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Are physiological and behavioral immune responses negatively correlated? Evidence from hormone-linked differences in men's face preferences

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ABSTRACT

Behaviors that minimize exposure to sources of pathogens can carry opportunity costs. Consequently, how individuals resolve the tradeoff between the benefits and costs of behavioral immune responses should be sensitive to the extent to which they are vulnerable to infectious diseases. However, although it is a strong prediction of this functional flexibility principle, there is little compelling evidence that individuals with stronger *physiological* immune responses show weaker *behavioral* immune responses. Here we show that men with the combination of high testosterone and low cortisol levels, a hormonal profile recently found to be associated with particularly strong physiological immune responses, show weaker preferences for color cues associated with carotenoid pigmentation. Since carotenoid cues are thought to index vulnerability to infectious illnesses, our results are consistent with the functional flexibility principle's prediction that individuals with stronger *physiological* immune responses show weaker *behavioral* immune responses.

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1. Introduction

Pathogens have been a major selection pressure on all organisms, including humans (Schaller, 2011; Schaller et al., 2015; Schaller and Park, 2011; Tybur and Gangestad, 2011) The footprint of this selection pressure can be seen in the complex, effective mechanisms involved in the physiological immune system, such as antibody production (Czerkinsky et al., 1987). In addition to this physiological immune system, recent research has revealed the existence of a behavioral immune system that also functions to prevent and manage infectious diseases. These behavioral immune responses include behaviors, emotions, and cognitions that minimize contact with potential sources of pathogens (Tybur and Gangestad, 2011; Tybur et al., 2013).

Because behavioral immune responses can be costly (e.g., they can carry opportunity costs) the behavioral immune system would be expected to show functional flexibility. That is, the extent to which individuals are vulnerable to infectious diseases should affect how they resolve the tradeoff between the possible benefits (e.g., reduced risk of contracting infectious diseases) and costs (e.g., increased risk of incurring opportunity costs) of behavioral immune responses (Schaller et al., 2015; Tybur et al., 2013). A strong prediction of this functional flexibility principle is that individuals with stronger physiological immune responses will show weaker behavioral immune responses. However, although studies have tested for correlations between questionnaires that measure the strength of behavioral immune responses and self-reported infectious disease frequency and/or recency (de Barra et al., 2014, Stevenson et al., 2009), only one of these studies reported significant correlations (Stevenson et al., 2009) Moreover, significant correlations in this study were observed for only one of the two behavioral immune response questionnaires administered (Stevenson et al., 2009). Thus, there is little compelling evidence that individuals with stronger physiological immune responses show weaker behavioral immune responses.

Questionnaires for assessing vulnerability to infectious disease may be prone to reporting biases, which can obscure real relationships between variables and also cause spurious associations (van de Mortel, 2008). One method for avoiding such biases is to assess vulnerability to infectious disease by examining factors that are known to moderate physiological immune responses. Recent work suggests that stress and sex hormones are related to physiological immune responses. For example, Gettler et al. (2014) reported that men with higher salivary testosterone levels had stronger physiological immunity to infectious illnesses (as indexed by salivary secretory immunoglobulin A) and reported fewer cold/flu symptoms than did men with low testosterone levels. However, Rantala et al. (2012) demonstrated that, although men with higher testosterone levels showed stronger physiological immune responses to a hepatitis B vaccine, this relationship was significantly stronger among men who also had low cortisol levels. If the behavioral immune system does show functional flexibility, Rantala et al.'s (2012) results suggest that behavioral immune responses may be

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weakest among men with the combination of high testosterone and low cortisol.

Aversions to cues of poor health in conspecifics are thought to be a major component of the behavioral immune system (Park et al., 2012; Tybur et al., 2013). One such cue is low levels of carotenoid-related skin color. Carotenoids are pigments found in fruit and vegetables that play an important antioxidative role in disease resistance (Hughes, 1999; Sies, 1993). If not expended in this role, carotenoids are stored in skin tissue, giving skin a yellower, darker appearance (Alaluf et al., 2002). Consequently, yellower, darker facial skin may be a cue of good health and absence of disease (Jones et al., 2016; Lefevre et al., 2013; Lefevre and Perrett, 2014; Whitehead et al., 2012a, 2012b). People also show strong aversions to faces with low levels of carotenoid cues (Lefevre et al., 2013; Lefevre and Perrett, 2014) and perceive them to be unhealthy (Whitehead et al., 2012a; Stephen et al., 2011). Such aversions are thought to function, at least in part, to minimize contact with individuals who are currently ill (Lefevre et al., 2013; Lefevre and Perrett, 2014). The tendency to perceive faces in which carotenoid cues were increased to be particularly healthy has been reported when white participants in the UK judge the health of white faces and when black participants in South Africa judge the health of black faces, suggesting these perceptions are stable across different cultures and skin-color phenotypes (Stephen et al., 2011). Moreover, the human visual system is particularly sensitive to variation in facial skin coloration, relative to similar variation in non-face stimuli (Tan and Stephen, 2013).

In the current study, we investigated whether individual differences in men's preferences for faces manipulated along the three main color axes (yellow, lightness, red; Commission Internationale de L'Éclairage, 1976) were predicted by the interaction between their salivary testosterone and cortisol levels. Men's color preferences, testosterone levels, and cortisol levels were estimated by averaging their scores on these variables across five weekly test sessions in order to obtain reliable estimates of each man's typical hormone levels and preferences. If individuals who show stronger physiological immune responses do show weaker behavioral immune responses, as the functional flexibility principle suggests, men with higher testosterone levels would show weaker aversions to the absence of color cues associated with high susceptibility to infectious disease in faces and this relationship would be particularly strong among men who also had low cortisol levels.

The functional flexibility principle suggests that the combined effects of testosterone and cortisol may predict men's preferences for facial cues associated with infectious disease risk, such as the yellower and darker coloration associated with carotenoid pigmentation (Lefevre and Perrett, 2014, Whitehead et al., 2012b), but not facial cues that are associated with illnesses that are not contagious. Since facial redness is associated with oxygenated blood and, consequently, may be a cue of cardiovascular health (Stephen et al., 2009a), we also investigated the combined effects of testosterone and cortisol on men's preferences for facial redness. By contrast with our predictions for preferences for yellower, darker coloration, we did not expect these preferences to be related to men's testosterone and/or cortisol levels.

Because the behavioral immune responses are thought to function primarily to protect individuals from contracting infectious illnesses during social interactions with both women and men (e.g., Tybur et al., 2013), we would not expect it to be modulated by stimulus sex. By contrast, responses that were specific to opposite-sex faces would implicate responses relevant to mate choice, rather than behavioral immune responses.

2. Methods

2.1. Participants

Forty-seven heterosexual men participated in the study (mean age = 21.99 years, SD = 3.19 years). All participants were students at the University of Glasgow (Scotland, UK). None of these men were currently taking any form of hormonal supplement and all indicated that they had not taken any form of hormonal supplement in the 90 days prior to participation. Participants were all of the heterosexual men tested in the first semester who met these criteria and completed the study. One additional man was tested but excluded from the dataset because his average cortisol level was more than five standard deviations above the mean for the rest of the sample.

2.2. Face stimuli

First, digital face photographs of 10 young adult white men and 10 young adult white women were taken against a constant background and under standardized diffuse lighting conditions. Participants were instructed to pose with a neutral expression and look directly at the camera. A GretagMacbeth 24-square miniColorChecker chart was included in each image for use in color calibration. The 20 face images were then color calibrated using a least-squares transform from an 11-expression polynomial expansion developed to standardize color information across images (Hong et al., 2001).

Next, we used methods described in Stephen et al. (2009b) to independently manipulate these face images' yellowness, lightness, and redness in CIELab color space (Commission Internationale de L'Éclairage, 1976). CIELab color space is modeled on the human visual system and consists of three independent color axes: yellow (b*), lightness (L*), and red (a*). Two versions of each of the original faces were manufactured by manipulating yellow: one in which yellow was increased by 1.5 units and one in which yellow was decreased by 1.5 units. Two additional versions of each of the original faces were manufactured by manipulating lightness: one in which lightness was increased by 1.5 units and one in which lightness was decreased by 1.5 units. Two final versions of each of the original faces were manufactured by manipulating red: one in which red was increased by 1.5 units and one in which red was decreased by 1.5 units. Importantly, these color manipulations only affect the manipulated color dimension (e.g., altering redness does not affect yellowness, and vice versa) and do not affect shape information or eye color (Stephen et al., 2009b). This technique for manipulating color information in faces has also been used in many other previous studies (e.g., Whitehead et al., 2012a; Stephen et al., 2011). These color manipulations, in which color values were increased or decreased by 1.5 units, are within the normal range of coloration for white adult faces (Whitehead et al., 2012b).

2.3. Procedure

All participants completed five weekly test sessions. All test sessions took place between 2 pm and 5 pm to minimize diurnal variation in hormone levels (Papacosta and Nassis, 2011). During each test session, participants provided a saliva sample via passive drool (Papacosta and Nassis, 2011). Participants were instructed to avoid consuming alcohol and coffee in the 12 h prior to participation and avoid eating, smoking, drinking, chewing gum, or brushing their teeth in the 60 min prior to participation. Saliva samples were frozen immediately and stored at −32 °C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis, where they were assayed using the Salivary Testosterone Enzyme Immunoassay Kit 1-2402 (M = 180.47 pg/mL, SD = 38.70 pg/mL) and the Salivary Cortisol Enzyme Immunoassay Kit 1-3002 (M = 0.19 μg/dL, SD = 0.08 μg/dL). All assays passed Salimetrics' quality control.

In each test session, participants also completed a facial color preference test that assessed their preference for facial yellowness, lightness, and redness. On this facial color preference test, the 30 pairs of male faces and 30 pairs of female faces (each pair consisting of two versions of a face; one version with increased color values and one version with decreased color values) were presented on a color-calibrated monitor. Participants were instructed to click on the face in each pair they

thought was more attractive. Male and female faces were presented in separate blocks and both trial and block order were fully randomized. The side of the screen on which any given image was presented was also fully randomized. This type of facial color preference test has been used in previous studies to assess preferences for aspects of facial coloration (Lefevre and Perrett, 2014). The screen was calibrated using xRite i1 Display Pro colorimeter prior to testing. We also used principal component analysis to investigate possible intercorrelations among different aspects of men's color preferences. The local ethics committee approved all aspects of the procedure.

3. Results

First, we calculated the proportion of trials on which each participant chose the image with increased color values as the more attractive separately for each combination of test session and color axis (yellow, red, lightness). Preliminary analyses using linear mixed models in which test sessions were grouped by participant to test for within-subjects effects of testosterone and cortisol on color preferences showed no significant within-subject effects of men's testosterone or cortisol on any aspect of color preference (all $|t| < 1.20$, all $p > 0.24$). Because of this, and because color preferences were highly consistent across test sessions (Cronbach's alphas: yellow = 0.76, lightness = 0.76, red = 0.81), we averaged scores for each color axis across test sessions.

One sample *t*-tests comparing average color preferences with the chance value of 0.5 showed that men preferred faces with increased yellow over versions with decreased yellow ($t = 4.94$, $p < 0.001$, M = 0.59, SEM = 0.02), preferred faces with increased red over versions with decreased red ($t = 6.08$, $p < 0.001$, M = 0.62, SEM = 0.02), but did not prefer faces with increased lightness over versions with decreased lightness ($t = 1.10$, $p = 0.28$, M = 0.52, SEM = 0.02).

Men's hormone levels were also highly consistent across test sessions (Cronbach's alphas: testosterone = 0.91, cortisol = 0.76). Consequently, we also averaged these values across test sessions. Average testosterone and average cortisol levels were then centered on their means for analyses.

Next, we subjected the three color-preference scores to principal component analysis (with no rotation). The first component produced explained approximately 55% of the variance in scores and was strongly positively correlated with preferences for facial yellowness ($r = 0.92$), strongly negatively correlated with preferences for facial lightness ($r = -0.85$), but only weakly positively correlated preferences for facial redness ($r = 0.26$). We labeled this component *dark yellow* component as it reflected preferences for yellower, darker skin. Men who scored high on this component showed stronger preferences for yellower and darker skinned faces. The second component explained approximately 35% of the variance in scores and was strongly positively correlated with preferences for facial redness ($r = 0.95$), positively correlated with preferences for facial lightness ($r = 0.38$), and weakly positively correlated with preferences for facial yellowness ($r = 0.09$). We labeled this component *light red* component as it reflected preferences for redder and lighter skin.

We then investigated individual differences in scores on the *dark yellow* component using a regression analysis in which average testosterone level (centered), average cortisol level (centered), and the interaction term were entered simultaneously as predictors. This analysis revealed a significant negative effect of average testosterone level ($t = -2.37$, standardized beta = −0.44, $p = 0.022$) and a significant positive effect of the interaction term ($t = 2.83$, standardized beta = 0.46, $p = 0.007$). The effect of average cortisol level was not significant ($t = 1.01$, standardized beta = 0.17, $p = 0.32$). These results indicate that men with higher testosterone levels generally showed weaker preferences for yellower and darker skin coloration in faces and that this relationship was particularly strong among men with low cortisol (Fig. 1). Repeating this analysis for scores on the *light red* component showed no significant effects (all absolute $t < 0.84$, all absolute standardized beta < 0.16, all $p > 0.40$).

Finally, we analyzed preferences for facial yellowness, lightness, and redness separately. For facial yellowness, the regression analysis revealed a significant negative effect of average testosterone level ($t = -2.21$, standardized beta = −0.41, $p = 0.033$) and a significant positive effect of the interaction term ($t = 2.65$, standardized beta = 0.43, $p = 0.011$). The effect of average cortisol level was not significant ($t = 0.77$, standardized beta = 0.13, $p = 0.45$). An additional analysis, in which sex of face was included as a within-subject factor, showed that none of these effects were qualified by significant interactions with sex of face (all $p > 0.32$). For facial lightness, the regression analysis revealed a positive effect of average testosterone level that was not significant ($t = 1.71$, standardized beta = 0.33, $p = 0.094$) and a significant negative effect of the interaction term ($t = -2.36$, standardized beta = −0.39, $p = 0.023$). An additional analysis showed that none of these effects were qualified by significant interactions with sex of face (all $p > 0.52$). The effect of average cortisol level was not significant ($t = -0.70$, standardized beta = −0.12, $p = 0.49$). These analyses confirmed that men with high testosterone levels generally showed weaker preferences for carotenoid cues in faces and that this relationship was particularly strong among men with low cortisol. The corresponding analysis of preferences for facial redness showed no significant effects (all absolute $t < 1.14$, all absolute standardized beta < 0.23, all $p > 0.26$). An additional analysis showed no significant interactions with sex of face (all $p > 0.46$).

Repeating all of the analyses described above excluding three participants who reported non-white ethnicity did not alter the patterns of significant results. Including participant age as an additional predictor also did not alter any of these patterns of significant results.

4. Discussion

Our analyses of preferences for color cues in faces revealed that men with higher testosterone levels generally showed weaker preferences for yellower and darker skin coloration, which are characteristic of increased carotenoid pigmentation (Lefevre et al., 2013, Lefevre and Perrett, 2014; Whitehead et al., 2012a, 2012b). Importantly, this relationship was particularly strong among men who had low cortisol. Previous research has demonstrated that men with the combination of high testosterone and low cortisol show the strongest physiological immune responses (Rantala et al., 2012), while other research has implicated carotenoids in immune function (Hughes, 1999; Sies, 1993). Consequently, our results suggest that men with a hormonal profile associated with a stronger physiological immune response may show a weaker behavioral immune response (i.e., show weaker aversions to individuals displaying color cues associated with high vulnerability to infectious disease). Thus, our results are consistent with the functional flexibility principle's prediction that individuals who are likely to show stronger physiological immune responses will show weaker behavioral immune responses (Schaller, 2011; Schaller et al., 2015; Schaller and Park, 2011; Tybur and Gangestad, 2011).

By contrast with our results for preferences for yellower and darker skin coloration, our analyses of preferences for facial redness found that these were not related to men's testosterone or cortisol levels. Since previous research (Stephen et al., 2009a) suggests that facial redness is a cue of blood oxygenation and, consequently, may be a cue of cardiovascular health (i.e., aspects of physical condition that carry no direct infectious disease risk), this pattern of results is also consistent with the functional flexibility principle.

That the relationships between men's hormone levels and color preferences were not affected by the sex of faces judged also suggests that our findings reflect a behavioral immune response to the threat of contagious disease, rather than reflecting preferences that are specific to mating contexts or contexts implicated in intrasexual competition only. In other words, because our findings are unaffected by stimulus

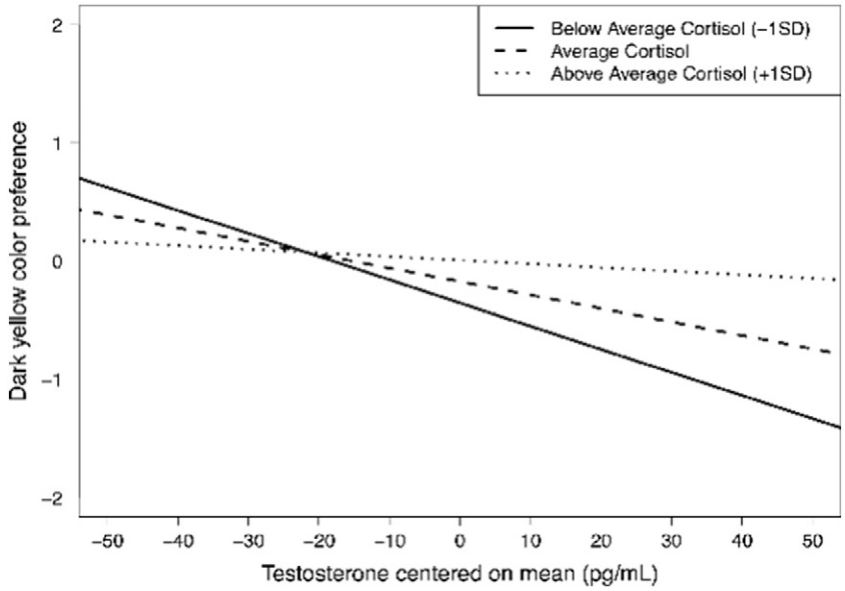

Fig. 1. The interaction between average testosterone and average cortisol for scores on the *dark yellow* component. Men with higher testosterone levels generally showed weaker preferences for dark yellow facial coloration. However, this relationship was particularly strong among men with low cortisol.

sex, it is unlikely that they are driven by mechanisms employed in either mate choice specifically or in assessments of the quality of potential competitors for mates only.

While our study employed measures of men's hormone levels and color preferences taken on multiple occasions, our sample size is relatively small ($N = 47$) and we used an indirect measure of men's immunocompetence. Investigating the links between face preferences and physiological immune responses using larger samples and more direct measures of immune responses is needed to clarify the potential link between physiological immune responses and face preferences. Additionally, although increasing carotenoid consumption causes darker, yellower skin (Whitehead et al., 2012b), and carotenoids are implicated in physiological immune function (Hughes, 1999; Sies, 1993), further work is needed to demonstrate more direct links between these components of facial coloration and immune function.

In summary, we show that men with higher testosterone levels have weaker preferences for yellower and darker coloration cues in faces and that this relationship is particularly strong among men who have low cortisol. In combination with recent work reporting that men with the combination of high testosterone and low cortisol show particularly strong physiological immune responses (Rantala et al., 2012), our results provide preliminary support for functional flexibility in the behavioral immune system by suggesting that men with stronger physiological immune responses show relatively weaker behavioral immune responses. More generally, while studies have reported that between-individual differences in women's hormone levels predict differences in their judgments of others' attractiveness (Bobst et al., 2014, Roney and Simmons, 2008), the current study is one of the first to report associations between measured hormone levels and differences in men's judgments of others' attractiveness.

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