

Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces

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Previous studies demonstrating changes in women's face preferences have emphasized increased attraction to cues to possible indirect benefits (e.g. heritable immunity to infection) that coincides with periods of high fertility (e.g. the late follicular phase of the menstrual cycle). By contrast, here we show that when choosing between composite faces with raised or lowered apparent health, women's preferences for faces that are perceived as healthy are (i) stronger during the luteal phase of the menstrual cycle than during the late follicular, fertile phase, (ii) stronger in pregnant women than in non-pregnant women and (iii) stronger in women using oral contraceptives than in women with natural menstrual cycles. Change in preference for male faces was greater for short- than long-term relationships. These findings indicate raised progesterone level is associated with increased attraction to facial cues associated with possible direct benefits (e.g. low risk of infection) and suggest that women's face preferences are influenced by adaptations that compensate for weakened immune system responses during pregnancy and reduce the risk of infection disrupting foetal development.

Keywords: attractiveness; faces; menstrual cycle; hormones; pregnancy; oral contraception

1. INTRODUCTION

Masculine physical traits in males are thought to advertise immunity to infection because only males with strong immune systems can overcome the immunosuppressive effects of high levels of testosterone and develop masculine characteristics (Zahavi 1975; Folstad & Karter 1992). Studies have reported that women's preferences for men's faces with masculine proportions change across the menstrual cycle (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001). At times that are characterized by high fertility (i.e. the late follicular phase), attraction to men's faces with masculine proportions is stronger than during less fertile phases of the cycle (e.g. the luteal and early follicular phases). Attraction to masculine males is thought to increase during periods of high fertility because it is only at these times that genetic benefits can be obtained for future offspring (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001). The effect of menstrual cycle phase on attraction to facial masculinity occurs when male faces are judged, but not when female

faces are judged (Johnston *et al.* 2001), and when males are judged for possible short-term relationships, but not long-term relationships (Penton-Voak *et al.* 1999; Johnston *et al.* 2001). These findings for effects of relationship context are consistent with the hypothesis that attraction to masculine men is generally stronger for short-term than long-term matings, as there are costs (in terms of low investment) associated with choosing a masculine long-term partner (Mazur & Booth 1998; Perrett *et al.* 1998).

Women agree when attributing health to faces and express strong attraction to male faces that are perceived as healthy (Jones *et al.* 2001, 2004; Rhodes *et al.* 2003). While facial characteristics associated with acute illness (e.g. pallor) contribute to an unhealthy appearance (Roujeau 2001), apparent facial health might also be a cue to the strength of men's immune systems. If apparent health in male faces is associated with possible indirect benefits (heritable immunity to infection), women's preferences for apparent health might be expected to exhibit the same pattern across the menstrual cycle that has been reported for attraction to masculine face shapes (i.e. increased during the late follicular phase of the menstrual cycle). Furthermore, attraction to apparent health in male faces might be expected to increase during the late follicular phase when male faces are judged for short-term relationships (Penton-Voak *et al.* 1999; Johnston *et al.* 2001) or judged for general attractiveness (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000), but not when male faces are judged for long-

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term relationships (Penton-Voak *et al.* 1999; Johnston *et al.* 2001), or when female faces are judged (Johnston *et al.* 2001). If attraction to putative cues to the strength of men's immune systems is strongest during periods of high fertility, non-pregnant women with natural cycles might express stronger attraction to apparent health in male faces than pregnant women or women using oral contraceptives.

A different set of predictions about the possible effects of menstrual cycle phase, pregnancy and oral contraceptive use on attraction to apparent health in faces is suggested by studies reporting changes in food preferences during pregnancy. During pregnancy, aversion to foods likely to be contaminated with infectious bacteria increases (Flaxman & Sherman 2000; Fessler 2002). This is thought to compensate for weakened immune system responses and protect the developing foetus (Flaxman & Sherman 2000; Fessler 2002). The increased progesterone levels that appear to trigger these aversions (Flaxman & Sherman 2000; Fessler 2002) are also a characteristic of the luteal phase of the menstrual cycle (Burkit *et al.* 1993; Johnson & Everitt 1995; Gilbert 2000). Strategies that minimize risk of infection might also be elicited during the luteal phase of the menstrual cycle in women with natural cycles (Fessler 2001). Such strategies might compensate for immunosuppression caused by raised progesterone level during the luteal phase of the menstrual cycle (Fessler 2001) or be a by-product of a mechanism for avoiding contagion during pregnancy. As cues to acute illness are visible in faces and contribute to attributions of poor health (Roujeau 2001), attraction to apparent health in faces might increase during the luteal phase of the menstrual cycle or during pregnancy, owing to possible direct benefits (e.g. low risk of infection). Furthermore, because most oral contraceptives raise progesterone levels (Gilbert 2000), women using oral contraceptives might also express stronger preferences for apparent health in faces than women with natural cycles. If changes in attraction to apparent health across the menstrual cycle, during pregnancy or associated with oral contraceptive use reflect strategies to reduce risk of infection during social interactions, these effects should be unaffected by the sex of the face judged.

We conducted a series of studies to test these different predictions. In studies 1–3 we tested for effects of menstrual cycle phase on attraction to apparent health in faces (study 1, between groups design; studies 2 and 3, within subject design). In study 4, we compared pregnant women's preferences for apparent health in faces with the preferences of non-pregnant women with natural cycles, whereas in study 5 we compared preferences for apparent health in faces between women with natural cycles and women using oral contraceptives.

2. STUDY 1

The aim of study 1 was to test for an effect of menstrual cycle phase on attraction to male faces manipulated in apparent health. We compared attraction to apparent health in male faces between the late follicular (14–20 days until onset of menses) and luteal (< 14 days until onset of menses) phases of the menstrual cycle (see Johnston *et al.* 2001). This comparison maximizes the contrast both in fertility (high in late follicular phase, low in luteal) and

underlying hormonal status (progesterone low in late follicular phase, high in luteal).

(a) Methods

(i) Stimuli manufacture

Four pairs of male faces varying in apparent health were manufactured for use in study 1. Each pair comprised two versions of a composite 'base face', one with decreased cues to apparent health and the other with increased cues to apparent health.

First, colour images (1200 × 1000 pixels) of 80 Caucasian male faces (age: mean = 20.8 years, s.d. = 1.3, range = 18–30 years) were captured under diffuse flash lighting with neutral expression and hair off the face. These face images, with hairstyle and clothing masked, were rated for health by eight men and seven women (age: mean = 23.3 years, s.d. = 2.7, range = 19–30 years) using a 1 (low health) to 7 (high health) point integer scale. Faces were presented in a random order. As inter-rater agreement for these ratings was high (Cronbach's alpha, $\alpha = 0.81$), ratings for each face were averaged across all participants. Two composite images ('healthy' and 'unhealthy') were generated by marking the same 179 facial landmarks on each face and averaging shape, colour and texture of the 25 face images with highest and lowest health ratings using image manipulation software (see Benson & Perrett (1991) and Tiddeman *et al.* (2001) for methods). These composites were made symmetric by averaging each composite with a mirror-reflected version of itself.

Next, four 'base faces' were created by averaging the shape, colour and texture of four random sets of three of the 80 male faces. 'Base faces' refer to composite face images with different apparent identities. These 'base faces' were subsequently transformed along a linear continuum of apparent health. The four 'base faces' were transformed in shape, colour and texture (see Tiddeman *et al.* (2001) for methods) by $\pm 50\%$ of the difference between the 'healthy' and 'unhealthy' composites. This resulted in four pairs of male faces that varied in apparent health but were matched in other respects (e.g. figure 1). These four face pairs were presented to participants in the study.

(ii) Participants

The participants in the study were 639 heterosexual women (age: mean = 22.56 years, s.d. = 1.69, range = 20–25 years) who reported regular cycles when asked if their cycle was regular or irregular, cycle lengths of 26–32 days (mean = 28.9 days, s.d. = 1.17), < 21 days until next onset of menses and no hormonal contraceptive use or pregnancy. All women were resident in the UK.

(iii) Procedure

The four face pairs varying in apparent health were presented on-screen using a two-alternative forced choice paradigm, in randomized order and interspersed with filler trials. Participants were told that they would be shown pairs of faces and to choose the face in each pair they preferred by clicking on the options below that face. Participants indicated the extent to which they preferred a particular face by choosing from the options: 'guess', 'slight preference', 'preference' and 'strong preference'. All participants reported their age, sexual orientation, hormonal contraceptive use, pregnancy status, whether cycle was regular, usual cycle length, date of onset of menstrual period before testing, residency and partnership status. In common with previous studies of individual differences in face preferences (Little *et al.* 2001, 2002; Little & Jones 2003) and cyclic changes in behaviour (Fessler &

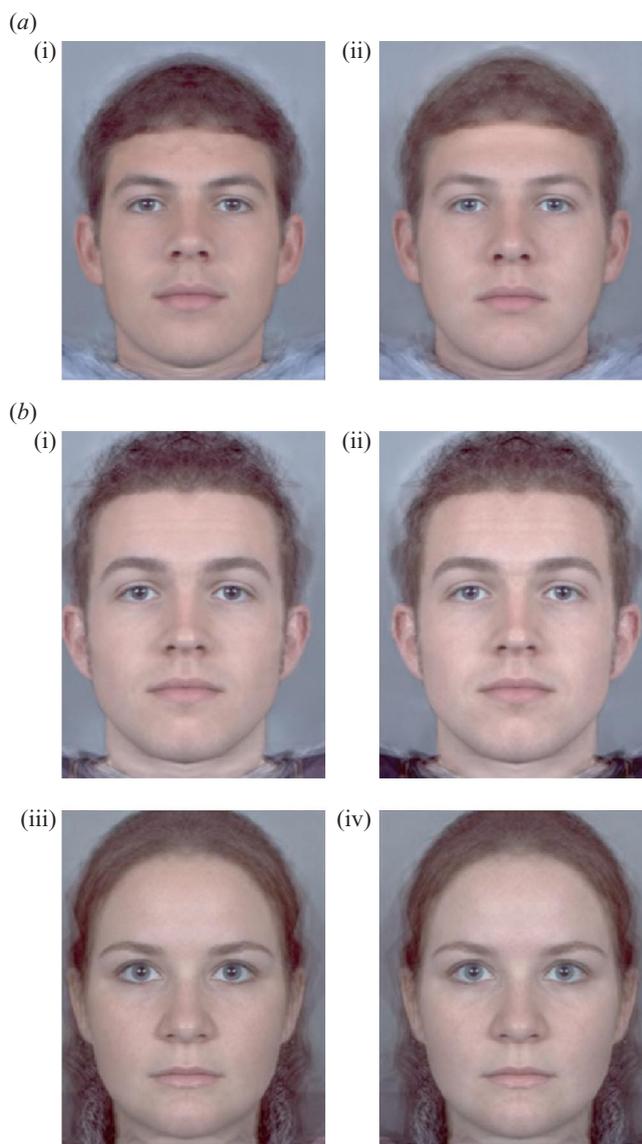


Figure 1. (a) Example stimuli used in study 1. Male 'base face' with (i) raised and (ii) lowered apparent health. 'Base faces' were manipulated in two-dimensional shape, colour and texture. (b) Example stimuli used in study 2. (i) and (ii) male; and (iii) and (iv) female 'base faces' with (i) and (iii) raised and (ii) and (iv) lowered apparent health. 'Base faces' were manipulated in colour and texture.

Navrrette 2003), the experiment was run across the World Wide Web. Participants were recruited through the BBC Science and Nature Web site (<http://www.bbc.co.uk.sn/>) by following links to an on-line study of face preferences. Duplicate entries were removed using computer Internet protocol (ip) address and similarity on an independent 16-item questionnaire (see Kraut *et al.* 2004).

(iv) Initial processing of data

Reported cycle length and date of onset of menstrual period before testing were used to assign participants to luteal ($n = 377$, < 14 days calculated until onset of next period, mean = 6.9, s.d. = 3.9) or late follicular ($n = 262$, 14–20 days calculated until onset of next period, mean = 16.8, s.d. = 2.1) groups. Responses were recoded using the following scale: 1 = strong preference for

low apparent health, to 8 = strong preference for high apparent health. For each participant, the mean preference strength for apparent health, was calculated (across four face pairs) and converted to a percentage of maximum preference for apparent health.

(b) Results

Univariate ANOVA (dependent variable: percentage of maximum preference; between subject factor: cycle phase (late follicular, luteal); covariate: age) indicated a significant effect of cycle phase ($F_{1,636} = 14.727$, $p < 0.001$; figure 2) and no effect of age ($F_{1,636} = 1.051$, $p = 0.306$). Attraction to apparent health was significantly stronger during the luteal phase of the cycle (mean = 76.19%, s.e.m. = 0.64) than during the late follicular phase of the cycle (mean = 72.34%, s.e.m. = 0.77). In both phases, attraction to faces with raised apparent health was significantly greater than chance (one sample *t*-tests comparing the percentage of maximum preference for apparent health with 50% (i.e. chance): both $p < 0.001$).

3. STUDY 2

Findings from study 1 indicated women in the luteal phase of the menstrual cycle expressed stronger attraction to apparent health in male faces than did women in the late follicular phase of the menstrual cycle. Study 2 was performed to establish if this finding generalized to a within-subject comparison of preferences for apparent health in faces. In study 2 we compared the effect of menstrual cycle phase (luteal, late follicular) on attraction to apparent health in male and female faces. Menstrual cycle phase has been found to influence preferences for masculinity in male faces, but not female faces (Johnston *et al.* 2001). If the effect of cycle phase on preferences for apparent health reflects shifts in attraction to cues to possible direct benefits (e.g. low risk of infection) menstrual cycle phase might affect preferences for apparent health in both male and female faces. As reporting of cycle data is prone to error (Gangestad & Thornhill 1998), in study 2 we confirmed that measured pregnanediol:creatinine ratios were high on test days assigned to the luteal phase (indicating ovulation had occurred). New stimuli were manufactured with more subtle cues to apparent health defined by colour and texture.

(a) Methods

(i) Stimuli manufacture

Twelve new pairs of faces (six female and six male) were manufactured. Six new pairs of female faces varying in apparent health were manufactured by transforming six female 'base faces' (made by averaging the shape, colour and texture of six random sets of three female faces) using composites of the 20 faces judged the least and most healthy from a sample of 60 photographs of female faces (age range of faces = 19–24 years; four male and four female raters, age range of raters = 17–26 years; inter-rater agreement, $\alpha = 0.82$). Photography, face rating and computer graphic procedures were as in study 1, except faces were transformed by $\pm 30\%$ of the colour and texture differences between the healthy and unhealthy composites. By contrast with the previous study, two-dimensional shape of stimuli was not altered.

Six new pairs of male faces varying in apparent health were manufactured in the same way by transforming six male 'base faces' using healthy and unhealthy male composites. 'Healthy' and 'unhealthy' composites and the six 'base faces' used were

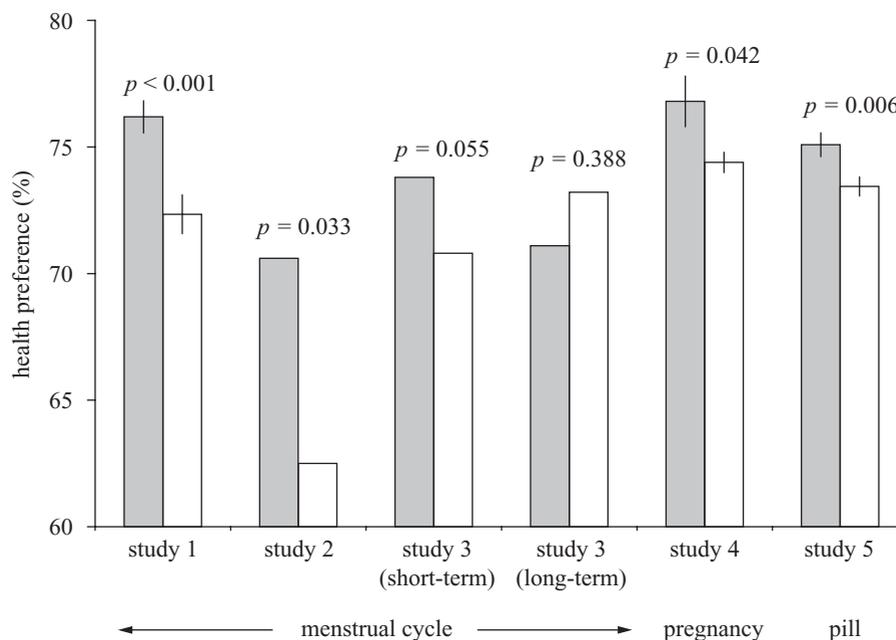


Figure 2. Effects of menstrual cycle phase (studies 1–3), pregnancy (study 4) and oral contraceptive use (study 5) on women's preferences for composite faces with raised apparent health. Two-tailed p -values shown are for main effects of cycle phase in univariate (study 1) and repeated-measures (study 2) ANOVA, paired samples t -tests (study 3), independent samples t -test (study 4) and a main effect of oral contraceptive use in univariate ANOVA (study 5). The s.e.m. is given for between-subject comparisons (studies 1, 4 and 5), but not for within-subject comparisons (studies 2 and 3). Preferences in studies 1, 4 and 5 are for male faces, in study 2 for both male and female faces, and in study 3 for male faces judged for short-term and long-term relationships. Relationship context interacted with cycle phase in study 3 ($p = 0.041$). In all conditions, attraction to apparent health was significantly greater than chance (50%, all $p < 0.01$). Collectively, these findings indicate that increased attraction to apparent health in faces is associated with conditions characterized by raised progesterone level (the luteal phase of the menstrual cycle, pregnancy and during oral contraceptive use). For studies 1 and 3–5, the y -axis is the mean preference expressed as a percentage of maximum preference for apparent health. For study 2 the y -axis records the percentage of trials (out of 12 possible) on which faces with increased apparent health were chosen. Filled bars, high progesterone and low fertility; open bars, low progesterone and high fertility.

made from a sample of 60 male faces (and their health ratings) that were selected at random from the 80 male faces used to manufacture stimuli for study 1 (inter-rater agreement for health ratings of sample of 60, $\alpha = 0.79$). Male 'base faces' made for study 2 were made from different faces to those that were used to make 'base faces' in study 1.

Examples of male and female stimuli used in study 2 are shown in figure 1*b* (middle and bottom rows).

(ii) Participants

Participants in the study were 30 heterosexual female university undergraduates (age: mean = 19.68 years, s.d. = 1.38, range = 18–23 years; cycle length: mean = 29.46 days, s.d. = 2.7, range = 23–35 days) reporting no hormonal contraceptive use, not being pregnant and not having used hormonal contraceptives in the past three months. Cycle lengths for each participant were calculated from the dates reported for onsets of at least two periods of menstrual bleeding before, during and after testing.

(iii) Procedure

Women were tested at six weekly intervals. On each test day, the 12 pairs of health stimuli were presented on-screen using a forced-choice paradigm, in a random order, and interspersed with filler trials. Participants responded to the instruction 'choose the face which is most attractive'. Participants were given a sample bottle before each test day and were asked to provide a sample of mid-stream urine collected

from the first urination of the morning of testing. On each test day, participants also reported cycle data as in study 1.

(iv) Initial processing of data

Suspected luteal phase and late follicular phase test days were identified as in study 1. As the luteal phase of the menstrual cycle is characterized by pregnanediol: creatinine ratios of 0.5 or greater (Bonello & Norman 2002; Joseph-Horne *et al.* 2002), suspected luteal phase test days were discarded if pregnanediol: creatinine ratios were less than 0.5 (as ratios indicated these test days were not post-ovulation). After this process, preferences during both luteal and late follicular phases were available for 19 women. For these women, the pregnanediol: creatinine ratio increased from late follicular to luteal test days and was more than 0.5 during the luteal phase. Late follicular measures are therefore likely to reflect a pre- or peri-ovulatory state.

A potential order confound was examined by comparing the mean order of test days assigned to luteal and late follicular phases using a paired-samples t -test. This analysis indicated that assigning test days to late follicular and luteal phases did not confound cycle phase and order of testing ($p = 0.69$). The percentage of trials (out of 12 possible) on which faces with increased apparent health were chosen was calculated as a measure of preference for apparent health in study 3. For male faces, this percentage was calculated separately for luteal and late follicular phases. Corresponding values were also calculated for female faces.

(b) Results

Repeated-measures ANOVA (dependent variable: percentage of trials on which apparent health preferred; within-subject factors: sex of face presented (male, female), phase (late follicular, luteal)) indicated no significant main effect of sex of face presented ($F = 0.28$, d.f. = 1,18, $p = 0.606$) and sex of face did not interact with cycle phase ($F = 0.362$, d.f. = 1,18, $p = 0.362$). There was, however, a significant main effect of cycle phase ($F = 5.34$, d.f. = 1,18, $p = 0.033$; figure 2). Attraction to apparent health in faces was stronger during the luteal phase of the menstrual cycle (mean = 70.6%, s.e.m. = 3.3) than during the late follicular phase (mean = 62.5%, s.e.m. = 3.0). In all conditions, women demonstrated attraction to faces with raised apparent health that was significantly greater than chance (all $p < 0.008$).

4. STUDY 3

Both between-groups (study 1) and within-subject tests (study 2) indicated that attraction to apparent health in faces was stronger during the luteal phase of the menstrual cycle than during the late follicular phase. These findings may reflect increased contagion avoidance when progesterone level is high and the body prepares for pregnancy. Men and women who appear healthy might also be perceived as reliable sources of care and support. Thus, the cyclic enhancement in attraction to apparent health observed in studies 1 and 2 may reflect increased desire for sustained friendship and support when progesterone level is high. If this were the case, the effect of cycle phase on women's preferences for apparent health in male faces might be more pronounced when judging the attractiveness of males as possible long-term partners than when judging the attractiveness of males for short-term relationships. In study 3 we therefore tested the effect of relationship context on cyclic shifts in women's preferences for male faces with raised apparent health.

(a) Methods**(i) Stimuli manufacture**

Six pairs of faces varying in apparent health were used in the study. These face pairs were manufactured in the same way as those used in study 1.

Six 'base faces' were manufactured by combining six different sets of 10 male faces. These sets of faces were randomly selected from the sample of 80 male faces used to manufacture stimuli in study 1, but were different to those used to make 'base faces' in studies 1 and 2. Three of the six new 'base faces' were transformed in apparent health using the 'healthy' and 'unhealthy' composites manufactured in study 1. The three remaining 'base faces' were transformed using 'healthy' and 'unhealthy' composites manufactured from an independent sample of Caucasian male faces ($n = 58$, age: mean = 21.2 years, s.d. = 2.8, range = 18–27 years). First, masked versions of the 58 faces were rated for health by 12 female and two male participants (age: mean = 25.4 years, s.d. = 5.6, range = 21–27 years; inter-rater agreement, $\alpha = 0.75$) using a 1 (low) to 7 (high) scale. 'Healthy' and 'unhealthy' composites were then manufactured by averaging the 20 male faces that were rated most or least healthy (as in study 1).

(ii) Participants

Participants in the study were 31 female university undergraduates (age: mean = 21.25 years, s.d. = 1.02, range = 18–23 years; cycle length: mean = 30.25 days; s.d. = 2.73, range = 23–34 days) reporting no hormonal contraceptive use, not being pregnant and not having used hormonal contraceptives in the last three months. Cycle lengths for each participant were calculated as in study 2.

(iii) Procedure

Participants were tested at four weekly intervals. On each test day, the procedure was identical to that used in study 1, except that six pairs of faces were presented and participants saw each pair twice: once in a block where faces were judged for short-term relationships and once in a block where judgements were for long-term relationships. The order of these blocks was randomized. In both blocks, health pairs were interspersed with filler trials. Long- and short-term relationships were defined as in Perrett *et al.* (2002). Urine samples were collected as in study 2.

(iv) Initial processing of data

The authenticity of suspected luteal phase and late follicular phase test days was confirmed using the diary and hormonal criteria as in study 2. Following this procedure, preferences for both luteal and late follicular phases were available for 22 women. Assigning test days to the late follicular and luteal phases did not confound cycle phase and order of testing ($p = 0.78$). For the short-term condition, mean preference strengths on luteal and late follicular test days were calculated separately and converted to percentages of maximum health preference as in study 1. Corresponding values were also calculated for the long-term condition.

(b) Results

Preferences were analysed using a repeated-measures ANOVA (dependent variable: percentage of maximum preference; within-subject factors: relationship context (long-term, short-term), phase (late follicular, luteal)). This analysis showed no significant main effects of relationship context ($F = 0.19$, d.f. = 1,21, $p = 0.89$) or cycle phase ($F = 0.68$, d.f. = 1,21, $p = 0.797$). There was, however, a significant interaction between cycle phase and relationship context ($F = 4.72$, d.f. = 1,21, $p = 0.041$).

A paired samples *t*-test indicated the difference in attraction to apparent health between the luteal phase of the cycle and the late follicular phase when faces were judged for a short-term relationship was very near significance (luteal: mean = 73.8%, s.e.m. = 2.4; late follicular: mean = 70.8%, s.e.m. = 2.3, $t = 2.30$, d.f. = 21, $p = 0.055$; figure 2). By contrast, when faces were judged for a long-term relationship, a paired samples *t*-test showed no difference between the luteal and late follicular phases (luteal: mean = 71.1%, s.e.m. = 2.2; late follicular: mean 73.21%, s.e.m. = 2.1, $t = 0.98$, d.f. = 21, $p = 0.388$). In all conditions, preferences for faces with raised apparent health were significantly greater than would be expected by chance (all $p < 0.001$).

5. STUDY 4

Findings from studies 1–3 suggest that increased attraction to apparent health in faces is associated with the luteal phase of the menstrual cycle and, hence, raised progesterone levels. As increased progesterone levels are also a

characteristic of pregnancy (Burkit *et al.* 1993; Gilbert 2000), in study 4 we compared pregnant and non-pregnant women's preferences for apparent health in male faces. Stimuli and testing procedure were the same as in study 1.

(a) *Methods*

One hundred and fifteen heterosexual women reporting pregnancy (age: mean = 26.51 years, s.d. = 3.0, range = 20–30 years, 87% from UK, 98% with a partner; days since onset of last period of menstrual bleeding: mean = 111, s.d. = 64, range = 20–240) were matched in terms of age, partnership and country of residency to 857 control non-pregnant heterosexual women reporting regular cycles when asked if their cycle was regular or irregular, and no use of hormonal contraceptives (age: mean = 26.58 years, s.d. = 2.9, range = 20–30 years, 86% from UK, 98% with a partner). Non-pregnant women were selected to represent an even sample through the entire menstrual cycle (cycle length: mean = 28.9, s.d. = 1.3 days, days until next period: mean = 14.7, s.d. = 8.2, range = –4–32 days). As in studies 1 and 3, responses were converted to percentages of maximum preference for apparent health.

(b) *Results*

Attraction to apparent health of pregnant women and the control group was examined with an independent samples *t*-test. This analysis indicated that pregnant women expressed greater attraction to apparent health than women with natural cycles did (pregnancy: mean = 76.8%, s.e.m. = 1.003, natural cycle: mean = 74.39%, s.e.m. = 0.419, $t = 2.776$, d.f. = 970, $p = 0.042$; figure 2). Both pregnant and non-pregnant women expressed attraction to faces with raised apparent health that was significantly greater than chance (all $p < 0.001$).

6. STUDY 5

Findings from studies 1–4 suggest increased attraction to apparent health coincides with conditions that are characterized by high progesterone levels (i.e. the luteal phase of the menstrual cycle, pregnancy). As most oral contraceptives also raise progesterone levels (Gilbert 2000), study 5 compared attraction to apparent health in male faces between women with natural menstrual cycles and women using oral contraceptives. Women using oral contraceptives are more likely to be in long-term relationships than women not using oral contraceptives (Little *et al.* 2002), and partnership status (i.e. having a partner or not) has been found to influence preferences for masculine proportions in male faces (Little *et al.* 2002). In study 5, we therefore considered a possible effect of partnership status on preferences for apparent health. Stimuli and testing procedure were the same as in studies 1 and 4.

(a) *Methods*

Participants in the study were 1570 heterosexual women reporting oral contraceptive use (age: mean = 22.58 years, s.d. = 1.66, range = 20–25 years, 83% from UK, 74.9% with a partner) and 1325 heterosexual women reporting no oral contraceptive use and regular cycles (age: mean = 22.58 years, s.d. = 1.68, range = 20–25 years, 71.3% from UK, 44.5% with a partner; days since last period of menstrual bleeding: mean = 13.749, s.d. = 8.214, range = 0–31 days; cycle length: mean = 28.89, s.d. = 1.249, range = 26–32 days). As in studies 1 and 4, responses were converted to percentages of maximum preference for apparent health.

(b) *Results*

Univariate ANOVA (dependent variable: percentage maximum health preference; between-subject factors: oral contraceptive use (yes, no), partnership status (partnered, single), UK residence (yes, no); covariate: age) revealed significant main effects of oral contraceptive use ($F_{1,2886} = 7.475$, $p = 0.006$; figure 2) and UK residence ($F_{1,2886} = 4.497$, $p = 0.034$) but no main effects of partnership status ($F_{1,2886} = 0.067$, $p = 0.796$) or age ($F_{1,2886} = 0.011$, $p = 0.916$). There were no significant interactions (all $F < 2.118$, all $p > 0.140$). Women using oral contraceptives expressed stronger attraction to apparent health (mean = 75.09%, s.e.m. = 0.47) than women not using oral contraceptives (mean = 73.44%, s.e.m. = 0.38) and UK residents expressed stronger attraction to apparent health (mean = 74.90%, s.e.m. = 0.50) than non-UK residents (mean = 73.63%, s.e.m. = 0.28). Pill users, women with natural cycles, UK residents and non-UK residents all expressed attraction to faces with raised apparent health that was significantly greater than chance (all $p < 0.001$).

7. DISCUSSION

In studies 1–3, attraction to apparent health in faces was stronger during the luteal phase of the menstrual cycle than during the late follicular phase of the cycle. Although the sex of the face presented did not alter the effect of menstrual cycle phase on health preferences (study 2), there was a significant interaction between cycle phase and the relationship context for which male faces were judged (long-term or short-term, study 3). Attraction to apparent health in male faces appeared to be stronger during the luteal phase of the menstrual cycle than during the late follicular phase when male faces were judged for possible short-term relationships ($p = 0.055$), but not long-term relationships ($p = 0.388$). In studies 4 and 5, attraction to apparent health in male faces was stronger in pregnant women and women using oral contraceptives (high progesterone levels) than in women with natural cycles (relatively low progesterone levels). Collectively, these findings suggest that increased attraction to apparent health in faces coincides with conditions that are characterized by raised progesterone levels, rather than conditions that are characterized by high fertility. Previous studies examining the effect of menstrual cycle on face preferences have employed self-reporting diaries to estimate cycle phase. By contrast, our studies 2 and 3 confirmed high progesterone metabolite for test days assigned to the luteal phase (indicating ovulation had actually occurred).

Increased attraction to faces with a healthy appearance in the luteal phase of the menstrual cycle, pregnancy and during oral contraceptive use supports the claim that strategies to reduce the risk of infection are elicited by increased progesterone levels (Flaxman & Sherman 2000; Fessler 2001, 2002). This is potentially adaptive as it may compensate for weakened immune system responses and reduce the risk of infection disrupting foetal development (Flaxman & Sherman 2000; Fessler 2001). Although apparent health in faces may be a cue to both underlying long-term health condition and current absence of illness, our findings suggest it is the latter of these qualities that is important for

hormone-mediated variation in women's preferences for faces tested here.

Intriguingly, increased attraction to apparent health during conditions characterized by high progesterone levels appears to be relevant for avoiding infection during social interactions with both men and women (study 2), and may have more influence when choosing partners for short-term than for long-term interactions (study 3). This latter finding suggests that the effect of cycle phase on preferences for apparent health does not reflect a drive to acquire long-term investment.

In study 5, women residing in the UK expressed stronger attraction to apparent health than did women who were not UK residents. This may be because difference in experience with faces of the type judged (white British males) and manifestations of health in this population contributes to variation in health preferences. The absence of an interaction between oral contraceptive use and UK residence, however, suggests that experiential and hormonal effects on preferences for apparent health are independent.

Increasing apparent health in male face images also increases attributions of masculinity (Boothroyd *et al.* 2005). Enhancement of attraction to male masculinity during the follicular menstrual phase (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001) will therefore work against the preference for apparent health that we find associated with raised progesterone states. It is noteworthy that increased attraction to apparent health during the luteal phase of the menstrual cycle appears to override aversion to masculinity in this phase.

Previous studies (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001), demonstrating that attraction to masculine proportions in male faces is strongest during the late follicular phase of the menstrual cycle, have emphasized indirect benefits of such preferences (e.g. offspring inheriting immunity to infection). By contrast, attraction to apparent health in faces, in the luteal phase of the menstrual cycle, in pregnancy and during oral contraceptive use, suggests that hormonal profile alters preferences for individuals offering direct benefits (e.g. low risk of infection). While hormone-mediated variations in preferences for masculine proportions and apparent health in faces show very different patterns, both evince adaptive design in women's face preferences.

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REFERENCES

- Benson, P. J. & Perrett, D. I. 1991 Synthesising continuous-tone caricatures. *Image Vision Comput.* **9**, 123–129.
- Bonello, N. & Norman, R. J. 2002 Soluble adhesion molecules in serum throughout the menstrual cycle. *Hum. Reprod.* **17**, 2272–2278.
- Boothroyd, L., Jones, B. C., Burt, D. M., Cornwell, R. E., Little, A. C., Tiddeman, B. P. & Perrett, D. I. 2005 Facial masculinity is related to perceived age but not perceived health. *Evol. Hum. Behav.* (In the press.)
- Burkit, H. G., Young, B. & Heath, J. W. 1993 *Functional histology*. Edinburgh: Churchill Livingstone.
- Fessler, D. M. T. 2001 Luteal phase immunosuppression and meat eating. *Biol. Forum* **94**, 403–426.
- Fessler, D. M. T. 2002 Reproductive immunosuppression and diet. *Curr. Anthropol.* **43**, 19–61.
- Fessler, D. M. T. & Navarrete, C. D. 2003 Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evol. Hum. Behav.* **24**, 406–417.
- Flaxman, S. M. & Sherman, P. W. 2000 Morning sickness: a mechanism for protecting mother and embryo. *Q. Rev. Biol.* **75**, 113–148.
- Folstad, I. & Karter, A. J. 1992 Parasites, bright males and the immunocompetence handicap. *Am. Nat.* **139**, 603–622.
- Gangestad, S. W. & Thornhill, R. 1998 Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proc. R. Soc. B* **265**, 927–933. (doi:10.1098/rspb.1998.0380)
- Gilbert, S. F. 2000 *Developmental biology*. Sunderland, MA: Sinauer.
- Johnson, M. H. & Everitt, B. J. 1995 *Essential reproduction*. Oxford: Blackwell Science.
- Johnston, V. S., Hagel, R., Franklin, M., Fink, B. & Grammer, K. 2001 Male facial attractiveness: evidence for a hormone-mediated adaptive design. *Evol. Hum. Behav.* **22**, 251–267.
- Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M. & Perrett, D. I. 2001 Facial symmetry and judgements of apparent health: support for a 'good genes' explanation of the attractiveness-symmetry relationship. *Evol. Hum. Behav.* **22**, 417–429.
- Jones, B. C., Little, A. C., Feinberg, D. R., Tiddeman, B. P., Penton-Voak, I. S. & Perrett, D. I. 2004 The relationship between shape symmetry and visible skin condition in male facial attractiveness. *Evol. Hum. Behav.* **25**, 24–30.
- Joseph-Horne, R., Mason, H., Batty, S., White, D., Hillier, S., Urquhart, M. & Franks, S. 2002 Luteal phase progesterone excretion in ovulatory women with polycystic ovaries. *Hum. Reprod.* **17**, 1459–1463.
- Kraut, R., Olson, J., Banaji, M., Bruckman, A., Cohen, J. & Couper, M. 2004 Psychological research online: report of board of scientific affairs advisory group on the conduct of research on the internet. *Am. Psychol.* **59**, 105–117.
- Little, A. C. & Jones, B. C. 2003 Evidence against perceptual bias views for symmetry preferences in human faces. *Proc. R. Soc. B* **270**, 1759–1763. (doi:10.1098/rspb.2003.2445)
- Little, A. C., Burt, D. M., Penton-Voak, I. S. & Perrett, D. I. 2001 Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proc. R. Soc. B* **268**, 39–44. (doi:10.1098/rspb.2000.1327)
- Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M. & Perrett, D. I. 2002 Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proc. R. Soc. B* **269**, 1095–1100. (doi:10.1098/rspb.2002.1984)
- Mazur, A. & Booth, A. 1998 Testosterone and dominance in men. *Behav. Brain Sci.* **21**, 353–363.
- Penton-Voak, I. S. & Perrett, D. I. 2000 Female preference for male faces changes cyclically: further evidence. *Evol. Hum. Behav.* **21**, 39–48.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. 1999 Menstrual cycle alters face preference. *Nature* **399**, 741–742.
- Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L. & Akamatsu, S. 1998 Effects of sexual dimorphism on facial attractiveness. *Nature* **394**, 884–887.

- Perrett, D. I., Penton-Voak, I. S., Little, A. C., Tiddeman, B. P., Burt, D. M., Schmidt, N., Oxley, R., Kinloch, N. & Barrett, L. 2002 Facial attractiveness judgements reflect learning of parental age characteristics. *Proc. R. Soc. B* **269**, 873–880. (doi:10.1098/rspb.2002.1971)
- Rhodes, G., Chan, J., Zebrowitz, L. A. & Simmons, L. W. 2003 Does sexual dimorphism in human faces signal health? *Proc. R. Soc. B* **270** (Suppl. 1), S93–S95. (doi:10.1098/rsbl.2003.0023)
- Roujeau, J. C. 2001 Clinical criteria and risk factors. *Annls Dermatol. Venereol.* **128**, 376–381.
- Tiddeman, B. P., Burt, D. M. & Perrett, D. I. 2001 Prototyping and transforming facial textures for perception research. *IEEE Comput. Graphics and Applicat.* **21**, 42–50.
- Zahavi, A. 1975 Mate selection: a selection for a handicap. *J. Theor. Biol.* **53**, 205–214.

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