Women's hormone levels modulate the motivational salience of facial attractiveness and sexual dimorphism

Short title: Hormones, motivation, and faces

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Abstract

The physical attractiveness of faces is positively correlated with both behavioral and neural measures of their motivational salience. Although previous work suggests that hormone levels modulate women's perceptions of others' facial attractiveness, studies have not yet investigated whether hormone levels also modulate the motivational salience of facial characteristics. To address this issue, we investigated the relationships between within-subject changes in women's salivary hormone levels (estradiol, progesterone, testosterone, and estradiol-to-progesterone ratio) and within-subject changes in the motivational salience of attractiveness and sexual dimorphism in male and female faces. The motivational salience of physically attractive faces in general and feminine female faces, but not masculine male faces, was greater in test sessions where women had high testosterone levels. Additionally, the reward value of sexually dimorphic faces in general and attractive female faces, but not attractive male faces, was greater in test sessions where women had high estradiol-to-progesterone ratios. These results provide the first evidence that the motivational salience of facial attractiveness and sexual dimorphism is modulated by within-woman changes in hormone levels.

1. Introduction

Facial attractiveness is a particularly salient social cue that influences many important social outcomes. For example, people prefer to mate with, date, associate with, hire, and vote for attractive individuals (see Langlois et al., 2000 for a meta-analytic review). Several lines of evidence also demonstrate that physically attractive faces have motivational salience. For example, the extent to which people will key press to increase the length of time for which they can view faces is correlated with the physical attractiveness of the faces (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2013). Additionally, compared to viewing physically unattractive faces, viewing physically attractive faces elicits greater activation in brain regions implicated in motivation and the processing of rewards, such as the nucleus accumbens and medial orbitofrontal cortex (see Bzdok et al., 2011 and Mende-Siedlecki et al., 2013 for meta-analytic reviews). Moreover, behavioral measures of motivational salience predict neural measures of faces' reward value better than do perceptions of attractiveness measured by ratings (Aharon et al., 2001).

Several lines of evidence suggest that changes in women's hormone levels during the menstrual cycle may affect their perceptions of others' facial attractiveness (see Gildersleeve et al., 2014 for a meta-analytic review). For example, studies have reported that women's preferences for masculine men are positively correlated with their estradiol (e.g., Roney & Simmons, 2008; Roney et al., 2011) or testosterone (e.g., Welling et al., 2007; Bobst et al., 2014) levels. By contrast with the relatively large number of studies

investigating how women's *perceptions* of others' attractiveness covary with changes in women's hormone levels, no previous studies have tested for effects of women's hormone levels on the *motivational salience* of facial attractiveness. This is surprising, given the importance of attractiveness for social interaction (Langlois et al., 2000) and research suggesting that women's testosterone (Hermans et al., 2010) or estradiol (Dreher et al., 2007) modulates the extent to which financial incentives activate brain regions involved in motivation and the processing of reward.

In light of the above, we investigated the hormonal correlates of within-woman changes in the motivational salience of male and female facial attractiveness. Women (none of whom were using any form of hormonal supplement, such as hormonal contraceptives) were each tested once a week for five weeks (i.e., each woman completed five weekly test sessions). In each of these test sessions, the motivational salience of male and female facial attractiveness was assessed and a saliva sample was collected. The motivational salience of faces was measured using a standard key-press task that has previously been shown to be a particularly good predictor of neural measures of the reward value of faces (Aharon et al., 2001). Saliva samples were analyzed for estradiol, progesterone, and testosterone levels.

Many previous studies of hormone-mediated responses to faces have emphasized the potential importance of sexually dimorphic facial characteristics, particularly in men's faces (reviewed in Gildersleeve et al., 2014). Since the relationship between men's facial attractiveness and sexual

dimorphism is complex (reviewed in Roney et al., 2011), with many studies finding no correlation between sexual dimorphism and attractiveness, we also tested for possible effects of hormone levels on the motivational salience of sexual dimorphism in faces. Given that sexual dimorphism and attractiveness are more reliably and highly correlated in female than male faces (see Rhodes, 2006 for a meta-analytic review), the effects of hormone levels on responses to attractiveness and sexual dimorphism in female faces may be more similar than the corresponding effects for male faces.

2. Methods

2.1 Participants

Fifty heterosexual women (mean age=21.2 years, SD=2.89 years) participated in the study. All participants were students at the University of Glasgow (Scotland, UK). None of these women were currently pregnant, breastfeeding, or 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. All participants provided written, informed consent.

2.2 Face stimuli

Stimuli were full-color face images of 50 white adult men (mean age=24.2 years, SD=3.99 years) and 50 white adult women (mean age=24.3 years, SD=4.01 years). Photographs were taken under standardized photographic conditions and depicted individuals who were posed front on to the camera with neutral emotional expressions and direct gaze. Images were aligned on pupil position and masked so that clothing was not visible.

In order to establish the attractiveness of the faces for comparison with motivational salience, the 50 male faces were rated for attractiveness by 100 heterosexual women and 100 heterosexual men (mean age=24.7 years, SD=5.87 years) using a 1 (much less attractive than average) to 7 (much more attractive than average) scale. A different set of 100 heterosexual women and 100 heterosexual men (mean age=25.0 years, SD=5.56 years) rated the 50 female faces using the same 7-point scale. Participants were randomly allocated to rate either male or female faces. Trial order within each block was fully randomized.

Inter-rater agreement was high for attractiveness ratings of both the male (Cronbach's α=.99) and female (Cronbach's α=.99) faces. Because mean ratings derived from female and male raters' scores were highly correlated for both male (r=.97, N=50, p<.001) and female (r=.96, N=50, p<.001) faces, we combined ratings from female and male raters to produce a single attractiveness score for each face. These facial attractiveness scores were used in our main analyses (see Results).

In order to establish the sexual dimorphism of the faces for comparison with motivational salience, the 50 male faces were rated for masculinity by 100 heterosexual women and 100 heterosexual men (mean age=24.4 years, SD=5.32 years) using a 1 (much less masculine than average) to 7 (much more masculine than average) scale. A different set of 100 heterosexual women and 100 heterosexual men (mean age=24.3 years, SD=5.19 years)

rated the 50 female faces for femininity using a 1 (much less feminine than average) to 7 (much more feminine than average) scale. Other than the rating scale used, the procedure was identical to the procedure used to collect attractiveness ratings.

Inter-rater agreement was high for sexual dimorphism ratings of both the male (Cronbach's α=.99) and female (Cronbach's α=.99) faces. Because mean ratings derived from female and male raters' scores were highly correlated for both male (r=.97, N=50, p<.001) and female (r=.97, N=50, p<.001) faces, we combined ratings from female and male raters to produce a single sexual dimorphism score for each face. These sexual dimorphism scores were used in our main analyses (see section 3).

Attractiveness and sexual dimorphism ratings were highly correlated for female faces (r=.86, N=50, p<.001). The correlation between attractiveness and sexual dimorphism ratings for male faces (r=.31, N=50, p=.031) was significantly weaker (Fisher r-to-z transformation: z=4.72, p<.001).

2.3 Procedure

In order to investigate how hormone levels might modulate the motivational salience of faces, each of the 50 women in our main study completed five weekly test sessions. During each test session, participants provided a saliva sample via passive drool (Papacosta & Nassis, 2011). Each woman's test sessions took place at the same time of day to control for possible effects of diurnal changes in hormone levels (Veldhuis et al., 1988; Bao et al., 2003).

In each test session, participants completed two versions of a standard key-press task, similar to those used to assess the motivational salience of faces in previous studies (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2013). Following Aharon et al. (2001) and Levy et al. (2008), and because the faces had been rated in single-sex blocks (see section 2.2), male and female faces were presented in separate blocks of trials. In one version of the task (male face version), the 50 male faces described in section 2.2 were presented in a fully randomized order. In the other version of the task (female face version), the 50 female faces described in section 2.2 were presented, again in a fully randomized order. Within each test session, participants completed the male face version of the task and the female face version in a random order.

In each version of the key-press task, participants controlled the viewing duration of each face image by repeatedly pressing designated keys on their keyboard after initiating each trial by pressing the space bar. Participants could increase the length of time a given face was displayed by alternately pressing the 7 and 8 keys and/or decrease the length of time a given face was displayed by alternately pressing the 1 and 2 keys. Each key press increased or decreased the viewing duration by 100ms. The default viewing duration for each image (i.e., the length of time a face remained onscreen if no keys were pressed) was 4 seconds. Participants were told that the key-press task would last for a total of 3.5 minutes in order to discourage responses aimed at changing the length of engagement with the task. However, in reality, the total length of the key-press task was dependent on participants' responses. All

participants key-pressed at least once in each version of the task in all test sessions. Participants completed a block of practice trials at the start of each test session to ensure they understood the task (face images were not shown in this block of practice trials).

Following previous studies of the motivational salience of faces (Aharon et al., 2001; Levy et al., 2008; Hahn et al., 2013), key-press scores for each face were calculated by subtracting the number of key presses made to decrease viewing time from those made to increase viewing time. These scores were calculated separately for each participant and for each test session and served as the dependent variable in our analyses (see section 3). Faces with greater key press scores are those with greater motivational salience (Aharon et al., 2001).

2.4 Hormonal Assays

Saliva samples were frozen immediately and stored at -32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis. Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and avoid eating, drinking, chewing gum or brushing their teeth in the 60 minutes prior to participation. Samples were assayed by Salimetrics using the Salivary 17β-Estradiol Enzyme Immunoassay Kit 1-3702 (M=4.27 pg/mL, SD=1.07 pg/mL), Salivary Progesterone Enzyme Immunoassay Kit 1-1502 (M=148.82 pg/mL, SD=65.63 pg/mL), and Salivary Testosterone Enzyme Immunoassay Kit 1-2402 (M=82.99 pg/mL, SD=21.25 pg/mL). All assays passed Salimetrics' quality

control. Estradiol, progesterone, and testosterone were assayed because
changes in these hormones have been implicated in studies of within-woman
changes in perceptual judgments of faces (reviewed in Roney et al., 2011).
We also calculated estradiol-to-progesterone ratio (M=0.03, SD=0.02) from
women's estradiol and progesterone data because estradiol-to-progesterone
ratio is correlated with fertility (Landgren et al., 1980; Baird et al., 1991) and
some researchers have suggested that women's responses to facial cues
may covary with estrogen-to-progesterone ratio (e.g., Frost, 1994).

2.5 Analyses

We used multilevel analyses with cross-classified structures to test for within-
subject effects of hormone levels on the motivational salience of faces.
Separate analyses were carried out for attractiveness and sexual dimorphism.
All continuous predictors were centered on their grand means. Key-press
scores served as our dependent variable in both analyses and both analyses
were conducted using R (R Core Team, 2013), *lme4* (Bates et al., 2014), and
lmerTest (Kuznetsova et al., 2013). In both sets of analyses, random effects
of session nested within participant, face, and the interaction between
participant and face were included. The equations and full results for each
model are given in our Supplemental Materials.

3. Results

3.1 Attractiveness

Testosterone, *estradiol*, *progesterone*, and *estradiol-to-progesterone ratio*
were entered for each participant's test session to test for independent within-

subject effects of the different hormone measures on key-press scores. *Facial attractiveness* and *sex of face* (0 = female, 1 = male) were entered for each face (see the section 2.2 for details of these ratings). Interactions between *facial attractiveness* and each of the hormone measures*, between *sex of face* and each of the hormone measures*, between *facial attractiveness* and *sex of face*, and among *facial attractiveness, sex of face* and each of the hormone measures were also included in our initial model*.

This initial analysis revealed no three-way interactions among *facial attractiveness, sex of face* and any of the hormone measures (all |t| < 1.30, all p > .19), except for *estradiol-to-progesterone ratio* (t = -2.22, p = .027). There were no significant two-way interactions between *sex of face* and any of the hormone measures or *facial attractiveness* (all |t| < 1.57, all p > .11). The effect of *facial attractiveness* interacted with *testosterone* (t = 5.71, p < .001) and *estradiol-to-progesterone ratio* (t = 2.43, p = .015), but not *estradiol* or *progesterone* (both |t| < 0.82, both *p* > .41).

To interpret these results, all non-significant interactions were removed from the model. The three-way interaction among *facial attractiveness, sex of face,* and *estradiol-to-progesterone ratio* was significant in this reduced model (t = -2.75, p = .006). For female faces, there was a significant positive effect of *facial attractiveness* (t = 9.43, p < .001), confirming that more attractive female faces generally had greater motivational salience, and no effect of *estradiol-to-progesterone ratio* (t = -0.14, p = .89). However, the effect of female *facial attractiveness* on key-press scores was greater in test sessions with higher

estradiol-to-progesterone ratio (t = 3.31, p < .001). For male faces, there was also a significant positive effect of *facial attractiveness* (t = 10.72, p < .001), and the effect of *estradiol-to-progesterone ratio* was not significant (t = 0.52, p = .60). By contrast with our results for female faces, the effect of male *facial attractiveness* on key-press scores did not vary as a function of *estradiol-to-progesterone ratio* (t = -0.70, p = .48).

There was also a significant positive effect of *testosterone* (t = 2.39, p = .018), indicating that key-press scores were generally greater in test sessions with higher testosterone levels. These effects were qualified by the significant interaction between *facial attractiveness* and *testosterone* (t = 6.66, p < .001), indicating that the positive effect of *facial attractiveness* on key-press scores was more pronounced in test sessions with higher testosterone levels. Note that our initial model showed no significant three-way interaction among *sex of face*, *facial attractiveness*, and *testosterone*.

3.2 Sexual dimorphism

Our initial model was identical to the initial model in the previous set of analyses, except that *sexual dimorphism* ratings (see section 2.2 for details of these ratings) were used in place of *attractiveness* ratings. This initial analysis revealed no three-way interactions among *sexual dimorphism, sex of face* and any of the hormone measures (all |t| < 1.56, all p > .11), except for *testosterone* (t = -4.67, p < .001). There were significant two-way interactions between *sexual dimorphism* and *estradiol-to-progesterone ratio* (t = 2.66, p = .008), *sexual dimorphism* and *testosterone* (t = 5.44, p < .001), *sexual*

dimorphism and *sex of face* (t = -3.31, p = .001), and *sex of face* and *testosterone* (t = -2.71, p = .007). No other interactions were significant (all |t| < 0.95, all p > .34).

All non-significant interactions were then removed from the model. In this reduced model, there was a significant interaction between *sexual dimorphism* and *estradiol-to-progesterone ratio* (t = 3.39, p < .001), indicating that sexual dimorphism had a greater effect on key-press scores in test sessions with higher estradiol-to-progesterone ratios. Note that our initial model showed no significant three-way interaction among sex of face, sexual dimorphism, and estradiol-to-progesterone ratio.

The three-way interaction among *sexual dimorphism, sex of face,* and *testosterone* that was significant in the full model was also significant in the reduced model (t = -4.68, p < .001). For female faces, there was a significant positive effect of *sexual dimorphism* (t = 5.09, p < .001), showing that more feminine female faces generally had greater motivational salience. There was also a significant positive effect of *testosterone* (t = 3.38, p < .001), indicating that the motivational salience of female faces in general was greater in test sessions with higher testosterone. These effects interacted (t = 5.42, p < .001), indicating that the effect of female *sexual dimorphism* on key-press scores was greater in test sessions with higher testosterone. For male faces, the effect of *sexual dimorphism* was not significant (t = 0.51, p = .61). There was a significant positive effect of *testosterone* for male faces (t = 2.12, p = .035), indicating that the reward value of male faces in general was greater in

test sessions with higher testosterone. Unlike for female faces, these effects did not interact (t = -1.12, p = .26).

Including *participant age* or *session order* (1, 2, 3, 4, 5) in our attractiveness and sexual dimorphism models did not alter the pattern of results.

4. Discussion

Consistent with the results of previous behavioral (e.g., Hahn et al., 2013) and neuroimaging (see Bzdok et al., 2011 and Mende-Siedlecki et al., 2013 for meta-analytic reviews) studies, physically attractive male and female faces generally had greater motivational salience than relatively unattractive faces. Consistent with previous research suggesting that sexual dimorphism and attractiveness are more strongly and reliably correlated in female faces than male faces (see Rhodes, 2006 for a meta-analytic review), we also found that female, but not male, faces with higher sexual dimorphism generally had greater motivational salience. Our analyses also suggested that the motivational salience of facial attractiveness and sexual dimorphism was modulated by changes in women's hormone levels, however.

The effect of physical attractiveness on the motivational salience of faces interacted with the effect of women's salivary testosterone level. Furthermore, this interaction was not qualified by a higher-order interaction involving sex of face, suggesting that testosterone has similar effects on the motivational salience of attractiveness for male and female faces. Attractiveness had greater positive effects on the motivational salience of faces in test sessions

where women had higher salivary testosterone levels. This pattern of results was also observed for sexual dimorphism in female faces, but was not observed for sexual dimorphism in male faces. Our results then suggest that women's testosterone levels modulate the motivational salience of facial attractiveness, consistent with the results of studies in which administering testosterone to women increased responses to financial incentives in brain regions implicated in motivation and reward processing (Hermans et al., 2010). Consequently, our data present new, converging evidence that testosterone plays a potentially important role in reward sensitivity (McCall & Singer, 2012). Some prior work suggests that viewing faces *in general* is rewarding (e.g., Kawabata & Zeki, 2008). This being the case, that we found the motivational salience of faces *in general* to be greater when testosterone levels were high also supports McCall and Singer's (2012) proposal.

The effect of sexual dimorphism on the motivational salience of faces interacted with the effect of women's estradiol-to-progesterone ratio. Moreover, this interaction was not qualified by a higher-order interaction involving sex of face, suggesting that estradiol-to-progesterone ratio has similar effects on the motivational salience of sexual dimorphism for male and female faces. Faces with high sexual dimorphism had greater motivational salience when estradiol-to-progesterone ratio was high. A similar pattern of results was also evident for female, but not male, facial attractiveness. Given strong associations between estradiol-to-progesterone ratio and conception risk (Landgren et al., 1980; Baird et al., 1991), these results are consistent with other research suggesting that women's attraction to masculine men is

greater when conception risk is high (see Gildersleeve et al., 2014 for discussion). Our results also suggest that women may be more sensitive to female attractiveness at this time. That attractive, feminine female faces have greater motivational salience to women when their estradiol-to-progesterone ratio is high is, perhaps, surprising, given that some previous research has suggested that women derogate the attractiveness of other women when conception risk is high (Fisher, 2004). That attractive, feminine female faces have greater motivational salience to women when their estradiol-to-progesterone ratio is high suggests that women do not necessarily increase avoidance of attractive competitors for mates when conception risk is high. We speculate here that greater motivational salience for attractive, feminine female faces when estradiol-to-progesterone ratio is high may function to facilitate enhanced monitoring of attractive competitors and/or modeling of those competitors' behaviors at points in the menstrual cycle when women are thought to be more likely to compete for high-quality mates (Fisher, 2004). Estradiol-to-progesterone ratio and testosterone may have different effects on responses to male faces because, while estradiol-to-progesterone ratio is a very good predictor of conception risk across the menstrual cycle (Landgren et al., 1980; Baird et al., 1991), testosterone may be more sensitive to situational factors related to competition for resources and mating (van Anders et al., 2011).

In conclusion, our analyses of salivary hormone levels suggest that the motivational salience of facial attractiveness is modulated by within-woman changes in testosterone levels and, to a lesser extent, estradiol-to-

progesterone ratios. Previous studies have demonstrated that the motivational salience of attractive faces is variable by showing that other types of facial cue (e.g., emotional expression or gaze direction) can modulate responses to physically attractive versus physically unattractive faces in brain regions involved in motivation and reward processing (Kampe et al., 2001; O'Doherty et al., 2003). Here we present new evidence that the motivational salience of physically attractive faces is variable, finding that within-woman changes in hormone levels also modulate the motivational salience of physically attractive faces. Moreover, these changes in the reward value of facial attractiveness may contribute to changes in women's actual behavior towards physically attractive and unattractive individuals during the menstrual cycle (e.g., Senior et al., 2007; Lucas & Koff, 2013).

5. Acknowledgments

6. References

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