kurtosis between ± 1.0). All facial and body measurements were linearly related to attractiveness, except body adiposity, which showed a curvilinear relationship, peaking at a body fat percentage of 12%. A squared transformation was used to linearize body adiposity [30]. We tested the direct relationship between antibody response and attractiveness measures using Pearson's correlations and constructed separate path models for body and facial attractiveness using multiple regression analyses with attractiveness as dependent variable and adiposity, masculinity and antibody response as independent variables (Fig. 1). In addition, we used multiple mediator models to test specific indirect effects (i.e. the effect of one potential mediator on the relationship between antibody response and attractiveness, controlling for the other potential mediator). Support for mediation was evaluated using non-parametric bias-corrected bootstrapping analysis — as recommended for small sample sizes [35] — and the more conventional Sobel Test [30, 35]. In these bootstrap analyses (10 000 bootstrap samples), mediation is significant if the 95% bias-corrected confidence intervals for the indirect effect do not include 0 [30, 35].

To address the second aim, correlations between circulating testosterone and (a) adiposity, and (b) masculinity, were tested using Pearson's correlation analysis (two-tailed). To address the third aim, we tested the relationship between each female rater's attractiveness judgements and the average masculinity score for each male

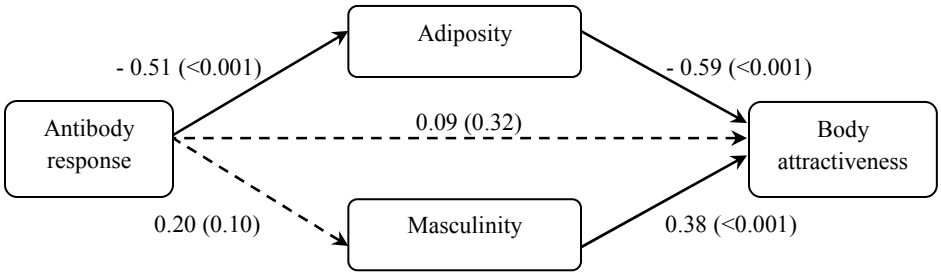

Figure 1a

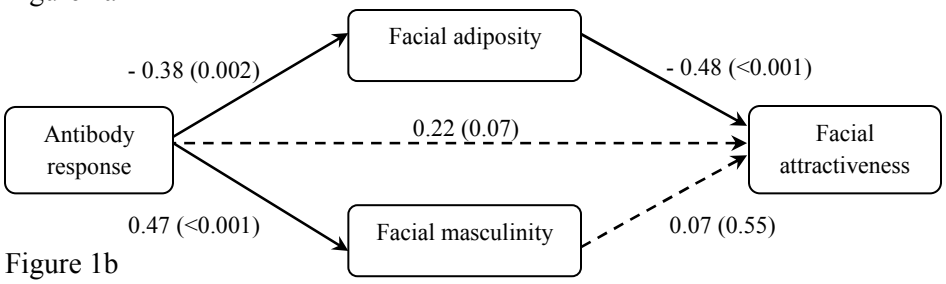

Figure 1b

Figure 1. Path coefficients for body (1a) and facial (1b) mediation models.
Standardised regression coefficients and associated p-values in brackets. N=69.
Dotted lines indicate non-significant coefficients ($p > 0.05$). Facial attractiveness was log transformed.

image using Spearman's rank order correlations (two tailed), in accordance with Stephen *et al.* [15]. All analyses were performed in SPSS 20.0 with the addition of a macro for bootstrapping and Sobel test analyses [35]. Data deposited in the Dryad repository: http://dx.doi.org/10.5061/dryad.pb7nb

3. Results

3.1. Body measurements

Antibody response was significantly correlated with bodily attractiveness (r_{69} = 0.47, $p < 0.001$). In the multiple regression model, body adiposity and masculinity, but not antibody response, significantly predicted bodily attractiveness (Fig. 1a). Adiposity was also significantly predicted by antibody response, while masculinity was not (Fig. 1a). Adiposity significantly mediated the relationship between antibody response and bodily attractiveness, but masculinity did not (Table 1). This finding was consistent for both the bias-corrected bootstrapping analysis and the Sobel test (Table 1), indicating that only the indirect effect through adiposity significantly mediates the relationship between antibody response and bodily attractiveness. This pattern of results was also observed after excluding males that did not show any antibody response after Hepatitis B vaccination (Table S2). Moreover, a significant pairwise contrast between the indirect effects showed that the specific indirect effect through adiposity is significantly larger than the specific indirect effect through masculinity. Circulating testosterone levels were significantly correlated with adiposity (r_{69} = 0.54, $p < 0.001$), but not masculinity (r_{69} = 0.21, $p = 0.084$). The correlation between testosterone and adiposity was significantly stronger than the correlation between testosterone and masculinity (Steiger's $Z=2.32$, $df = 66$, $p = 0.015$).

Table 1. Mediation analyses for indirect effects **(**N = 69; BC, bias-corrected; SE, standard error. Effect refers to the specific indirect effect of antibody response on attractiveness through each mediator**)**

		BC Bootstrap 95% CI			Sobel Test	
	Effect	**SE**	**Lower**	**Upper**	**SE**	**p**
Body attractiveness						
Adiposity	0.16	0.05	0.09	0.27	0.04	<0.001
Masculinity	0.04	0.03	-0.01	0.11	0.03	0.11
Total Indirect	0.20	0.06	0.09	0.34	0.05	<0.001
Adiposity vs masculinity	0.12	0.05	0.04	0.22	0.05	0.010
Facial attractiveness						
Adiposity	0.05	0.02	0.02	0.09	0.02	0.015
Masculinity	0.02	0.02	-0.01	0.06	0.02	0.26
Total Indirect	0.07	0.02	0.02	0.12	0.03	0.011
Adiposity vs masculinity	0.03	0.03	-0.02	0.08	0.03	0.30

All but one of the female raters (96.6%) showed a positive correlation between body attractiveness judgements and averaged masculinity scores for each male image, a relationship that was significant in 69.0% (e.g. 20/29) of cases (all $r_{s69} \geq 0.25$, $p < 0.05$). The single negative correlation between masculinity and attractiveness was not significant ($r_{s69} = -0.01$, $p = 0.95$).

3.2. Face measurements

Antibody response was significantly correlated with facial attractiveness ($r_{69} = 0.43$, $p < 0.001$), in line with previously reported findings utilising the current sample [29]. In

the multiple regression model, facial adiposity significantly predicted facial attractiveness, while facial masculinity and antibody response did not (Fig. 1b). Both adiposity and masculinity were significantly predicted by antibody response (Fig. 1b). Fig. S2 illustrates the facial features associated with high and low antibody response. As with the body measurements, adiposity significantly mediated the relationship between antibody response and facial attractiveness, while masculinity did not (Table 1; Table S2). There was no significant difference between the specific indirect effect through adiposity and the specific indirect effect through masculinity (Table 1). Circulating testosterone levels were significantly correlated with adiposity ($r_{69} = 0.52$, $p < 0.001$) and masculinity ($r_{69} = 0.38$, $p = 0.001$). There was no significant difference in the testosterone-adiposity and testosterone-masculinity correlations (Steiger's $Z=1.04$, $df = 66$, $p = 0.28$).

Most of the female raters (75.9%) showed a positive correlation between facial attractiveness judgements and averaged masculinity scores for each male image, but the relationship was only significant in 24.1% (7/29) of cases (all $r_{s69} \geq 0.27$, $p < 0.05$). None of the negative correlations between masculinity and facial attractiveness were significant (all $r_{s69} \geq -0.14$, $p > 0.05$).

4. Discussion

Results show that adiposity is consistently and significantly associated with (a) antibody response and (b) attractiveness in both the body and the face of a group of Latvian men. Masculinity, on the other hand, was not significantly related to both attractiveness and antibody response in either the body or the face. Moreover, adiposity is a significant mediator of the relationship between antibody response and attractiveness for both body and face measures, while masculinity does not

significantly contribute to the relationship above and beyond the contribution of adiposity for either body or face measurements. These findings indicate that women in this study use adiposity, and not masculinity, as a cue to immunocompetence when judging the attractiveness of men.

We should point out two potential caveats to these findings. First, masculinity might be a comparatively better cue to immunocompetence in populations with a higher variance in masculinity and a lower variance in adiposity. Second, other factors, apart from adiposity and masculinity, might also affect the relationship between immune response and attractiveness. However, the direct relationship between antibody response and attractiveness reported here and in Rantala *et al.* [29] is no longer significant once adiposity and masculinity are controlled for, indicating that these two factors mediate the relationship (at least for the given sample size). This finding builds on a growing body of evidence showing that labile conditional cues, such as adiposity and skin colour, might be better indicators of mate quality than more stable conditional cues, such as masculinity [4, 15, 36]. Previous research largely supports the findings presented here in four ways. First, in accordance with our findings, previous work showed that measures of adiposity are significantly associated with attractiveness in the face [20] and the body [8, 17]. Second, 4% of men in our sample were underweight, 65% healthy weight and 30.4% overweight or obese according to criteria developed by Gallagher *et al.* [33]. One would therefore expect a negative relationship between adiposity and immunity in our sample, which is indeed what we observed. Our results are therefore consistent with previous findings on the role of obesity, and overweight status, on the immune system [21].

Third, although this is the first study, to our knowledge, to test the relationship between masculinity and a direct measure of immunity, previous studies also found

mixed results regarding the relationship between masculinity and indirect measures of immunity [e.g. 5, 7, 14]. Fourth, in accordance with our results, previous studies found a significant positive association between body masculinity and attractiveness [11]. We found no significant association between facial masculinity and attractiveness, not surprising given that previous studies also found mixed results regarding the relationship between masculinity and attractiveness [e.g. 6, 12, 15]. The lack of a significant association between facial masculinity and attractiveness cannot be attributed to women showing opposing individual preferences for masculine and feminine looking male faces. For one, the women in this study were tested in the fertile phase of their menstrual cycle when masculinity preferences are enhanced [9]. Second, we found no evidence that some women strongly preferred feminine, as opposed to masculine, looking faces or bodies in this study.

Although we found that masculinity does not underlie the relationship between immune response and attractiveness, masculinity could still affect sexual selection in other ways. For example, masculine men might simply outcompete their less masculine rivals [37]. Women might also prefer masculine men because of direct benefits they can provide or because of other indirect benefits such as genetic quality in terms of dominance or competitiveness [37, 38]. Indeed, Peters *et al.* [10] did find a positive association between masculinity and mating success.

A second basic assumption of the ICHH is that testosterone is positively associated with cues that indicate mate quality [3]. Although we have no information on the adolescent testosterone levels that would have played a role in the production of secondary sexual traits [39], adult testosterone levels in our study were more closely correlated with adiposity than with masculinity (although not significantly so for facial measures).

In summary, our results show that adiposity, and not masculinity, underlies the relationship between immune response and attractiveness. Compared to masculinity, adiposity is also more strongly associated with circulating testosterone levels. Taken together, these findings highlight the role of adiposity as a cue to male quality in modern human societies.

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