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Women's pupillary responses to sexually significant others during the hormonal cycle

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Abstract

Women's sexual preferences can change over the hormonal cycle, as several studies, based on responses to questionnaires, diaries, and ratings of photographs, have indicated increased sexual interests around the time of ovulation. However, fewer studies have measured changes in attention or interest to sexually significant stimuli in terms of physiological responses that are not under voluntary control and measure sexual interest indirectly (i.e., without mention of sexual feelings or activities). In the present study, we indexed changes in sexual interest in terms of changes in the eye pupil's size. Pupillary diameter is known to have a proportional relation to the observer's level of interest and attention to a visual stimulus as well as to physical pleasure. Fourteen women (7 being "pill" users) viewed photos on a computer screen while their pupil diameters were recorded using an infrared eye-tracking device. Three measures were taken for each participant during three time windows that estimated the ovulatory, luteal, and menstrual phase of the cycle. We found an increase in mean pupil diameter for sexually significant stimuli during the fertile phase and this pupillary change was also specific to pictures of the participants' actual sexual partners. Moreover, this effect was only seen for women who did not use oral contraceptives. These findings confirm that women's attention for sexually significant stimuli is higher during their fertile phase of the menstrual cycle, and that changes in sexual interest are implicitly measurable using pupillometry.
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Keywords: Sexual stimuli; Pupillometry; Hormonal cycle; Oral contraceptive

Human mating can occur at times different from ovulation cycle and, in fact, most human sexual activity is non-reproductive and decoupled from the control of underlying hormonal mechanisms. Many evolutionary thinkers have also been fascinated by the fact that human females do not advertise their fertility, as some other primates do (e.g., by genital swelling; Domb and Pagel, 2001; Zinner et al., 2004), and that – essentially – human females "conceal" their fertile window to potential mates and, to some extent, to themselves (Burley, 1979). Such apparent loss of estrus presents a "problem" to evolutionary thinkers (Barrett et al., 2002, p. 112) since it would seem to create uncertainty about paternity (Hrdy, 1981).

However, several researchers have questioned whether the human unrestricted mating pattern is really different from the normal anthropoid primate reproductive biology (Dixson, 1998; Pawlowski, 1999; Wallen, 2001). Also, modern hominids have not entirely lost cyclical estrus (Wallen, 1990, 1995; Hrdy, 2000); instead, its manifestations have become much subdued. In fact, diary studies have shown that human females report to be more interested and think more often about sex (including increased autosexual behavior and interest in erotica) during the follicular phase (Schreiner-Engel et al., 1981; Stanislaw and Rice, 1988; Zillmann et al., 1995; Slob et al., 1996). Most importantly, women report to be more likely to initiate heterosexual encounters during their ovulatory period, when sexual intercourse could result in reproduction (Adams et al., 1978; Bullivant et al., 2004). In addition, at least in modern Western societies, women report to be more prone to fantasize or have sexual intercourse with a man other than their current partner during the fertile phase of the cycle (Gangestad et al., 2002; cf. Sheldon et al., 2006). Also, female faces are judged by men as more attractive when photographed during the fertile window of the cycle than when photographed during the luteal phase (Roberts et al., 2004).

During the late follicular period, females experience a peak in estrogen followed by a rise in progesterone. In female laboratory animals, a priming with estrogen followed by exposure to progesterone leads to female-typical sexual behaviors (Zehr et al.,

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1998; Pfaff et al., 2004). Oral contraceptives lead to heightened progesterone level and a suppression of the estrogen peak in midcycle as well as that of testosterone (Morris et al., 1987; Graham and Sherwin, 1993). This difference in hormonal levels is thought to be the reason why women on oral contraceptives do not report an increase in sexual behavior at the time of ovulation (Adams et al., 1978).

Indeed, during the hormonal cycle, several motivational (Fessler, 2003; Haselton et al., 2007), perceptual (Krug et al., 1994; Furlow, 1996), and cognitive (Hampson, 1990; Kimura, 1999) aspects of the human female can change. Importantly, women's sense of attraction towards men, as measured by facial preference, can be rather different during the phases of the hormonal cycle (Penton-Voak et al., 1999; Johnston et al., 2001; Koehler et al., 2002; Penton-Voak et al., 2003; Jones et al., 2005). However, most of this evidence has been based on responses to questionnaires, self-report in diaries, or ratings of photographs. Although these results have converged in indicating increased sexual interests around the time of ovulation, there is one important caveat when interpreting ratings or direct, explicit, responses to guided questions; that is, these may simply reflect the participants' beliefs that there should be a difference in motivation along the cycle, without this necessarily mirroring a physiological change in the actual drive or sexual interest.

Hence, it seems particularly important that converging evidence must be found between the studies that measure sexual interest with questionnaires, diaries, and ratings of photographs, and those using more objective responses (i.e., physiological responses that are not under voluntary control) as well as indirect testing methods (e.g., where sexual feelings are not mentioned). In addition, emotional reactions typically involve extensive cognitive processing but some "core" emotional response can occur unconsciously (e.g., "liking", Berridge, 2003; Berridge and Winkielman, 2003). That is, implicit affective reactions that remain unconscious can be manifested in observable affective reactions (either behavior or physiological responses; LeDoux, 1996; Damasio, 1999; Zajonc, 2000). Most relevantly, explicit subjective reports are necessarily limited to what can be consciously introspected (cf. Sheldon et al., 2006). Hence, subjective reports may miss affective reactions that occur without a person being aware of the causal event (Berridge, 2003). In fact, explicit and implicit motives often diverge (Woike et al., 2003).

Pupillometry or measurements of changes in the eye pupil's diameter would seem to constitute one physiological variable that may be particularly appropriate for measuring, in an implicit but objective manner, someone's level of interest or attention towards a stimulus (Kahneman, 1973) or cognitive effort (Hess and Polt 1964; Kahneman and Beatty, 1966; Just and Carpenter, 1993). Hence, relevant stimuli for the organism (cognitively engaging or emotionally significant stimuli, including the sexual) might also trigger an unconscious attentional response that is then reflected in the autonomic response of pupillary dilation (Kahneman and Peavler, 1969). Indeed, early pupillometric research found that pupil diameter increases while participants watched nude pictures of the other sex (Hess and Polt, 1960; Hess et al., 1965; Garrett et al., 1989) and the effect generalizes to sexual auditory stimuli (Dabbs, 1997). Pupillometry can also directly index sexual pleasure: Bernick and colleagues (1971) reported a positive correlation between pupil size and duration of erection in men who were watching an erotic movie. Whipple and colleagues (1992) found a significant increase in pupil diameter in females during orgasm (after genital self-stimulation) compared to sexual imagery and resting periods. In this study, measurements of systolic blood pressure and heart rate were also taken during the same conditions; interestingly, pupillary size and systolic blood pressure were the best measures for discriminating the self-stimulated orgasm from the other states.

Thus, the current study examines whether the different phases of the menstrual cycle influence the autonomic response of pupillary size, which is not under voluntary control of the subject, while the participants view photo images of individuals who vary in terms of their sexual desirability. As mentioned above, previous studies have suggested that both sexual interest and activities change over the cycle. The goal of this study was to seek converging evidence by showing that women show more attention towards sexually desirable stimuli during their fertile phase of the cycle. Thus, we predicted that females would be more attentive to males during their follicular phase and especially to those "interesting" males who they already consider as sexually attractive (e.g., favorite actors) and could be of reproductive significance (i.e., boyfriends). Specifically, the present study monitored changes in pupillary diameter to facial portraits as an index of changes of interest towards significant individuals during the hormonal cycle. As opposed to conscious judgment of attraction, pupil dilation is not under direct voluntary control of the subject. This makes pupillometry a particularly fruitful way to examine the phenomenon of sexual attractiveness. We predicted that pupillary size would be largest during the ovulatory phase and specifically when presenting images of sexually significant desirable objects (i.e. the boyfriends and the favorite actors) but not of other men who were judged as non-attractive (although they could be celebrities) or of individuals who were unlikely to be a current object of desire (e.g., photos of the other participants' boyfriends or of other women, i.e. actresses). Finally, since previous studies (e.g., Adams et al., 1978) have suggested that cycles in sexual desire are flattened or inexistent in women using oral contraceptives (which would also be expected on the basis the effect of contraceptive pills on the hormonal peak of estrogen), we predicted that only the participants in the present study who did not use the pill would show the predicted effects.

Method

Participants

The participants were 14 female students at the University of Tromsø in Norway, ranging from 21 to 24 years old, mean age 22.5 years. The only requirement for participating in the study was having a current relationship with a boyfriend. The length of these romantic relationships ranged from 2 months to 6.5 years. All women were requested to provide a recent photograph of their romantic partner. The participants were told that the purpose of the study was to examine their pupillary reactions to photographs. Since the menstrual cycle is fundamentally a within-subject concept, we adopted a design in which all participants were tested 3 times in different moments of their cycle. We used the reverse cycle day (RCD) method to predict the day of ovulation, since this method is least demanding for the participants and several previous studies that

have used day-in-cycle have been successful in predicting other effects of theoretical interest (e.g., Adams et al., 1978; Kimura, 1999; Gangestad and Thornhill, 1998; Penton-Voak et al., 1999; DeBruine et al., 2005; Jones et al., 2005; Haselton and Gangestad, 2006). We expected a higher activation of the autonomic nervous system in the ovulatory phase (12–15 after the first day of menses) than during a segment of the luteal phase (days 20–23) or the menstrual phase (days 1–5).

Half of the participants in this study, at the time of the experiment, were using contraceptive pills and the other half did not. All participants reported having regular cycles. They also had normal vision or corrected with contact lenses. All participants were recruited among the experimenter's (L.F.) friends and acquaintances, since students in psychology may have been aware of cycle effects. Participation was voluntary but a lottery ticket was given as a reward at the end of each session. All participants were blind to the main hypothesis of the study and they were debriefed about the purpose of the study at the end of the third, final, session. At the debriefing session, no participant reported having specific knowledge of cycle effects on either sexual interest or pupillary responses.

Apparatus and stimuli

Pupil diameter was recorded from the participant's left eye by means of the Remote Eye Tracking Device (RED), built by SMI-SensoMotoric Instruments® from Teltow (Germany). The RED 2 can operate at a distance of 0.5–1.5 m and the recording eye tracking sample rate is 50/60 Hz – that is approximately every 20 ms, with resolution better than 0.1°. The eye-tracking device operates based on determining the position of two high contrast elements in the eye: the pupil and the corneal reflection. According to an independent calibration procedure, given the constant distance from the screen, the pupil diameter was recorded with a definition of about 500 pixels/mm. However, given that changes in diameter were used in the interpretation of data, the exact eye diameter was not needed. Illumination of the room does not interfere with the recording capabilities of this apparatus. The coordinates of all boundary points are fed to a computer, which, in turn, determines centroids of the two elements. The vectorial difference between the two centroids is the "raw" computed eye position, which in turn is used to compute the pupil diameter based on the horizontal and vertical projections of the pupil's ellipsoid at the different sampled positions. The pictorial stimuli were prepared using Adobe Photoshop 7.0, and presented by use of the slideshow feature of ACDsee© 32v2.4 software on a 49-cm flat colour monitor.

The participants were shown in total 20 photos of faces. These included 5 photos of currently famous male actors' faces (e.g., Brad Pitt). Importantly, for each participant, one of the photos showed the face of the actor that the participant had previously indicated to be her favorite actor (i.e., the actor they deemed to be most attractive in their opinion). There were also 5 photos of currently famous female actresses and, as for the male actors, one showed the face of the participant's favorite actress (i.e., the actress each participant deemed to be most attractive in their opinion for the opposite sex; e.g., Angelina Jolie). In addition, there were 5 photos of well-known (but rather neutral in terms of attractiveness) Norwegian celebrities (e.g., the national TV channel's "weather man"; or some aged politician). Most importantly, each participant saw also the face of her boyfriend plus 4 photos of some of the other participants' boyfriends. The pictures of the boyfriends were obtained from each of the participants prior to the first session and the rest of the photos were downloaded from the Internet by use of www.google.com (image search engine). The photos were then edited by the use of Adobe Photoshop 7.0© to show the face only and they were cropped to be the same size. A blue background surrounded each photo. In pupillometric studies, it is important that pupillary changes for different classes of pictures cannot be explained away simply in terms of differences in light level, either in the ambient or in average luminance of the pictures in each condition (Janisse, 1977; Garrett et al., 1989). Ambient light was kept constant during the study and, importantly, average luminance values were obtained for each of the pictures (by use of the histogram function in Adobe Photoshop 7.0©) and these showed that the least bright class of photos (Celebrities: Mean Luminance=115.9; SD=19.9) and the brightest class of pictures were both within 1 standard deviation of the other (Actresses: Mean Luminance=134.6; SD=24.3) and Actors (Mean Luminance=117.8; SD=20.7) and Boyfriends (Mean Luminance=118.0; SD=17.2) showed very similar intermediate values. Finally, artifacts based on difference in images' light levels cannot possibly explain any interactive effects with phases of the hormonal cycle.

All participants viewed each picture type in the same order and the same sequence was repeated in each session. Specifically, the following sequence was used: 1) Actor; 2) Actress; 3) Celebrity; 4) Other's boyfriend; 5) Actor; 6) Other's boyfriend; 7) Celebrity; 8) Actress; 9) Favorite Actor; 10) Actress; 11) Participant's Boyfriend; 12) Celebrity; 13) Actor; 14) Favorite Actress; 15) Other's boyfriend; 16) Celebrity; 17) Actor; 18) Other's boyfriend; 19) Celebrity; 20) Actress. Note that each participant's boyfriend's photo was seen as the 11th picture within the series of 20, which was intended to control possible effects on the pupillary response that may occur at the beginning of the presentation of a series of visual stimuli. For the same reason, the favorite actor and favorite actress pictures were positioned as the 9th and 14th pictures, respectively, within the series.

Procedure

The participants were tested in a windowless and sound-insulated laboratory while seated at a distance of 72 cm in front of the computer screen. To stabilize and reduce head movements, their chins were placed in a height adjustable headrest. They were asked to look at the screen while the experimenter adjusted the camera to achieve a good resolution of the pupil. At the beginning of each trial, a standard routine of calibration was used. The eye position was recorded at 9 standard calibration points, appearing as white plus signs on a blue background, corresponding to a regularly spaced 3×3 matrix. Eye position is relevant for the exact computation of pupillary horizontal and vertical diameters, since the projection of the eye pupil in the camera changes with eye position. Each participant was then instructed to fixate at each location while the eye position was sampled at a rate of 1000 Hz for 100 ms near the middle of this interval. The participants were then told to fixate on the monitor and maintain their gaze at all times on the slideshow of photos appearing on screen.

The same sequence of pictures was shown to each participant in each of the three recording sessions. Pupillary diameters were recorded during the presentation of the photos, starting from the onset of the picture on screen and for the duration of 10 s. No other task was given to the participant than that of looking at the screen whenever a picture appeared on it. At the end of each session, the participants were given a questionnaire where they would rate the attractiveness of the people seen on the photos. They would rate the photos on a scale from 1 to 7, where 7 represented "extremely attractive" and 1 "least attractive". While filling this questionnaire, they were also given the opportunity to see each of the photos again in the same sequence. The same procedure was conducted during a session occurring during either the ovulatory phase, the luteal phase or the menstrual phase of each participant. Since we used the RCD method to predict the day of ovulation (Lenton et al., 1984; Thornhill and Gangestad, 1999), each participant when first contacted reported the first day of menses and from that the first session was scheduled. As a result, for the Pill group, there were 3 participants who had their first session while in the luteal phase; 2 while in the ovulatory phase, and 2 while in the menstrual phase; for the No-Pill group, there were 2 participants who began testing while in the luteal phase; 2 while in the ovulatory phase, and 3 while in the menstrual phase. All 14 women completed all of the 3 test sessions and each participant was scheduled for three consecutive phases so that no participants had a session that did not follow immediately after one of the other estimated phases.

Results

Pupillary changes

First, we computed the mean pupil size for each participant in each of the estimated phases of the hormonal cycle (ovulatory, luteal and menstrual; or their day count equivalents for the participants using oral contraceptives) and these three values were averaged to compute the mean pupillary size for each participant. This value was then used to compute a ratio between the mean pupillary value for each of the 6 different conditions (boyfriend, favorite actor, others' favorite actors, favorite actress, others' favorite actresses and celebrities) over each participant's overall mean pupil size so as to obtain a mean pupillary change (no

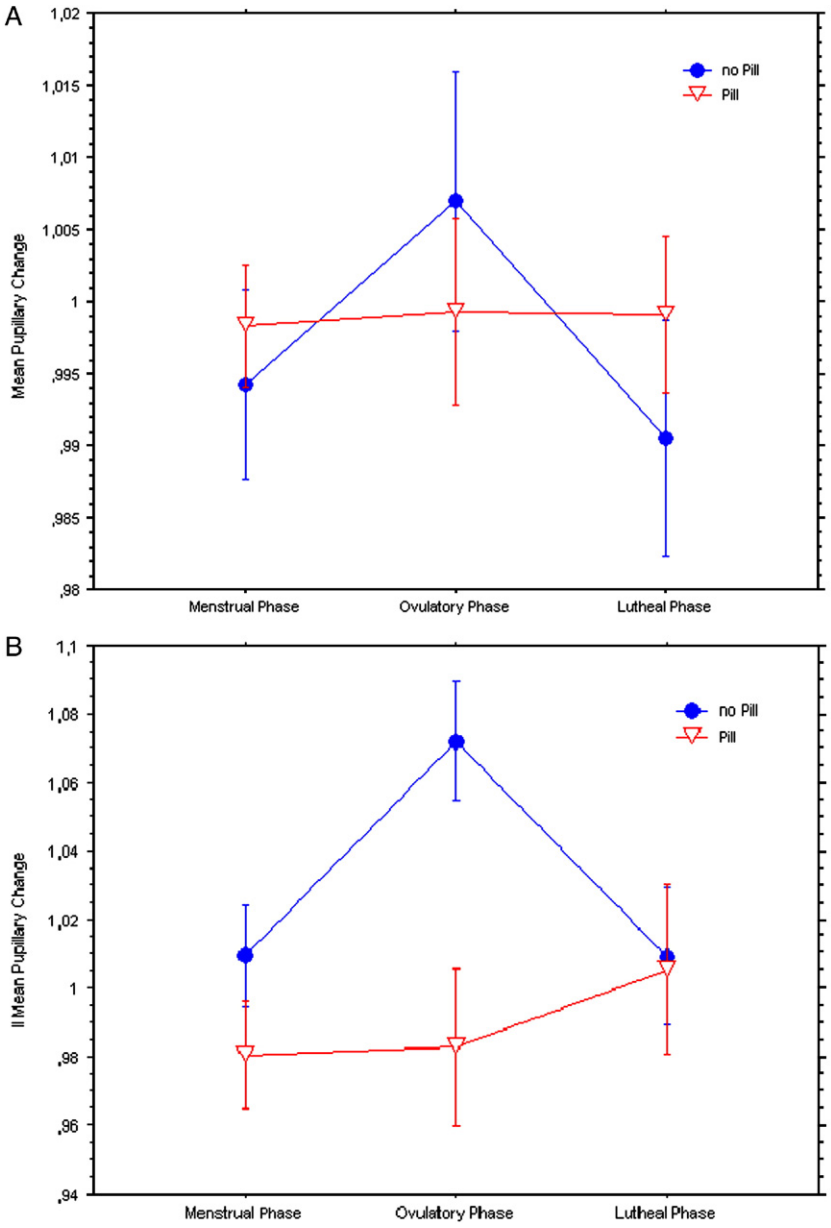

Fig. 1. (A) Mean pupillary change of participants using no oral contraceptives (circles) and of participants using the pill (triangles) in the three estimated phases of the cycle. Bars show 95% confidence intervals. (B) Mean pupillary change of participants using no oral contraceptives (circles) and of participants using the pill (triangles) in the three estimated phases of the cycle (Ovulatory; Luteal; Menstrual) while viewing a photo of their boyfriends. Bars show 95% confidence intervals.

change=1; dilation >1; constriction <1) for each participant in each session and condition. This obtained measure is appropriate for comparisons between participants, since there exist individual differences in pupil size that may result in different absolute values of pupillary size for each group of participants.

We first performed a repeated-measures ANOVA, with Photo (boyfriend, favorite actor, others' favorite actors, favorite actress, others' favorite actresses, celebrities, and others' boyfriends) and Phase (ovulatory, luteal and menstrual) as the within-subject factors. Pill (yes, no) was used as the between-subjects factor. Change in Mean Pupil Diameter (i.e., average of horizontal and vertical diameters) was the dependent variable. This analysis revealed a main effect of Photo, $F(6,72)=13.1$, $p<.0001$ (Lambda=78.7; Power=1.00), a main effect of Cycle, $F(2,24)=4.9$, $p=.02$ (Lambda=9.8; Power=.76). Most importantly, Photo had an interactive effect with Pill, $F(6,72)=4.1$, $p=.001$ (Lambda=24.9; Power=.97) as well as with Cycle, $F(12,144)=2.1$, $p=.01$ (Lambda=25.5; Power=.93). Moreover, Cycle interacted with Pill, $F(2,24)=4.4$, $p=.02$ (Lambda=8.7; Power=.70). Essentially, the above effects of Photos and Cycle can be summarized as effects due to pupillary changes of the group that did not use the pill, whereas the interactive effects of Pill were accounted by the absence, or reduction of a change in pupil size over Cycle or Photo, of the of the group that did use the pill. The difference between pill users and no-users is best illustrated by the interactive effects of Pill and Cycle, shown in Fig. 1, and that of Pill and Photo, shown in Fig. 2.

Since the Pill users showed no change in pupillary size over the selected time windows of the cycle, we analyzed in a repeated-measures separate ANOVA the No-Pill participants only ($N=7$),

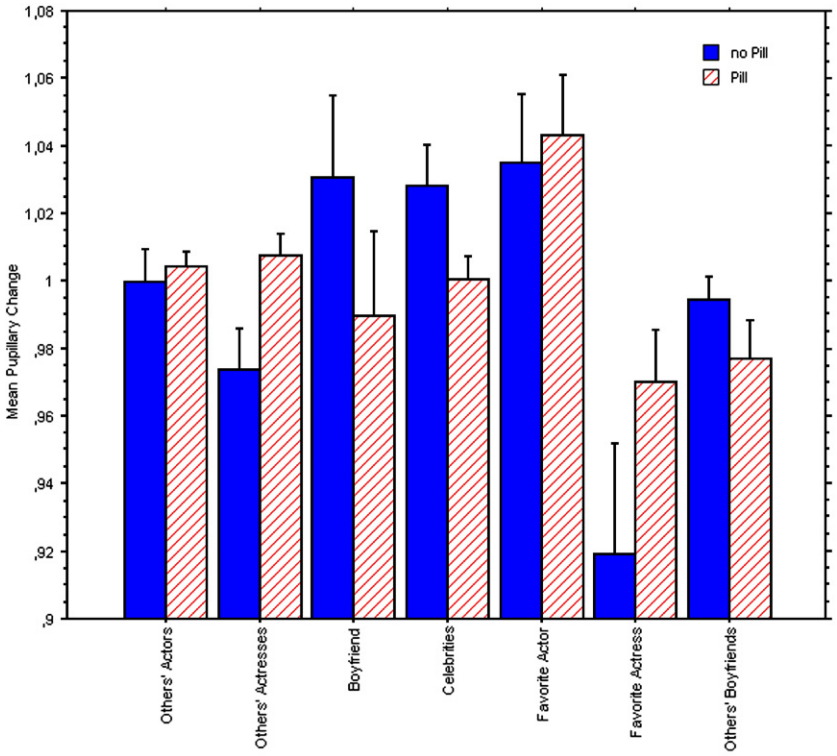

Fig. 2. Mean pupillary change for each photo of participants using no oral contraceptives (filled column) and participants using the pill (striped column). Bars show 95% confidence intervals.

with Photo (boyfriend, favorite actor, others' favorite actors, favorite actress, others' favorite actresses, celebrities, and others' boyfriends) and Cycle (ovulatory, luteal and menstrual) as the within-subject factors. This analysis revealed a main effect of Photo, $F(6,36)=7.9$, $p<.0001$ (Lambda=47.2; Power=1.00) and Cycle, $F(2,72)=7.7$, $p=.007$ (Lambda=15.4; Power=0.90). Increases in pupillary sizes occurred for the photos of the boyfriends (Mean Change=1.03; SD=.038), favorite actors (Mean

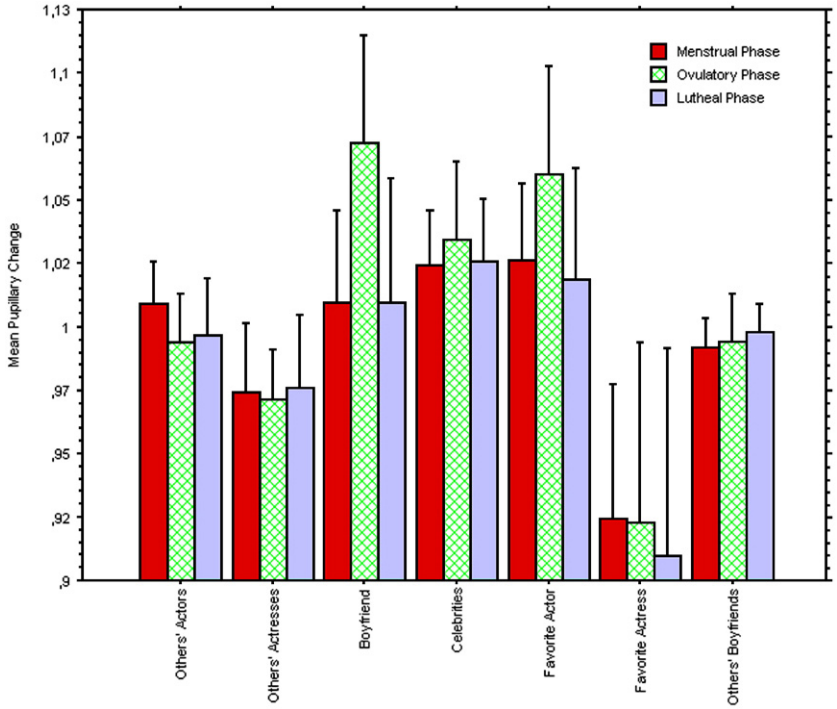

Fig. 3. Mean pupillary change for each photo in participants using no oral contraceptives in the three estimated phases of the cycle. Bars show 95% confidence intervals.

Change=1.04; SD=.032), and the celebrities (Mean Change=1.028; SD=.024); instead, there were no changes for others' favorite actors (Mean Change=1.00; SD=.017) as well as others' boyfriends (Mean Change=.995; SD=.009); decreases in pupillary sizes occurred for favorite actress (Mean Change=919; SD=.072) as well as others' favorite actresses (Mean Change=974; SD=.026). Regarding the main effect of Cycle, there was an increase in pupillary size during the estimated ovulatory phase (Mean Change=1.007; SD=.009); in contrast, mean pupillary size decreased during the menstrual and luteal time windows (Mean Change=.994; SD=.005; Mean Change=.990; SD=.012, respectively).

Most importantly, there was a highly significant interaction between Photo and Cycle, $F(12,72)=2.91$, $p=.002$ (Lambda=34.9; Power=0.98). As shown in Fig. 3, the greatest changes occurred for the two sexually relevant stimuli (boyfriend and favorite actor) and only during the estimated ovulatory phase.

In order to further explore these effects, which were predicted, we performed two separate one-way ANOVAs on the pupillary responses to the Boyfriend photos alone or to the Favorite Actor alone. The analysis for the Boyfriend in the seven No-Pill participants showed a change in pupil diameter that was statistically significant for Cycle, $F(2,12)=8.62$, $p=.005$ (Lambda=17.2; Power=.92). As shown in Fig. 3 (bars represent 95% confidence intervals), during the ovulatory phase, the participants showed a peak in mean pupil diameter compared to the luteal and menstrual phases. This effect supports our hypothesis that sexually relevant stimuli are processed differently during the estimated fertile phase and in a way that is consistent with an increase in interest/attractiveness that is specific to targets of sexual desire during this part of the hormonal cycle.

In contrast, the analysis of the Favorite Actor, despite showing the same trend as that seen with Boyfriend pictures (see Fig. 3), failed to reach significance for the factor of Cycle, $F(2,12)=2.89$, $p=.09$ (Lambda=5.8; Power=.45). As indicated by the estimate of statistical Power, this was rather low for this analysis but it is likely that a significant effect could be found with larger sample sizes than that of the present study.

Interestingly, there were two unexpected findings: (1) the low pupil diameter's mean for Favorite Actress in both Pill and No-Pill groups (see Fig. 2); this effect did not show any cyclic variations in the group using no oral contraceptives (see Fig. 3) but appeared rather stable over sessions; (2) the increased pupil diameter's mean for Celebrities in both Pill and No-Pill groups (see Fig. 2); again, this effect was stable over sessions or cycle.

In a separate ANOVA, we also analyzed the data of the Pill users ($N=7$). This showed only a significant main effect for Photo, $F(6,36)=12$, $p<.0001$ (Lambda=72.1; Power=1.00). Pupil diameters were largest for the favorite actor (see Fig. 2). However, there was no hint of cyclic fluctuations as found for No-Pill participants. This null finding was also expected on the basis the effect of contraceptive pills on the hormonal peak of estrogen and by women's self-reports on sexual desire and activities over the cycle.

Attractiveness ratings

As done earlier for the pupil diameters, we first performed a repeated-measures ANOVA, with Photo (boyfriend, favorite actor, others' favorite actors, favorite actress, others' favorite actresses, celebrities, and others' boyfriends) and Phase (ovulatory, luteal and menstrual) as the within-subject factors. Pill (yes, no) was used

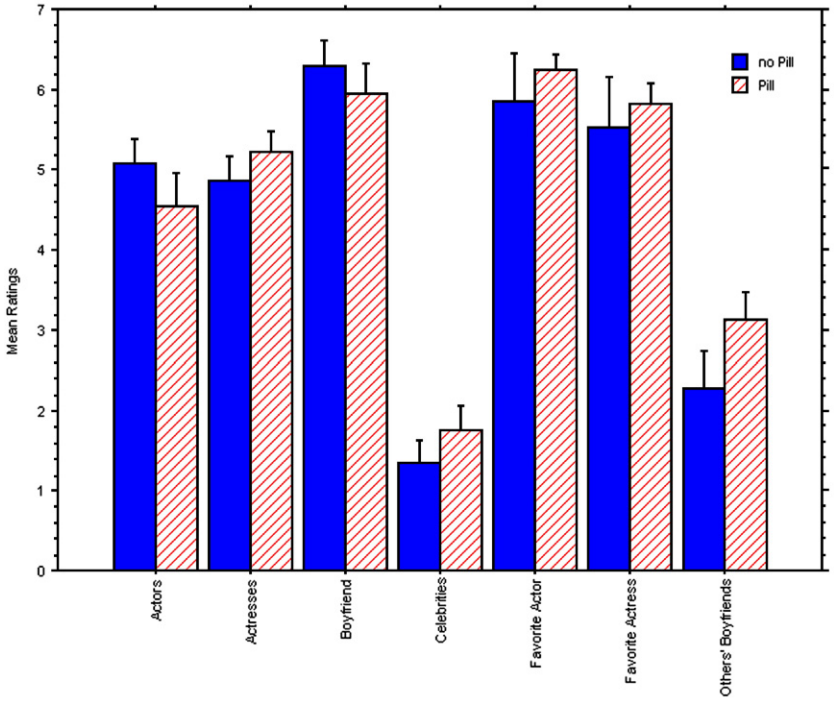

Fig. 4. Mean attractiveness ratings for each photo of participants using no oral contraceptives (filled column) and participants using the pill (striped column). Bars show 95% confidence intervals.

as the between-subjects factor. Mean Attractiveness Score was the dependent variable. There was only a significant main effect of Photo, $F(6,72)=104.4$, $p<.0001$ (Lambda=627; Power=1.00). When viewing the participants' ratings of attractiveness (see Fig. 4), the Boyfriend, the Favorite Actor and Favorite Actress stand out with high ratings. This was expected since participants should find their boyfriend attractive and the choice of Favorite Actor/Actress also directly reflects the participants' judgments of how attractive they deem a particular actor or actress to be.

As discussed earlier, an unexpected finding was the low pupil diameter's mean for Favorite Actress in both Pill and No-Pill groups (see Fig. 2) which was also in complete contrast with the subjective ratings of attractiveness (see Fig. 4), since the Favorite Actress obtained a rather high mean score=5.7 (SD=1.05). The reverse relationship between pupil diameters and ratings was instead observed for the Celebrities, where participants showed large pupil diameters (compare Figs. 3 and 4), which also had not been anticipated. Celebrities' attractiveness ratings obtained the lowest mean=1.6 (SD=.67). However, as expected for both conditions, pupil diameters and ratings were stable over the cycle.

Regression analyses of attractiveness ratings and pupillary changes

To assess whether pupillary changes simply reflect a pupillary response to attractive photos instead of sexually significant stimuli per se, we first performed a simple regression between each attractiveness rating (as collected at the end of each session) and the corresponding mean pupillary change for each participant and regardless of phase of the cycle. This analysis revealed no significant relationship ($R^2<.0001$). An additional simple regression between each attractiveness rating (as collected at end of each session) and the corresponding mean pupillary change for only the No-Pill participants and only during their ovulatory phase also failed to reveal a significant relationship ($R^2=.006$). Indeed, as shown in Figs. 2 and 4, there was no consistent relation between means of pupillary change and of attractiveness, since photos of actresses (either own favorite or others') showed small pupillary sizes despite the high attractiveness ratings and the celebrities showed the inverse relation (large pupillary sizes despite the low attractiveness ratings). Hence, we can rule out the possibility that the attractiveness levels of the photos exerted a gating effect on the pupillary responses.

Eye position

Given the length of each of the pupillary recording (10 s), one would like to know whether the participants showed sustained attention to the photos or whether they may have looked for a substantial part of each recording outside of the area of the screen corresponding to the photo. This was checked by analyzing the eye position's data, since infrared pupillometry entails keeping track of eye position in order to compute the correct size of the pupil's horizontal and vertical diameter from its orthogonal projection into camera. Thus, we selected a region of interest on the screen that corresponded to the screen's area where the photos were shown and we then computed (by use of the BeGaze software©) the percentage of time the eye spent within such region of interest. This occurred on average for 96% of the time (SD=5%; range: 92–99%). A repeated-measures ANOVA, with Photo, Phase, and Pill as factors and percentage of time as the dependent variable, showed no significant differences. Hence, we conclude that the pictures were indeed attended overtly by all of the participants in each session.

Discussion

Using the infrared pupillometric method, we recorded pupil diameters of female participants while they were viewing photos of individuals of sexual significance (boyfriend or favorite actor) as well as photos of other individuals who were rated low in attractiveness (e.g., others' boyfriends or celebrities). Pupillary measurements were taken three times for each participant, within 3 time windows of each woman's menstrual cycle that estimated the occurrence of the ovulatory, luteal and menstrual phases. Thus, the goal of this study was to explore possible differences in autonomic activation across the menstrual cycle in response to images of sexually attractive individuals. Specifically, pupillary changes were measured in relation to whether they were above and below the average pupillary size over all sessions and conditions and, as a result, these ranged from a decrease in size of about −8% to an increase of about 8%. The maximum increase was measured when our female participants were in their estimated ovulatory phase and when they were looking at their boyfriends' pictures (Fig. 3). The findings confirmed the presence of cyclic differences in pupillary diameters while watching facial portraits of sexually interesting individuals. Remarkably, the participants using contraceptive pills did not show cyclic fluctuations of pupil sizes. As hypothesized by, for example, Adams et al. (1978), such a flattening of responses could result from the higher progesterone levels and suppression of estrogens during the fertile period. In addition, circulating testosterone in females, also related to sexual motivation (Morris et al., 1987), peaks at midcycle but can be suppressed in women using oral contraceptives (Graham and Sherwin, 1993).

The most important finding was that the No-Pill participants showed a significant increase in pupil diameter during their estimated ovulatory phase. Indeed, the effect was highly specific to the appearance of the photos of their boyfriends. However, a similar effect approached significance when the participants viewed photos of their favorite actors. Assuming that a favorite actor represents the most likely candidate for an extra-pair sexual encounter, an increased response to such a target of interest would be entirely consistent with previous reports that women (at least, in Western societies) report to be more prone to fantasize or have sexual intercourse with a man other than their current partner during the fertile phase of the cycle (e.g., Gangestad et al., 2002; Haselton and Gangestad, 2006).

We conclude that women show more autonomic system activation when viewing photos of sexually desirable subjects during their fertile phase; thus, changes in pupil diameters might index changes in sexual interest or sexual arousal. Alternatively, these increased pupillary dilations may reflect non-specific

changes in general arousal, which could in turn influence sexual attraction (cf. Foster et al., 1998). Estrogen has influence on arousal both at the level of the central nervous system (Klaiber et al., 1982; Shaywitz et al., 1999; Fernandez et al., 2003; Goldstein et al., 2005) and the autonomic nervous system (Dye, 1992). However, if the measured pupillary changes at ovulation had only been an increased responsiveness of the sympathetic system to salient stimuli, one should have expected increased pupil dilations to several of the classes of visual stimuli, if not all, we had included in the study; yet there was little indication of widespread effects (as it can be seen in Fig. 3). Instead, increased pupil dilations not only were time-locked to the ovulatory phase but they were specifically restricted to one class of photographic stimuli (i.e., the boyfriend's photo) and, perhaps, also to the favorite actors' photos. Other classes of pictures that were also rated high in attractiveness (e.g., favorite actress or all actresses' and actors' photos) did not evoke any detectable pupillary change along the cycle.

If we accept the possibility that pupillary size can reliably index sexual interest, the present findings are highly consistent with earlier research showing that women have a general increase in sexual activity, attraction and interest when in their fertile period (e.g., Adams et al., 1978; Haselton and Gangestad, 2006; Jones et al., 2005; Gangestad et al., 2005). In other words, by monitoring the physiological parameter of pupillary size we can measure women's changes in attention towards targets of sexual desire and successfully tap into a high-level psychological appraisal of affective–sexual interest.

Finding converging psychophysiological evidence to women's self-reports of sexual interest would seem important, since interpreting ratings or direct, explicit, responses to guided questions entails a fundamental caveat: These explicit responses may simply reflect the participants' beliefs that there should be a difference in motivation along the cycle, without this necessarily mirroring a physiological change in the actual drive or sexual interest. For example, such beliefs may originate from the non-specific effects of high levels of circulating estrogen; that is, around the time of ovulation, women are more likely to feel self-confident, restless, and they have improved sense of smell (Doty et al., 1981) and visual perception (Parlee, 1983; Maguire and Byth, 1998). All these are signs of enhanced motor and sensory capability that are likely to reflect cyclic variations in arousal more than specific changes in sexual motivation. Most importantly, it is well known that menstruation is defined in many socio-cultural contexts in negative terms (Walker, 1997). Thus, given the increased sense of well being and arousal of periods of the cycle distant from the menstrual period (Clayton et al., 1999), one cannot discard the possibility that women may simply believe that they should feel more attracted and attractive, and consequently more sexually active, in the former than the latter phases of the cycle. Indeed, a study by Ruble (1977) examined the effect of menstrual expectations on reporting symptoms, in which participating women were led to believe they were in different phase of the cycle that they actually were. Expectations but not hormonal state determined the content of the women's reports. Ruble's (1977) study is a good example of the importance of beliefs and biases in mediating explicit reports (cf. Rosnow and Rosenthal, 1997), especially when concerning feelings and behavior during the cycle.

Interestingly, despite the small sample size of the present study, the results were clear, which may have resulted from choosing "ecologically valid" stimuli. Specifically, there was no doubt that the present stimuli were of sexual interests to the participants, since the images showed individuals (boyfriends) that are already partners to each participant's "real-life" sexual activity. Moreover, some of the stimuli may have also been part of the participants' "real-life sexual fantasies" (i.e., the favorite actor). Previous studies' attempts to induce increases in physiological responses by using erotic pictures (e.g., Garrett et al., 1989) or films (or fantasies) involving strangers may have tended to be relatively ineffective. Some of these studies have also measured sexual arousal in terms of maximum pulse amplitude and maximum blood volume in the vagina (by use of photoplethysmography) during various phases of the cycle. For example, Meuwissen and Over (1992) observed only negligible changes in physiological responses over the course of the cycle and concluded that there was no support for the claim that female sexual response varied systematically across the menstrual cycle. Similar negative findings for changes in vaginal blood volume, vaginal pulse amplitude, or labial temperature as a function of phase of the menstrual cycle had been reported in other studies (e.g., Hoon et al., 1982). More recently, an eye-tracking study of gaze while viewing erotica (Rupp and Wallen, 2007) showed no change in women's looking patterns during the hormonal cycle. In contrast, Slob and colleagues (1991, 1996) monitored changes in the temperature of a labium minus in women watching erotic films and found an increase of labial temperature in women during their follicular phase; however, this physiological response to erotic films appeared to habituate rapidly from a first session to a second session. Also, in the study of Slob et al. (1996), no correlations were found between subjective sexual arousal measurements and the objective physiological changes.

In general, a lack of consensus between studies using objective methods and those using introspective methods would seem rather worrisome, but a more appealing possibility is that while the vaginal response to fantasy may differ negligibly during the cycle, the level of sexual interest and drive may be under significant hormonal control. Thus, a caveat of several studies that one needs to consider is that of ecological validity. A lack of it could obscure the detection of reliable physiological sexual response differences (Meston and Gorzalka, 1996). Attempts to induce increases in sexual arousal may be relatively ineffective with films or fantasies that include strangers compared to those that involve real-life sexual partners and activities (Masters and Johnson, 1966). In fact, introducing real-life elements into the laboratory (e.g., Bartels and Zeki, 2000) may be particularly beneficial when studying female participants (cf. Chivers et al., 2004).

Remarkably, in the present study, several of the pictures not only failed to evoke cyclic fluctuations in mean pupillary change but they actually resulted in lower than average pupillary responses. For example, pupillary responses to Favorite Actress were the smallest (about −8%; see Fig. 3). It may seem puzzling that the mean pupillary diameter for Favorite Actress was markedly smaller than for any of the other groups of photos,

especially in the light of the fact that these very pictures received a very high score on attractiveness (Fig. 4). One possible reason for such an inverse relationship between ratings of attractiveness and pupillary size might be that, even though these women are deemed beautiful, the female participants did not considered them as targets of sexual interest. Hess and Polt (1960) found that female participants had an increase in pupillary size of about 20% (as measured from a baseline consisting of control patterns) when watching pictures of nude males, but the pupillary change was reduced to about one third of that of the nude males when they were watching instead pictures of nude females. Additionally, pupillary narrowing for female stimuli could be accounted in terms of intrasexual competition, since women can rate other women's facial attractiveness lower on days with high estrogen levels (Fisher, 2004), so to decrease a rival's perceived value.

Another unexpected relation between ratings and pupillary diameters occurred with the images of celebrities (i.e., individuals who equaled the actors in fame but who were rated low in attractiveness). Although this stimuli were intended to constitute a somewhat neutral group to compare with the other "sexually interesting" groups of photos, it turned out that pupil sizes were overall much larger than expected for a group of "neutral" faces (Figs. 2 and 3), despite the attractiveness ratings for the same faces were, as expected, the lowest (Fig. 4). We surmise that such a contrast originated from the fact that participants tended to find the occasional appearance of a photo of these celebrities as "comical" instead of just neutral. Indeed, several participants laughed when they saw these photos, and several participants later explained their reaction of surprise in seeing a few elderly, unattractive, men mixed among a majority of young males (the boyfriends) and other unusually attractive individuals (Hollywood actors and actresses). Hence, the pupil dilations might be explained by another kind of activation of the autonomous nervous system in response to positive emotions, namely: Humor and laughter.

To conclude, female hormonal levels do influence what would seem a most natural behavior: Women's preferences for men and their interest in sexual activities. As most of the previous studies have used subjective methods like self-reports, the approach of the present study is rather different and perhaps was capable of revealing emotional and attentional responses that the participants themselves might have been not aware of (cf. Berridge and Winkielman, 2003). Finally, the present findings suggest that measurement of pupillary sizes is a promising method for investigating the effect of hormones on, at least, females' interest in sex. Indeed, pupillometry could be especially useful whenever a non-invasive, non-verbal, tool for measuring sexual interest might be preferred. Because measuring pupil size is so easy and convenient, particularly with the recently developed infrared eye-tracking technology, this method is now often preferred over other psychophysiological methods (e.g., galvanic skin response) when studying the relation between human autonomic activity and cognitive or emotional processes (Loewenfeld, 1993; Steinhauer and Hakerem, 1992).

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