Facial coloration tracks changes in women's estradiol

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Summary Red facial coloration is an important social cue in many primate species, including humans. In such species, the vasodilatory effects of estradiol may cause red facial coloration to change systematically during females' ovarian cycle. Although increased red facial coloration during estrus has been observed in female mandrills (*Mandrillus sphinx*) and rhesus macaques (*Macaca mulatta*), evidence linking primate facial color changes directly to changes in measured estradiol is lacking. Addressing this issue, we used a longitudinal design to demonstrate that red facial coloration tracks within-subject changes in women's estradiol, but not within-subject changes in women's progesterone or estradiol-to-progesterone ratio. Moreover, the relationship between estradiol and facial redness was observed in two independent samples of women ($N = 50$ and $N = 65$). Our results suggest that changes in facial coloration may provide cues of women's fertility and present the first evidence for a direct link between estradiol and female facial redness in a primate species.
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1. Introduction

Facial coloration appears to function as an important social cue in many non-human primate species (Setchell and Dixson, 2001; Waitt et al., 2003; Setchell et al., 2006; Dubuc et al., 2009; Higham et al., 2010). For example, facial redness is associated with status in male mandrills (*Mandrillus sphinx*, Setchell and Dixson, 2001) and attractiveness in male rhesus macaques (*Macaca mulatta*, Waitt et al., 2003). In some species of non-human primate, facial coloration may also function as a fertility cue (Setchell et al., 2006; Dubuc et al., 2009; Higham et al., 2010). For example, female rhesus macaques' (Dubuc et al., 2009) and mandrills' (Setchell et al., 2006) facial skin becomes redder during the fertile phase of their ovarian cycles, complementing findings for similar changes in the color of female hindquarter skin (Dixson, 1998). Female rhesus macaques' facial skin may

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also become darker during the fertile phase of their ovarian cycles (Higham et al., 2010).

The majority of research examining these changes in facial coloration has focused on investigating the ultimate functions of these color changes (Setchell et al., 2006; Dubuc et al., 2009; Higham et al., 2010, 2011). Consequently, research into the proximate mechanisms through which these changes in facial coloration might occur has been neglected. It has been assumed that the vasodilatory effects of estradiol (Sobrino et al., 2009) drive these changes in facial coloration (Dixson, 1998; Dubuc et al., 2009), as well as the analogous changes in the color of female hindquarter skin (Dixson, 1998; Dubuc et al., 2009). Estradiol may increase blood flow to blood vessels close to the surface of the skin, increasing skin redness (Dixson, 1998; Dubuc et al., 2009). While this potential mechanism for changes in female skin color has been widely accepted, there is no direct evidence that changes in female skin color closely track within-subject changes in estradiol (Dubuc et al., 2009). Consequently, a critical assumption of the assumed proximate mechanism for changes in primate skin coloration during the ovarian cycle remains untested.

Recent work suggests that facial skin coloration may also function as an important social cue in humans. For example, increasing red, yellow, and light skin coloration increases the perceived health of white European and black African women's faces (Stephen et al., 2009a, 2009b; Re et al., 2011). Increasing red and yellow facial skin coloration also increases women's attractiveness (Re et al., 2011; Whitehead et al., 2012a, 2012b). These effects are thought to primarily reflect responses to facial cues of cardiovascular health (Stephen et al., 2009a) and good diet (Stephen et al., 2011; Whitehead et al., 2012b). However, other research suggests that facial skin coloration may be a viable cue to women's current fertility status. For example, one recent study reported that women's facial skin was redder on the day of ovulation, when fertility and estradiol are both high, than it was at the end of the luteal phase, when fertility and estradiol are both low (Oberzaucher et al., 2012). However, the relationship between estradiol and fertility is not linear; estradiol can also be relatively high in the mid-luteal phase, when fertility is low (Alliende, 2002). Accordingly, another study comparing women's facial skin coloration between the high-fertility, high-estradiol ovulatory phase and the low-fertility, high-estradiol mid-luteal phase found no differences in coloration between these points of the cycle (Samson et al., 2011). If women's facial skin coloration does change systematically during the menstrual cycle, it is plausible that the vasodilatory effects of estradiol drive these color changes. However, like research on color changes in other primates, it has not yet been established that changes in women's facial skin coloration do, in fact, track changes in estradiol.

In light of the above, we used a longitudinal design to investigate the relationships between changes in objective measures of women's facial coloration and changes in their salivary estradiol, progesterone, and estradiol-to-progesterone ratio during the menstrual cycle. We investigated these relationships in two independent samples of women in which each woman was tested in five weekly test sessions. Following other recent studies of women's facial coloration (Stephen et al., 2009b, 2011; Samson et al., 2011; Whitehead et al., 2012a), we measured facial coloration on the red (a*), yellow (b*), and light (L*) axes in CIELab color space (Commission Internationale de L'Éclairage, 1976). Note that our study design focuses on the relationship between measured hormone levels and facial coloration. This approach has been used in several recent studies of women's responses to facial cues (Pisanski et al., 2014; Wang et al., 2014; Hahn et al., 2015) and allows for a more direct test of associations between hormone levels and aspects of facial coloration than a simple comparison of color measures obtained during different phases of the menstrual cycle would allow.

2. Methods

2.1. Participants

All participants were students at the University of Glasgow and each completed five weekly test sessions. Participants were recruited only if they were not currently using any hormonal supplements (e.g., oral contraceptives), had not used any form of hormonal supplements in the 90 days prior to their participation, and had never used sunbeds or tanning products. None of the participants reported being pregnant, having been pregnant recently, or breastfeeding. We tested two independent samples of women. Sample 1 consisted of 50 white women (mean age = 20.9 years, SD = 2.38 years). Sample 2 consisted of 66 white women (mean age = 21.5 years, SD = 2.95 years). No woman appeared in both samples. All women provided written informed consent to participate.

2.2. Color measures

In each of the five test sessions, each participant first cleaned her face with hypoallergenic face wipes to remove any make up. A full-face digital photograph was taken a minimum of 10 min later. Photographs were taken in a small windowless room against a constant background, under standardized diffuse lighting conditions, and participants were instructed to pose with a neutral expression. Camera-to-head distance and camera settings were held constant. Since women may be more likely to wear red or pink clothing during the fertile phase of their menstrual cycle (Beall and Tracy, 2013) and these changes in clothing could influence measures of facial coloration due to reflectance, participants wore a white smock covering their clothing when photographed. Photographs were taken using a Nikon D300S digital camera and a GretagMacbeth 24-square ColorChecker chart was included in each image for use in color calibration.

Next, face images were color calibrated using a least-squares transform from an 11-expression polynomial expansion developed to standardize color information across images (Hong et al., 2001). Skin patches (150 × 150 pixels) were then extracted from the same fixed location (relative to the pupil) on the left and right cheeks of each woman's five face images. The average red (a*), yellow (b*), and light (L*) values for each patch were then measured in CIELab color space (Commission Internationale de L'Éclairage, 1976). Color measures obtained from images in this way produce similar results to spectrophotometry

CIELab values measured directly from the skin (Coetzee et al., 2012). Previous work reporting estrous-linked changes in macaque (Dubuc et al., 2009), mandrill (Setchell et al., 2006), and human (Oberzaucher et al., 2012) facial redness also used color measures from face photographs. Average red (Sample 1: $M = 15.4$ units, SD = 1.91 units; Sample 2: $M = 14.4$ units, SD = 1.43 units), yellow (Sample 1: $M = 18.2$ units, SD = 2.60 units; Sample 2: $M = 20.0$ units, SD = 2.62 units), and light (Sample 1: $M = 74.2$ units, SD = 3.42 units; Sample 2: $M = 72.2$ units, SD = 2.85 units) values of the two patches for each face image were used in subsequent analyses. These average values were calculated separately for each of the five face images per woman.

2.3. Hormone assays

Participants provided a saliva sample via passive drool (Papacosta and Nassis, 2011) in each test session. 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. Each woman's test sessions took place at approximately the same time of day to control for possible effects of diurnal changes in hormone levels (Veldhuis et al., 1988; Bao et al., 2003).

Saliva samples were frozen immediately and stored at $-32\,^{\circ}\text{C}$ until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis, where they were assayed using the Salivary 17β-Estradiol Enzyme Immunoassay Kit 1-3702 (Sample 1: $M = 4.68$ pg/mL, SD = 0.92 pg/mL; Sample 2: $M = 3.75$ pg/mL, SD = 1.41 pg/mL) and Salivary Progesterone Enzyme Immunoassay Kit 1-1502 (Sample 1: mean = 152.5 pg/mL, SD = 65.5 pg/mL; Sample 2: $M = 140$ pg/mL, SD = 91.5 pg/mL). All assays passed Salimetrics' quality control. We also calculated estradiol-to-progesterone ratio for each woman's individual test sessions (Sample 1: mean = 0.05, SD = 0.04; Sample 2: $M = 0.04$, SD = 0.04), since estradiol-to-progesterone ratio is highly correlated with fertility across the menstrual cycle. One woman in Sample 2 was identified as a potential outlier because she showed an unusually large change in estradiol across the five test sessions. We excluded this woman from all analyses, but note here that including her in the dataset did not alter the pattern of significant results.

2.4. Analyses

We tested for within-subject effects of salivary estradiol, progesterone, and estradiol-to-progesterone ratio on aspects of facial coloration using multilevel modeling with test sessions grouped by participant (five test sessions per participant). Analyses were conducted using R (R Core Team, 2013), lme4 (Bates et al., 2014), and lmerTest (Kuznetsova et al., 2013). To test for within-subject effects of hormone levels on each color value, values on the color axis were entered as the dependent variable at the test session level and values for salivary estradiol, progesterone, and estradiol-to-progesterone ratio were simultaneously entered as predictors, again at the test session level. Data from Sample 1 and Sample 2 were analyzed separately. The

full outputs for each of our models are included in our supplemental materials.

3. Results

Analyses of values on the red color axis revealed significant, positive, within-subject effects of estradiol in both samples of women (Sample 1: $t = 2.57$, $p = .011$; Sample 2: $t = 3.37$, $p < .001$, Fig. 1). These results indicate that, consistent with our predictions, women's faces were significantly redder in test sessions where salivary estradiol was relatively high. By contrast with these results for estradiol, these analyses showed no significant effects of either progesterone (Sample 1: $t = 1.23$, $p = .22$; Sample 2: $t = -0.76$, $p = .45$), or estradiol-to-progesterone ratio (Sample 1: $t = -0.05$, $p = .96$; Sample 2: $t = -0.65$, $p = .52$).

Analyses of values on the yellow color axis revealed no significant effects of estradiol (Sample 1: $t = -1.83$, $p = .068$; Sample 2: $t = -1.94$, $p = .054$), progesterone (Sample 1: $t = -1.17$, $p = .24$; Sample 2: $t = 0.27$, $p = .79$), or estradiol-to-progesterone ratio (Sample 1: $t = 0.19$, $p = .85$; Sample 2: $t = 1.24$, $p = .22$).

Analyses of values on the light color axis revealed no significant effects of estradiol in either sample of women (Sample 1: $t = -0.71$, $p = .48$; Sample 2: $t = -1.46$, $p = .14$). There was, however, a significant, negative, within-subject effect of progesterone in Sample 1 ($t = -2.20$, $p = .029$), but not Sample 2 ($t = 0.05$, $p = .96$). The effect of estradiol-to-progesterone ratio was not significant in Sample 1 ($t = -0.12$, $p = .91$), but there was a significant, positive, within-subject effect of estradiol-to-progesterone ratio in Sample 2 ($t = 2.24$, $p = .026$).

Our main analyses showed significant positive effects of estradiol on redness and negative effects of estradiol on yellowness that approached significance. Repeating our analyses of redness, this time with values on the yellow color axis as an additional predictor, showed significant positive effects of estradiol in both samples (Sample 1: $t = 2.15$, $p = .033$; Sample 2: $t = 2.91$, $p = .004$). By contrast, repeating our initial analyses of yellowness, this time with values on the red color axis as an additional predictor, showed that the effects of estradiol were clearly not significant in either sample (Sample 1: $t = -0.98$, $p = .33$; Sample 2: $t = -0.26$, $p = .79$). These results indicate that the tendency for women's faces to be less yellow when estradiol is high is a byproduct of the effect of estradiol on facial redness.

An additional analysis of facial redness combining data from Sample 1 and Sample 2 showed a significant within-subject effect of estradiol on facial redness ($t = 4.42$, $p < .001$) and no other significant effects (both absolute $t < 0.50$, both $p > .62$). The effect of estradiol remained significant when facial yellowness was added to the model ($t = 3.58$, $p < .001$). An additional analysis of facial yellowness combining data from Sample 1 and Sample 2 showed a significant negative effect of estradiol ($t = -2.87$, $p = .004$) and no other significant effects (both absolute $t < 1.12$, both $p > .26$). As in our earlier analyses, this negative effect of estradiol on yellowness was an artifact of the estradiol-linked change in redness (effect of estradiol when facial redness was added to the model: $t = -1.01$, $p = .31$). An additional analysis of facial lightness combining data from
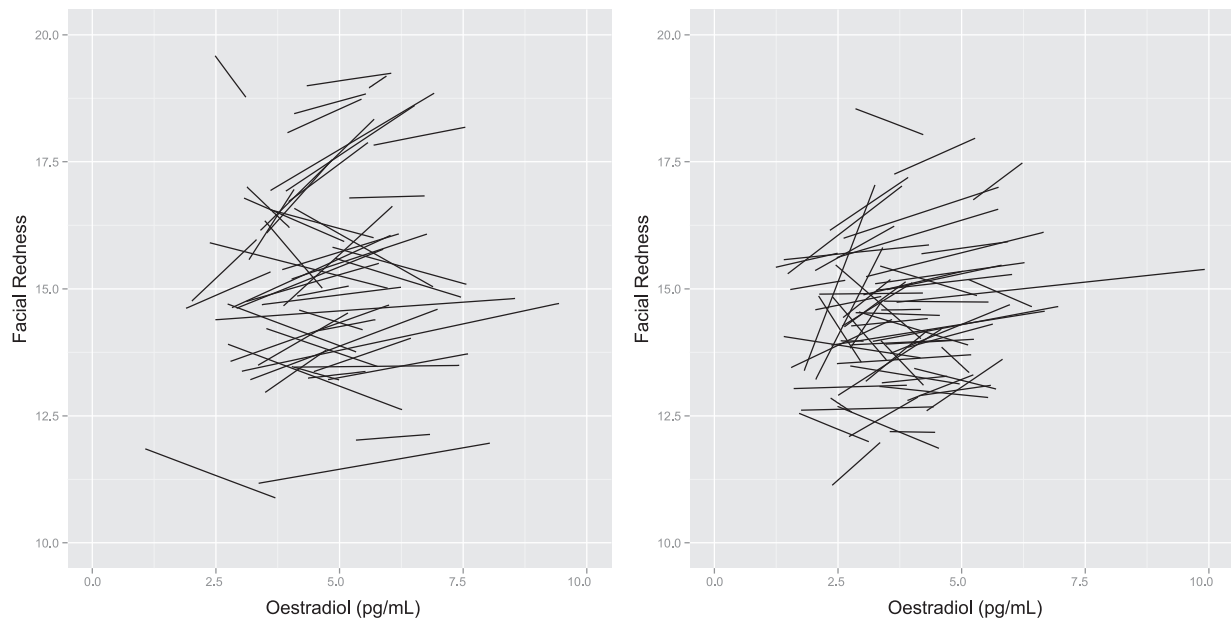
Figure 1   Changes in *facial redness* as a function of estradiol in Sample 1 (left panel) and Sample 2 (right panel). Graphs show lines of best fit for each individual participant.

Sample 1 and Sample 2 showed a weak positive effect of estradiol-to-progesterone ratio ($t = 1.76$, $p = .080$) and no other effects (both absolute $t < 1.44$, both $p > .15$).

Further analyses showed that all the significant effects of estradiol described above remained significant when estradiol-to-progesterone ratio was dropped from each model.

4. Discussion

We observed significant, positive, within-subject effects of estradiol on facial redness were in two independent samples of women. That women's facial redness tracks within-subject changes in estradiol complements changes in facial redness during the ovarian cycles of female rhesus macaques (Dubuc et al., 2009) and mandrills (Setchell et al., 2006). However, our data are the first to link changes in facial coloration directly to changes in measured estradiol, supporting the proposal that cyclic changes in facial redness in female primates with prominent facial skin are underpinned by change in estradiol (Setchell et al., 2006; Dubuc et al., 2009). Thus, our data provide new insight into the proximate mechanism through which cyclic changes in facial redness occur in female primates.

Although our data suggest that women's facial redness contains information about their current hormonal condition (i.e., their current estradiol level), facial redness might also contain information about women's fertility. Estradiol is generally high during the late follicular phase of the menstrual cycle, when fertility is also high (Gandara et al., 2007; Hambridge et al., 2013). However, estradiol can also be high during the mid-luteal phase of the menstrual cycle, when fertility is relatively low (Alliende, 2002). Consequently, assessed in isolation, changes in facial redness may not necessarily contain particularly useful information about

whether a woman is currently in the ovulatory phase of their menstrual cycle. Consistent with this proposal, in the current study estradiol-to-progesterone ratio, which is highly correlated with women's fertility across the menstrual cycle (Landgren et al., 1980; Baird et al., 1991), did not predict facial redness in either sample of women. However, menstrual cycles with larger changes in estradiol are less likely to be anovulatory cycles (Gandara et al., 2007; Hambridge et al., 2013) and women who show larger changes in estradiol over an individual menstrual cycle are less prone to anovulatory cycles generally (Hambridge et al., 2013). Thus, changes in facial redness may contain information about women's *general* fertility (i.e., the probability of ovulation occurring on that cycle and the extent to which a woman is prone to anovulatory cycles generally), even though they may not contain reliable information about position in the menstrual cycle. Whether estradiol-mediated changes in facial redness evolved specifically to signal this information, or are simply a low-cost functionless byproduct of the vasodilatory effects of estradiol, remains an open question.

Another open question is whether (or under what circumstances) the systematic changes in facial redness observed in the current study can be detected. Recent psychophysical experiments suggest that the human color perception system is optimized for detecting relatively subtle changes in facial redness, compared with detecting changes in the redness of other types of stimuli or detecting changes in facial coloration on other color axes (Tan and Stephen, 2013). Indeed, discrimination thresholds for within-subject changes in facial redness are very low (Re et al., 2011). Re et al. (2011) found the discrimination threshold for within-subject changes in facial redness to be 0.67 units, which is considerably smaller than the average change in redness between the test sessions with the lowest and highest facial redness in either of our samples (Sample 1: $M = 1.6$ units, SD = 0.6 units; Sample 2: $M = 1.4$ units, SD = 0.6 units).

While these results suggest that it is plausible that estradiol-mediated changes in facial redness would be detectable, variability *between* women in facial redness may mean that within-subject changes are much more apparent to individuals who interact with the woman regularly. Similar to recent findings for individual differences in detection of facial cues associated with hormonal condition in female rhesus macaques (Higham et al., 2011), individuals who are familiar with the woman may more easily detect color changes associated with hormonal condition. Of course, our results linking within-subject changes in redness directly to within-subject changes in estradiol indicate that women showing larger changes in estradiol (i.e., women who are less prone to anovulatory cycles both generally and in their current cycle) will generally be those in whom the redness change is most visible. Regardless of whether the estradiol-linked changes in women's facial redness observed in the current study can be detected, our results present strong support for the proposal that estradiol underpins the changes in skin coloration that have previously been reported in other primate species. Indeed, the changes in redness that were revealed in our study could simply be a vestigial remnant of this mechanism that serves no current function in humans.

While our results for facial redness were consistent between our two samples, results for facial lightness were more mixed. Lightness was negatively correlated with within-subject changes in progesterone in Sample 1 (but not Sample 2) and positively correlated with within-subject changes in estradiol-to-progesterone ratio in Sample 2 (but not Sample 1). Faces of women in Sample 1 were lighter when progesterone levels were low, as is the case during the follicular phase of the menstrual cycle, including the late follicular, fertile phase (Gandara et al., 2007; Hambridge et al., 2013). Faces of women in Sample 2 were lighter when estradiol-to-progesterone ratio was high, as is the case during the late follicular, fertile phase only (Gandara et al., 2007; Hambridge et al., 2013). Whether these different patterns of results were a consequence of Type 1 errors (i.e., were false positives) or a consequence of subtle differences in the characteristics of the samples is currently unclear, although the fact that no significant effects were observed for lightness when data from Sample 1 and Sample 2 were combined in a single analysis suggests they are likely to be false positives. Regardless of this issue, the results of our analyses of facial lightness suggest that the previously reported tendency for female rhesus macaques' faces to become darker during the most fertile phase of their ovarian cycle (Higham et al., 2010) does not necessarily generalize to female humans.

Our analyses of objective measures of facial coloration and measured hormone levels in two independent samples of women suggest that women's facial redness tracks changes in salivary estradiol. This finding complements previous work reporting changes in female facial redness during estrus in non-human primates (mandrills and rhesus macaques). Our results also support the proposal that estradiol underpins changes in female facial coloration during the ovarian cycle in primate species with conspicuous facial skin, potentially due to its vasodilatory effects (Setchell et al., 2006; Dubuc et al., 2009). The majority of studies investigating possible links between women's physical characteristics

and measured hormone levels have focused on correlations that occur *between* women (e.g., Jasienska et al., 2004; Law Smith et al., 2006; Durante and Li, 2009) and many of these results have not replicated in other samples (e.g., Puts et al., 2013; Grillot et al., 2014). By contrast with this emphasis on between-women differences, our data add to recent studies suggesting that aspects of women's facial appearance track within-subject changes in measured hormonal levels (Puts et al., 2013).

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Conflict of interest

None declared.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.psyneuen.2015.02.021.

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