

Visual cues to fertility are in the eye (movements) of the beholder

Elizabeth A. Necka^{a,*}, Omid Kardan^a, David A. Puts^b, Kelly E. Faig^a, Marc G. Berman^a,
Greg J. Norman^a

^a Department of Psychology, University of Chicago, United States of America

^b Department of Anthropology, Pennsylvania State University, United States of America

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ABSTRACT

Past work demonstrates that humans behave differently towards women across their menstrual cycles, even after exclusively visual exposure to women's faces. People may look at women's faces differently as a function of women's menstrual cycles. Analyses of participants' scanpaths (eye movement patterns) while they looked at women at different phases of their menstrual cycles revealed that observers exhibit more consistent scanpaths when examining women's faces when women are in a menstrual cycle phase that typically corresponds with peak fertility, whereas they exhibit more variable patterns when looking at women's faces when they are in phases that do not correspond with fertility. A multivariate classifier on participants' scanpaths predicted whether they were looking at the face of a woman in a more typically fertile- versus non-fertile-phase of her menstrual cycle with above-chance accuracy. These findings demonstrate that people look at women's faces differently as a function of women's menstrual cycles, and suggest that people are sensitive to fluctuating visual cues associated with women's menstrual cycle phase.

1. Introduction

Visual cues to ovulation are abundant in female non-human primates, providing signals of fertility that aid in successful reproduction (e.g., Higham et al., 2008, 2010; Setchell et al., 2006). Though it has long been assumed that ovulation is concealed in human females (Burley, 1979; Schoröder, 1993), growing evidence suggests women may differ in appearance at different phases of their menstrual cycles. For example, women near ovulation (i.e., at peak fertility) are often regarded as more attractive than women who are in less fertile phases of their cycles (Roberts et al., 2004; Samson et al., 2011; Bobst and Lobmaier, 2012; although see Bleske-rechek and Claire, 2011), and variations in attractiveness are generally related to estradiol and progesterone levels (Jones et al., 2018; Puts et al., 2013), hormones whose fluctuations across the menstrual cycle correspond with fluctuating fertility (Baird et al., 1991). Features of women's visual appearance such as facial shape (Bobst and Lobmaier, 2012; Lobmaier et al., 2016; Oberzaucher et al., 2012), skin pigmentation (Burriss et al., 2015; Jones et al., 2015), and body soft-tissue symmetry (Manning et al., 1996; Scutt and Manning, 1996) fluctuate across the menstrual cycle and may influence attractiveness and/or serve as visual cues of a woman's fertility status.

Fluctuations in women's appearance across the menstrual cycle,

however, are subtle. Though significant, some changes in visual appearance (e.g., skin color) may be too subtle to be detected by the human eye (Burriss et al., 2015). Yet people are indeed capable of distinguishing between women at more and less fertile points in their menstrual cycle on the basis of exclusively visual exposure to women's faces, suggesting humans are sensitive to at least some (or some combination) of these visual cues. For example, people's expectations about their social interactions with women differ depending on the woman's menstrual cycle phase, even when only exposed to pictures of the women's faces: men are more likely to expect they can get a date with a woman who is near her fertile-phase (Bobst and Lobmaier, 2012) and women are more likely to mate guard their partners from women who are in the fertile-phase of their menstrual cycle (Hurst et al., 2017).

What is the process by which people distinguish between women at more and less fertile points in their menstrual cycles on the basis of visual information alone? One possibility is that people process women's faces similarly regardless of women's menstrual cycle phase, and that differences in women's visual facial appearance influence later evaluative processes, with consequences for subsequent behavior. Alternatively, people may detect differences in women's visual facial appearance early in face processing, and exhibit differential spatial and temporal dynamics when looking at women's faces. We have recently demonstrated that after only 500 ms of exposure, women attend more

* Corresponding author.

E-mail address: enecka@uchicago.edu (E.A. Necka).

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to other women who are in a more fertile phase of their menstrual cycle than to those who are in a less fertile phase (Necka et al., 2018), suggesting that people may detect cues to women's fertility status early in face processing. Furthermore, a growing body of evidence suggests that how people scan faces depends on a number of psychosocial features of the face, including its social status (Gobel et al., 2015), emotional expression (Eisenbarth and Alpers, 2011; Schurigin et al., 2014), and the threat value of the face (Kampermann et al., 2017). Thus, we expected that there may be differences in how individuals look at women's faces as a function of the women's menstrual cycle phases.

We were specifically interested in studying people's eye movement patterns (i.e., their scanpaths) when they looked at women's faces at different menstrual cycle phases, rather than the aggregate spatial distribution of their fixations over time, because evidence suggests that the eye movements that people make when they look at faces are important for face learning and recognition. Eye movements enhance face learning (Henderson et al., 2005), and the dynamic process of how observers look at faces over time (i.e., transition from fixating on one facial feature to another) is a better predictor of whether they accurately recognize a previously learned face than the spatial distribution of eye fixations alone (i.e., the facial features that were fixated upon; Chuk et al. 2014). Thus, viewers may gain important information about faces not only from facial features that they attend to but also from the relations between the features (e.g., information obtained from eye movements but not fixations alone). Analytical strategies that account for both the unfolding temporal dynamics and the spatial patterns of observers' eye movements (e.g., scanpath analyses) may be better suited to capture variance in face-processing, especially in contexts where faces differ only subtly, than analyses that focus independently on eye movements to specific facial features.

In the present study, we examined if people exhibited systematic differences in eye movement patterns (scanpaths) when looking at pictures of women in fertile- or non-fertile menstrual-cycle phases from a stimulus set that has previously been shown to vary in appearance across the menstrual cycle (Puts et al., 2013). Given evidence that people detect visual cues of fertility on women's neutral faces, we hypothesized that a woman's fertility should alter the way that observers process her face, as measured by observers' eye movements. Specifically, we investigated whether there were systematic differences in observers' scanpaths when looking at women's faces in different menstrual cycle phases, and if we could use eye movements to classify whether observers were viewing the face of a woman in a fertile- or non-fertile-phase. We did not have specific hypotheses regarding how observers' scanpaths might vary as a function of stimulus fertility, only that they would differ. Importantly, our interest here is not the facial characteristics that fluctuate across the menstrual cycle and serve as visual cues to fertility but rather whether there are differences in the eye-movement patterns that observers exhibit when looking at the neutral faces of women at different points in their menstrual cycles.

2. Methods

2.1. Participants

Sixty-seven members of an urban campus community with normal or corrected-to-normal (e.g., contact lenses/glasses) vision provided informed consent to participate in an eye-tracking study about "judging emotions and personalities in faces" in exchange for cash compensation or course credit. Analyses were conducted on 54 participants aged 18–23 years old ($M = 19.69$, $SD = 1.12$; 24 Caucasian, 17 Asian, 6 Hispanic, 5 African American, and 2 other race; 35 female) with complete data after participants were excluded due to unsuccessful eye calibration ($n = 10$), eye-tracker malfunction ($n = 2$), or participant withdrawal ($n = 1$). With 29 stimuli that varied on one factor (fertility) with two levels, this sample size was sufficient to detect a medium sized effect with power $(1-\beta) = 0.80$ (jakewestfall.org/pangea/). There were

no effects of participant sex or ethnicity on any analyses; therefore, these factors are not discussed further.

2.2. Procedure

Because cognitive task has been shown to influence eye movement patterns (Kardan et al., 2015; Borji & Itti, 2014), we instructed all participants to engage in an identical emotion recognition task reported previously in Krems et al. (2015) and Maner et al. (2005). Briefly, participants viewed pictures of targets' faces and were told that the photos were taken immediately after targets had re-lived emotional events in their lives, which evoked anger, fear, happiness, or pride, and then concealed their emotions with a neutral facial expression. Each target purportedly completed this procedure in a random order, once for each emotion. In actuality, no targets completed the emotion re-living procedure; instead, they were simply told to assume a neutral expression for photographs (see 'Stimuli and areas of interest'). Participants were told that they would view a subset of each target's images and that their task was to judge the emotion targets had supposedly re-lived and assess targets' personalities based on the images.

Participants rested their forehead and chin on a desk-mounted support 87 cm away from a video monitor (BenQXL2420Z HD LED monitor, 60 Hz refresh rate, 1920×1080 , 53×30 cm). Eye position was noninvasively acquired from the right eye using a table-mounted video-based eye tracker (Eyelink 1000; SR Research) at 500 Hz. The eyetracker was calibrated using a 9-point grid; calibration was successful if measured error was $< 1^\circ$ for at least 8/9 points and Eyelink's algorithm validated calibration as "good" or "fair".

Each trial began with a central fixation cross for 1000 ms, followed by a 1600 ms presentation of a neutral target's face subtending a visual angle of $\approx 12^\circ$ in a random corner of the screen. After the image disappeared, participants judged (in a random order) how much they believed the target experienced anger, fear, happiness, and pride using a 100-point visual-analog scale ranging from "Not at all" to "Very Much" and selected which emotional experience they believed the target had been instructed to re-live in a forced-choice response. Finally, they answered three questions about their perception of the target's personality (to be reported elsewhere). Stimuli were presented randomly within two blocks: male and female (block order counterbalanced within participant sex). Male stimuli were included as part of a broader study and will not be discussed further. Within the female block, fertile-phase and non-fertile-phase targets were blocked (again, order was counterbalanced within participant sex).

In debriefing, only two participants reported suspicion that targets had not completed the emotional re-living procedure. However, because these participants' average responses were within 1 SD of the grand mean of responses for each behavioral variable, they were retained.

2.3. Stimuli and areas of interest

Color facial photographs of 29 regularly cycling premenopausal women not using hormonal contraceptives (a subset of those previously analyzed in Puts et al., 2013) were used as stimuli. All stimuli were Caucasian, to match the dominant race of our sample population and minimize effects of cultural exposure on facial emotion recognition and looking patterns (Briellmann et al., 2014; Elfenbein and Ambady, 2003; Zebrowitz et al., 2010).

Stimulus women were photographed twice, once in their anticipated late follicular phase (denoted here as their "fertile" phase) and once in their anticipated mid-luteal phase (denoted here as their "non-fertile" phase). Session order was counterbalanced across stimulus women. Stimulus women were selected from a broader stimulus set (reported in Puts et al., 2013) to maximize the likelihood that the anticipated "fertile" phase corresponded to a period of higher than normal odds of conception. Specifically, stimuli were selected if, at the time the

photographs were taken, their salivary estradiol-to-progesterone (E:P) ratio, a strong correlate of conception risk (Baird et al., 1991), met three criteria: (1) the ratio from photographs taken when targets were putatively *fertile* was above the average of all other E:P ratios within the stimulus set, (2) the ratio from photographs taken when targets were putatively *non-fertile* was less than the average of all other E:P ratios within the stimulus set, and (3) the E:P ratio from the photograph taken when the target was putatively *fertile* was larger than the E:P ratio from the photograph taken when the target was putatively *non-fertile*. Women who were wearing visible accessories were not utilized. Some stimuli within the stimulus set were related because targets were originally recruited for a study on sibling relationships; thus, for sibling pairs, only one sibling from each pair ($N = 6$)¹ was randomly selected for inclusion. After stimulus selection, 45% ($N = 13$) of the stimulus set was photographed first in their “fertile” phase and the remaining 55% ($N = 16$) was photographed first in their “non-fertile” phase. Previous analyses using the entirety of the present stimulus set revealed that progesterone was significantly associated with stimulus attractiveness (Puts et al., 2013); however, in the subset of stimuli used in the present analyses, no significant differences in attractiveness emerged between the fertile and non-fertile phase stimuli, $t(29) = 1.58$, $p = .125$, nor did a Bartlett's test of homogeneity of variances reveal a significant difference in the variance of the attractiveness of the two sets of stimuli, $K^2 = 0.454$, $p = .500$. (Attractiveness ratings were obtained from data previously analyzed in Puts et al. (2013)).

For each stimulus, 24 face regions were defined as areas of interest (AOIs), as in Schurgin et al. (2014), with the exception that ‘hair’ was divided into four distinct AOIs corresponding to the four quadrants of the face, using the center of the nose as a midpoint (Supplemental Fig. 1). Using the automated facial emotion recognition software Affectiva (McDuff et al., 2013), we verified that there were no differences between fertile- and non-fertile-phase stimuli in the degree of expression of the 7 different emotional expressions recognized by Affectiva (joy, sadness, disgust, surprise, anger, fear, and contempt) or in the overall valence of their facial expressions, all $ps > 0.153$ (see Table 1).

2.4. Behavioral analyses

To verify that any differences in eye movement patterns were not attributable to differences in perceptions of emotions on the faces of fertile- and non-fertile-phase stimuli, we analyzed participants' behavioral estimates of target's emotions. We assessed whether participants differed in the degree to which they thought fertile- or non-fertile-phase faces were experiencing each of the potential emotions (fear, anger, happiness, and pride) using mixed effects models that included random intercepts and slopes on the level of subject and of stimulus identity. t -Tests were computed using the package lmerTest in R (Kuznetsova et al., 2015).

2.5. Eye-movement analyses

Saccades were defined as any period during which the eye exceeded a velocity of 30°/second or an acceleration of 8000°/second², blinks were defined as any period for which pupil position was not tracked or the pupil was partially occluded, and fixations were defined as any period during which the pupil and corneal reflection were tracked and were not denoted as a blink or saccade. Gaze position was determined by tracking pupil and corneal reflection, and samples were smoothed using Stampe's (1993) algorithm to produce the lowest sample-to-sample artifact (SR Research, 2009). The manufacturer specified average accuracy for the desktop mounted system used here is 0.25° to 0.50°. We discarded fixations beginning prior to 1000 ms (i.e., the onset

Table 1

Results of automated analysis of facial expression in stimulus women's faces as a function of stimulus fertility using Affectiva.

Emotion	Fertile	Non-fertile	t	p
	M (SD)	M (SD)		
Joy	1.53E-3 (9.94E-4)	1.60E-3 (8.30E-4)	-0.63	0.535
Sadness	2.01 (6.11)	0.78 (2.96)	1.17	0.253
Disgust	0.42 (0.03)	0.42 (0.03)	-1.01	0.319
Surprise	0.27 (0.52)	0.20 (0.13)	0.829	0.414
Anger	2.88 (9.84)	0.88 (3.16)	1.17	0.253
Fear	0.04 (0.09)	0.02 (0.06)	1.07	0.295
Contempt	0.30 (0.27)	0.25 (0.18)	1.28	0.211
Valence	-2.21 (6.22)	-0.96 (3.61)	-1.47	0.153

Note. A paired samples t -test with 27 degrees of freedom revealed no significant differences in facial expressions of any emotions or in the valence of facial expressions.

of the stimuli) and fixations < 120 ms that were immediately preceded or followed by a blink (as per Holmqvist et al., 2011). For each trial, we analyzed participants' scanpaths (that is, how they looked at the face across time) in two distinct ways – one top-down guided by the facial features of the stimuli and the other data-driven by characteristics of the eye movement patterns.

In our first scanpath analysis, we computed scanpaths to different facial features (AOIs) by binning fixations to the image into 10 ms bins, determining the AOI associated with each bin within each fixation, and concatenating all fixations. Prior to analyses on these AOI scanpaths, we tested in a univariate fashion whether participants differed on the frequency or total duration of fixations to any individual AOI by summing the number of fixations to each AOI and averaging the total duration spent fixating on each AOI across the entire trial and testing for an effect of stimulus fertility. We then computed similarities in scanpaths by converting scanpaths to string sequences (e.g., “left-eye-right-eye-nose”) and submitted these strings for each subject to the Needleman-Wunsch algorithm for optimal realignment using the Matlab ScanMatch toolbox (Cristino et al., 2010). The Needleman-Wunsch algorithm is commonly used in bioinformatics to align genetic sequences, and optimally matches two sequences and computes a score indicating how well they align. Briefly, if two sequences are not perfectly aligned, then a character can be inserted, deleted, or substituted in the first sequence so that it matches the second sequence (see Fig. 1a). Substitutions, insertions, and deletions carry penalties that reduce the ‘optimality score’ of the alignment, where higher scores indicate more optimal alignment. In our analyses, we computed substitution penalties based on the inverse Euclidian distance between two AOIs, such that substituting a fixation to one region (i.e., “left cheek”) for a fixation to another proximal region (i.e., “left eye”) incurred a smaller penalty than substituting a fixation to a more distal region (i.e., “chin”). As recommended in Cristino et al. (2010), if two fixations were further apart than 96% of all saccade amplitudes, then they would be considered too dissimilar to be aligned via substitution and instead a character would be inserted or deleted. For more details on this approach, see Cristino et al. (2010).

For each subject, we obtained an $N \times N$ matrix of scanpath optimal alignment scores, where N is the number of stimuli out of the total 58 for which we had fixation data for that participant after cleaning for blinks ($mean = 56.49$, $SD = 1.56$). We then tested whether the fertility status of the stimuli from which we derived the scanpaths predicted how well the scanpaths aligned (i.e., the alignment score from the ScanMatch Toolbox). That is, we compared the alignment of scanpaths for all pairs of stimuli within subjects to determine if scanpaths were more similar when (a) both scanpaths were derived from eye movement patterns when looking at a fertile-phase stimulus (b) both scanpaths were derived from eye movement patterns when looking at a non-fertile phase stimulus, or (c) one scanpath was derived from eye movement

¹ For one sibling pair, both siblings were accidentally selected for inclusion. All results maintain following exclusion of the sibling pair.

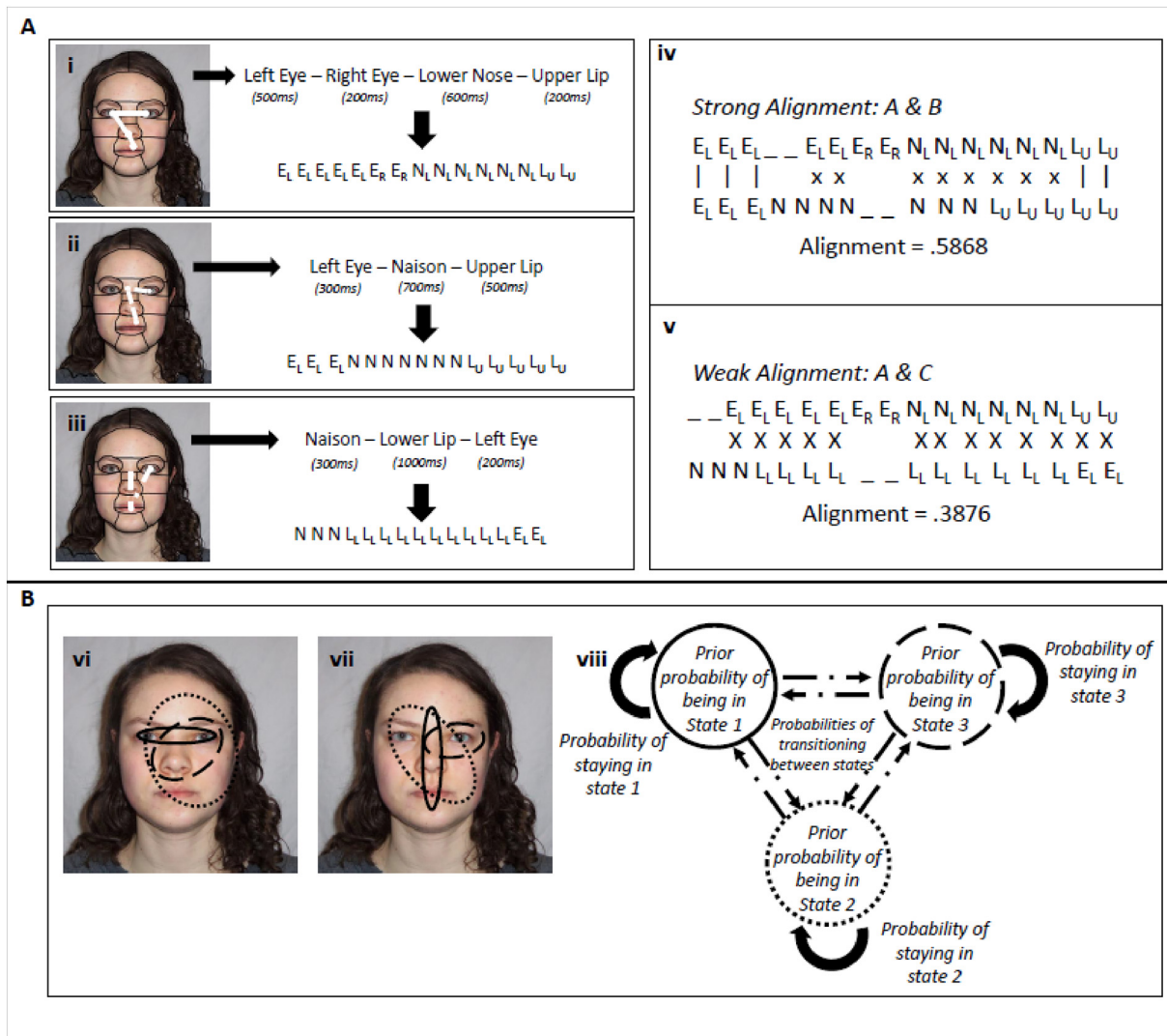


Fig. 1. Scanpath analyses.

Scanpaths were analyzed in two ways. (A) Scanpaths were first converted to string sequences (i–iii). Areas of interest for each fixation were repeated in the string sequence N times, where N is the total fixation duration divided by 10 ms bins (shown here as 100 ms bins for illustration purposes), rounded to the nearest integer. String sequences were then submitted to the Needleman-Wunsch algorithm for optimal alignment. The Needleman-Wunsch algorithm realigns the sequences to maximize their ‘alignment score’. Realignments can include inserting gaps into the sequences (as in the “_” characters in iv & v) or substituting one AOI for another (as in the “x” and “X” characters in iv & v). Alignment scores are higher (as in iv, the alignment between i and ii) if there are direct matches between the two sequences, few gaps, and/or if the substitutions are between relatively geographically proximal AOIs (e.g., substituting the left eye or the lower nose in sequence i for the naison in sequence ii, represented by lowercase “x”). Alignment scores are lower (as in v, the alignment between i and iii) if there are few or no direct matches between the two sequences, more gaps, and/or if the substitutions are between less proximal AOIs (e.g., substituting the left eye in sequence i for the lower lip in sequence ii, represented by uppercase “X”). In the event of too distal substitutions (e.g., the right-eye in i and the lower lip in iii), a gap is instead inserted into one of the sequences to shift the AOIs that are to be aligned (as in v, where two gaps in the second sequence ensure that the lower lip in sequence iii will never be substituted for the right eye in sequence i). (B) The spatial distribution of fixations and the distribution of fixation durations were used to determine up to three ‘hidden’ states using Hidden Markov Modeling (as demonstrated in vi and vii). From each model, we extracted the prior probability of being in each state and the probability of staying in each state or transitioning to another state (viii; adapted from Chuk et al. 2014; Chuk et al., 2017), as well as the center of each state (x and y coordinates), mean duration of fixations for each state, and the covariance between these features.

patterns when looking at a fertile-phase stimulus and the other was derived from eye movement patterns when looking at a non-fertile phase stimulus. To do this, we averaged the alignment scores of all fertile-fertile pairs of stimuli, all non-fertile-non-fertile pairs of stimuli, and all mixed-fertility-status (i.e., fertile-non-fertile) pairs of stimuli (excluding pairs of a woman during her fertile-phase with herself during her non-fertile phase) within each subject. We then conducted a one-way repeated-measures ANOVA with fertility-pair type (i.e., both fertile, both non-fertile, or mixed fertility status) as the within-subjects factor. In addition to the omnibus test, we examined two a-priori planned contrasts – specifically, whether fertile-fertile pairs were

aligned better than pairs of mixed-fertility status, and whether fertile-fertile pairs were aligned better than non-fertile-non-fertile pairs.

An alternative approach to analyzing scanpaths is to learn AOIs from the patterns of fixations, rather than defining AOIs based on features of the face. This approach accounts for fixations that may fall slightly outside of a region of interest and is less influenced by measurement error and decisions about areas of interest. Thus, in our second set of scanpath analyses, we used Hidden Markov Modeling (HMM) to determine the AOIs, and whether AOIs, the rate of transitioning between AOIs, or the amount of time spent in AOIs varied as a function of stimulus fertility. Briefly, HMMs are time series models that

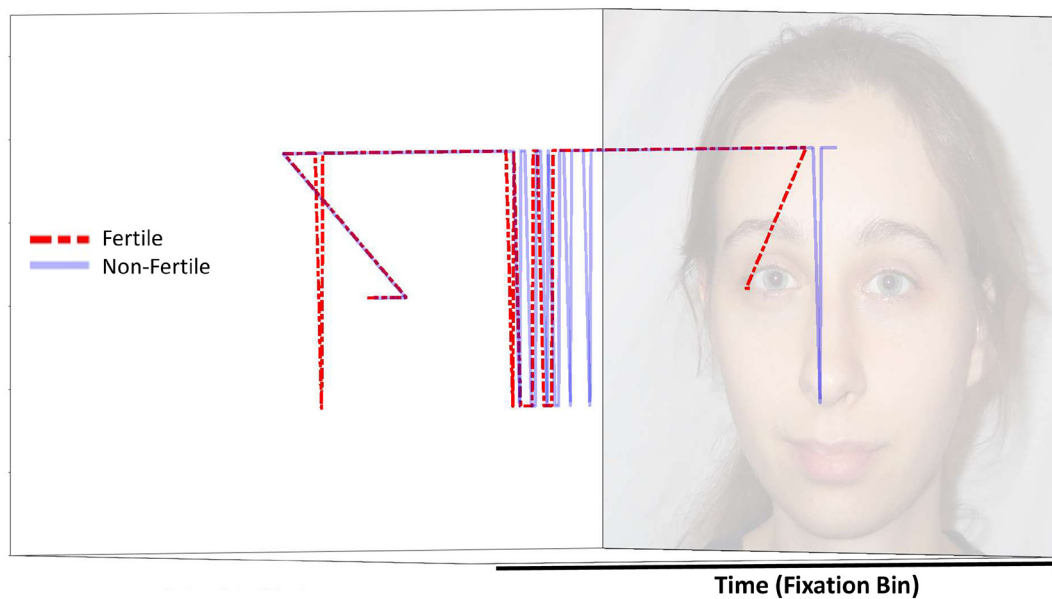


Fig. 2. Modal Scanpaths for fertile- and non-fertile-phase stimuli.

The modal scanpath was derived for fertile and non-fertile-phase stimuli for each participant by calculating which AOI was most commonly fixated to during each 10 ms bin of the scanpath. We then calculated across participants the AOI that was most commonly fixated to during each 10 ms bin for fertile and non-fertile phase stimuli. Modal scanpaths for fertile-phase stimuli are presented in red; modal scanpaths for non-fertile-phase stimuli are presented in blue. The z-axis corresponds to time (in 10 ms fixation bins for ScanMatch analysis). A representative stimulus is overlaid in the background for mapping scanpaths to appropriate AOIs. The modal scanpath is presented for visualization purposes only; unique scanpaths for each stimulus within each participant were analyzed using the ScanMatch toolbox (Cristino et al., 2010; see main text). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

use observable measurements (e.g., gaze positions and durations) to determine the 'hidden' (i.e., unobservable) dynamic process that generated those data (i.e., pattern of eye movements across time). HMMs assume that timeseries processes are comprised of various states and transitions to/from those states, such that a process's next state is determined by its current state, but that states cannot be directly observed and instead must be inferred using observable measurements (see Fig. 1b; for a more thorough explanation, see Haji-Abolhassani and Clark, 2014). We used the Matlab toolboxes Eye Movement Analysis with Hidden Markov Models (EMHMM, Chuk et al., 2017) and Scanpath Modeling and Classification with Hidden Markov Models (SMAC with HMM, Coutrot et al., 2018) to model scanpaths. These toolboxes determine hidden states (that is, areas of interest in the stimuli) by modeling the spatial distribution of all fixations as a Gaussian distribution, and determine the probability that a process (that is, participant's gaze pattern) transitions from one state to another. For more details on HMMs with eye movement data, see Chuk et al. 2014; Chuk et al., 2017 and Coutrot et al. (2018).

For each subject, we first concatenated for each stimulus the x- and y-coordinates of all fixations and transformed them into a standard space (since facial feature locations were not uniformly distributed across stimuli); we weighted these fixation coordinates by the duration of each fixation (in milliseconds). For each stimulus within each participant, we next trained an HMM with up to three hidden states. We used a variational approach, which selects the optimal number of hidden states by maximizing the log-likelihood of the data under models with varying numbers of states, up to an upper limit of three states (to limit overfitting and difficulties with interpretability beyond three states). Because the variational approach requires at least one more fixation than the number of states to be estimated, only scanpaths with four or more fixations (after cleaning for blinks) were included in HMM analyses ($mean = 52.31/58$ trials, $SD = 6.86$). Finally, we extracted thirty different parameters from each HMM – specifically, the prior probability of being in each state, the probability of transitioning between each state, and the centers and covariances for each state (i.e., x and y coordinates of the state center, mean fixation duration, and

covariance matrix coefficients). We used these parameters to train a linear discriminant classifier on whether a participant was observing a fertile- or non-fertile phase stimulus. This approach has previously been successfully used to quantify stimulus characteristics from eye-tracking data (Coutrot et al., 2018). We ran the classifier 10,000 times within each subject, each time training on data from ~90% of the trials (which were randomly selected) and testing the remaining ~10% of trials (i.e., a leave-N out cross validation). We extracted mean and median classifier accuracy for each participant, and submitted these values to a one-sample t-test and Wilcoxon sign-rank test, respectively. Two participants were excluded from this analysis because they did not have at least 30 trials with at least 4 fixations necessary to compute an HMM, and therefore the number of observations for the classifier was less than the number of parameters on which it was trained and the classifier could not be run. In a secondary analysis to verify that results could not be explained by variations in attractiveness, we also trained classifiers on the thirty HMM parameters for each participant using the same methods as above after first residualizing each parameter with respect to stimulus attractiveness, as measured in Puts et al. (2013).

3. Results

3.1. Behavioral analyses

To verify that any differences in eye movement patterns were not attributable to differences in perceptions of emotions on the faces of fertile- and non-fertile-phase stimuli, we analyzed participants' behavioral estimates of target's emotions using mixed effects models. There were no significant differences in participants' ratings of happiness ($B = 1.00$, $SE = 1.90$, $t(28.29) = 0.52$, $p = .604$), anger ($B = 0.38$, $SE = 2.30$, $t(28.72) = 0.16$, $p = .871$), fear ($B = -1.79$, $SE = 1.87$, $t(28.02) = -0.96$, $p = .347$), or pride ($B = 1.71$, $SE = 2.05$, $t(29.66) = 0.84$, $p = .409$) as a function of stimulus fertility.

3.2. Eye-movement analyses

To test whether there were systematic differences in how participants scanned the faces of women in their fertile- and non-fertile phases, we first examined the frequency and duration of fixations to each facial AOI in a univariate fashion. Univariate analyses failed to find any differences in how frequently participants fixated to (all p s > 0.073), or how long they fixated on (all p s > 0.155), any of the facial AOIs as a function of stimulus fertility status (Supplementary Table 1).

Qualitative assessment of modal scanpaths (Fig. 2) suggested that participants tended to look at the lips of fertile-phase women earlier in time than non-fertile-phase women's lips. Participants also showed a tendency to oscillate more between the lips and the eye region when looking at non-fertile-phase women's faces (as indicated by more frequent transitions between the eyes and the lips) later in the viewing period. We next computed a transition matrix to determine the average number of times that participants transitioned from one AOI to another as a function of the fertility of the face they were looking at. For each pair of AOIs, we computed the difference in how frequently each participant made that transition on average in fertile-phase faces and how frequently they made it in non-fertile-phase faces, such that more positive scores indicate transitions happened more frequently in fertile-phase faces and more negative scores indicate that transitions happened more frequently in non-fertile-phase faces (Fig. 3). Qualitative assessment of the transition matrix suggests potentially that for fertile-phase faces, participants tended to make transitions between AOIs that were closer together and oriented along the vertical plane (e.g., upper nose to upper lip) whereas they tended to make more sweeping transitions along the vertical plane in non-fertile-phase faces (e.g., forehead to lower lip). However, using a paired samples t -test to test whether the frequency of these different types of AOI transitions varied as a function of fertility status, none survived Bonferroni correction for multiple comparisons (all p s > 0.05; Supplemental Table 2).

We next compared the alignment of scanpaths for all pairs of stimuli within subjects to determine if scanpaths were more similar when both scanpaths were derived from eye movement patterns when looking at a fertile-phase stimulus, relative to when one or both of the stimuli was non-fertile. Scanpath analyses revealed that there were significant differences in how participants looked at fertile- and non-fertile-phase neutral faces, $F(2, 106) = 8.91$, $p = .002$, $\eta_G^2 = 0.01$ (Greenhouse-Geisser corrected) (Fig. 4). Specifically, scanpaths were more similar among pairs of fertile-phase faces (average alignment score = 0.62, $SD = 0.05$) than among pairs of faces with mixed fertility-status (average alignment score = 0.60, $SD = 0.06$; $t(53) = 4.79$, $p < 0.001$, mean difference = 0.02, SE of difference = $4E-4$, $d_z = 0.31$), or among pairs of non-fertile-non-fertile-phase faces (average alignment score = 0.61, $SD = 0.06$; $t(53) = 2.29$, $p = .026$, mean difference = 0.01, SE of difference = $7E-4$, $d_z = 0.65$). (Within-subject effect size estimates were computed by dividing the average within-subjects difference score between conditions by the standard deviation of the within-subjects difference scores (e.g., $\frac{\mu_{diff}}{\sigma_{diff}}$), equivalent to Cohen's d_z). In other words, participants exhibit more uniform patterns of eye movements (i.e., higher alignment scores) when looking at the faces of women who are fertile, and more variable patterns (i.e., lower alignment scores) when looking at the faces of women who are non-fertile.

We also measured scanpaths using a data-driven approach (using HMMs to determine AOIs). For each participant, we used parameters from the optimal HMM model derived for each stimulus to train a linear discriminant classifier; we used ~90% of stimuli in the training set to predict the fertility status of the remaining 10% of the stimuli. Mean within-subject classification accuracy across participants was 63.17%, which was significantly above chance accuracy, $t(51) = 10.52$, $p < 0.001$, $d = 1.46$, 95% CI = [60.66%, 65.69%]. Median accuracy (64.46%) was also significantly above chance, $z = 5.58$, $p < 0.001$,

$r = 0.65$, 95% CI = [63.33%, 71.67%]. Results held even when HMM parameters were residualized with respect to attractiveness (see supplemental results for more information). Taken together, these results suggest that scanpaths significantly differ when looking at fertile- and non-fertile-phase women's faces.

4. Discussion

In this study, we tested whether people exhibited differences in eye movement patterns when viewing the faces of women at different points in their menstrual cycle. We found that participants' scanpaths looking at fertile-phase faces were less variable than their scanpaths looking at non-fertile-phase faces, and could be used to predict with above chance accuracy whether participants looked at a fertile or non-fertile phase woman's face. These results suggest that humans are sensitive to changing features of women's faces and engage in differential visual processing of a woman's face as a function of the fertility status of the woman.

Though the present study establishes that differences in eye movement patterns exist as a function of whether people are viewing fertile or non-fertile-phase women's faces, no differences in transitions between AOIs emerged in univariate analyses. Qualitative assessment of the transition matrix suggests that observers saccade between facial AOIs that are in closer proximity to each other along the vertical axis of fertile-phase faces and look more frequently at lower regions of the face earlier during the looking period. One possibility is that observers exhibit greater sensitivity to second-order relations (e.g., the distance between facial features; Maurer et al., 2002) in fertile-phase faces. Sensitivity to second-order relations, particularly vertical relations, is instrumental for face recognition (Goffaux et al., 2009). Thus, one intriguing albeit yet unsubstantiated possibility is that observers engaged with fertile-phase faces in ways that optimized acquisition of information relevant for face recognition. This possibility should be taken as merely speculative, and future studies that experimentally manipulate face processing using paradigms such as a face-inversion task or the Bubbles (Gosselin and Schyns, 2001) paradigm and measure face recognition are necessary to empirically test this hypothesis.

It is worth considering why individuals may be more systematic in their attunement to women's fertility status. For men, the ability to detect visual cues of fertility potentially enhances their odds of successful reproduction by encouraging copulation when it would be most likely to result in offspring (i.e., when women are near ovulation). Men think that they have a better chance of getting a date with a woman whose face is prototypical of a woman near ovulation (Bobst and Lobmaier, 2012), an expectation that could encourage them to pursue a date (or mating opportunity), enhancing their reproductive odds. For women, detecting visual cues of fertility may help modulate expectations for intrasexual interactions. Near ovulation, women may engage in social behaviors that disadvantage women with whom they interact (e.g., Durante et al., 2014; Krems et al. 2015; Necka et al., 2016). An ability to detect and anticipate such behavioral changes would potentially allow women to preemptively respond to fertile-phase women, protecting themselves from disadvantageous social outcomes such as reduced monetary gains (e.g., Durante et al., 2014) or wandering partners (e.g., Hurst et al., 2017; Krems et al., 2016). Like the present study, however, this past work did not assess whether individuals were overtly aware of women's fertility status. Future research should further investigate whether differences in observers' scanpaths when looking at fertile and non-fertile phase women predict behavior towards them, and how observers' overt beliefs about the women relate to their looking behavior.

Importantly, much of the literature on fluctuations in women's behavior across the menstrual cycle is underpowered (Gangestad et al., 2016; Gonzales et al., 2015), and imprecision in ways that researchers have operationalized fertility in the past dampen the robustness of these findings (e.g., Wood et al., 2014). In the present study, we undertook

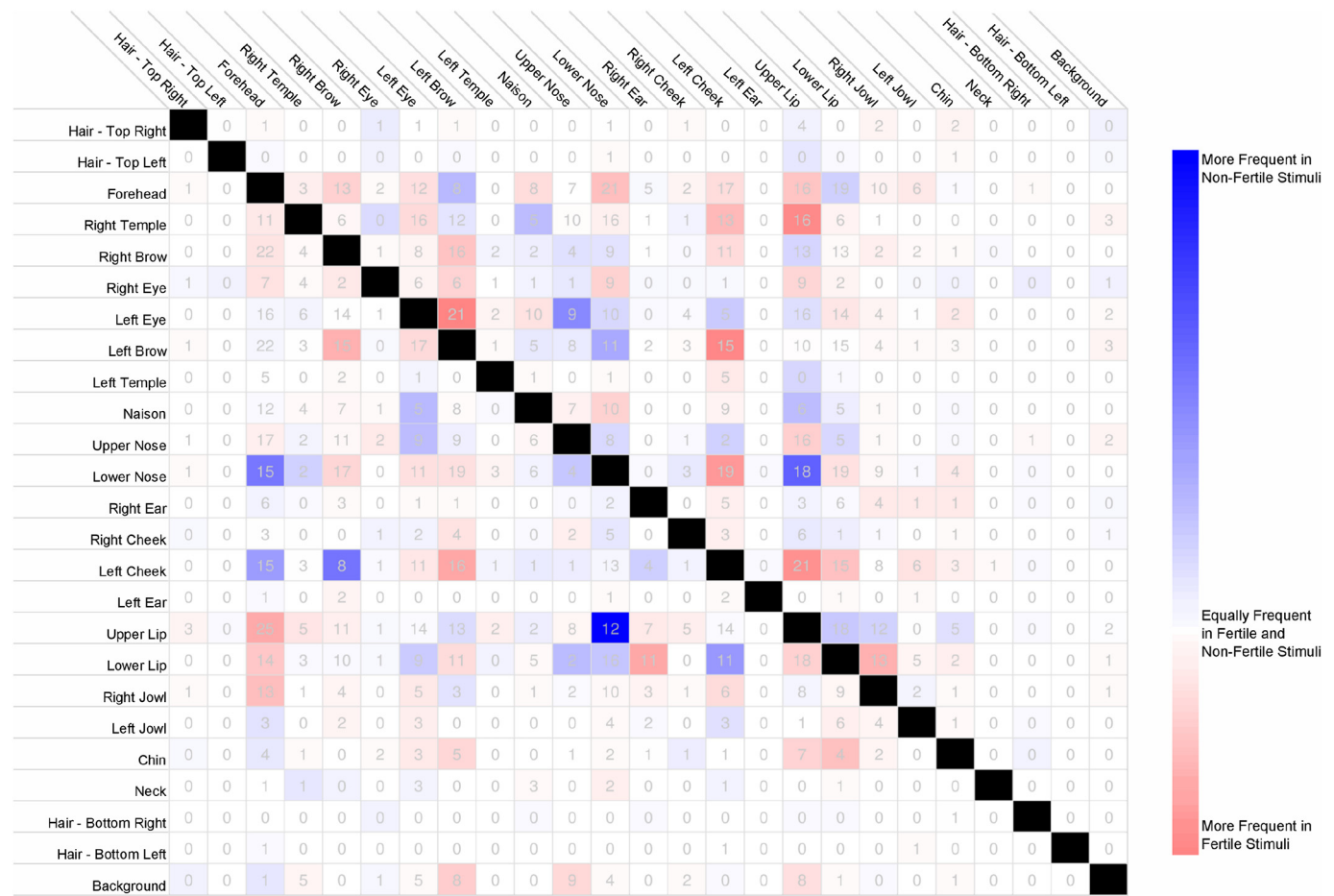


Fig. 3. Transition matrix for 25 AOIs as a function of stimulus fertility. For each stimulus, we computed how frequently participants transitioned from focusing on one AOI (originating AOI represented in rows) to another AOI (terminating AOI represented in columns). We then averaged within participants the relative frequency of transitions as a function of stimulus fertility – transitions that were more frequent on trials with fertile-phase stimuli are represented in red, and those that were more frequent on trials with non-fertile-phase stimuli are represented in blue. Represented here are the average frequencies of transitions, averaged across participants. Rows represent the AOI prior to transition, and columns represent the AOI to which participants' gaze transitioned; therefore, the frequency of transitions is not symmetrical around the diagonal. Numbers in each cell indicate the number of participants who demonstrated that transition; estimates where more participants exhibited the transition are more precise. Note that for description of AOIs, left and right refer to the stimulus woman's left or right, not the viewer's. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

multiple measures to validate that the stimuli we considered ‘fertile’ were actually in the fertile-phase of their menstrual cycles. We first classified our stimuli on the basis of stimulus women's self-reported menstrual cycle information, then verified fertility using their salivary estradiol-to-progesterone ratios to select women who had a higher probability of being near ovulation at the time that their ‘fertile’-phase photo was taken. We also used images of the same women across their menstrual cycles, rather than using images of some women at their fertile phase and others at non-fertile-phases, to verify that differences between phases pertained to fluctuations within, rather than between, women. This approach to stimulus selection and analysis reduces the likelihood that differences in our fertile- and non-fertile phase stimuli were confounded by factors other than fluctuating fertility across the menstrual cycle. However, because ovulation was not confirmed when stimulus women's ‘fertile’-phase photo was taken, we cannot be certain that women we classified as ‘fertile’ were indeed experiencing higher than normal odds of conception. Thus, a more conservative conclusion is that our data establish at minimum that viewers' eye movements differ when looking at women when women's ratio of estradiol-to-progesterone is high versus when it is low.

Though we believe women's fluctuating fertility across the menstrual cycle is the most theoretically grounded and parsimonious

explanation for differences in observers' eye gaze patterns, we acknowledge that it need not be the only explanation. For example, though fertility-related effects on attractiveness-enhancing behavior in humans (such as grooming behavior or wearing red) have received mixed support (e.g., Arslan et al., 2017; Beall and Tracy, 2013; Blake et al., 2017; Eisenbruch et al., 2015), evidence from a previously published study using stimuli studied here found that fluctuations in facial attractiveness within women tend to track with hormones putatively indicative of fertility (Puts et al., 2013), an effect that was conceptually replicated in a recent large-sample study (Jones et al., 2018; though see Catena, Simmons, & Roney, 2019). Significant differences in attractiveness between the subset of ‘fertile’- and ‘non-fertile’-phase stimuli used here did not emerge, nor did the variance in attractiveness between the two stimuli groups differ. Further, gaze patterns could be used to differentiate between ‘fertile’- and ‘non-fertile’-phase stimuli, even when parameters from scanpaths were first made linearly independent of attractiveness. It thus seems unlikely that the present findings could be explained by attractiveness, though it is possible that perceptions of attractiveness contributed in part to differences in eye movement patterns when observing fertile relative to non-fertile women. To the best of our knowledge, no published studies have studied how scanpaths differ on attractive or unattractive faces, though

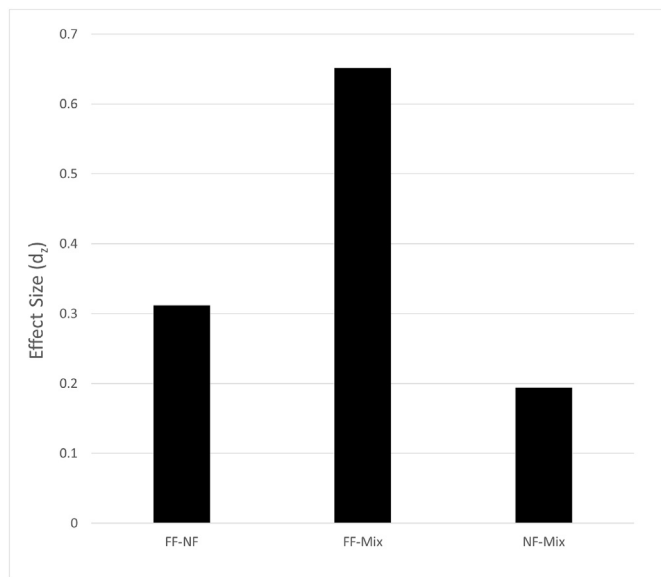


Fig. 4. Effect sizes for comparisons among ScanMatch Alignment Scores. Participants' scanpaths aligned more within pairs of fertile faces than when across pairs of different fertility statuses, as evidenced by higher alignment scores among fertile-fertile pairs than among fertile-non-fertile (mixed) pairs. Here, we demonstrate effect sizes for each comparison by computing the standardized difference between conditions within participants (e.g., $\frac{\mu_{diff}}{\sigma_{diff}}$), equivalent to Cohen's d_z . *FF-NF* = comparison of alignment scores between pairs of fertile faces and alignment scores between pairs of non-fertile faces, *FF-Mix* = comparison of alignment scores between pairs of fertile faces and alignment scores between pairs of fertile and non-fertile (mixed fertility status) faces, *NF-Mix* = comparison of alignment scores between pairs of non-fertile faces and alignment scores between pairs of fertile and non-fertile (mixed fertility status) faces.

convergent evidence suggests that attractive faces tend to capture gaze longer (Griffey and Little, 2014; Leder and Mitrovic, 2016; Mitrovic et al., 2018; Valuch et al., 2015). Further, several recent high-powered replications have demonstrated that women behave differently (at least towards men) and express differences in sexual desire across their menstrual cycles (Arslan et al., 2017; Roney and Simmons, 2013, 2016). To the extent that people associate changes in women's behavior with changes in their visual appearance across the menstrual cycle, they may develop expectations about social interactions with women that differ across the menstrual cycle and may be functional for fine-tuning social expectations and behaviors. Such expectations may be a more proximate mechanism to explain differences in people's gaze patterns when looking at the faces of women at different points in their menstrual cycle.

Our classifier used participants' scanpaths to detect whether they were observing a fertile or non-fertile-phase face with above chance accuracy, and average alignment scores differed significantly as a function of fertility, with moderate effect sizes. The magnitude of our alignment score differences is consistent with magnitudes that have previously been reported in literature using the same tools (Pellicano et al., 2011). Though our classifier did not perform as well as a classifier used previously to identify stimulus sex from eye movement data (Coutrot et al., 2016), stimulus fertility can reasonably be assumed to be much subtler than stimulus sex. In fact, given that humans exhibit a highly prototypical pattern for inspecting faces, it is to be expected that the similarities in visual inspection of faces (especially faces homogeneous on salient social and visual categories, such as race and sex) would dwarf any differences that might exist. That we found systematic differences in eye movement patterns as a function of fertility even given the overriding tendency for humans to exhibit characteristic patterns when looking at faces suggest that there are indeed differences

in visual processing as a function of women's fertility.

In summary, using analyses that accounted for both the spatial distribution and temporal dynamics of people's eye fixations, we found that people exhibit a less variable looking pattern when looking at the faces of fertile-phase women. Using eye movement data in multivariate analyses, we were able to determine with above chance accuracy whether participants were looking at a fertile- or non-fertile phase face. Together, these results demonstrate that people's eye movements differ as a function of whether they are looking at a woman's neutral face near peak fertility or when she is at a less fertile-phase of her menstrual cycle. Though visual cues to women's fertility status are subtle, the current results suggest that people differentially process women's faces as a function of the women's menstrual cycle phase.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2019.104562>.

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