

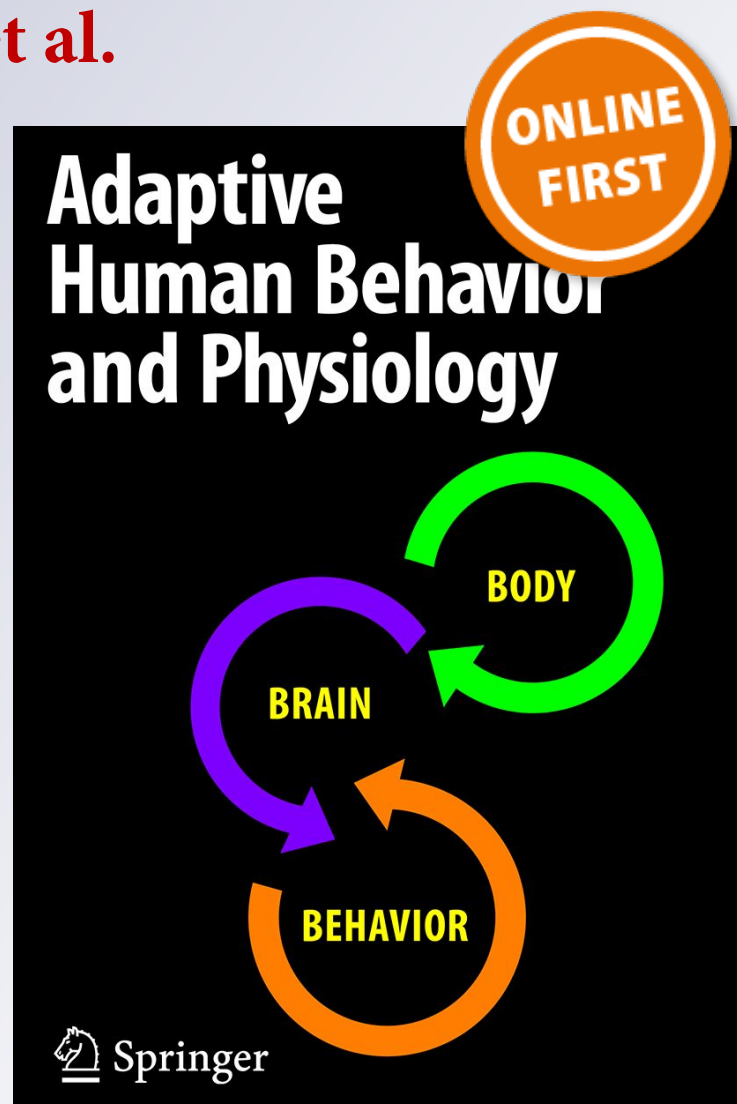
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# Women's Attention to and Memory for Fertile- and Non-Fertile Phase Women Across the Menstrual Cycle

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## Abstract

**Objectives** Across the menstrual cycle, women exhibit fluctuations in psychosocial motivations. Some evidence suggests that near ovulation, women exhibit increased status concerns and behaviors that could be considered intrasexually competitive in nature. Women are sensitive to other women's fertility, which may be useful for refining expectations about subsequent social interactions, particularly among women who are fertile themselves. Consistent with theories that attentional and memory processes are modulated by motivation, we hypothesized that women would exhibit attentional and memory biases for fertile-phase women, and potentially more so when they were in the fertile phase of their own cycle. However, individuals with higher visual working memory capacity (VWMC) are typically resistant to such biases; thus, we expected bias would be most pronounced among participants with lower VWMC. **Methods** Fifty-six premenopausal women who were not using hormonal contraceptives completed a visual selective attention task and a visual working memory task at two points in their menstrual cycle, near peak fertility (e.g., the late follicular phase) and during one of two low-fertile phases (either the early-follicular or the mid-luteal phase).

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Stimuli in the tasks were images of premenopausal women who were not using hormonal contraceptives in fertile- and non-fertile phases. We assessed participants' response times in the tasks as a function of the fertility of the stimulus woman, participants' cycle-phase, and participants' VWMC.

**Results** We demonstrate that when participants have lower VWMC, images of fertile-phase women capture their attention more than images of non-fertile-phase women. Furthermore, we show preliminary evidence that when participants have lower VWMC, they are faster to identify the face of a woman stored in visual working memory if she is in her fertile, relative to non-fertile, phase and participants are in the early-follicular phase of their own cycle.

**Conclusions** When VWMC is low, women are sensitive to visual cues of other women's fertility, such that they exhibit attentional biases for fertile-phase women, and memory biases for fertile-phase women that vary as a function of their own menstrual cycle phase. Our results suggest that visual cues of other's biological states alter early attentional processes in congruence with one's broader social goals and motivations.

**Keywords** Psychosocial motivation · Motivational relevance · Menstrual cycle · Ovulation · Fertility · Attention · Memory · Visual working memory · Selective attention · Attentional capture · Bias

Individuals attend to features of their environment in ways that are consistent with their psychosocial motivations (Brosch and Van Bavel 2012; Dietze and Knowles 2016). Visual attention tends to be value directed, such that stimuli that are motivationally relevant, though not necessarily task-relevant, capture attention (Anderson et al. 2011; Raymond and O'Brien 2009). Visual attention also plays a critical role in the encoding and maintenance of information in visual short term memory (Chun 2011; Gazzaley and Nobre 2012), such that attended items are better encoded (Gazzaley 2011), transferred to visual working memory (Schmidt et al. 2002), and maintained (Towler et al. 2015). Perhaps unsurprisingly then, visual working memory appears also to be modulated by motivational relevance, such that individuals are faster to respond to motivationally relevant stimuli stored in memory (Krawczyk and D'Esposito 2013; Krawczyk et al. 2007). Accumulating evidence suggests women's psychosocial motivations and behaviors may vary across their menstrual cycles, in ways that could affect how motivationally relevant they are to other women. The present study tested the extent to which fertile-phase women bias other women's attention and memory, and whether such bias depends on a woman's own fertility status. Notably, visual working memory capacity is predictive of individuals' attentional control abilities (Anderson et al. 2011; Fukuda and Vogel 2009; Fukuda and Vogel 2011; Gaspar et al. 2016); thus, the present study also examined how individual differences in visual working memory capacity moderated women's attention and memory for fertile-phase women.

In the late-follicular (i.e., fertile) phase of the menstrual cycle, when levels of estradiol and likelihood of conception are highest, and progesterone levels are lowest, women tend to demonstrate increased sexual desire (Bullivant et al. 2004; Jones et al.

2018a; Roney and Simmons 2013) and increased initiation of and engagement in sexual activity (Bullivant et al. 2004; Burleson et al. 2002). Concurrently, they tend to exhibit an attentional bias towards attractive men (Anderson et al. 2010) and courtship language (Rosen and López 2009). During this phase, women are also more likely to exhibit behavior that could be considered intrasexually competitive in nature (Durante et al. 2011; Piccoli et al. 2013), and to behave in ways that may improve their social status (e.g., increasing their own position relative to another woman; Lucas and Koff 2013; Durante et al. 2014). Consistent with evidence that motivational relevance directs attention, women are also more likely to have an attentional bias in this phase towards objects that convey or can be used to gain status (Lens et al. 2012; Zhuang and Wang 2014), especially when other attractive women are made salient (Zhuang and Wang 2014).

These converging motives to attain social status and mating-related opportunities when women are in the most fertile-phase of their cycles may make them particularly relevant for other women's motivated behavior. That is, to the extent that fertile-phase women's status-seeking motives or mating-related goals bring them into direct conflict with other women (e.g., by threatening their social status or mating opportunities), fertile-phase women may affect other women's capacity to achieve motivated end-states. Other women's fertility status is relevant for women, or may interfere with their psychosocial goals, in a number of ways. Partnered women, for example, are presumably motivated to maintain their romantic relationship, yet their partners may find fertile-phase women particularly attractive (Bobst and Lobmaier 2012; Haselton and Gildersleeve 2011), or fertile-phase women may even actively mate-poach their partners. Partnered women respond to this potential threat by mate-guarding their partners against fertile-phase women (Hurst et al. 2016) or avoiding social interactions with fertile-phase women outright (even when their partner is not present; Krems et al. 2016). Outside of the context of a romantic relationship, another woman's fertility should be relevant for women because fertile-phase women engage in behaviors that can limit one's own acquisition of resources or jeopardize one's own social standing (Durante et al. 2014).

Consistent with the supposition that a woman's fertility status is relevant to other women, anticipation of social interactions with other women may be made more efficient by sensitivity to the fertility status of other women. Like men, women are attuned to subtle visual cues of other women's fertility (Lobmaier et al. 2016), and can use visual appearances alone to discriminate between other women with probabilistically higher or lower odds of conception (Jones et al. 2018b; Puts et al. 2013; Roberts et al. 2004). If other women's fertility status is indeed motivationally relevant to women, such that fertile-phase women may be more likely to interrupt women's status- or mating-related behaviors or otherwise interfere with their ability to achieve motivated end-states, then we would expect women to exhibit heightened attention to and memory for fertile-phase women.

Yet such biases might depend on a woman's own cycle phase. Prior research indicates that women who present the most proximate threats to reproductive resources, including other fertile-phase women, are preferentially the targets of fertile-phase women's competitive behaviors (Durante et al. 2011, 2014; Lucas and Koff 2013; Necka et al. 2016, although see Eisenbruch and Roney 2016). When women are in the

fertile-phase of their own cycle, they may experience heightened motivations to attain status or engage in mating-related behaviors that would make potential interference with these motivations particularly salient. Thus, we expect that women's biases toward fertile-phase women should be enhanced when they themselves are in the fertile-phase of their own cycles.

In sum, we expected that fertile-phase women would be motivationally relevant to other women, particularly when they were in the fertile-phase of their own cycle, and that such motivational relevance would bias their attention toward and memory for fertile-phase women. We operationalized biases as faster responding to fertile-phase women in visual selective-attention and working-memory tasks. As stated previously, individuals with higher visual working memory capacity are more able to resist prolonged attentional capture and distraction by salient or motivationally-relevant stimuli (Anderson et al. 2011; Fukuda and Vogel 2009; Fukuda and Vogel 2011; Gaspar et al. 2016). Hence, even if fertile-phase women are motivationally relevant for these individuals, their strong attentional control abilities (at least under normal cognitive load conditions, as examined here) might protect them from exhibiting attentional biases, and this lack of attentional biasing should in turn preclude a memory bias. Thus, we expected the degree of attentional and memory biases towards fertile-phase women would depend on individual differences in a woman's own visual working memory capacity, such that biases should be most pronounced among women with lower visual working memory.

## Methods

All procedures were approved by the Institutional Review Board at the university with which the last author is affiliated. All study procedures were performed in accordance with relevant guidelines and regulations.

## Participants

Participants were recruited from an urban Midwestern US institution's campus community, prescreened, and selected only if they reported they were female, less than 40 years old, and not currently using hormonal contraceptives (inclusion criteria were masked by distractor questions during prescreening). After recruitment but prior to participation, participants' next menstruation was confirmed and backward counting methods were used to estimate the ovulatory period from the previous cycle. Scheduling was undertaken using these calculations to target the ovulatory period of the next menstrual cycle (see [Scheduling Protocol](#)). Fifty-nine participants chose to participate in the study and provided written informed consent prior to any procedures. Of these, one participant reported hormonal contraceptive use at study participation, one reported becoming pregnant between recruitment and participation, and one reported having an endocrine disorder. These participants were excluded. Analyses were conducted on the remaining 56 participants (mean age 21.96 years,  $SD = 3.95$ , range 18–38, 15 Caucasian), all of whom reported being premenopausal and not having used hormonal contraceptives in the three months preceding participation. Participants' menstrual cycle duration for the cycle immediately preceding participation (confirmed



by onset of menstruation) was on average 29.84 days ( $SD = 4.69$ , range = 21–44<sup>1</sup>). Sample size was determined a-priori based on guidelines in (Gangestad et al. 2016) suggesting that 55 participants are necessary to detect a medium-sized effect of participant fertility with 80% power in a within-subjects design where fertility was estimated as we did here, using backward counting with next menstruation confirmed and targeted participation during estimated high and low fertility phases.

## Scheduling Protocol

Participants participated at two points in their menstrual cycles. One session was during their late-follicular phase (e.g., approx. days –4 to 0, where 0 indicates the expected day of luteinizing hormone surge, calculated by subtracting 14 days [the approximate length of the luteal phase; Dixon et al., 1980], from the projected start date of participants' next cycle, based on the measured length of their last cycle and start date of their current cycle). In subsequent methods and results, we refer to this period as participants' 'fertile-phase' for brevity, but note that because we were unable to measure participants' hormonal profiles,<sup>2</sup> it may more accurately be referred to as their 'probabilistically fertile phase'.

Participants were quasi-randomly assigned to participate in one of two low-fertility phases: the early-follicular ( $N = 29$ ; days –10 to –6) or mid-luteal ( $N = 27$ ; days 6 to 10) phase (adjustment to random assignment was undertaken only for scheduling conflicts). Sessions were on average 7.93 days apart ( $SD = 2.91$ ). When possible, women participated in both sessions at approximately the same time of day to control for diurnal fluctuations in hormone concentrations.

Though we were unable to analyze participants' actual fluctuating hormone levels on both days of their participation, we were able to approximate them by computing participants' adjusted cycle day on a standard 28-day cycle and estimating their estradiol and progesterone levels from published values for standard cycles (reported in Garver-Apgar et al. 2008). For participants whose menstrual cycle duration for the cycle immediately preceding participation was not equal to 28 days, we computed their adjusted cycle day (based on a 28-day cycle) using the methods in Puts (2006). Specifically, for sessions that took place 15 or more days preceding the anticipated start date of their next menstrual cycle (that is, before the expected LH surge on day 0), adjusted cycle day was computed by multiplying participants' actual cycle day (e.g., –10 to –1, where 0 indicates the expected day of luteinizing hormone surge based on the expected start date of participants' next menstrual cycle) by the average number of days in a standard 28-day cycle prior to the LH surge (i.e., 13 days) and dividing by the number of days in participants' non-standard cycle prior to the expected LH surge (i.e., the measured length of participants' last cycle – 15; see Puts 2006 for more details).

<sup>1</sup> Ninety-five percent of women exhibit average cycle lengths between 15 and 44 days (Chiazze et al. 1968). We chose a priori to include only participants whose menstrual cycle duration immediately prior to participation fell within this range, and excluded no participants. Using a more conservative estimate of 23–35 days (Münster et al. 1992), as recommended by Blake et al. (2016), excludes 7 participants, but patterns of results do not change.

<sup>2</sup> At the end of each session, participants provided saliva via passive drool for assay; however, due to freezer malfunction, these data could not be analyzed.

## Procedure

Data reported here are part of a larger study on the relation between hormonal fluctuations across the menstrual cycle and social cognitive processes. Participants attended two one-hour sessions, during which they completed cognitive tasks and survey measures and were compensated with cash or course credit. Tasks were presented using E-Prime 2.0 and surveys were presented through Qualtrics. Electrocardiogram and impedance cardiography data were collected continuously (results will be reported elsewhere). Task order was pseudo-randomized between participants and was consistent between sessions. Following task completion, participants responded to survey measures (to be reported elsewhere).

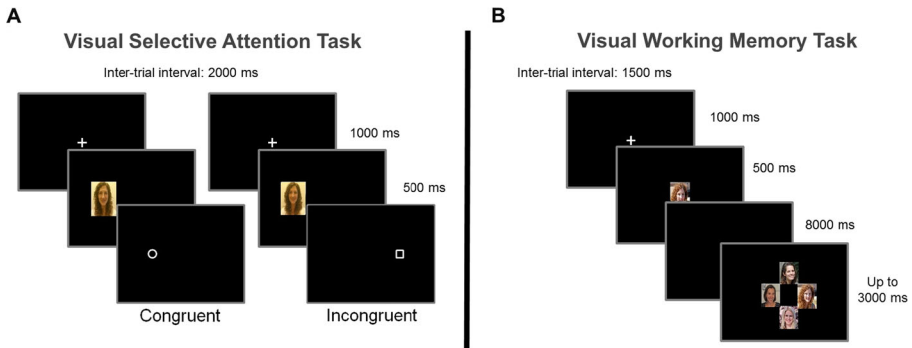
For tasks presented here, participants saw stimuli of color photographs of neutral faces of normally cycling Caucasian women in their late-follicular ('fertile') phase and mid-luteal ('non-fertile') phase from a previously published stimulus set (collection methods reported in Puts et al. 2013). Estradiol and progesterone were measured in stimuli women each time their photographs were taken. To ensure stimuli women were probabilistically fertile when their late-follicular photographs were taken, we selected from the larger stimulus set only women whose estradiol-to-progesterone (E:P) ratio (an approximate marker of ovulation; Baird et al. 1991) in their late-follicular photograph was greater than the average of all late-follicular photographs ( $N=47$  stimuli women). Stimuli have been previously rated by unacquainted women on perceived attractiveness (Puts et al. 2013). Control stimuli included pictures of neutral objects (pieces of furniture).

## Tasks

**Visual Selective Attention Task** Participants completed a modified exogenous cuing task (Posner and Cohen 1984) to assess biases in attention (Fig. 1a). Trials began with a fixation cross centered on the screen for 1000 ms. Next, a stimulus appeared randomly either left or right of center screen for 500 ms. The stimulus was either a neutral face of a woman in her late-follicular or mid-luteal phase or a neutral object. Immediately following stimulus disappearance, a small circle or square probe appeared randomly and with equal frequency in either the same location (congruent trial) or the opposite location (incongruent trial) as the stimulus. Participants identified the probe shape as quickly and accurately as possible using the keyboard, and their reaction time (in ms) was measured. Inter-trial intervals were 1500 ms. Participants completed three blocks of 24 trials each; stimulus type was randomized across trials. Participants completed eight practice trials before beginning and were reminded of response-shape associations before each block.

Incongruent trials required an attentional shift – a shift of attention away from the stimulus location to the probe location. In these trials, greater latency to respond can be interpreted as greater difficulty disengaging or moving attention from a currently attended stimulus or spatial location (Koster et al. 2004) (that is, greater latency on incongruent trials suggests the stimulus holds attention). During congruent trials, no attentional shift is necessary. Attention tends to facilitate responding, such that responses are faster if attention is already deployed to the spatial location where the probe appears. Thus, in congruent trials, faster responding is interpreted as a greater





**Fig. 1** Visual Selective Attention and Visual Working Memory Tasks. **a** The visual selective attention task. A stimulus appeared on the left or right side of the screen for 500 ms, after which a probe appeared in either the same location as (congruent) or opposite location of (incongruent) the stimulus. Participants' task was to accurately identify the shape of the probe as quickly as possible. **b** The visual working memory task. A sample stimulus appeared for 500 ms, followed by a delay of 8000 ms during which there was nothing on the screen. Following the delay, an array of four stimuli appeared, one of which was identical to the initial sample stimulus. Participants' task was to identify as quickly and as accurately as possible which image matched the sample

attentional bias, that is, greater attentional orienting toward or capture by the stimulus (c.f., Koster et al. 2004; Salemink et al. 2007). Though we hypothesized that attentional biases of both types would emerge, because congruent and incongruent trials in the visual selective attention task assessed different constructs we analyzed these trial types independently (as in Dewall et al. 2011).

**Visual Working Memory Task** To assess visual working memory biases, participants completed a modified delayed-match-to-sample task with a visual search component (Fig. 1b). Each trial began with a centered fixation cross for 1000 ms. Next, a stimulus (i.e., the “sample”) appeared centered for 500 ms, followed by an 8000 ms delay where no stimuli were present. After the delay, the sample and three comparison stimuli were presented for up to 3000 ms (or until response) in a diamond array. The location of the sample was randomized and each location within the diamond array was equally represented. Participants identified as quickly and accurately as possible which image matched the sample in memory using the keyboard's arrow keys. Accuracy and response time (in ms) were recorded. Inter-trial intervals were 1000 ms. Participants completed two practice trials before beginning.

Participants completed three blocks of ten trials each, with sample stimulus-type varying by block. Sample stimuli were the neutral face of a woman in her late-follicular or mid-luteal phase or a neutral object. The neutral objects block was used as a measure of visual working memory (VWMC; see section “Visual Working Memory Capacity as a Moderator”), whereas the blocks with the neutral faces of cycling women were used as experimental blocks. In each trial, the sample was randomly selected from a set of four stimuli which were matched prior to the experiment; the other stimuli from the set were used as comparisons that trial. For experimental blocks, comparison stimuli fertility (i.e., same or opposite fertility status as the sample) varied between participants (but was consistent across sessions) for exploratory purposes. This was not a key variable of interest but is included as a covariate in all analyses.

## Visual Working Memory Capacity as a Moderator

Our measure of VWMC was participants' accuracy (i.e., percent correct) on the control (i.e., neutral object) condition of the delayed match-to-sample task. We excluded trials on which participants did not respond before trial time-out at 3000 ms (2.95% of trials). Descriptive statistics are reported in Table 2. Participants' accuracy on the control condition of the delayed match-to-sample task during each session was used as a moderator in all analyses, given that we expected attentional and memory biases to vary as a function of participants' VWMC (becoming most apparent when visual working memory capacity is lower).

## Data Analysis

We utilized mixed effects models, implemented in lme4 (Bates et al. 2015) in R (Team 2008) to assess participants' response times. Mixed effects models are preferred when observations are not independent (e.g., each participants' response to any given stimulus is not independent of their responses to other stimuli); and ignoring correlated error terms can lead to biased standard error estimation (Hox 2002; Raudenbush and Bryk 2002). Further, mixed effects models can be used to account for variance between stimuli, as well as between participants (Judd et al. 2012), making them useful when factors vary between stimuli within participants, as in our data. In other words, rather than using a repeated-measures ANOVA, where we would have to average reaction times across all stimuli of each fertility type, we opted to use mixed-effects models, which allow us to measure the effect of fertility both within individual participants as well as within individual stimulus women.

Because VWMC tends to be a stable individual difference measure (Xu et al. 2017), we were primarily interested in looking at the effect of VWMC between-subjects. However, given mixed past evidence that different forms of working memory may fluctuate across the menstrual cycle (e.g., Phillips and Sherwin 1992; Rosenberg and Park 2002), measuring VWMC at only one point during the menstrual cycle may confound within-subject fluctuations with between-subject (trait-like) differences. Thus, to account for both potential sources of variance, we modeled VWMC both within- and between- subjects by including a random slope of the effect of visual working memory capacity on responses (thus accounting for individual subjects' changes in VWMC across their cycle) and a fixed effect of visual working memory on responses (thus accounting for between-participant differences).

Parameter estimates were obtained using maximum likelihood estimation and significance was tested using two-tailed tests and the Satterthwaite approximation for degrees of freedom (using lmerTest; Kuznetsova et al. 2017). Planned contrasts for session type (i.e., participant fertility) compared participants' responses in the non-fertile early-follicular and mid-luteal phases to their responses in the fertile late-follicular phase. In other words, two planned contrasts for session type existed – a first comparing the effect of the non-fertile early-follicular phase relative to the fertile late-follicular phase (conducted only among participants who completed their non-fertile session during their early follicular phase) and a second comparing the effect of the non-fertile mid-luteal phase relative to the fertile late-follicular phase (conducted only among participants whose non-fertile session was during their mid-luteal phase).

However, the omnibus test of the effect of session type (fertile- vs non-fertile) includes data from all participants and incorporates variance both within- and between- participants. Follow-up analyses for the effect of session type replaced the categorical variable of participant fertility (i.e., fertile/non-fertile) with the continuous variable of participants' imputed estradiol-to-progesterone (E:P) ratios, which served as an approximate marker of ovulation such that higher E:P levels are associated with greater fertility (Baird et al. 1991). Planned contrasts for stimulus type compared fertile to non-fertile stimuli in both tasks and, in the visual attention task, faces to neutral objects.

For analyses of the visual selective attention task, we controlled for the visual field to which stimuli were presented (attention to visual fields may vary with cycle phase; Thimm et al. 2014) and probe-response congruency (i.e., whether probe laterality was congruent with correct keyboard response laterality, which could impact response times). For the visual working memory task analyses, we controlled for whether comparison stimuli matched the fertility status of the sample. Continuous covariates were grand centered to aid in interpretation of coefficients, and deviation contrast coding was used for nominal covariates.

When significant effects were obtained during initial hypothesis testing, we tested robustness by controlling for participant demographic covariates of age, ethnicity (coded Caucasian/non-Caucasian to account for small *n*s in each non-Caucasian cell), sexual orientation (coded heterosexual, non-heterosexual, or other), and whether participants were currently involved in a romantic relationship (see Table 1 for sample characteristics). As further exploratory analyses, we tested the extent to which stimulus estradiol, progesterone, and attractiveness, all of which covary with fertility in the published literature, as well as within our stimulus set specifically, explained effects associated with stimulus fertility in multilevel mediation models using the bootstrapping method with 5000 iterations. Neuroendocrine predictors were log-transformed in all analyses.

Full mixed model specifications are reported in [Supplementary Materials](#). All data for the current study are available from the corresponding author upon request.

## Results

### Demographics

Participants who completed their low-fertile session in their early-follicular phase and participants who completed their low-fertile session in their mid-luteal phase were not significantly different from each other on any demographic variables, including age, race, sexuality, romantic relationship status, the cycle day on which they participated in their fertile sessions, and menstrual cycle length prior to participating (all *ps* > .213).

### Visual Working Memory Capacity

Participants exhibited 92.10% accuracy (*SD* = 6.72%) across both sessions. Accuracy did not vary by cycle phase,  $F(2,75.5) = 1.57$ ,  $p = .215$ , and planned contrasts revealed no significant differences across sessions,  $ps > .158$ . There were no differences in

**Table 1** Sample characteristics

	<i>N</i>
<b>Ethnicity</b>	
Caucasian	15
Asian (Non-Caucasian)	21
African American (Non-Caucasian)	7
Hispanic (Non-Caucasian)	7
Other (Non-Caucasian)	6
<b>Sexuality</b>	
Heterosexual	43
Bisexual (Non-Heterosexual)	4
Homosexual (Non-Heterosexual)	1
Decline to label my sexuality (Other)	7
Other	1
<b>Romantic Relationship Status</b>	
Involved in Romantic Relationship	21
Not Involved in Romantic Relationship	35

VWMC during the late-follicular phase as a function of whether it was participants' first or second session,  $t(52.6) = -.54$ ,  $p = .594$ . Descriptive statistics are reported in Table 2.

### Attentional Bias–Visual Selective Attention Task

Response times less than 200 ms and greater than 3 *SD* (1358 ms) were removed (1.43% of trials). Remaining response times were log-transformed. Incorrect responses (3.43% of remaining trials) were excluded, though patterns of effects maintain even when including these trials. There were no differences in response times,  $p = .425$ , or

**Table 2** Descriptive statistics

<i>Cognitive task performance by participant menstrual cycle phase</i>			
	Early-follicular phase	Late-follicular phase	Mid-luteal phase
Visual working memory capacity	96.63% (6.34%)	92.48% (9.30%)	89.65% (10.84%)
<b>Visual selective attention</b>			
Accuracy	97.03% (2.77%)	96.55% (3.98%)	95.94% (4.35%)
Response time (ms)	642.24 (106.52)	636.30 (98.37)	640.57 (83.79)
<b>Visual working memory</b>			
Accuracy	96.20% (4.75%)	95.43% (7.50%)	94.55% (4.58%)
Response time (ms)	1289.35 (231.47)	1292.11 (214.17)	1275.58 (173.77)

Visual working memory capacity refers to accuracy on the block of neutral objects of the Visual Working Memory Task, and is used as a moderator in all analyses. Visual Working Memory Accuracy and Response Time refer to accuracy and response times on blocks with fertile and non-fertile phase women's faces

accuracy,  $p = .668$ , during the late-follicular phase as a function of whether it was participants' first or second session (Table 2).

**Attentional Bias to Fertile Women** We first examined our hypothesis that women preferentially attend to fertile-, relative to non-fertile-, phase women, particularly when visual working memory is low. For congruent trials, where faster responding can be taken as evidence of attentional bias, a significant interaction between stimulus type and VWMC emerged,  $F(2,153.6) = 4.19$ ,  $p = .017$ . Planned comparisons (Table 3) revealed VWMC moderated responses to fertile versus non-fertile stimuli,  $B = .21$ ,  $SE = .10$ ,  $t(1372) = 2.14$ ,  $p = .032$  (Fig. 2), such that when working memory was poorer, participants exhibited greater bias toward fertile stimuli (i.e., responded quicker to the probe). Using Preacher et al.'s (2006) computational tool for testing two-way interactions (Case 3) in multilevel modeling, we examined the simple slopes of the association between stimulus-type and response times among observations 1 *SD* above and below mean VWMC. Among those lower in working memory, faster responses to fertile, relative to non-fertile faces, were observed,  $B = -.03$ ,  $SE = .01$ ,  $z = -2.63$ ,  $p = 9E-4$ , whereas the simple slope was nonsignificant among those with higher working memory,  $B = 3E-4$ ,  $SE = .01$ ,  $z = .28$ ,  $p = .780$ . Our second planned contrast comparing faces to objects revealed a non-significant interaction between VWMC and stimuli type on response times,  $B = .15$ ,  $SE = .09$ ,  $t(82) = 1.75$ ,  $p = .084$ . Controlling for covariates, the significant moderation of the effect of stimulus fertility on response times by VWMC maintained,  $F(2,139.2) = 4.19$ ,  $p = .017$ . However, for incongruent trials, neither stimulus type ( $p = .460$ ) nor the interaction between stimulus type and VWMC ( $p = .666$ ) predicted response times (Supplementary Table 1).

In exploratory analyses, we probed the extent to which neuroendocrine and physical appearance fluctuations associated with stimulus fertility interacted similarly with participants' visual working memory. We removed stimulus fertility and its interaction with VWMC from our model and inserted stimulus progesterone, estradiol, and attractiveness (based on ratings from women unacquainted with our stimuli and participants reported in Puts et al. 2013) and their respective interactions with VWMC. Stimulus progesterone levels interacted significantly with VWMC,  $F(1,166.7) = 6.03$ ,  $p = .015$ , such that stimuli with lower progesterone elicited faster responses among participants lower in visual working memory. However, neither stimulus estradiol nor attractiveness interacted with participants' VWMC to predict response times, all  $ps > .079$ . Thus, we proceeded to formally test the extent to which progesterone mediated the moderating (interaction) effect of stimulus fertility and VWMC on response times in a multilevel mediation model, controlling for estradiol and attractiveness (Fig. 3). We expected that any indirect effect of stimulus fertility through progesterone would depend on participants' visual working memory because, though we observed a bias toward fertile-phase stimuli when participants' working memory was low, we observed no association between stimulus fertility and response times when working memory was high. Thus, we measured the extent to which the indirect effect depended on a moderator (here, VWMC), called the index of moderated mediation (Hayes 2015). The index of moderated mediation was statistically significant ( $-.013$ , 95% CI =  $[-.03, -7E-4]$ ), indicating that the indirect effect of stimulus fertility on response times through progesterone varied with participants' VWMC. These results, though exploratory, suggest that neuroendocrine fluctuations across a woman's

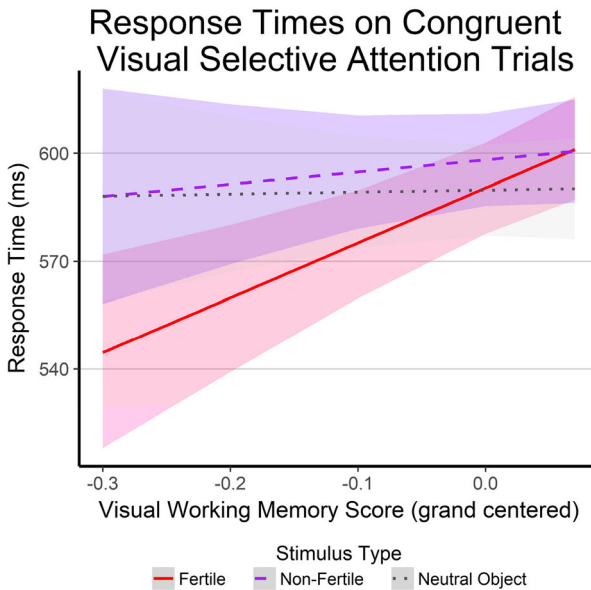
**Table 3** Table of results from linear mixed-model examining women’s attentional bias to fertile-phase women

*Fixed effects of stimulus fertility and visual working memory capacity on RT in congruent trials of the visual selective attention task*

	<i>B (SE)</i>	<i>t (df)</i>	<i>p</i>
Intercept	6.37 (.02)	297.95 (61)	<2e-16
Visual Working Memory Capacity	0.11 (.14)	.80 (20)	0.433
Stimulus Type: Fertile vs. Non-Fertile	-0.01 (.01)	-1.60 (3625)	.110
Stimulus Type: Faces vs. Objects	0.01 (.01)	1.04 (2664)	0.299
Probe-Response Congruency	0.05 (.01)	7.57 (3667)	4.75E-14
Visual Field of Stimulus	-0.02 (.01)	-2.29 (3671)	0.022
Visual Working Memory Capacity x Stimulus Type: Fertile vs. Non-Fertile	0.21 (.01)	2.14 (1372)	0.032
Visual Working Memory Capacity x Stimulus Type: Faces vs. Objects	0.15 (.09)	1.75 (82)	0.084

Degrees of freedom and *p*-values were calculated using the Satterthwaite approximation in the R package lmerTest (Kuznetsova et al. 2017)

menstrual cycle may affect her appearance in ways which bias other women’s attention, but that they do so differently for women with lower relative to higher visual working memory (i.e., biasing only those women with relatively low working memory.)



**Fig. 2** Response Times in the Visual Selective Attention Task on Congruent Trials. When participants had lower visual working memory, they exhibited an attentional bias on congruent trials, such that they responded more quickly to fertile, relative to non-fertile, faces. Fitted values for raw response times are shown here, though analyses were conducted on log-transformed RTs. Visual working memory capacity is grand centered across all sessions and all participants, such that negative scores indicate lower than average visual working memory capacity and positive scores indicate higher than average visual working memory capacity. Shaded regions indicate +/- 1 standard error

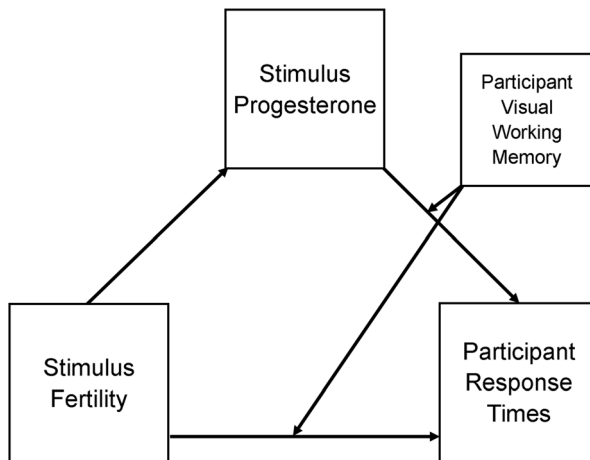


**Attentional Bias to Fertile Women among Fertile Women** We next examined whether participants' cycle phase moderated their attention to fertile women. For both congruent and incongruent trials, there was neither an omnibus three-way interaction between VWMC, stimulus type, and session type, nor a significant effect for either planned comparison for session type,  $ps > .239$  (Supplementary Table 2). In a model in which we replaced participant's session type with participants' imputed E:P ratio, we still failed to find a significant three-way interaction between VWMC, stimulus type, or session type,  $ps > .108$ . Thus, we observed no significant evidence that participants' cycle phase biased the time it took them to respond to probes which immediately followed images of fertile, relative to non-fertile, women.

### Memory Bias–Visual Working Memory Task

Trials on which participants failed to respond before trial time-out at 3000 ms (2.18% of trials) were excluded. As with the selective attention task, response times greater than 3 *SD* above the mean response time (2798 ms) were removed (1.21% of remaining trials). No response times were less than 200 ms. Response times were log transformed before analysis. Response times in the late-follicular phase did not differ as a function of whether it was participants' first or second session,  $p = .151$  (Table 2).

**Memory Bias for Fertile Women** We first examined our hypothesis that women better recall the faces of fertile, relative to non-fertile women, particularly when visual



**Fig. 3** A model testing whether the effect of stimulus fertility on participants' response times on congruent trials in the visual selective attention task as a function of participant visual working memory could be explained by stimulus progesterone. Participant visual working memory moderated the effect of stimulus fertility on response times, such that participants responded faster to fertile-phase stimuli when visual working memory was low (Fig. 2). In exploratory analyses, we found that it also moderated the effect of stimulus progesterone on response times, such that participants responded faster to stimuli with lower levels of progesterone (independent of their fertility status) when visual working memory was low. We tested the moderated mediation model, controlling for estradiol levels and attractiveness, with 5000 simulations. Results revealed that the indirect effect of stimulus fertility on participant response times through progesterone depended significantly on participant visual working memory

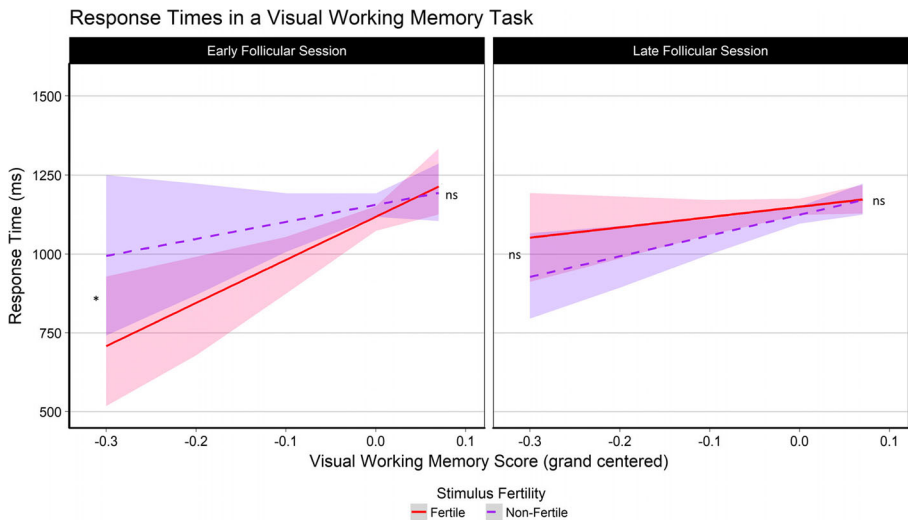
working memory is low. We observed no significant interaction between VWMC and stimulus fertility ( $p = .930$ ), nor a significant main effect of stimulus fertility ( $p = .237$ ). Interestingly, we observed a significant effect of comparison stimuli fertility, such that participants responded more slowly on trials where comparison stimuli were of the same fertility status (e.g., fertile or non-fertile) as the sample,  $F(1,70.3) = 11.83$ ,  $p = .001$  (Supplementary Table 3).

**Memory Bias for Fertile Women among Fertile Women** We next examined whether participant and stimulus cycle-phases might interact to predict response times, such that fertile women would exhibit a memory bias in favor of fertile women's faces (i.e., quicker response times), particularly when visual working memory is low. A weak but significant three-way interaction between stimulus fertility, session type, and VWMC emerged,  $F(2,77.1) = 3.24$ ,  $p = .045$  (Fig. 4), and substituting participants' session type with their imputed E:P ratio revealed a consistent three-way interaction,  $F(1,209.4) = 10.654$ ,  $p = .001$ . The three-way interaction between stimulus fertility, VWMC, and our planned contrast comparing early to late-follicular sessions was significant,  $B = 1.28$ ,  $SE = .50$ ,  $t(280.8) = 2.536$ ,  $p = .012$ ; however, the three-way interaction between our planned contrast comparing late-follicular to mid-luteal sessions and stimulus fertility and VWMC was not,  $B = .35$ ,  $SE = .39$ ,  $t(35.4) = .91$ ,  $p = .368$  (Table 4). Decomposition of the significant interaction revealed that when participants were in the early-follicular phase, they demonstrated a bias toward identifying fertile faces stored in visual working memory (e.g., faster RTs) when they had lower working memory,  $B = .14$ ,  $SE = .06$ ,  $z = 2.54$ ,  $p = .011$ , but not when they had higher working memory,  $B = -.04$ ,  $SE = .04$ ,  $z = -.88$ ,  $p = .380$ . However, when participants were in their late-follicular phase, they were not biased to more quickly recognize fertile faces, regardless of whether they had lower,  $B = -.04$ ,  $SE = .02$ ,  $z = -1.47$ ,  $p = .142$ , or higher,  $B = 1e-3$ ,  $SE = .02$ ,  $z = .07$ ,  $p = .946$ , levels of working memory. Consistent with previous analyses, a significant main effect of comparison stimulus fertility emerged, such that participants were slower to respond when comparison stimuli were of the same fertility status as the sample stimulus,  $B = .18$ ,  $SE = .03$ ,  $t(101) = 6.97$ ,  $p = 3E-10$ . Controlling for covariates, the significant three-way interaction between session type, stimulus fertility, and VWMC maintained,  $F(2, 109.1) = 3.17$ ,  $p = .046$ .

In exploratory analyses, we assessed whether stimulus neuroendocrine and physical appearance fluctuations were associated with participants' memory biases differentially across the menstrual cycle by removing stimulus fertility and its associated interaction terms from our model and inserting stimulus progesterone levels, estradiol levels, and attractiveness scores and their interactions with participants' session type and VWMC. No three-way interaction terms were significant, all  $ps > .212$ .

## Discussion

The present study is the first, to our knowledge, to demonstrate that visual cues of a woman's fertility status shape attentional and memory processes in other women. We observed that women's attention is captured by fertile-phase women, and that they are quicker to identify fertile-phase women stored in memory when they are in the early-



**Fig. 4** Response Times in a Visual Working Memory Task. Response times to recognize women's neutral faces as a function of stimulus fertility, session type, and visual working memory capacity (fitted values for raw response times are shown here, though analyses were conducted on log-transformed RTs). Visual working memory capacity is grand centered across all sessions and all participants, such that negative scores indicate lower than average visual working memory capacity and positive scores indicate higher than average visual working memory capacity. Participants were faster to recognize the neutral faces of fertile women than they were to recognize the neutral faces of non-fertile women in a visual working memory task when they were in their early follicular phase (left panel) and had lower visual working memory. However, when they were in the most probabilistically fertile phase of their cycle (late follicular phase; right panel), there was no difference in the speed to recognize the neutral faces of fertile and non-fertile women, regardless of visual working memory capacity. Shaded regions indicate  $\pm 1$  standard error

follicular phase of their menstrual cycle. These effects are evident only in circumstances where attentional control abilities are compromised (e.g., when participants have lower visual working memory). We discuss the implications of these findings below.

As predicted, for women more susceptible to visual attentional capture (e.g., those with poorer visual working memory capacity; Fukuda and Vogel 2009), fertile-phase women capture attention more than non-fertile-phase women, as evidenced by participants' quicker identification of probes that replace fertile faces. Interestingly, we observed an effect of fertile-phase women on attentional biases in congruent trials (which index attentional orienting) only, and this effect did not depend on a woman's own menstrual cycle phase. Though the present data allow only speculation as to why we observed an attentional bias exclusively in trials indexing attentional orienting, but not in those indexing attentional engagement, one possibility could be that in our task, stimulus fertility affected earlier stages of face processing (such as face categorization; Liu et al. 2002) that are involved in initial attentional orienting and speeded responses on congruent trials, but not later stages of face processing (e.g., face identification or emotion recognition; Batty and Taylor 2003; Liu et al. 2002; Puce et al. 1999) that could delay attentional disengagement and slow responses on incongruent trials. In other words, fertile-phase women may initially capture attention to facilitate recognition of a face, but the devotion of additional attentional resources that might delay disengagement from fertile-phase women's faces may depend on other factors, such as the context in which women encounter a fertile-phase woman, that were not captured in

**Table 4** Table of results from linear mixed-model examining women's memory bias to fertile-phase women as a function of their own menstrual cycle phase

*Fixed effects of stimulus fertility, participant fertility, and visual working memory capacity on RT in visual working memory task*

	<i>B (SE)</i>	<i>t (df)</i>	<i>p</i>
Intercept	6.94 (.02)	334.23 (121)	<2E-16
Visual Working Memory Capacity	.39 (.39)	.99 (28)	.332
Stimulus Fertility: Non-Fertile	4.64E-3 (.02)	.31 (1213)	0.757
Session Type: Early Follicular vs Late Follicular	.03 (.04)	.79 (68)	0.432
Session Type: Mid-Luteal vs Late Follicular	.01 (.03)	.34 (68)	0.733
Distractor Fertility Status: Same as Sample	.18 (.03)	6.97 (101)	3.40E-10
Visual Working Memory Capacity x Stimulus Type: Non-Fertile	-.21 (.20)	-1.04 (75)	0.304
Visual Working Memory Capacity x Session Type: Early Follicular vs Late Follicular	-1.14 (1.09)	-1.05 (24)	0.305
Visual Working Memory Capacity x Session Type: Mid-Luteal vs Late Follicular	.86 (.59)	1.46 (12)	0.171
Stimulus Fertility: Fertile vs Non-Fertile x Session Type: Early Follicular vs Late Follicular	-.06 (.03)	-1.78 (1067)	0.076
Stimulus Fertility: Fertile vs Non-Fertile x Session Type: Mid-Luteal vs Late Follicular	-.02 (.04)	-.63 (927)	0.531
Visual Working Memory Capacity x Stimulus Fertility: Fertile vs. Non-Fertile x Session Type: Early Follicular vs Late Follicular	1.28 (.50)	2.54 (281)	0.012
Visual Working Memory Capacity x Stimulus Fertility: Fertile vs. Non-Fertile x Session Type: Mid-Luteal vs. Late Follicular	.35 (.39)	.91 (35)	0.368

Degrees of freedom and p-values were calculated using the Satterthwaite approximation in the R package lmerTest (Kuznetsova et al. 2017)

our visual selective attention task. However, this interpretation should be treated as speculative, and further work is necessary to explicitly test this possibility.

Exploratory mediation analyses demonstrated that the effect of stimulus fertility on participants' attention may be explained through stimulus progesterone levels, even controlling for attractiveness, when participants have lower visual working memory. This suggests that coordinated changes in women's visual appearance associated with their progesterone levels may convey socially relevant biological information, independently of information conveyed by attractiveness. Women near ovulation (i.e., with probabilistically the highest odds of conception) are often regarded as more attractive by both men and women than women who are in less fertile phases of their menstrual cycles (Bobst and Lobmaier 2012; Roberts et al. 2004; although see Bleske-Rechek et al. 2011), and ratings of facial attractiveness are generally related to estradiol and progesterone levels (Jones et al. 2018b; Puts et al. 2013), hormones whose fluctuations across the menstrual cycle correspond with fluctuating levels of fertility. However, attractiveness alone is likely an insufficient cue to a woman's fertility (c.f., Havlicek et al. 2015; Jones et al. 2018b), and a number of other facial features may also fluctuate

in appearance across the menstrual cycle, including face shape (Bobst and Lobmaier 2012; Lobmaier et al. 2016; Oberzaucher et al. 2012), skin pigmentation (Burriss et al. 2015; Jones et al. 2015), or soft-tissue symmetry (Manning et al. 1996; Scutt and Manning 1996). Though beyond the scope of the present paper, the finding that women (with lower VWMC) exhibited an attentional bias for fertile-phase women that was mediated by stimulus progesterone, independently of stimulus attractiveness, suggests that women may be using an amalgam of visual cues to track subtle cues of other women's fertility. How these fluctuating features work in synchrony to convey socially relevant biological information is a ripe area for future research.

Given evidence that fertile-phase faces tend to capture women's attention more than non-fertile-phase faces in the visual selective attention task (when participants were susceptible to attentional capture), we also expected them to capture attention in our visual working memory task. Past work has shown that faces attended during encoding are better retained in visual working memory (Towler et al. 2015) and motivationally relevant stimuli stored in memory are more efficiently recognized (Krawczyk and D'Esposito 2013; Krawczyk et al. 2007). We thus expected women's attentional biases with respect to fertile-phase faces (among those with lower visual working memory) would translate to faster identification of fertile-phase faces in the visual working memory task. However, we did not find that women with lower visual working memory capacity demonstrated a memory bias for fertile-phase women across the board; rather, we found that women with lower visual working memory exhibited memory biases that were dependent upon their own cycle phase. Women more efficiently identified fertile-phase faces only when they were in their early-follicular phase (and had lower visual working memory). Though we expected that a woman's own fertility status might moderate her memory bias for fertile-phase women, the direction of this effect was not as we predicted: we expected a stronger bias (more rapid identification of fertile-phase women) among other *fertile*-phase women (i.e., women in the late-follicular phase), not among women in their *non-fertile* early-follicular phase.

It is worth considering why we might have observed this pattern of effects. One potential explanation is that two separate mechanisms jointly account for women's response times in the visual working memory task: the persistence of the internal representation of a face in visual working memory and the decision-making process guiding behavioral selection of the stimulus which matches one's internal representation. An attentional bias toward fertile-phase faces would quicken responding in the visual working memory task only to the extent that improved visual working memory for fertile-phase faces without also introducing more deliberation into the decision-making phase of the task. More cautious or deliberate responding (for example, disconfirming distractor faces before confirming the target fertile-phase face) would eradicate any benefit (i.e., quicker responding) gained from more privileged representation of fertile-phase faces in visual working memory among those with an attentional bias to fertile-phase faces (i.e., those with lower visual working memory).

Under this interpretation, when women in their fertile- and mid-luteal phase, they may have been more judicious when judging fertile-phase women, such that even though they had an attentional bias towards fertile-phase women (when visual working memory was lower), they were slower to select which face matched the fertile-phase face held in memory, whereas when women were in their early-follicular phase, they

did not behave more cautiously towards a fertile-phase woman. Indeed, this interpretation is consistent with evidence that estradiol, which is higher among women in their late-follicular and mid-luteal phases than among women in their early-follicular phase, diminishes impulsive choice among women (Dimitroff 2014; Smith et al. 2014). Further, characterizing performance on the visual working memory task as resulting from two distinct processes helps resolve why we did not observe an effect of a woman's own fertility on attentional biases towards fertile-phase women, but we did observe an effect on memory biases. This finding demands replication, especially given that results did not emerge precisely as hypothesized.

An important feature of the present results is that effects were observed only when women had lower visual working memory capacity. Here, we treated visual working memory capacity as a trait, consistent with work suggesting that visual working memory capacity is robust across time and different testing contexts (Xu et al. 2017). Our results suggest that within-woman fluctuations in attention and memory for other women may be more pronounced in women who have lower levels of visual working memory capacity, or in women who exhibit more dramatic changes in visual working memory capacity across (and thus have lower visual working memory capacity in parts of) their cycle. However, we do not take this to mean that fertile-phase women are motivationally relevant *only* to women who have lower levels of visual working memory. We may have failed to detect attentional biases in women with higher working memory with the present tasks because individuals with higher levels of visual working memory capacity recover quickly even in the event of attentional capture (Fukuda and Vogel 2011). This does not preclude the possibility that such biases exist. Indeed, future work that taxes visual working memory resources to a greater degree (for example, by placing participants under cognitive load) may yet reveal biases for fertile-phase women among women with higher visual working memory capacity as well.

Note that in all analyses, we treated women's visual working memory capacity as capable of fluctuating across the cycle (i.e., by modeling working memory capacity as a random effect within subjects), consistent with previous evidence that some forms of working memory may fluctuate across the menstrual cycle (e.g., Phillips and Sherwin 1992; Rosenberg and Park 2002) or with levels of estradiol, one of the primary hormones that fluctuates across the menstrual cycle (e.g., Hampson and Morley 2013; Hampson et al. 2015). Though we did not observe systematic differences in women's visual working memory capacity as a function of cycle phase, the inclusion of visual working memory capacity as an important moderator capable of fluctuating with cycle phase, as well as our distinction between fertile-phase and non-fertile phase women as targets of attentional and memory processes, may help to explain why we observe systematic differences in attention towards and memory for other women across women's menstrual cycle, where other authors have failed to find differences (c.f., Anderson et al. 2010).

One important limitation of the present work is that hormonal states were estimated based on cycle days but were not confirmed with hormonal assays. Women exhibit substantial variation in their ovulatory cycles, and the median validity of most 'counting methods' for estimating fertility is only approximately .5 (Gangestad et al. 2016). Here, we followed guidelines for increasing the validity of our experimental design using counting methods (i.e., using a within-subject design where participation was targeted to days with high probability of being within the ovulatory window, based



on backward counting methods with next menstruation confirmed), and collected the suggested sample size to have adequate power to assess within-subjects effects of participant fertility. Additionally, we imputed estimated levels of estradiol and progesterone, and found that E:P ratio (a proximate marker of fertility, Baird et al. 1991) exhibited the same effect on attention and memory as our categorical variable of participant's menstrual cycle phase. Specifically, E:P was not a significant moderator of the effect of other women's fertility on attentional biases when participant's VWMC was low, but it was a significant moderator of the effect of other women's fertility on memory biases when participants' VWMC was low, suggesting that women's biases in memory for fertile-phase women (when VWMC is low) depend on their own fertility status. Still, because hormonal states were not confirmed with assays, future work should replicate and extend the findings that pertain to our participants' fertility status. Though there is potential ambiguity surrounding participants' fertility, this does not impact our finding that all women exhibit an attentional bias towards fertile-phase women when visual working memory capacity is lower, as stimulus fertility was confirmed with hormonal assays (as described in Puts et al. 2013).

One assumption underlying the present work is that other women's fertility is indeed relevant for women's broader social goals, which can direct attention even without explicit awareness (Moskowitz et al. 2004). Evidence suggests, for example, that other women's fertility status affects women's mate-guarding behavior (Hurst et al. 2016; Krems et al. 2016), presumably because fertile-phase women pose a threat to the stability of their romantic relationships, and that fertile-phase women tend to dehumanize other women (Piccoli et al. 2013) and to seek status gains over other women (Durante et al. 2014). If one accepts that other women's fertility may be behaviorally relevant for women (see Necka et al. 2016 for further discussion), then our findings are consistent with a theory of exogenous attentional control that proposes that stimuli are more likely to involuntarily capture attention if they are congruous with current goals (Folk et al. 1992). Though the present data do not permit examination of why fertile-phase women may be relevant to other women, one possibility is that women may be vigilant to threats of status loss posed by their fertile peers, which could in turn affect mating opportunities. The present data suggest that an important direction for future research is to further characterize how women's fertility status affects their tendency to engage in behaviors that may be construed as intrasexually competitive in nature. Such research would further elucidate why fertile-phase women may be motivationally relevant to other women.

Taken together, the present findings suggest women are sensitive to other women's fluctuating fertility on the basis of static visual cues alone, and that women's attention toward and memory for other women may be biased by those other women's fertility. These findings are consistent with previous work demonstrating that women in their fertile-phase behave in ways that may make them more motivationally relevant to other women. We argue that attentional biases index women's sensitivity to the fertility status of other women, and this sensitivity may help women levy accurate expectations about social interactions with other women and adjust their behavior accordingly. Further, this study presents preliminary evidence that women's own cycle phase may modulate how attentional biases manifest in memory. In sum, women's fertility status, as conveyed by visual cues, may affect other women's lower order social processing.

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**Author Contributions** EAN, DAP, and GJN conceived of the experimental procedures. EAN, KVH, and DAP generated experimental materials. EAN, KF, KVH, and SJD collected the data. EAN, IML, ML, and GJN analyzed the data. EAN drafted the manuscript and all authors provided critical edits and revisions.

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**Conflict of Interest** The authors declare they have no conflict of interest.

**Ethical Approval and Informed Consent** All procedures were approved by the Institutional Review Board at the university with which the last author is affiliated. All participants provided written informed consent.

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