Evolution and Human Behavior 37 (2016) 117–124

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

The pupils are the windows to sexuality: pupil dilation as a visual cue to others' sexual interest☆

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ARTICLE INFO

Article history:
Initial receipt 18 December 2014
Final revision received 21 September 2015

Keywords:
Person perception
Social vision
Pupil dilation
Reverse correlation
Sexual interest

ABSTRACT

In order to ensure successful mating opportunities, it is critical that human perceivers accurately infer others' sexual interests. But how do perceivers achieve these inferences? For over 50 years, scientists have documented that the pupils dilate in response to sexual arousal. Despite the potential importance of this cue for mate selection, however, extant data have focused almost exclusively on the perspective of the individual experiencing arousal. Here, we demonstrate that outside observers exploit pupil dilation as a visible cue to others' sexual interests. We used reverse-correlation methods to derive facial images based on perceivers' mental representations of both state-based (sexually aroused, sexually unaroused) and trait-based (sexually promiscuous, sexually non-promiscuous) markers of sexual interest. Next, we explored the phenotypic features that differentiated these faces, specifically the dilation of the pupils contained within each reverse-correlation image. Consistent with the notion that pupil dilation is a reliable cue to sexual arousal, sexually interested faces contained objectively larger and darker pupils than did sexually disinterested faces. Moreover, these differences were perceptually obvious to naïve observers. Collectively, our results suggest that perceivers attend to an external cue – pupil dilation – when forming decisions about others' state-based and trait-based sexual interests.

1. Introduction

Artists and philosophers have long contended, "The eyes are the windows to the soul." The notion that the eyes convey important information about one's inner state to observers is also backed by scientific evidence. For instance, certain features of the eye – most notably, the pupils – have been shown to change in response to sexual arousal (Dabbs, 1997; Hess & Polt, 1960; Tombs & Silverman, 2004). Moreover, successful human mating requires that perceivers accurately interpret the sexual interests of those around them: The formation of close interpersonal relationships hinges upon inferences about others' sexual receptivity (Buss & Schmitt, 1993). Some have even argued that the motivation to select appropriate mates has shaped the progress of human evolution (Miller, 2000). Despite the weighty consequences of perceivers' inferences about others' sexual interests and the fact that the pupils reliably dilate in response to sexual arousal, it remains unclear whether perceivers exploit pupillary information when inferring others' sexual interests. Here, we examine the communicative function of pupil dilation by testing whether perceivers use the pupils as a marker of others' sexual interests.

The pupils readily adapt to perceptual environments, contracting and relaxing in response to physical changes such as light intensity (Lowenstein & Loewenfeld, 1962) or experiential changes such as habituation (Lowenstein, Feinberg, & Loewenfeld, 1962). Pupil size also covaries with internal psychological states (Janisse, 1977), including sexual interest. Indeed, a seminal study revealed that heterosexual women's pupils tended to dilate when viewing photographs of nude men whereas heterosexual men's pupils tended to dilate when viewing photographs of nude women (Hess & Polt, 1960). Although participants' pupils dilated in response to other visually salient images as well (e.g., mothers and babies), the effect was especially pronounced for sexually arousing stimuli. Subsequent studies replicated this basic pattern with more diverse stimuli, revealing that the pupils also dilate in response to imagined (Whipple, Ogden, & Komisaruk, 1992) and auditory sexual stimuli (Dabbs, 1997). For example, in one study, participants' pupils dilated significantly more to sexually provocative auditory stimuli (e.g., a couple having sex) than to other highly valenced auditory stimuli (e.g., a couple fighting) or controls (e.g., a greeting by a flight attendant; Dabbs, 1997).

The pupillary responses that coincide with exposure to sexually arousing stimuli respond to changes in both stimulus and perceiver. For example, pupil dilation reacts to variation in the sexual interest value of the stimulus itself. In several studies, heterosexual observers' pupil dilation increased linearly as the amount of clothing on opposite-sex models decreased (Hamel, 1974; Nunnally, Knott, Duchnowski, & Parker, 1967). Other studies have revealed that pupil

☆ This research was supported by a National Science Foundation Graduate Research Fellowship (Lick). We gratefully acknowledge members of the Social Communication Lab for their assistance with data collection and their feedback on earlier drafts of this manuscript.
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http://dx.doi.org/10.1016/j.evolhumbehav.2015.09.004
1090-5138/

dilation is sensitive to perceivers' sexual orientations, insofar as gay men's pupils dilated more to photographs of nude men compared to nude women whereas straight men's pupils dilated more to photographs of nude women compared to nude men (Hess, Seltzer, & Shlien, 1965). Perhaps most compelling, pupil dilation is sensitive to hormonal fluctuations. In one recent study, women who were not using hormonal contraceptives experienced a marked increase in pupil dilation when viewing sexually relevant images (e.g., their boyfriends) but not when viewing sexually irrelevant images (e.g., same-sex actresses) during the fertile window of their ovulatory cycle (Laeng & Falkenberg, 2007).

Alongside the robust body of research documenting pupillary responses to sexually provocative stimuli are studies revealing that pupil dilation also coincides with the subjective experience of sexual arousal. For example, pupil dilation is positively correlated with self-reported sexual arousal among women (Hamel, 1974) and with self-reported erection among men viewing pornography (Bernick, Kling, & Borowitz, 1971). Animal models further corroborate this link between arousal and pupil dilation. In one study, copulation with a male rat induced pupil dilation among female rats, with the largest dilation occurring during the male's ejaculation. Severing the pelvic nerve that responds to genital stimulation greatly reduced female rats' pupillary responses to ejaculation, and completely eliminated pupillary responses to genital probing by an experimenter (Szechtman, Adler, & Komisaruk, 1985).

Thus, pupil dilation is a well-documented response to sexual arousal. It remains unclear, however, whether pupillary changes reliably communicate one's sexual interests to others. That is, scientists have yet to determine whether perceivers utilize pupil dilation as a valid cue when forming impressions of others' sexual interests. This possibility is feasible insofar as perceivers utilize the pupils to form more general impressions of others. For example, in two studies, perceivers provided more favorable evaluations of opposite-sex targets who displayed larger rather than smaller pupils (Hess & Petrovich, 1987; Tombs & Silverman, 2004). In another study, men and women who were asked to choose a partner from two confederates matched for attractiveness tended to prefer the confederate with artificially dilated pupils relative to the confederate with un-dilated pupils (Stass & Willis, 1967). These findings suggest that perceivers can and do attend to the pupils when forming impressions of others, although there has been no work on perceivers' use of pupillary information when judging sexual interest specifically.

In summary, prior research has yielded three important observations relevant to our work: (1) pupil dilation is an honest marker of sexual arousal, (2) perceivers use pupillary information to form general impressions of others, and (3) accurate impressions of others' sexual interests are critically important for mating success. Based upon these findings, we propose that perceivers may utilize pupillary information to judge others' sexual interests. We focus our investigation at two different levels of analysis. First, we examine state-based measures of sexual arousal, which assess whether observers believe a target to be aroused or unaroused in a given moment. Second, we examine trait-based measures of broader sexual strategies, which assess whether observers believe a target to be promiscuous or non-promiscuous in their sexual behavior more generally (Simpson & Gangestad, 1991). Recent evidence suggests that these indices of sexual interest may be related, insofar as expression of the dopamine D4 receptor gene is implicated in both behavioral promiscuity (Garcia et al., 2010) and basic sexual arousal processes (Ben Zion et al., 2006). Given this link between low-level physiological arousal and higher-level behavioral strategies, we contend that perceivers will expect sexually interested faces – whether interest is defined as state-based or trait-based – to contain more dilated pupils than sexually disinterested faces.

We used cutting-edge reverse-correlation techniques to test whether pupil dilation serves as a visual cue for inferring others' sexual interests. Reverse-correlation recently gained traction as a data-driven method for illustrating the visual cues that perceivers use to identify individuals belonging to particular social groups (Todorov, Dotsch, Wigboldus, & Said, 2011). In general, the method yields images that are thought to represent the visual heuristics perceivers use to form impressions of other people. Here, it allowed us to visualize perceivers' mental representations of sexually interested others, limiting demand characteristics while providing a visual snapshot of the cues that differentiate people with varying levels of sexual arousal and promiscuity. In this way, reverse-correlation provided a powerful method for testing whether the pupils are implicated in perceptions of others' sexual interest.

2. Method and materials

The study involved three distinct phases of data collection: (1) a *classification phase*, during which participants completed a reverse-correlation task from which we derived their mental representations of sexually interested and disinterested others, (2) a *validation phase*, during which we tested whether these representations conveyed sexual interest to naïve observers as intended, and (3) an *analysis phase*, during which we examined objective and subjective differences in the pupils contained within images created during the classification phase.

2.1. Classification phase

We created two base images (one female, one male) using FaceGen Modeler, which estimates phenotypic features based upon parameters observed in three-dimensional face scans of the human population (Blanz & Vetter, 1999). We began with FaceGen's average base face and set all phenotypic features (e.g., caricature) at their anthropometric mean. We then used the gender-morphing tool to create one male face of average masculinity and one female face of average femininity while holding other features constant. Thus, the base faces depicted sexually dimorphic phenotypes evident in the human population, with the female face displaying a visibly higher brow line, higher cheekbones, wider eyes, smaller nose, and fuller lips than the male face.

Next, using MATLAB scripts from prior research (Dotsch, Wigboldus, Langner, & van Knippenberg, 2008), we created 700 pairs of faces for each sex by adding or subtracting randomly generated noise patterns from the base images. The noise patterns consisted of 60 sinusoids: 6 orientations (0°, 30°, 60°, 90°, 120°, and 150°) × 5 spatial scales (1, 2, 4, 8, and 16 sinusoid patches), each of which spanned 2 cycles per patch (0, π/2), with random contrasts. We weighted the noise patterns at 0.525 before superimposing them over the base images. The addition of these noise patterns systematically altered the appearance of the face, such that each pair of images looked slightly different despite the fact that they were derived from the same base face.

Finally, we used custom software to present each pair of faces side-by-side in random order to participants. We conducted this study twice: Once to derive mental representations of state-based sexual interest (arousal) and once to derive mental representations of trait-based sexual interest (promiscuity). We describe the methods and results for these two sets of images in tandem below. For the sake of parsimony, we refer to the aroused and promiscuous images collectively as "sexually interested," and the unaroused and non-promiscuous images collectively as "sexually disinterested."

To derive mental representations of state-based sexual interest, 38 undergraduates (32 women) from the University of California, Los Angeles were randomly assigned to evaluate either male ($n = 17$ participants) or female faces ($n = 21$ participants). For all 700 pairs of faces, participants identified the image that best represented a sexually aroused individual by pressing keys labeled *left* and *right*. To derive mental representations of trait-based sexual interests, 40 undergraduates (33 women) from the University of California, Los Angeles were randomly assigned to evaluate either the male ($n = 21$ participants) or female faces ($n = 19$ participants). For all 700 pairs of faces, participants identified the image that best represented a sexually promiscuous individual by pressing keys labeled *left* and *right* (see Fig. 1 for an example).

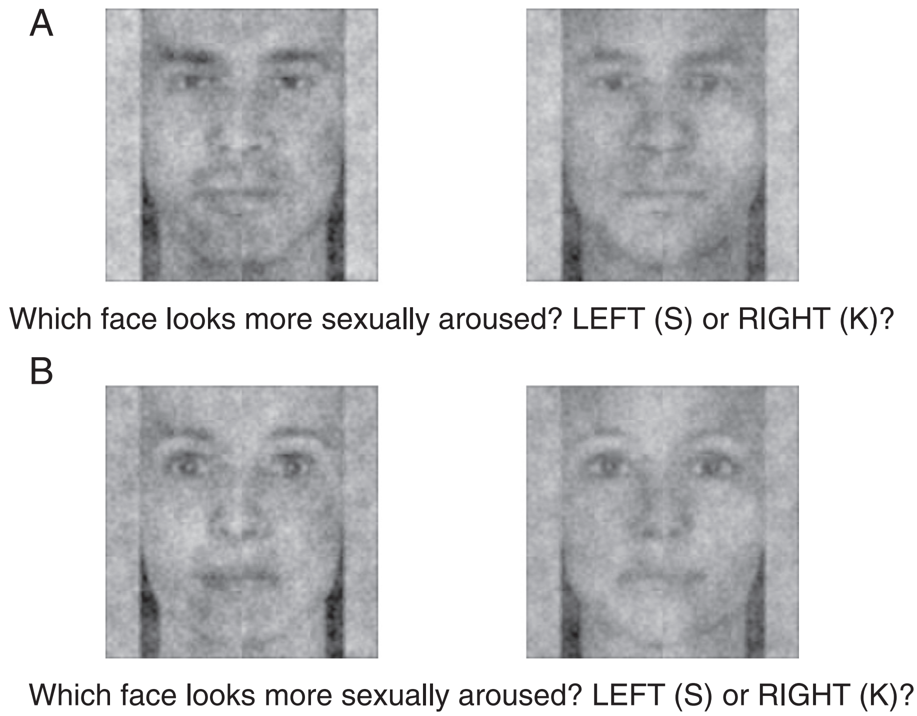

Fig. 1. Sample trial from Classification Phase, in which participants made 700 forced-choice decisions about which male face (A) or female face (B) looked more sexually aroused.

Sexual interest is a feature perceivers can judge both within and across sex categories, so there was no reason to believe that perceiver sex would affect the reliability of classification images. Indeed, we tested for main effects and interactions with perceiver sex in all analyses described below, but none of them were statistically significant (all *ps* > .17; $M_p = .56$, $SD_p = .26$). That is, we found no evidence that the cues in women's mental representations of sexually aroused/promiscuous women differed from the cues in their mental representations of sexually unaroused/non-promiscuous men (or vice-versa). The relatively large number of women in the classification phase was therefore not a concern, and we do not mention perceiver sex further.

Upon completion of data collection, we created composite aroused/unaroused and promiscuous/non-promiscuous images for each participant by averaging the noise patterns of the selected and unselected images and superimposing them over the original base faces. Recent evidence suggests that classification images based on the unselected images in a reverse-correlation task reflect the opposite of a given social category (Dotsch & Todorov, 2012). For example, figures not selected as female approximated male body shapes in two recent studies (Johnson, Iida, & Tassinary, 2012; Lick, Carpinella, Preciado, Spunt, & Johnson, 2013). Therefore, we assumed that the unselected images represented facial features that participants deemed unaroused and non-promiscuous, respectively.[1]

[1] An additional study with the promiscuous mental representations substantiated this assumption. We conducted a third classification phase during which participants selected the face from each pair that appeared *less* promiscuous rather than *more* promiscuous. A sample of 51 Internet users from Amazon Mechanical Turk (see below) then rated how promiscuous (*1 = not at all promiscuous* to *9 = very promiscuous*) the images from these two classification phases appeared. Results indicated that the selected and unselected images from the original classification phase ("Which face looks more promiscuous?") were more differentiated than the selected and unselected images from the new classification phase ("Which face looks less promiscuous?"). That is, participants tended to rate the promiscuous and non-promiscuous faces as appearing more and less promiscuous, respectively, when they came from the original classification phase described above as opposed to the additional classification phase described here, *Bs* = 0.97 and 0.18, *SEs* = 0.06 and 0.06, *ts* = 17.57 and 2.87, *ps* < .001 and = .004, 95% CIs [0.86, 1.08] and [0.06, 0.31]. This is likely because the additional classification phase required participants to think in the negative (i.e., *less* promiscuous), which is cognitively difficult and may have resulted in noisy composite images. For this reason, all forthcoming analyses examined images from the original classification phase, which best differentiated sexually interested from sexually disinterested facial features.

Altogether, the reverse-correlation procedure resulted in 156 classification images (38 aroused, 38 unaroused; 40 promiscuous, 40 non-promiscuous) that represented the facial cues perceivers associated with men's and women's state-based and trait-biased sexual interest.

2.2. Validation phase

Having derived perceivers' mental representations of sexually interested and disinterested men and women, we conducted preliminary studies to ensure that the images were perceptually valid. In the first study, 32 Internet users from Amazon Mechanical Turk (13 male, 8 White, $M_{Age} = 38.66$ years) viewed the 76 state-based classification images (aroused/unaroused) in random order and rated the apparent arousal of each one on a 9-point rating scale (*1 = not at all sexually aroused* to *9 = very sexually aroused*). We analyzed these ratings using multilevel regression models to account for the fact that responses were nested within the cross-classification of perceiver (multiple ratings from each perceiver) and target (two images from each participant in the classification phase). Specifically, we regressed arousal ratings onto image type (sexually aroused, sexually unaroused) while accounting for both levels of nesting. As expected, sexually aroused images were rated as appearing more aroused ($M = 4.99$, $SD = 2.40$) than were sexually unaroused images ($M = 3.24$, $SD = 2.17$), $B = 1.75$, $SE = 0.07$, $t = 26.18$, $p < .001$, 95% CI [1.62, 1.88] (Supplementary Data File 1, available on the journal's website at www.ehbonline.org).

In the second validation study, 51 Internet users from Amazon Mechanical Turk (31 male, 19 White, $M_{Age} = 36.18$ years) viewed the trait-based classification images (promiscuous/non-promiscuous) in random order and rated the apparent promiscuity of each one on a 9-point rating scale (*1 = not at all promiscuous* to *9 = very promiscuous*). Again, we analyzed the data using multilevel models, regressing promiscuity ratings onto image type (sexually promiscuous, sexually non-promiscuous) while controlling for nesting within perceiver and target. As expected, sexually promiscuous images were rated as appearing more promiscuous ($M = 5.84$, $SD = 1.82$) than were sexually non-promiscuous images ($M = 4.87$, $SD = 1.89$), $B = 0.97$, $SE = 0.06$, $t = 17.57$, $p < .001$, 95% CI [0.86, 1.08] (Supplementary Data File 2, available on the journal's website at www.ehbonline.org). Collectively, these findings indicate that the reverse-correlation method produced classification images that differed in their apparent sexual interest as expected.

2.3. Analysis phase

Having created and validated the classification images, we next tested our primary hypothesis about pupil dilation as a visual cue differentiating perceivers' mental representations of sexually interested and disinterested faces. We accomplished this using both objective and subjective measures of the pupils contained within each classification image. We reasoned that dilated pupils would appear larger and darker relative to constricted pupils, and that perceivers' mental representations of sexually interested faces would contain these cues to a greater degree than perceivers' mental representations of sexually disinterested faces.

2.3.1. Pupil size

We first examined the size of the pupils contained within each classification image by using the Quick Selection Tool in Adobe Photoshop (Adobe Systems, 2000) to crop the pupils from the left and right eyes of each image in a data-driven manner. This tool precisely defines the edges of a given feature by detecting changes in the properties of adjacent pixels. Specifically, we selected a 10-pt brush and centered the cursor in the middle portion of the eyes in each classification image. By dragging the brush outward from the center, the Quick Selection Tool automatically analyzed the qualities of surrounding pixels, outlining each pupil's boundary based upon differences in color, tonal range, and texture of neighboring pixels. This procedure therefore allowed us to define the edges of each pupil systematically based upon qualities of the image itself, without relying on subjective judgments about the boundary of each pupil. We operationalized the size of each pupil as the area of the cropped selection in square pixels, and we hypothesized that the pupils in mental representations of sexually interested faces (aroused, promiscuous) would be larger in absolute size than the pupils in mental representations of sexually disinterested faces (unaroused, non-promiscuous).

2.3.2. Pupil luminance

Next, we examined the luminance of each pupil. We again used the Adobe Quick Selection Tool (Adobe Systems, 2000) to crop the pupils from the left and right eyes of each classification image, recording the average luminance within each pupil using a 51-pixel sampling space. This measure is expressed as a percentage, with higher values indicating more white light in the image. We hypothesized that pupils in mental representations of sexually interested faces (aroused, promiscuous) would have smaller luminance values (i.e., would be darker) than pupils in mental representations of sexually disinterested faces (unaroused, non-promiscuous).

2.3.3. Perceptual salience

Finally, we tested whether objective variability in pupil size and luminance resulted in perceptually salient differences to naïve observers. To do so, we conducted four additional social perception studies. The first two were modeled after a recent study in which participants made forced-choice judgments about each pair of classification images created during the classification phase (Lick et al., 2013). Specifically, Internet users from Amazon Mechanical Turk viewed all pairs of aroused/unaroused images ($N = 42$; 43% male, 74% White, $M_{Age} = 34.29$) or all pairs of promiscuous/non-promiscuous images ($N = 45$; 49% male, 78% White, $M_{Age} = 29.35$) side-by-side and made forced-choice judgments about which image had more pronounced pupils. Thus, perceivers were shown a side-by-side comparison of the reverse-correlation images from each participant in the classification phase and asked to choose which one had more pronounced pupils. We defined "pronounced" for participants as pupils that were notably larger and darker relative to the other image. We hypothesized that participants would tend to choose the sexually interested classification images (aroused, promiscuous) as having more pronounced pupils more often than the sexually disinterested classification images (unaroused, non-promiscuous). As a more powerful test of this hypothesis, the second two studies required Internet users from Amazon Mechanical Turk to view each of the aroused/unaroused classification images ($N = 33$; 43% male, 74% White, $M_{Age} = 34.29$) or promiscuous/non-promiscuous classification images ($N = 39$; 39% male, 69% White, $M_{Age} = 30.61$) individually in random order and rate how pronounced the pupils appeared on a 9-point rating scale (*1 = pupils are not at all pronounced* to *9 = pupils are extremely pronounced*). Here, we hypothesized that perceivers would tend to rate the pupils contained in mental representations of sexually interested faces (aroused, promiscuous) as appearing more pronounced than the pupils in mental representations of sexually disinterested faces (unaroused, non-promiscuous), even when the images appeared one at a time. Collectively, the hypothesized results would reveal objective differences in pupil size and luminance across mental representations of sexually interested and disinterested faces that are perceptually evident to naïve observers.

3. Results

For measures of pupil size and luminance, the pattern of results was identical when examining each pupil separately. Therefore, we collapsed across the left and right pupils by averaging the size and luminance measures for each classification image. For each measure, we present results for the aroused/unaroused classification images first, followed by results for the promiscuous/non-promiscuous classification images. For sample eye regions from the images in each of these categories, see Fig. 2.

3.1. Pupil size

First, we tested whether the size of the pupils varied as a function of arousal in classification images depicting state-based sexual arousal. Because we derived two images from each participant in the classification phase (one aroused, one unaroused), the images were statistically dependent at the target level. In order to account for this dependence, we structured the data in wide format and subtracted the average pupil size in the aroused image from the average pupil size in the unaroused image for each creator. We then subjected this difference score to a one-sample t-test against a null value of zero. As expected, sexually aroused images had larger pupils than did sexually unaroused images ($M_{diff} = 120.21$, $SD_{diff} = 191.01$, 95% CI [57.43, 183.00]), $t(37) = 3.88$, $p < .001$, $d = 0.63$. Importantly, however, pupil size differed in the base images of men and women to begin with (855 and 990 square pixels, respectively), so we conducted an additional analysis to test whether target sex moderated this effect. Specifically, we conducted an independent samples t-test comparing the difference in pupil size as a function of image type (aroused, unaroused). This difference did indeed vary as a function of target sex, $t(29.03) = -2.12$, $p = .043$ (df corrected for unequal variances). The pupils were larger in aroused relative to unaroused images of both women ($M_{diff} = 173.17$, $SD_{diff} = 228.89$, 95% CI [68.98, 277.35]), $t(20) = 3.47$, $p = .002$, $d = 0.76$, and men ($M_{diff} = 54.79$, $SD_{diff} = 103.25$, 95% CI [1.71, 107.88]), $t(16) = 2.19$, $p = .044$, $d = 0.53$, though the effect was stronger for the women (Fig. 3; Supplementary Data File 3, available on the journal's website at www.ehbonline.org).

We conducted a similar analysis to test whether the size of the pupils varied as a function of trait-based promiscuity. Specifically, we subjected the difference in pupil size between promiscuous and non-promiscuous classification images to a one-sample t-test against a null value of zero. As expected, sexually promiscuous images had larger

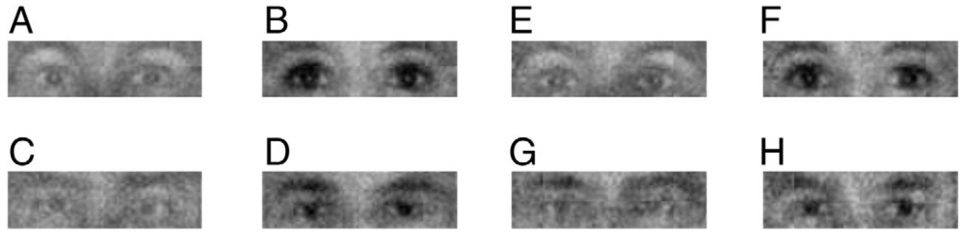

Fig. 2. Eye regions from classification images: non-promiscuous female (A), promiscuous female (B), non-promiscuous male (C), promiscuous male (D), unaroused female (E), aroused female (F), unaroused male (G), aroused male (H).

pupils than did sexually non-promiscuous images (M_{diff} = 135.98, SD_{diff} = 189.72, 95% CI [75.30, 196.65]), $t(39) = 4.53$, $p < .001$, $d = 0.72$. As before, however, this difference varied as a function of target sex, $t(25.57) = -3.47$, $p = .002$ (*df* corrected for unequal variances). The pupils were larger in promiscuous relative to non-promiscuous images of both women (M_{diff} = 234.87, SD_{diff} = 214.63, 95% CI [131.42, 338.32]), $t(18) = 4.77$, $p < .001$, $d = 1.09$, and men (M_{diff} = 46.50, SD_{diff} = 105.04, 95% CI [−1.31, 94.31]), $t(20) = 2.03$, $p = .056$, $d = 0.44$, though the effect was stronger for the women (Fig. 3; Supplementary Data File 4, available on the journal's website at www.ehbonline.org).

3.2. Pupil luminance

Second, we tested whether the average luminance of the pupils varied as a function of sexual arousal in each classification image. Using an analytic strategy identical to that described above, we conducted a one-sample *t*-test on the difference in luminance as a function of image type (aroused, unaroused). This comparison indicated that sexually aroused images had darker pupils than did sexually unaroused images (M_{diff} = −7.17, SD_{diff} = 6.54, 95% CI [−9.32, −5.02]), $t(37) = -6.76$, $p < .001$, $d = -1.10$. Importantly, however, pupil luminance differed in the base images of men and women to begin with (15.5% and 16%, respectively), so we conducted an additional analysis to test whether target sex moderated this effect. Specifically, we conducted an independent samples *t*-test that compared the difference in the size of pupils as a function of image type (aroused, unaroused). This difference did indeed vary as a function of target sex, $t(36) = 2.17$, $p = .037$. The pupils were darker in aroused relative to unaroused images of both women (M_{diff} = −9.14, SD_{diff} = 6.67, 95% CI [−12.18, −6.11]), $t(20) = -6.28$, $p < .001$, $d = -1.37$, and men (M_{diff} = −4.74, SD_{diff} = 5.64, 95% CI [−7.63, −1.84]), $t(16) = -3.47$, $p = .003$, $d = -0.84$, though the effect was stronger for the women (Fig. 4; Supplementary Data File 3, available on the journal's website at www.ehbonline.org).

We next tested whether the luminance of the pupils varied as a function of promiscuity in trait-based classification images. Specifically, we conducted a one-sample *t*-test on the difference in luminance as a function of image type (promiscuous, non-promiscuous). This comparison indicated that sexually promiscuous images had darker pupils than did sexually non-promiscuous images (M_{diff} = −10.20, SD_{diff} = 11.01, 95% CI [−13.72, −6.68]), $t(39) = -5.86$, $p < .001$, $d = -0.93$. Unlike the previous analysis, however, this difference did not vary as a function of target sex, $t(38) = 0.71$, $p = .485$. The pupils were darker in promiscuous relative to non-promiscuous images of both women (M_{diff} = −11.50, SD_{diff} = 10.79, 95% CI [−16.70, −6.30]), $t(18) = -4.64$, $p < .001$, $d = -1.07$, and men (M_{diff} = −9.02, SD_{diff} = 11.33, 95% CI [−14.18, −3.87]), $t(20) = -3.65$, $p = .002$, $d = -0.80$, and the magnitude of the effect was similar for both sexes (Fig. 4; Supplementary Data File 4, available on the journal's website at www.ehbonline.org).

3.3. Perceptual salience (forced-choice)

Finally, we tested whether the objective differences we observed in the pupils of sexually interested and disinterested classification images were perceptually salient to naïve observers. We again tested this possibility separately for the state-based (aroused, unaroused) and trait-based (promiscuous, nonpromiscuous) images. In the first set of analyses, we examined participants' decisions regarding pupil prominence in a two alternative forced-choice design. Because of its forced-choice nature, we calculated the proportion of trials on which participants chose sexually aroused faces as having more pronounced pupils than sexually unaroused faces. Overall, participants rated sexually aroused faces as having more pronounced pupils than sexually unaroused faces 75% of the time, and this proportion was significantly greater than chance

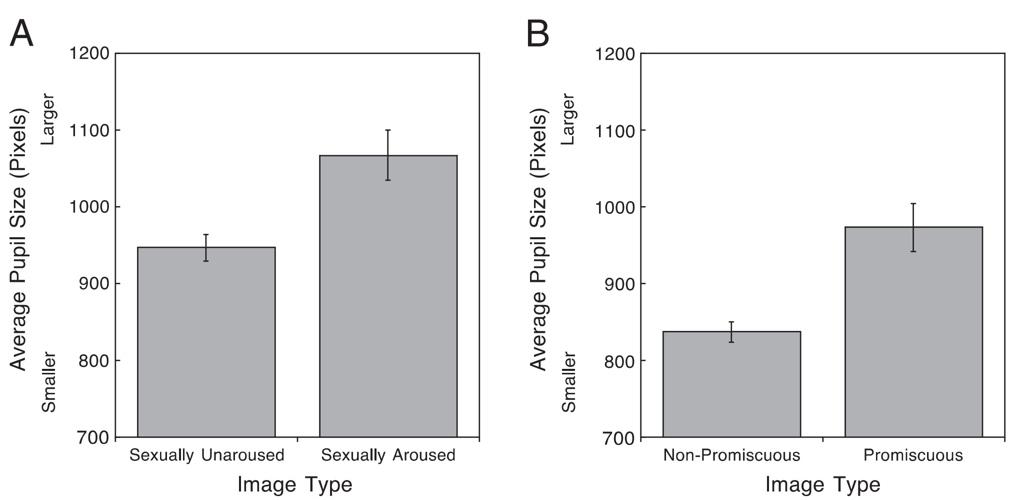

Fig. 3. Differences in the average pupil size as a function of classification image type. Sexually aroused faces had larger pupils compared to sexually unaroused faces (A). Sexually promiscuous faces had larger pupils compared to sexually non-promiscuous faces (B). Error bars represent standard errors around the mean within each image type.

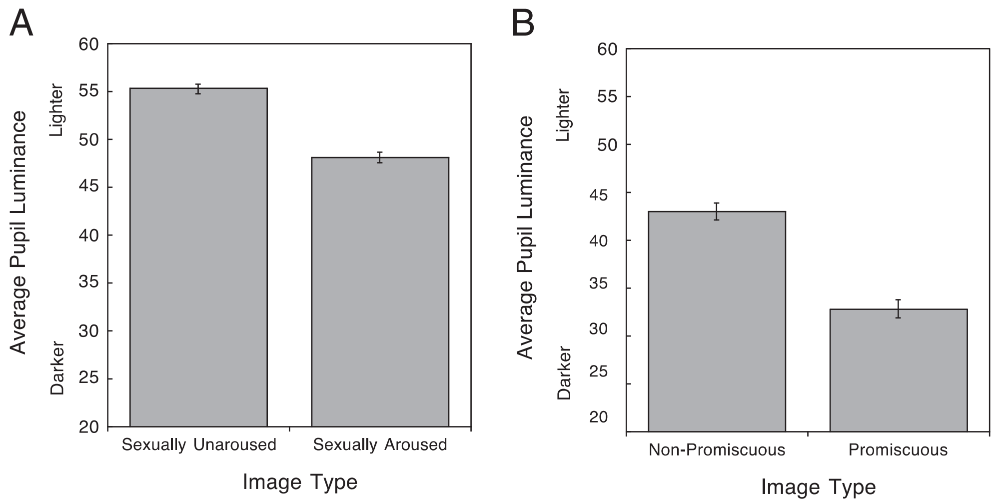

Fig. 4. Differences in the average pupil luminance as a function of classification image type. Sexually aroused faces had darker pupils compared to sexually unaroused faces (A). Sexually promiscuous faces had darker pupils compared to sexually non-promiscuous faces (B). Error bars represent standard errors around the mean within each image type.

(i.e., 50%), $t(41) = 12.24$, $p < .001$, $d = 1.92$, 95% CI [0.21, 0.29].[2] The results were consistent across both sexes, though the tendency to identify the pupils in sexually aroused faces as more pronounced than the pupils in sexually unaroused faces was stronger for female faces (79%) than for male faces (70%), $ts = 9.83$ and 11.93, $ps < .001$, $ds = 1.53$ and 1.82, 95% CIs [0.23, 0.35] and [0.17, 0.23], respectively (Supplementary Data File 5, available on the journal's website at www.ehbonline.org).

We conducted a similar analysis to test whether participants' forced choice ratings of pupil prominence varied as a function of trait-based sexual promiscuity. Again, we calculated the proportion of trials on which participants chose sexually promiscuous faces as having more pronounced pupils than sexually non-promiscuous faces. Overall, participants rated sexually promiscuous faces as having more pronounced pupils than sexually non-promiscuous faces 74% of the time, and this proportion was significantly greater than chance (i.e., 50%), $t(44) = 11.18$, $p < .001$, $d = 1.71$, 95% CI [0.19, 0.28].[3] The results were consistent across both sexes, although the tendency to rate the pupils in sexually promiscuous faces as more pronounced than the pupils in sexually non-promiscuous faces was stronger for female faces (80%) than male faces (67%), $ts = 11.32$ and 8.44, $ps < .001$, $ds = 1.67$ and 1.21, 95% CIs [0.25, 0.36] and [0.13, 0.22], respectively (Supplementary Data File 6, available on the journal's website at www.ehbonline.org).

3.4. Perceptual salience (continuous)

Finally, we compared continuous ratings of pupil dilation for each state-based classification image. As before, we used multilevel regression models to account for the fact that these ratings were nested within the cross-classification of perceiver (multiple pupil ratings from each participant) and target (two images from each creator in the classification phase). Specifically, we regressed ratings of pupil dilation onto classification image type (aroused, unaroused) while accounting for both levels of nesting. As expected, pupils in sexually aroused faces were perceived as being more pronounced than were pupils in sexually unaroused faces, $B = 0.93$, $SE = 0.08$, $t = 11.66$, $p < .001$, 95% CI [0.77, 1.09]. Moreover, this effect was moderated by a two-way interaction with Target Sex, $B = 0.52$, $SE = 0.15$, $t = 3.50$, $p = .001$, 95% CI [0.23, 0.81]. Perceivers rated the pupils in sexually aroused faces as more pronounced than the pupils in sexually unaroused faces of both sexes, though the effect was stronger for the women, $Bs = 1.27$ and 0.75, $SEs = 0.10$ and 0.11, $ts = 12.18$ and 7.12, $ps < .001$, 95% CIs [1.07, 1.48] and [0.55, 0.96] (Supplementary Data File 7, available on the journal's website at www.ehbonline.org).

We conducted a similar analysis to test whether participants' ratings of pupil prominence varied as a function of trait-based sexual promiscuity. Specifically, we regressed ratings of pupil dilation onto classification image type (promiscuous, non-promiscuous) while accounting for nesting at both the perceiver and target levels. As expected, the pupils in sexually promiscuous faces were perceived as being more pronounced than the pupils in sexually non-promiscuous faces, $B = 1.39$, $SE = 0.07$, $t = 19.81$, $p < .001$, 95% CI [1.25, 1.52]. Moreover, this effect was moderated by a two-way interaction with Target Sex, $B = 0.57$, $SE = 0.14$, $t = 4.07$, $p < .001$, 95% CI [0.29, 0.84]. Perceivers rated the pupils in sexually promiscuous faces as more pronounced than the pupils in sexually non-promiscuous faces of both sexes, though the effect was stronger for the women, $Bs = 1.68$ and 1.12, $SEs = 0.10$ and 0.10, $ts = 16.65$ and 11.57, $ps < .001$, 95% CIs [1.49, 1.88] and [0.93, 1.30] (Supplementary Data File 8, available on the journal's website at www.ehbonline.org).

4. General discussion

Using data-driven methods with both objective and subjective outcome measures, we found that perceivers use a fleeting marker of sexual arousal – pupil dilation – to evaluate others' sexual interests. Specifically, the pupils contained in perceivers' mental representations of sexually interested faces were objectively larger and darker than the pupils contained in their mental representations of sexually disinterested faces, and these differences were perceptually salient to naïve observers. Pupil dilation therefore appears to be an external cue that reliably and validly differentiates perceivers' mental representations of sexually interested vs. sexually disinterested others. These findings provide important methodological and theoretical insights to multiple areas of research in human psychology.

Methodologically, our use of reverse-correlation techniques to test perceivers' mental representations of sexual interest expands the repertoire of this relatively new analytic tool. The current findings showcase the utility of reverse-correlation for examining subtle differences within particular facial regions to which perceivers might attend when forming impressions of others. Given the widespread scientific focus on the eyes as predictors of emotion perception (Adams & Kleck,

[2] Confidence intervals refer to the proportion of trials on which participants are expected to choose sexually aroused faces as having more pronounced pupils than sexually unaroused faces, over and above a null value of 50%.

[3] Confidence intervals refer to the proportion of trials on which participants are expected to choose sexually promiscuous faces as having more pronounced pupils than sexually non-promiscuous faces, over and above a null value of 50%.

2005), gaze direction (Hoffman & Haxby, 2000), and visual attention (Hoffman & Subramaniam, 1995), future researchers may use similar techniques to explore ocular features contained in other mental representations.

Theoretically, this work expands scientific approaches to the perceptual correlates of sexual arousal. Classic research on this topic focused on pupil dilation among individuals who themselves experienced arousal. Ours is the first known study to test the communicative function of this response. Insofar as reverse-correlation classification images reveal perceivers' mental representations of social categories, our findings indicate that perceivers exploit pupil dilation when making decisions about others' sexual interests. This work has widespread theoretical applications. First, it broadens our understanding of self-presentational tactics evident across historical time periods and cultural contexts. For example, our findings help to explain antiquated beauty practices, such as Renaissance women's use of deadly nightshade in order to enlarge their pupils and earn the title *belladonna* ("beautiful woman;" McCabe, 2011). Our work also offers some explanation for why Japanese animated cartoons often have exaggerated pupils: These features may subtly indicate sexual arousal, contributing to a notable sexualization of female characters in popular media (Durham, 2008). Finally, our findings provide a context for understanding recent fashion trends, including "baby doll" contact lenses that artificially increase the size of one's irises and pupils (www.eyecandys.com). These trends might make young women appear sexually interested to potential suitors.

Our findings also have implications for understanding the interpersonal dynamics governing mating strategies. Specifically, they suggest that perceivers use a fleeting cue to sexual arousal when making decisions about others' sexual interests. This heuristic is critical because pupil dilation is a well-documented and valid cue to sexual arousal, and therefore might help perceivers reach accurate judgments about others. In combination with *error management theory* (Haselton & Buss, 2000), this aspect of our findings proffers some novel predictions for future research. For example, error management theory suggests that human mating tendencies evolved to maximize benefits while minimizing costly mistakes. According to this logic, men should be especially apt to rely on pupil dilation when inferring women's sexual interests because the pupils are sensitive to sexual arousal and would therefore help men to avoid missing a mating opportunity with a potentially interested partner (i.e., a costly error). Future studies can now test this hypothesis empirically.

While perceivers' use of a momentary arousal cue (pupil dilation) to make decisions about others' sexual interests might sometimes yield accurate conclusions, it could also suggest a judgment bias similar to the fundamental attribution error (Ross, 1977). Indeed, the same facial marker was associated with ratings of state-based sexual arousal and trait-based sexual promiscuity in our studies. In fact, in an unreported pilot study ($N = 44$ mTurk users), we found that participants rated the promiscuous classification images ($M = 4.81$, $SD = 2.24$) as appearing more sexually aroused than the non-promiscuous classification images ($M = 3.43$, $SD = 1.98$), $B = 1.36$, $SE = 0.06$, $z = 22.71$, $p < .001$, 95% CI [1.24, 1.48]. These findings suggest a strong link between the visual correlates to state-based sexual arousal and more trait-like behavioral promiscuity. Although our findings join a literature suggesting a link between markers of sexual arousal and self-reported promiscuity (Ben Zion et al., 2006; Garcia et al., 2010), we still have much to learn about the validity of using pupil dilation as a cue to others' broader behavioral tendencies. The current studies cannot definitively address this issue, but they illuminate new methods that can shed light on the association between markers of momentary sexual arousal and judgments of promiscuous behavior more generally.

Finally, the current studies highlight new avenues for research on the factors guiding human approach and avoidance motivations. For instance, our data suggest that perceivers who are interested in finding a sexual mate may use pupil dilation as a cue to guide their search, leading them to feel more justified making an advance toward someone with relatively large pupils compared to someone with smaller pupils. On the other hand, perceivers who are disinterested in sexual encounters or who wish to stave off potential predators may use pupil dilation as a cue to avoid certain interactions, retreating from partners with visibly dilated pupils. Finally, there may be natural variability in pupil size (e.g., less pupil dilation among older adults; Winn, Whitaker, Elliott, & Phillips, 1994) and luminance (e.g., darker irises that make the pupil appear dilated due to an unclear boundary between the dark-hued iris and pupil) that may lead to biased judgments of sexual interest toward individuals from certain groups. With the current findings as a guide, future studies can examine these and other consequences of perceivers' attention to pupil dilation when forming impressions of others' sexual interests.

In summary, poets and philosophers have long claimed that the eyes are the windows to the soul. After imaging perceivers' mental representations of sexually interested and disinterested men and women, we offer an extension of this statement. On the basis of current evidence, we contend that the pupils in particular act as windows to others' sexuality.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2015.09.004.

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