



# **RESEARCH PAPER**

# Head Tilt and Fertility Contribute to Different Aspects of Female Facial Attractiveness

Danielle Sulikowski\*, Darren Burke†, Jan Havlíček‡ & S. Craig Roberts§

\* School of Psychology, Charles Sturt University, Bathurst, NSW, Australia

† School of Psychology, University of Newcastle, Ourimbah, NSW, Australia

‡ Department of Zoology, Faculty of science, Charles University, Prague, Czech Republic

§ Division of Psychology, School of Natural Sciences, University of Stirling, Stirling, UK

#### Correspondence

Dr Danielle Sulikowski, School of Psychology, Charles Sturt University, Bathurst, NSW, Australia. E-mail: danielle.sulikowski@ymail.com

Received: February 23, 2015 Initial acceptance: April 12, 2015 Final acceptance: June 18, 2015 (M. Herberstein)

doi: 10.1111/eth.12412

**Keywords:** face attractiveness, head tilt, menstrual cycle, fertility

### Abstract

Subjective attractiveness ratings of facial portraits of women taken at the fertile phase of the menstrual cycle are higher than those of portraits of the same women taken during non-fertile periods. As female faces tilted downward are rated as more attractive and female courtship behaviours change across the menstrual cycle, we investigated whether systematic downward tilt of women's faces during the fertile phase might be responsible for increased attractiveness ratings. In the original study (Proc. R. Soc. Lond. B, 271, 2004, S272), the fertile-phase portrait of each woman was deemed more attractive in 56–62% of cases. When the portraits were reclassified by head pitch, the more downward-tilted portrait was preferred in 64–73% of cases. The fertile-phase portrait was no more likely to be the downward-tilted one, however, suggesting that effects of fertility on attractiveness are not simply due to changes in head position. We also had these portraits rated (N = 130) for physical attractiveness and behavioural allure. Fertile-phase portraits were rated as more physically attractive than non-fertile portraits, while more downward-tilted portraits were rated as more behaviourally alluring than less downward-tilted ones. These data not only confirm reported effects of head tilt and fertility on perceived female attractiveness, but also suggest that these factors influence different components of the attractiveness percept.

# Introduction

Although human females lack the overt oestrus displays seen in some primates (involving obtrusive genital swellings that act as broadcast signals of fertility, Nunn 1999), a variety of detectable aspects of human female behaviour and appearance vary across the menstrual cycle. Behaviourally, females at the follicular (fertile), compared to the luteal (non-fertile), stage of the menstrual cycle tend to adopt a more attractive gait (Fink et al. 2012; but see also Provost et al. 2008), wear more revealing clothing (Durante et al. 2008), dance in a more attractive way (Fink et al. 2012), may self-report a greater degree of flirtatious behaviour (Haselton & Gangestad 2006) and speak in a way that is judged to be both more attractive and

Ethology **121** (2015) 1–8 © 2015 Blackwell Verlag GmbH

more flirtatious (Puts et al. 2013). Physically, female body odour becomes more attractive (Kuukasjärvi et al. 2004; Havlíček et al. 2006; Gildersleeve et al. 2012), and faces, breasts and other soft tissue body parts become more symmetrical (Manning et al. 1996; Scutt & Manning 1996; Oberzaucher et al. 2012). For a current review and theoretical implications, see Havlíček et al. (2015).

Roberts et al. (2004; and later Bobst & Lobmaier 2012; Oberzaucher et al. 2012 and Puts et al. 2013; but see also Bleske-Rechek et al. 2011) have demonstrated that photographs of female faces (with neutral expressions) taken at the fertile phase of the cycle are judged to be more attractive than those taken at the luteal phase. Puts et al. (2013) showed that such increases in facial attractiveness are associated with

cyclical fluctuations in sex hormones (primarily progesterone and to a lesser extent oestradiol). Changes in apparent facial shape and texture (Bobst & Lobmaier 2012; Oberzaucher et al. 2012) may contribute to cyclical fluctuations in facial attractiveness. It remains unknown, however, whether other factors may also contribute to changes in facial attractiveness across the menstrual cycle.

Burke & Sulikowski (2010) previously reported that female faces viewed from slightly above the horizontal (corresponding to a slightly downward-tilted face) are perceived by both males and females to be more feminine and more attractive. This viewpoint coincides with the perspective that a (slightly taller) male would typically have of a (slightly shorter) female's face. The apparent changes in face shape created by perceiving the face from above the horizontal are the same differences measured by Oberzaucher et al. (2012, see Fig. 2, pg. 171) between ovulatory and luteal face images - a narrower lower nose, less robust bottom half of face and fuller lips. Such features are also presumed to indicate high levels of oestrogens (Thornhill & Grammar 1999) including oestradiol, which is positively associated with natural conception rates (Lipson & Ellison 1996). This raises the prospect that at least some of the reported changes in apparent face shape (as measured from flat photographs) occurring across the menstrual cycle may have been due to women tilting their head slightly downward in the fertile-phase images, compared to the luteal phase images. Given the many behavioural cues of female attractiveness (cited above), which intensify at the fertile phase of the menstrual cycle, it is plausible that females may adjust their head pitch across the cycle, being more likely to maximize their apparent facial attractiveness during the fertile period. Such cyclic changes in behaviour, unlike changes in physical appearance, could potentially be employed strategically and directed specifically towards desirable individuals.

We wanted to test whether the increased attractiveness of images of females at the fertile phase of the cycle originally reported by Roberts et al. (2004) was (at least, partly) attributable to females being more likely to tilt their head slightly more downward during the fertile, compared to the non-fertile-phase photograph. To test this, we re-examined the stimuli that were used by Roberts et al. (2004), which consisted of a fertile-phase image and a non-fertile-phase image of each of 48 individual females. In the original study, the pairs of images were rated for attractiveness using a forced-choice test paradigm. For Study 1 of this article, we determined which of the two images of each female was the more downward-tilted image, examined the contingency between head tilt and fertility and re-analysed the preference ratings collected by Roberts et al. (2004).

# Study 1: Preferences for Downward-tilted and Fertile-phase Images

# Methods and Results

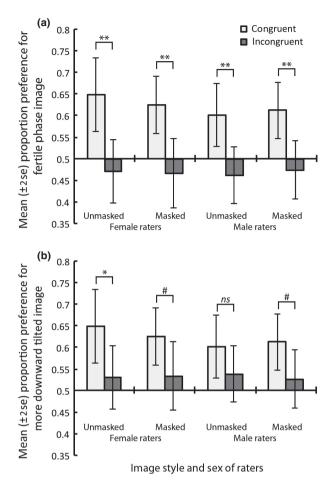
To determine which face of each identity pair was the more downward-tilted face, the identity pairs were presented to seven raters (two males, five females, including DB and DS), naïve as to which was the fertile-phase image, who judged which image of each pair was the most downwardly tilted. Each image pair was presented twice, once with each image on the left and right, respectively. Based on these ratings, an image was determined to be the more downwardtilted one if five of the seven raters chose that image twice as being the more downwardly tilted one, a criterion with an associated cumulative probability  $(N \ge 5)$  of p = 0.013. This allowed us to identify the downward-tilted image in 40 of the 48 identity pairs. The remaining 8 identity pairs were judged again as above by five of the original seven raters. The more downward-tilted face of 5 of these pairs was then determined based on that face being chosen more than twice as often as its pair across both sets of ratings, a criterion with an associated cumulative probability (N  $\ge$  17) of p = 0.032. This left three identity pairs for which the most downward-tilted image could not be reliably identified. The following analyses consider only the other 45 identity pairs. (SCR and JH did not reveal to DS and DB which face of each pair was the fertile-phase image until after this classification process was complete).

For 21 of the 45 identities, the fertile-phase image was also the more downward-tilted one - not a significant association, with cumulative binomial probability  $(x \ge 21)$  of p = 0.724. Roberts et al. (2004) originally presented the identity pairs to male (N = 130) and female (N = 131) participants requiring them to choose which image of each pair was the most attractive. In that study, the images were presented as the full portrait shot (unmasked) and again with a black mask covering the hair, ears, neck and shoulders, leaving only the face itself visible (masked). Here, we reconsider these original preferences with respect to head tilt, rather than fertility. The more downward-tilted face was preferred (i.e. was chosen by more than 50% of participants) as the more attractive one for 33 of 45 identities (73%) by both male and female raters when the faces were presented unmasked and for 30 and 29 identities of 45 (67% and 64%), for male and female raters respectively, when the faces were presented masked. All of these represent significant cumulative binomial preferences (unmasked p = 0.001, masked male p = 0.008, masked female p = 0.036). As binomial splits based on a 50% criterion are insensitive to preference strengths, we also analysed the mean relative frequencies with which the more downward-tilted image of each pair was chosen (with image pair, rather than rater, as the unit of analysis). The  $\bar{x}$  ( $\pm$ SE) preferences for the unmasked downward-tilted faces were 0.59  $\pm$  0.03 for female raters and 0.57  $\pm$  0.02 for male raters and for the masked images,  $0.58\pm0.03$  for female raters and  $0.57\pm0.02$  for male raters. All of these also represent significant preferences for the downward-tilted faces (compared to a null  $\bar{x}$  of 0.5, all  $t_{44} > 2.82$ , all p < 0.005, Cohen's *d*: 0.42 - 0.45).

For comparison, when just these 45 identities were considered (as opposed to all 48 as reported in the original study), the more fertile image was chosen as the more attractive one by males 25 times (56%, p = 0.276) and by females 26 times (58%, p = 0.186) when masked and by males 26 times (58%, p = 0.186) and by females 28 times (62%, p = 0.068) when unmasked. Considered parametrically, the  $\bar{x}$  $(\pm SE)$  preferences for the unmasked fertile faces were  $0.55\pm0.02$  for female raters and  $0.53\pm0.03$  for male raters, and for the masked images,  $0.54 \pm 0.03$ for female raters and  $0.54 \pm 0.02$  for male raters. Although none of these represent statistically significant preferences for the fertile faces (compared to a null  $\bar{x}$  of 0.5, all  $t_{44} < 1.79$ , all p > 0.081, Cohen's *d*: 0.16–0.27), this does not mean that the original preferences reported by Roberts et al. (2004; which were statistically significant for most subgroups of face stimuli and raters) were driven solely by the presence of the three identities removed from the current analyses. In the original study, preferences were reported separately for male and female participants from the United Kingdom and the Czech Republic, while in this study preferences, data from both countries were combined. The mean fertile face preferences calculated from all 48 identities (with data combined from both countries) ranged from 0.54 to 0.56 (as compared to the 0.53 to 0.55 preference range reported above for the 45 identities included in the current study).

To determine whether the effects of tilt and fertility on perceived attractiveness were additive, we split the stimulus identities into those for whom the downward-tilted image was also the fertile-phase image (congruent, n = 21) and those for whom it was not (incongruent, n = 24). One-sample t-tests confirmed that the preference for the fertile/down-tilted faces in the congruent group of identities was significantly greater than 0.5 for both masked and unmasked faces rated by both males and females (all  $t_{20} > 2.78$ , all p < 0.012, Cohen's d: 0.61–0.81), confirming, not surprisingly, that faces that were both fertile and more downward-tilted were preferred over faces that were neither fertile nor more downwardtilted. In the incongruent group, the competing effects of tilt and fertility effectively balanced out, with no significant preferences expressed for either downward-tilted/non-fertile faces or less downward-tilted/ fertile faces chosen (all  $t_{23} < 1.25$ , all p > 0.227, Cohen's *d*: 0.17–0.25).

We then compared the preferences for the fertile faces in the incongruent group (where all fertile faces were also the less downward-tilted face), with the strength of preference for the more downward-tilted/ fertile faces in the congruent group. We also compared the preferences for the more downward-tilted faces in the incongruent group, with the strength of preference for the downward-tilted/fertile faces in the congruent group. For these analyses, we treated stimulus identity as the basic replicate; the preference scores of males and females judging masked and unmasked faces, respectively, as  $2 \times 2$  within-group measures (participant sex  $\times$  masked/unmasked); and the congruent vs. incongruent groups of identities as a between-groups factor. The preference for fertile (and more downward-tilted) faces in the congruent group of identities was significantly stronger than the preference for fertile (and less downward-tilted) faces in the incongruent groups of identities  $(F_{1,43} = 13.308, p = 0.001, \omega^2 = 0.214, \text{ Cohen's } d:$ 1.11), confirming that downward tilt increases the preference for fertile female faces (see Fig. 1a). Similarly, the preference for more downward-tilted (and fertile) faces in the congruent group of identities was also significantly stronger than the preference for more downward-tilted (and not fertile) faces in the incongruent groups of identities ( $F_{1.43} = 4.554$ , p = 0.039,  $\omega^2 = 0.073$ , Cohen's *d*: 0.65), confirming that fertility increases the preference for more downward-tilted female faces (see Fig. 1b). Construction of 90% CIs around the above effect sizes (which are equivalent to 95% CIs around d-family effect sizes, see Steiger 2004) gives overlapping effect size estimates of the effect of tilt on fertility preferences  $(0.071 < \omega^2 < 0.393)$  and the effect of fertility on tilt preferences  $(0.003 < \omega^2 < 0.244)$ , and so we cannot



**Fig. 1:** Preferences for (a) fertile-phase images were significantly stronger if the fertile image was also the more downward-tilted image (congruent faces) than if it were the less downward-tilted image (incongruent faces). Similarly, preferences for (b) more downward-tilted images were significantly stronger if the downward-tilted image was also the fertile image than if it were not. \*\*p < 0.01 \*p < 0.05 "p < 0.1 ns not significant.

conclude that the effect of tilt, although on average larger than the effect of fertility, is actually reliably larger.

### Discussion

While we found no evidence that the increase in attractiveness at the fertile phase could be attributed to head tilt, we did find that head tilt significantly influenced the attractiveness preferences and that the preferences for fertile-phase images were stronger when those faces were also tilted further down. Similarly, preferences for the more downward-tilted faces were stronger when those faces were also fertile. We have previously demonstrated an effect of head tilt on attractiveness ratings only for computer-generated faces, systematically tilted approx.  $\pm 15^{\circ}$ . The current findings greatly increase the ecological validity of the effect of head tilt on perceived attractiveness, by extending it to photographs of real faces and to the subtle variations in head tilt that likely occur during normal interactions – when these images were originally taken, the models were instructed to look directly at the camera, so differences in tilt are slight and incidental.

As there was no tilt-fertility contingency, we decided to further explore the types of cues that could explain the increase in attractiveness at the fertile phase of the cycle and the perceived reason for the effect of head tilt. Although we have previously suggested that a downward-tilted female face appears more attractive because that perspective accentuates the feminine facial features (Burke & Sulikowski 2010), it is also the case that a downward-tilted face could be perceived as more submissive (Mignault & Chaudhuri 2003). Similarly, physical changes in the face over the menstrual cycle relating to symmetry of soft tissue (Manning et al. 1996; Scutt & Manning 1996; Oberzaucher et al. 2012) and/or skin appearance (Farage et al. 2009; Oberzaucher et al. 2012) could be responsible for the effects of fertility on attractiveness. Alternatively, fertile images may have been more likely to contain subtle positive facial expressions that increased their attractiveness. Even though models were instructed to keep a neutral face. it is possible that slight expression changes still occurred, just as instructions to look straight at the camera did not preclude the observed effects of tilt. To help differentiate between these alternatives, we had the stimulus faces rated for their 'physical attractiveness', an instruction designed to focus participants' attention on the physical features of the face and for their 'behavioural allure', designed to focus attention on any aspect of the models' behaviour.

# Study 2: Ratings of Behavioural Allure and Physical Attractiveness

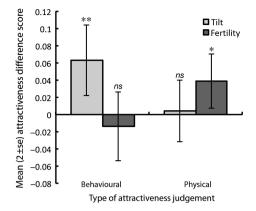
### Methods and Results

The 90 images (45 identities) were individually rated by 28 males (aged 21–65,  $\bar{x} = 37.5$ , SD = 10.9) and 102 females (aged 18–59,  $\bar{x} = 34.8$ , SD = 9.7). All participants were undergraduate students who participated as part of course requirements and all provided informed consent prior to participation. Data collection was approved by the Charles Sturt University, School of Psychology Ethics Committee (approval number 113/2011/68) and complied with the ethical standards laid down in the 1964 Declaration of Helsinki.

Faces were rated for their 'physical attractiveness' (participants were instructed to rate the physical attractiveness of each woman's face) and for their 'behavioural allure' (participants were instructed to allow this rating to be influenced by anything the model was doing, but to try and not let her actual physical attractiveness affect the rating). The images were presented once each, in random order, to obtain the physical attractiveness ratings, and then a second time in a different randomized order to obtain the allure ratings. Ratings were given in this order by all participants as informal pilot testing suggested that the allure ratings would be very low (because all images were of neutral expressions of women not doing anything especially alluring) if participants were not first aware of the limited range of 'allure' present in the images.

Ratings were provided on a scale from 1 (labelled 'least attractive/alluring') to 10 ('most attractive/alluring'). The raw ratings given by each participant were converted into four difference scores, which represented the mean difference in physical attractiveness (and behavioural allure) scores given to the fertile, compared to the non-fertile images, and given to the more downward-tilted, compared to the less downward-tilted images. The difference score was positive if the fertile/more downward-tilted images received the higher mean rating from that participant and negative if these image types received the lower mean rating.

These four difference scores were then subjected to a 2  $\times$  2 repeated-measures ANOVA, with rating type (two levels: behavioural and physical) and cue (two levels: fertility and head tilt) as the repeated measures. Participant sex was originally included in the model, but subsequently removed as it was not involved in any significant main effects or interactions. There was no main effect of either cue ( $F_{1,129} = 0.028$ , p = 0.867) or rating type ( $F_{1,129} = 0.948$ , p = 0.332), but the two measures significantly interacted  $(F_{1,129} = 8.578, p = 0.004, \eta_{\rho}^2 = 0.062)$ , as shown in Fig. 2. This occurred because participants rated the downward-tilted faces as more behaviourally alluring (mean significantly greater than zero as per a onesample *t*-test, *t*<sub>129</sub> = 2.991, p = 0.003, Cohen's *d*: 0.26) and the fertile faces as more physically attractive  $(t_{129} = 2.504, p = 0.014, Cohen's d: 0.22)$ . On the other hand, more downward-tilted faces were not rated as more physically attractive ( $t_{129} = 0.203$ , p = 0.840) and fertile faces were not rated as more behaviourally alluring ( $t_{129} = 0.709$ , p = 0.479).



**Fig. 2:** More downward-tilted faces were rated as more behaviourally alluring, but not more physically attractive, than less downward-tilted faces, while fertile-phase images were rated a more physically attractive, but not more behaviourally alluring, than non-fertile-phase images. \*p < 0.05 \*\*p < 0.01.

#### Discussion

The ratings revealed that the contribution of head tilt to attractiveness is perceived to be behavioural, while the contribution of fertility is perceived as physical. This suggests that the effects of head tilt and fertility on these stimuli are not just mutually strengthening, but likely due to different cues. Skin colour and tone likely change across the menstrual cycle (Oberzaucher et al. 2012) as a result of changes in peripheral blood flow (Bartelink et al. 1990) and changes in skin thickness and suppleness as a result of fluctuating oestrogen levels (Farage et al. 2009). The latter of these mechanisms may also contribute to fullness of lips (Fink & Neave 2005; Oberzaucher et al. 2012) and increased apparent symmetry of soft facial tissues, although decreases in asymmetry during the fertile phase of the cycle have been reported only for extraface soft tissues (Manning et al. 1996; Scutt & Manning 1996). While the source of the increase in physical attractiveness in the images used in the current study is uncertain, our ratings do suggest that potential subtle differences in posture and/or facial expression between the fertile and non-fertile images are not likely to account for the original preference (measured as an overall attractiveness preference) for fertile images reported by Roberts et al. (2004).

Fertile-phase faces were not judged as more behaviourally alluring than non-fertile-phase faces. This may appear inconsistent with reports, making use of another face image set, that found fertile-phase images to be more 'sociable' and 'likeable' (as well as more attractive, healthy and sexy, Oberzaucher et al. 2012). It is possible that these differences have arisen due to the use of different face sets. Another potential explanation is that descriptors such as 'sociable' and 'likeable' are thought (by raters) as stable traits and are in fact more influenced by the perceived physical attractiveness of the model in the image (the attractiveness halo effect, Eagly et al. 1991), than by any behavioural cues present in the image. The instruction in our study to rate the images based on their behavioural allure may therefore have directed participants away from the physical cues that influence subjective personality judgements and towards cues perceived to relate more to immediate motivation and intention.

The behavioural allure of the downward-tilted images could be due to head pitch being perceived as a social signal (as discussed by Burke & Sulikowski 2010), with backward-tilted heads more dominant and forward-tilted ones more submissive (Mignault & Chaudhuri 2003; although see also Hehman et al. 2013 reporting that, for more severe tilts maintaining direct gaze, both upward- and downward-tilted faces of both sexes are rated as more intimidating). It is not immediately clear, however, that a submissive social signal (or an intimidating one) would be interpreted by raters as 'alluring'. Alternatively, slight changes in pitch may affect the perceived position of the mouth, with a downward-tilted face appearing as though the corners of the mouth are turned upward in a slight smile and the opposite for a backwardtilted face (Lyons et al. 2000). Thus, more downward-tilted faces may have been more likely to appear as though they were smiling, even only slightly, increasing the allure ratings. Of course, as the two photographs of each identity in the stimulus set were taken weeks apart, it is also possible that the models' moods at the time of the respective photograph sessions differed. Perhaps models who were more likely to tilt their head slightly downward (when asked to look straight at the camera) were also more likely to pose a more relaxed, inviting face (when asked for a neutral expression). In this hypothetical scenario more downward-tilted faces may have been actually, not just apparently, more welcoming.

The latter interpretation cannot account for the original effect of tilt on attractiveness reported by Burke & Sulikowski (2010), as stimuli in that study presented identical model faces viewed from different perspectives. However, both social dominance/sub-missiveness and apparent changes in facial expression could potentially account for the effects seen in that original study (where only overall attractiveness judgements were made, Burke & Sulikowski 2010) as

well as the effects seen in the behavioural allure ratings being reported here. Clearly, the precise mechanisms by which perceived attractiveness is affected by slight changes in the vertical angle from which a (female) face is viewed require further scrutiny. In any case, the current data suggest that it is unlikely that an illusory increase in femininity alone, induced by slight changes in perspective (in terms of making the eves and forehead appear larger, while the jaw appears smaller), can account for the increase in physical attractiveness. If this were the case, we would have seen effects of tilt in the physical attractiveness ratings as well as (or even more strongly) than in the behavioural allure ratings when, in fact, we observed the opposite pattern. It is more likely that the effect of tilt was due to illusory (or actual) changes in facial expression, or due to the tilted head itself being perceived as an alluring cue.

# **General Discussion**

When Roberts et al. (2004) originally investigated preferences for the fertile vs. non-fertile-phase images (the same preference data that we re-compared here with respect to head tilt), they asked participants to simply choose the most attractive image, without specifying any particular component or type of attractiveness. Those original preferences favoured both fertile and down-tilted images (compared to non-fertile and less down-tilted images, respectively), meaning that the original preferences were based on a combination of both physical and behavioural cues. That we were able to subsequently separate the effects of such cues, with simple self-report instructions, suggests that they each impact on different components of the subjective attractiveness percept.

In Study 1 of this article, the effects of tilt on attractiveness preferences appeared to be somewhat larger than those of fertility. Although not a statistically significant difference (and so potentially not a difference at all), the effects of tilt and fertility on behavioural and physical attractiveness ratings, respectively, were more similar in size in Study 2. Study 1 required participants to directly compare faces of the same identity, while Study 2 did not. Study 1 may therefore have artificially encouraged a greater reliance on behavioural rather than on physical cues, because participants were looking at two images that were obviously of the same person and so may have (not consciously) discounted apparent physical differences as image artefacts. Although interesting, even if true, this suggests that the potentially stronger effects of tilt in Study 1 are an artefact of the study design and not

necessarily indicative of any real-life difference in the importance of tilt and fertility on subjective attractiveness.

It is tempting to suggest that physical cues of attractiveness may inform a 'mate quality' judgement, while behavioural cues inform an 'intentions' judgement. Kniffen & Wilson (2004) asked participants to ignore previous interactions with familiar people and provide purely physical judgements of their attractiveness. In this case, participants were unable to guarantine judgements based on physical cues from the effects of personality variables. The personality cues that affected the judgements in this case, however, were traits likely to contribute to overall mate quality, such as kindness and intelligence (Shackelford et al. 2005), rather than signals of immediate intentions. Perhaps, therefore, conscious attractiveness judgements may be able to separate cues of attractiveness that are related to enduring mate quality, from those related to transient intention, but are less able to separate the effects of different cues signalling the same underlying trait.

The distinction between judgements of mate quality and judgements of intention (both of which appear to influence global attractiveness percepts) is probably less clear-cut, however, than suggested above. For example, in this study, physical judgements of attractiveness increased for images at the fertile stage of the cycle. While one could argue that immediate short-term mate quality also increases with increasing likelihood of conception, we know that women at the fertile stage of the cycle may also become more flirtatious (Haselton & Gangestad 2006; Puts et al. 2013) and potentially more ready to engage in sexual behaviour (Adams et al. 1978) including extra-pair matings (Gangestad et al. 2002). So in this instance, with respect to short-term mating behaviour, physical changes in a female's face associated with cycling fertility could indicate increased proceptivity and/or receptivity. Conversely, a woman's self-perceived attractiveness (which is a good predictor of her others-perceived attractiveness, Rand & Hall 1983) may be linked to her reproductive strategy (as measured by the SOI, Clark 2004; and relative preferences for more masculine males, Little et al. 2001). This could potentially produce reliable differences in the amount of 'alluring' behaviour typically expressed by females towards a given male, providing a reliable behavioural cue of physical mate quality. Further investigations of the perceived affordances of different types of attractiveness judgements and cues are required to untangle these possibilities.

### Conclusions

In the current study, we found no evidence that head tilt could account for the effects of fertility on female facial attractiveness originally reported by Roberts et al. (2004). This does not necessarily preclude head tilt from contributing to effects of menstrual cycle on facial attractiveness in other studies (Oberzaucher et al. 2012), but it does rule out head tilt as a sole explanatory factor. Our findings also imply that the effects of fertility on attractiveness are perceived as 'physical', while effects of head tilt on attractiveness are perceived as 'behavioural'. The physical effects of menstrual cycle phase are consistent with previous reports of changes in shape and skin texture across the menstrual cycle (Bobst & Lobmaier 2012; Oberzaucher et al. 2012). Future studies are required to ascertain the effects of head tilt on perceived 'behavioural' attractiveness, with dominance/submissive posturing and changes in perceived facial expression as two potential candidates.

# Acknowledgements

DS is supported by a Charles Sturt University Research Compact Grant. DB is supported by an Australian Research Council Discovery Project Grant (DP0986420). S.C.R. was supported by the Wellcome Trust and a British Academy Mid-Career Fellowship. J.H. is supported by the Czech Science Foundation (grant 14-02290S). The authors declare that they have no conflict of interest.

# **Literature Cited**

- Adams, D. B., Ross Gold, A. & Burt, A. D. 1978: Rise in female-initiated sexual activity at ovulation and its suppression by oral contraceptives. N. Engl. J. Med. 21, 1145—1150.
- Bartelink, M. L., Wollersheim, H., Theeuwes, A., van Duren, D. & Thien, T. 1990: Changes in skin blood flow during the menstrual cycle: the influence of the menstrual cycle on the peripheral circulation in healthy female volunteers. Clin. Sci. **78**, 527 —532.
- Bleske-Rechek, A., Denkinger, K., Webb, R. M., Erickson, L. & Nelson, L. A. 2011: Physical cues of ovulatory status: a failure to replicate enhanced facial attractiveness and reduced waist-to-hip ratio at high fertility. Evol. Psychol. 9, 336—353.
- Bobst, C. & Lobmaier, J. S. 2012: Men's preference for the ovulating female is triggered by subtle face shape differences. Horm. Behav. 62, 413–417.

Burke, D. & Sulikowski, D. 2010: A new viewpoint on the evolution of sexually dimorphic human faces. Evol. Psychol. **8**, 573—585.

Clark, A. P. 2004: Self-perceived attractiveness and masculinization predict women's sociosexuality. Evol. Hum. Behav. **25**, 113—124.

Durante, K. M., Li, N. P. & Haselton, M. G. 2008: Changes in women's choice of dress across the ovulatory cycle: naturalistic and laboratory task-based evidence. Pers. Soc. Psychol. Bull. **34**, 1451—1460.

Eagly, A. H., Ashmore, R. D., Makhijani, M. G. & Longo, L.C. 1991: Beautiful is good, but..: a meta-analytic review of research on the physical attractiveness stereotype.Psychol. Bull. 110, 109–128.

Farage, M. A., Neill, S. & MacLean, A. B. 2009: Physiological changes associated with the menstrual cycle. Obstet. Gynecol. Surv. **64**, 58—72.

Fink, B. & Neave, N. 2005: The biology of facial beauty. Int. J. Cosmet. Sci. **27**, 317–325.

Fink, B., Hugill, N. & Lange, B. P. 2012: Women's body movements are a potential cue to ovulation. Personality Individ. Differ. 53, 759—763.

Gangestad, S. W., Thornhil, R. & Garver, C. E. 2002: Changes in women's sexual interests and their partner's mate retention tactics across the menstrual cycle: evidence for shifting conflicts of interest. Proc. R. Soc. Lond. B **269**, 975–982.

Gildersleeve, K. A., Haselton, M. G., Larson, C. M. & Pillsworth, E. G. 2012: Body odor attractiveness as a cue of impending ovulation in women: evidence from a study using hormone-confirmed ovulation. Horm. Behav. **61**, 157—166.

Haselton, M. G. & Gangestad, S. W. 2006: Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. Horm. Behav. 49, 509—518.

Havlíček, J., Dvořáková, R., Bartoš, L. & Flegr, J. 2006: Non-advertized does not mean concealed: body odour changes across the human menstrual cycle. Ethology 112, 81—90.

Havlíček, J., Cobey, K. D., Barrett, L., Klapilová, K. & Roberts, S. C. 2015: The spandrels of Santa Barbara? A new perspective on the peri-ovulation paradigm Behav. Ecol. doi: 10.1093/beheco/arv064.

Hehman, E., Leitner, J. B. & Gaertner, S. L. 2013: Enhancing facial features increases intimidation. J. Exp. Soc. Psychol. 49, 747—754.

Kniffen, K. M. & Wilson, D. S. 2004: The effect of nonphysical traits on the perception of physical attractiveness: three naturalistic studies. Evol. Hum. Behav. 25, 88—101.

Kuukasjärvi, S., Eriksson, C. J. P., Koskela, E., Mappes, T., Nissinen, K. & Rantala, M. J. 2004: Attractiveness of women's body odors over the menstrual cycle: the role of oral contraceptives and receiver sex. Behav. Ecol. **15**, 579—584.

Lipson, S. F. & Ellison, P. T. 1996: Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. Hum. Reprod. **11**, 2090—2096.

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. Lond. B 268, 39–44.

Lyons, M. J., Campbell, R., Plante, A., Coleman, M., Kamachi, M. & Akamatsu, S. 2000: The Noh Mask effect: vertical viewpoint dependence of facial expression perception. Proc. R. Soc. Lond. B **267**, 2239—2245.

Manning, J. T., Scutt, D., Whitehouse, G. H., Leinster, S. J.
& Walton, J. M. 1996: Asymmetry and the menstrual cycle in women. Ethol. Sociobiol. 17, 129–143.

Mignault, A. & Chaudhuri, A. 2003: The many faces of a neutral face: head tilt and perception of dominance and emotion. J. Nonverbal. Behav. **27**, 111–132.

Nunn, C. L. 1999: The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. Anim. Behav. **58**, 229—246.

Oberzaucher, E., Katina, S., Schmehl, S. F., Holzleitner, I. J. & Grammer, K. 2012: The myth of hidden ovulation: shape and texture changes in the face during the menstrual cycle. J. Evol. Psychol. **10**, 163—175.

Provost, M. P., Quinsey, V. L. & Troje, N. F. 2008: Differences in gait across the menstrual cycle and their attractiveness to men. Arch. Sex. Behav. 37, 598—604.

Puts, D. A., Bailey, D. H., Cárdenas, R. A., Burriss, R. P., Welling, L. L. M., Wheatly, J. R. & Dawood, K. 2013: Women's attractiveness changes with estradiol and progesterone across the menstrual cycle. Horm. Behav. 63, 13—19.

Rand, C. S. & Hall, J. A. 1983: Sex differences in the accuracy of self-perceived attractiveness. Soc. Psychol. Q. **46**, 359—363.

Roberts, S. C., Havlicek, J., Flegr, J., Hruskova, M., Little, A. C., Jones, B. C., Perrett, D. I. & Petrie, M. 2004: Female facial attractiveness increases during the fertile phase of the menstrual cycle. Proc. R. Soc. Lond. B **271** (Suppl.), S270—S272.

Scutt, D. & Manning, J. T. 1996: Symmetry and ovulation in women. Hum. Reprod. **11**, 2477–2480.

Shackelford, T. K., Schmitt, D. P. & Buss, D. M. 2005: Universal dimensions of human mate preferences. Personality Individ. Differ. **39**, 447–458.

Steiger, J. H. 2004: Beyond the *F* test: effect size confidence intervals and tests of close fit in the analysis of variance and contrast analysis. Psychol. Methods 9, 164—182.

Thornhill, R. & Grammar, K. 1999: The body and face of woman: one ornament that signals quality? Evol. Hum. Behav. **20**, 105—120.