THE UNIVERSITY OF CHICAGO

INTRASEXUAL VIGILANCE IN WOMEN:
SOCIAL, COGNITIVE, AND NEUROENDOCRINE MECHANISMS

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE SOCIAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY

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CHICAGO, ILLINOIS
AUGUST 2016

To all of the minds who have challenged, inspired, and nurtured my own.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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SPECIAL THANKS

I owe tremendous thanks to many extraordinary individuals, without whom this dissertation would not have been possible. First and foremost, I am extremely grateful to Greg Norman, who welcomed me into his lab with open arms, challenged me, encouraged me, talked me off the cliff on a regular basis, helped me become a better scientist, and taught me about the type of advisor I hope to someday become. Greg's zeal for science is contagious and especially motivating. His sheer delight and 'pleasure in finding things out' reminds me day in and day out why I chose this career, and it is an honor and pleasure to be able to work with him. I am indebted also to the incredible faculty who have helped sculpt my thinking and provided astute wisdom regarding all things academe, especially Howard Nusbaum, Boaz Keysar, Marc Berman, Anne Henly, and John Cacioppo. In addition, I am thankful for the guidance of Rob Tigner, Michele Breault, Karen Vittengl, Michael Kelrick, and Terri Lindenberg, early mentors who opened my eyes to this wonderful science and encouraged me to pursue graduate studies.

I would also like to extend my sincerest gratitude to the wonderful Kasey Van Hedger, Kelly Faig, Stephanie Dimitroff, Karen Smith, and Ken Onishi, my lab-mates in the Social Psychophysiology and Neuroendocrinology Lab, for their patience, comments, critique, encouragement, laughs, and for embracing whole-heartedly my inner-nerd. I am grateful to my cohort for their support throughout the trials and tribulations of graduate school, specifically Ivo Gyurovski and Natalie Wheeler, whom I hope remain my lifelong colleagues and friends. Thank you to the research assistants who have helped collect the data presented here, including Ali Calentino, Nealey DuVernay, Adam Picker, Audrey Sung, and Arielle Von Hippel. Thank you also to my collaborators, David Puts, Omid Kardan, Maike Luhmann, Louise Hawkley, and Moriah Sokolowski, and to my colleagues and friends, Stephen Gray, Stephen Van Hedger, Nicole Baltazar, Anna Matejko, Stephanie Bugden, Naveen Khetarpal, Rebecca Rosen, Ellie Shockley, Aly Light, and Sebastian Lehmann, for their hard work, ideas, and stimulating conversations. Many amazing friends are owed thanks for reminding me when things are tough why I fell in love with psychology in the first place, and for listening to and exciting at my ideas while they're still only half-baked, specifically Leigh Harmon, Meg Burik, Katie Kohloff, Daniel King, Maddie Schmitt, Emily Cunningham, Danielle DiGiacomo, Randy Bame, and Gerardo Delgado, among many others. Special thanks also to one amazing Polish Tatra Sheepdog and two awesome kitties for always putting a smile on my face.

For their encouragement, love, and eternal support, I want to thank my siblings, the talented and charming Dianna and Christopher Necka, my grandparents Judy and Vernon Muschetto, Anna and Bruno Necka, and Rose Muschetto, and the rest of my family, especially Mark Necka and Margi Leddin. Most importantly, for instilling in me a lifelong curiosity and passion for learning, for providing me with the unconditional love and unwavering support that enabled me to pursue my dreams, and for teaching me the importance of hard work, persistence, and patience, I want to thank my parents, Valerie and William Necka, without whom none of this would be possible.

Finally, I would like to thank Ian Lyons, my partner in life and the man who has been there through the good, the bad, and the ugly. Thank you for your kindness, compassion, and love, and for believing in me when I didn't believe in myself. I look forward to our continued adventures, to thriving in sharing with one another our discoveries, and to continuing to flourish and grow in our mutual curiosity about the human mind and spirit and our zest for life.

ABSTRACT

Hormones facilitate the coordination of social and cognitive processes which are fundamental to life by exerting synergistic effects on individuals' physiology and behavior. In this dissertation, I use the model of the human female's menstrual cycle to examine how endogenous fluctuations in circulating hormones are related to changes in both an individual's social behaviors and perceptions and those of their conspecifics. When women are in the most probabilistically fertile phase of their menstrual cycle, they tend to exhibit behavior characteristic of status competition with other women. Analogous motivations among probabilistically fertile women may put fertile-phase women in direct competition with each another. In three studies, I test the hypothesis that women are more vigilant towards fertile-phase women, particularly when they are in the fertile-phase of their own menstrual cycle, based on visual cues to other women's fertility. In Study 1, I demonstrate that women behaviorally distinguish between fertile- and non-fertile-phase women as a function of their own fertility status, such that probabilistically fertile women give fewer resources to other fertile-phase women. In Study 2, I demonstrate that women attend to fertile-phase women more than non-fertile-phase women and, when they are in the fertile-phase of their own cycle, are slower to indicate that a fertile-phase woman matches one held in memory. These effects are observed only when women have low visual working memory, which is related to increased susceptibility to attentional capture. In Study 3, I find evidence that women differentially attend to some features of fertile- and non-fertile-phase women's neutral faces, but not features associated with emotional expressivity which typically conveys threat. Taken together, this work extends previous research which has demonstrated that women engage in greater intrasexual competition when they are probabilistically fertile by considering women's sensitivities to other women's hormonal and associated motivational states.

I discuss this work in the context of hormones’ coordination of physiological and behavioral responses to changing fitness demands.

GENERAL INTRODUCTION

Hormones exert synergistic effects on physiology and behavior, facilitating the coordination of social and cognitive processes which are fundamental to life. For example, the gonadal hormone estradiol increases the likelihood that females engage in behaviors which increase their likelihood of conception, while also serving an essential role in preparing uterine and follicular tissues for successful reproduction. As one example, among female rodents, estradiol is associated with an increased likelihood of exhibiting lordosis, an arching of the back to facilitate male penetration, in response to the tactile stimulation of her flanks by a mounting male rodent (Davidson, Rodgers, Smith, & Bloch, 1968; Pfaff, Schwartz-Giblin, McCarthy, & Kow, 1994). As another, in female humans, increases in estradiol are associated with heightened desire for and initiation of sexual intercourse, as well as increased receptivity towards male advances (Bullivant et al., 2004; Flowe, Swords, & Rockey, 2012; Guéguen, 2009; Roney & Simmons, 2013). Hormones thus modify the likelihood that an organism exhibits certain behaviors, behaviors which complement the physiological processes that they promote (Nelson, 2010).

Hormones can also influence the physiology and behavior of an organism's conspecifics. For example, recent evidence suggests that higher estrogen levels in one mouse within a caged pair can lead to subsequent increases in estrogen levels in the cagemate, an effect hypothesized to occur through the cagemate's dermal or nasal exposure to the other mouse's urine and neuroendocrine components therein (Guzzo, Jheon, Imtiaz, & DeCatanzaro, 2012; Guzzo, Pollock, & DeCatanzaro, 2013). In humans, preliminary evidence suggests that hormones secreted by the apocrine glands of the axillae (i.e., armpits) of human females may influence both behavioral and hormonal responsivity of other individuals who are exposed to their scent

(Maner & McNulty, 2013; Miller & Maner, 2010, 2011; Woodward, Thompson, & Gangestad, 2015). Thus, hormones may play a role as social signals which influence conspecifics' perceptions of and behaviors toward an individual.

In this dissertation, I use a model of the human female menstrual cycle as a way to examine endogenous fluctuations in circulating hormones and associated changes in an individuals' and their conspecifics' behavior. Accumulating evidence suggests that gonadal hormones which fluctuate across the menstrual cycle are associated with changes in women's mating-related psychology and behavior (c.f., Bullivant et al., 2004; Roney & Simmons, 2013), as well as with changes in men's perceptions of and behavior towards them (Haselton & Gildersleeve, 2011). Yet only recently has empirical work begun to examine the relationship between a woman's menstrual cycle phase and her social perceptions of and interactions with other women. Broadly construed, the present project aims to assess how a woman's menstrual cycle phase **(a)** is related to her perceptions of and behavior towards other women, **(b)** is related to other women's perceptions of and behaviors towards her, and **(c)** is related to other women's perceptions of and behaviors towards her differentially across those other women's menstrual cycles. The present work is built on the assumption that fertile-phase women share analogous motivations with other fertile-phase women (i.e., motivations which track fertility). To the extent to which motivated end-states (e.g., high social status; access to mating partners) are limited by other women's demands for or achievement of identical end-states, other fertile-phase women may thus impair a woman's ability to achieve her desired end-state. The present dissertation focuses specifically on fluctuations in women’s vigilance and competitive behavior towards other women as a function of both women’s menstrual cycle phase.

Background

Fluctuations in conception probability and mating-related psychology and behavior

Each month, the average pre-menopausal woman mounts a neuroendocrine cascade which is necessary for successful reproduction (see Figure 1). During the end of the menstrual cycle and into the beginning of the next cycle (which begins with menstruation), gonadotropin-releasing hormone (GnRH) is released from the hypothalamus in pulses, prompting the pituitary gonadotroph cells to secrete luteinizing hormone (LH) and follicle-stimulating hormone (FSH) in a similarly pulsatile fashion (Buffet, Djakoure, Maitre, & Bouchard, 1998). These hormones promote growth of follicles within the ovary (the follicular phase) until one follicle obtains dominance, a process which lasts an average of 14 days, although there is considerable inter-women and intra-women (inter-cycle) variability (Lenton, Landgren, & Sexton, 1984). The early follicular phase is characterized by low levels of gonadal hormones, whereas the late follicular phase is characterized by mounting levels of estrogen and ends with ovulation, the release of the egg (ovum) from the follicle into the fallopian tubes. This marks the start of the luteal phase, during which the now empty follicle reorganizes to become the corpus luteum and begins to release estradiol and progesterone to prevent maturation of further ovulation and to thicken the uterine endometrial lining for implantation of a fertilized egg. If fertilization of the egg and implantation of the zygote do not occur, the corpus luteum regresses and, in the case of humans, the enriched endometrial tissues of the uterine lining are shed through the reproductive tract in a process known as menstruation.

The ovum is viable for fertilization for only approximately 24 hours after ovulation (Royston, 1982; Weinberg & Wilcox, 1995); thus, there are only a few days during each menstrual cycle when a woman has a high probability of becoming pregnant. Clinical studies examining the likelihood of conception in humans suggest that the five days prior to and the day of ovulation itself represent a probabilistic ‘fertile window’ during which the probability of clinical pregnancy from a single act of unprotected sexual intercourse is relatively high (6.1% to 8.1%; Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001). This phase of the menstrual cycle has been associated with a variety of changes in mating-related psychology and behavior which are thought to deflect male attention away from other women and increase the likelihood of attracting a potential mate (Gangestad, Thornhill, & Garver-Apgar, 2005). For instance, during the late follicular, pre-ovulatory phase, women are more interested in initiating sexual intercourse (Bullivant et al., 2004), are more receptive to male advances (Flowe et al., 2012; Guéguen, 2009), and report having greater sexual desires and fantasies (Roney & Simmons, 2013), effects which are associated with circulating levels of estrogen and progesterone (Roney & Simmons, 2013). Furthermore, women are more likely to behave in ways that can increase their attractiveness to males, such as wearing revealing clothing (Durante, Li, & Haselton, 2008) and dancing and walking suggestively (Fink, Hugill, & Lange, 2012). These effects are largely consistent with research in non-human mammals, which suggests that females exhibit heightened sexual receptivity (welcoming of male advances) and proceptivity (active initiation of intercourse) during the periovulatory phase of the ovulatory cycle (Beach, 1976; Bonsall, Zumpe, & Michael, 1978; Nadler, Collins, Miller, & Graham, 1983).

Fluctuations in physical attributes which may convey relevant biological information

Women tend to exhibit fluctuations in physical attributes which correspond with hormonal fluctuations across the menstrual cycle and may serve as cues that index their probabilistic fertility. Women are typically considered more attractive during their fertile phase (Haselton & Gildersleeve, 2011). During the fertile phase, when estrogen is high and progesterone is low, women tend to be rated as having more attractive faces (Roberts et al., 2004), and their faces tend to be more round (Bobst & Lobmaier, 2012) and red (Jones et al., 2015; although it is unclear whether changes in coloration are apparent to the human eye; Burriss et al., 2015). Such visual cues may communicate biologically relevant information. For example, based on static visual cues alone, men are more likely to choose women near the fertile phase of their cycle as being more attractive, caring, flirtatious, and likely to date them (Bobst & Lobmaier, 2012). Women may share male’s perceptions of fertile-phase women. For example, women tend to guard their romantic partners, particularly their sexually desirable romantic partners, from fertile-phase women, perhaps as a way to mitigate the potential that fertile-phase women may pose to the stability of their romantic relationship (Krems, Neel, Neuberg, Puts, & Kenrick, 2016). Indeed, women choose fertile-phase women as being more likely than non-fertile-phase women to steal away their preferred dates (Lobmaier, Bobst, & Probst, 2016), but notably only when their own levels of estradiol are high, a point to which we will return.

Fluctuating endogenous hormones across the cycle may also modulate other physical attributes. The hormones which characterize the luteal phase of the menstrual cycle are associated with decreased female vocal attractiveness and flirtatiousness (Puts et al., 2013), and voices are rated as more attractive near the late follicular phase of the cycle (Bryant & Haselton, 2009; Pipitone & Gallup, 2008; although see Fischer et al., 2011). Evidence for estrogen receptors in the larynx are suggestive of a putative role for estrogen in modulating voice dynamics (Amir & Biron-Shental, 2004; Ferguson, Hudson, & McCarty Jr., 1987; Raj, Gupta, Chowdhury, & Chadha, 2010). Further, women may also exhibit olfactory changes across the menstrual cycle, with their scents rated as more attractive when they are near ovulation (Gildersleeve, Haselton, Larson, & Pillsworth, 2012; Havlíček, Dvořáková, Bartoš, & Flegr, 2006).

Fluctuations in intrasexual competitive behaviors

Shifts in women's mating-related behavior and visual, vocal, and olfactory characteristics increase their attractiveness to men during their late follicular phase, but may effective only to the extent that a man is not otherwise involved with another woman. Given that both time and the number of accessible men are finite, a woman's ability to secure a mate during the approximately six-day 'fertile window' in which her likelihood of conception is high is constrained by the influence of other women who are also vying for his attention. Thus successful reproduction depends not on a woman's ability to attract a mate in a vacuum, but rather on her ability to attract him in the presence of a number of competing and attractive alternatives. Indeed, work across phylogeny suggests that successful intrasexual competition can increase opportunities to conceive and chances of offspring survival (Stockley & Bro-Jørgensen, 2011). It is thus possible that engaging in intrasexual competition may increase a female's odds of reproductive success. This notion is encapsulated in the Ovulatory Competition Hypothesis, which predicts that near ovulation women should exhibit increases in behaviors characteristic of intrasexual competition (Durante, Griskevicius, Cantú, & Simpson, 2014).

Indeed, a growing body of literature suggests that women may be more likely to engage in competitive-like behaviors during their late follicular, probabilistically fertile- phase. Near ovulation, women dehumanize other women (Piccoli, Foroni, & Carnaghi, 2013) and give other women fewer resources (Durante et al., 2014). Furthermore, near the probabilistically fertile phase, self-promoting behavior, which is largely perceived as an effective tactic for attracting members of the opposite sex (Buss, 1988), tends to be elicited more by the presence of other women than of potential mates. During the late follicular phase, women prefer to purchase sexier clothing items when primed with images of attractive women, but not when primed with images of unattractive women or of attractive or unattractive men (Durante, Griskevicius, Hill, Perilloux, & Li, 2011; Zhuang & Wang, 2014). Although preliminary, this work suggests that some behaviors which have previously been construed as being motivated by a woman's desire to attract a mate may actually be indirectly motivated by such concerns. This research points to the possibility that hormonal influences on women's behavior may promote status competition with other women which intensifies near ovulation.

Competition can be costly, however, potentially leading women to overlook objectively better outcomes in favor of advancing their position *relative* to another woman (Durante et al., 2014). Thus, women often compete selectively, engaging in competition only with women who present proximate threats to reproductive resources, such as attractive women and women who live nearby (Durante et al., 2014, 2011; Lucas & Koff, 2013). Analogous motivations among probabilistically fertile women may result in fertile-phase women being the most relevant competitors for other fertile-phase women, putting fertile-phase women in direct competition with each other. Evolutionarily, analogous mating-related motivations among fertile-phase women may have led them to compete with each other for access to potential mates. More proximally, women's heightened concern with their general social standing near ovulation may make them more cognizant of or perturbed by other fertile-phase women's status striving.

This possibility poses the question, to what extent do women distinguish between other women as a function of the other women's hormonal profiles, and does their ability or tendency to do so change across their own menstrual cycle? I expect that vigilance to fluctuating visual cues of other women's fertility is important for a woman to accurately discern the likelihood that another woman may threaten her own status or likelihood of reproduction, and that vigilance is therefore particularly strong among women who are in the late follicular (i.e., 'fertile') phase of their menstrual cycle, for whom information about others' biological states and associated mating- and status-related motives and behaviors is especially relevant. Past research suggests that among women who exhibit hormonal profiles characteristic of high conception likelihood (e.g., higher levels of estradiol and lower levels of progesterone), olfactory cues from other women in the late follicular, but not luteal, phase of their cycle prompt increases in endogenous salivary testosterone (Woodward et al., 2015), a response which is sometimes related to anticipation of competition (Bateup, Booth, Shirtcliff, & Granger, 2002). Even among women whose probability of conception is low, estradiol may play a role in women's ability to detect cues to other women's fertility or to assess such cues as a potential threat (Lobmaier et al., 2016). Taken together, these findings suggest a role for a woman's fertility status, or potentially some components of the neuroendocrine profile associated with peak fertility, in discerning and differentially responding to other women's fertility.

The present project

The present project addresses three primary research questions: **(a)** are fluctuating hormones throughout the menstrual cycle associated with women's behavior towards and perceptions of other women? **(b)** are women's behaviors towards and perceptions of other women influenced by those other women's fertility status (as conveyed by fluctuating visual characteristics across the menstrual cycle)? and **(c)** does the effect of a woman's fertility (as conveyed by fluctuating visual cues) on other women's behaviors toward and perceptions of women depend upon those other women's own hormonal states?

Assessment and manipulation of fertility

In the current project, I refer to women who are in their late follicular, probabilistically fertile phase of their menstrual cycle (e.g., the six days preceding and including ovulation) as "fertile" and women who are in their early follicular, probabilistically non-fertile phase of their menstrual cycle or who are in their mid-luteal, probabilistically non-fertile phase of their menstrual cycle as "low-fertile" or "non-fertile". In the present project, cycle phase is generally assessed using a forward-counting method (in which women report the start date of their last menstrual cycle and researchers count forward, assuming a normal cycle length, to determine women's current cycle day and phase of their cycle) and a backward-counting method (in which women report the start date of their next menstrual cycle and researchers count backward, assuming a normal cycle length, to determine what women's cycle day and phase of their cycle was on the day they participated). For studies which assess the probabilistic fertility of participants, only participants who are not currently using hormonal birth control are included, as hormonal contraceptives artificially manipulate endogenous hormonal fluctuations across the cycle. For studies which manipulate the probabilistic fertility of stimuli, a stimulus set of naturally cycling premenopausal women who were not using hormonal contraceptives is used (Puts et al., 2013). Stimulus women were photographed twice throughout their menstrual cycle, once in the late follicular (i.e., 'fertile') phase and once in the luteal (i.e., 'non-fertile') phase of their cycle, and their voices were recorded at each time-point. Women's circulating estrogen and progesterone were measured and their facial and vocal attractiveness and flirtatiousness were rated by naïve male and female observers (see Puts et al., 2013 for further details).

Definition of Competitive Psychology and Behaviors

For the purpose of the present project, I construe behaviors which improve a woman's status *relative* to another woman (regardless of outcome) as generally competitive behaviors. Women tend to engage in subtle forms of competition, avoiding physical aggression and overt displays of competition unless they are high-ranking in their social group and their rank is well-secured (Benenson, 2013). Furthermore, women tend to disguise their competition, engaging in acts such as enforcing equality among their female peers, derogating other women, and using social exclusion to punish those who defect (Benenson, 2013; Benenson et al., 2013; Buss & Dedden, 1990; Campbell, 2004; Fisher, 2015). Thus, because competition can manifest in so many varied ways, I define competitive psychology as any desires, thoughts, or intentions to improve one's status *relative* to another person (regardless of outcome).

Overview of studies

In **Study 1**, I test whether women's behavior towards another woman varies as a function of both women's fertility status. Specifically, I examine women's resource distribution in a behavioral economic game, and whether allocation of resources varies as a function of a woman's own fertility status and the fertility status of the woman against whom she supposedly plays the economic game. **Study 1** asks if women's vigilance in preserving resources for themselves and keeping them from potential competitors is heightened if either or both they and their competitor are probabilistically fertile. In **Study 2**, I test whether women's attention towards other women and ability to identify other women from memory varies as a function of both women's fertility statuses. Given the strong association between attentional capture and visual working memory, I look particularly at women who have poorer visual working memory capacity, as these women should be most susceptible to attentional capture, and their attention to women may be related to their ability to identify them from memory. In **Study 3**, I consider that one potential explanation for women's heightened vigilance toward fertile-phase women may be that women are biased to see emotional expressions which convey aggressive intent on the neutral faces of fertile-phase women where there are none. To test this, I measure women's propensity to judge neutral emotional expressions as expressions of anger and to look at facial features which typically convey physical traces of angry expressions in the neutral faces of fertile and non-fertile women. Taken together, these studies test women's vigilance towards other women on multiple behavioral levels, and whether such vigilance varies with woman's probabilistic fertility and the fertility of her conspecifics.

Appendix A: Figure for General Introduction

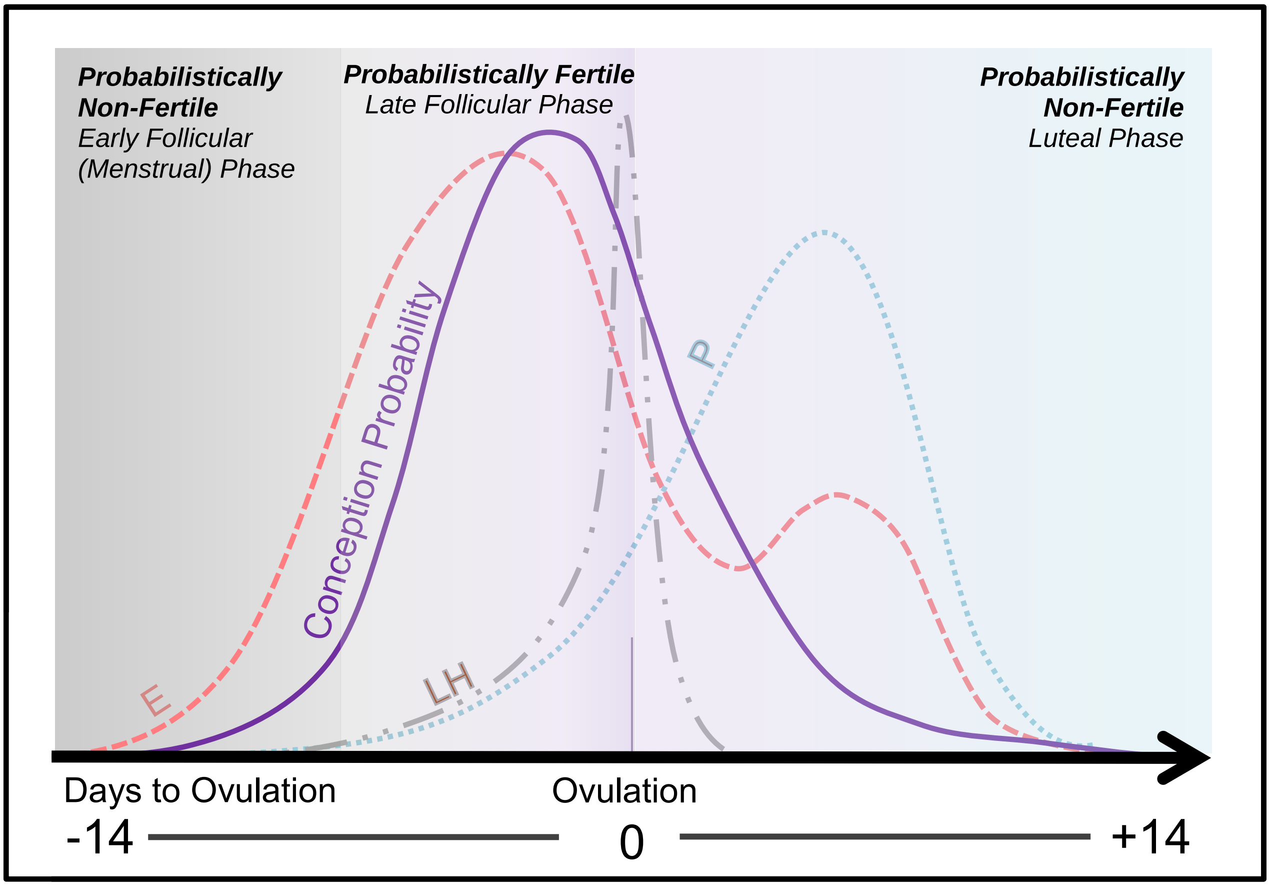

Figure 1. A schematic representing the Human Ovarian Cycle.
During the early follicular phase, estrogen (E, pink) levels begin to rise as follicles grow. As one follicle gains dominance, estrogen levels begin to mount and in a positive feedback loop provoke a surge of luteinizing hormone (LH, gray) from the pituitary gland, which triggers the release of the ovum (egg) into the fallopian tubes at ovulation. Clinical data on the probability of conception (purple) from a single act of unprotected intercourse suggest that the five days prior to and the day of ovulation are when likelihood of conception is highest. Following ovulation, the luteal phase begins and levels of progesterone (P, blue), secreted from the corpus luteum, rise. Note that hormones and conception probability are all on different scales and this schematic is not drawn to scale.

CHAPTER 1: STUDY 1

Introduction

There are only approximately six days in the average premenopausal woman's regular ovulatory cycle during which intercourse may result in conception (Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001). During the late follicular (i.e., "fertile") phase of a woman's cycle, she is more likely to demonstrate mating-related psychology and behavior such as interest and engagement in, and potentially even initiation of, sexual behavior (Bullivant et al., 2014; Roney & Simmons, 2013). Near ovulation, women also tend to behave in ways that can increase their attractiveness to males, wearing revealing clothing (Durante, Li, & Haselton, 2008) and dancing and perhaps walking suggestively (Fink, Hugill, & Lange, 2012; but see Provost, Quinsey, & Troje, 2008). In addition to attracting potential mates directly, these behaviors may also divert male attention from other women. That is, these behaviors may be one way in which women compete with each other.

Indeed, fertile women's self-promoting behavior is elicited more by the presence of other women than of potential mates. For example, during their fertile phase, women preferred to purchase sexier clothing items when primed with images of attractive women, but not when primed with images of unattractive women or of attractive or unattractive men (Durante, Griskevicius, Hill, et al., 2011). Other behaviors associated with aspects of competition have also been observed in women near ovulation (although see Cobey, Klipping, & Buunk, 2013), such as dehumanizing other women (Piccoli, Foroni, & Carnaghi, 2013) and giving other women fewer resources (Durante, Griskevicius, Cantú, & Simpson, 2014)[1].

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[1] Because research in this area is often underpowered, extant findings should be taken as suggestive of a relationship between fertility and competition, but not as definitive.

Furthermore, fluctuations in competitive behavior throughout the estrous cycle can be observed across species, with competition tending to be highest among female mammals near estrous (Stockley & Bro-Jørgensen, 2011). In yellow baboons (*Papio cynocephalus*), for example, ovulating and pre-ovulating estrous females are more likely to form attack coalitions against other females (Wasser, 1983). Moreover, pre-ovulating (but not ovulating) estrous females are more likely to be the targets of such attacks (Wasser, 1983; Rowell, 1972), the effect of which is an increase in the number of cycles before conception (Wasser & Starling, 1988). A negative association between adult sex ratio (females/males) and birth rate in this species suggests that some attacks may reflect female competition for mating opportunities (Dunbar & Sharman, 1983). Yellow baboons live in multi-male, multi-female societies in which females mate promiscuously with multiple males. By contrast, humans tend to exhibit mildly polygynous mating with a high degree of social monogamy. Within socially monogamous relationships, women may exhibit mixed mating strategies, seeking out extra-pair copulations with mates of higher genetic quality than their long-term partner during peak fertility (Gangestad & Haselton, 2015). To the extent that mating opportunities with males of high genetic quality are limited, women may therefore confront increased mating competition when they are near peak fertility.

Successful intrasexual competition can increase opportunities to conceive and chances of offspring survival (Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011). However, intrasexual competition can also be costly, potentially leading women to overlook objectively better outcomes in favor of advancing their position *relative* to other women (Durante et al., 2014). Thus, women often compete selectively, engaging in competition preferentially with women who present proximate threats to reproductive resources, such as attractive women and women who live nearby (Durante et al., 2014, 2011; Lucas & Koff, 2013).

Given that women have only a few days each month during which they are likely to conceive, the competitors who also experience increased conception risk and mating motivation during those days (e.g., other fertile women) may especially challenge a woman's ability to attract prospective mates' attention, thereby potentially decreasing her chances of reproduction.

Like men, women are attuned to subtle physical and behavioral cues to other women's fertility, such as facial and vocal attractiveness (Puts et al., 2013). These cues may induce competitive responses in women. For example, across four experiments, Krems, Neel, Neuberg, Puts, & Kenrick (2016) found that, after viewing photographs of other women taken during either their fertile or non-fertile ovulatory-cycle phases, partnered women consistently reported intentions to socially avoid fertile-phase (but not non-fertile-phase) women—but only when their own partners were highly desirable. Viewing fertile-phase women also increased women's sexual desires for their (highly desirable) partners. In another study, women experienced heightened levels of endogenous salivary testosterone (which may facilitate competitive behaviors) when exposed to olfactory cues from other women who were in the late follicular, but not luteal, phase of their cycle (Maner & McNulty, 2013). Preliminary findings also suggested that women with endocrine profiles consistent with the late follicular phase may be the only ones to exhibit this effect (Woodward, Thompson, & Gangestad, 2015), indicating that both a woman's own fertility and that of a potential rival could be important for mounting a testosterone response. In other words, a woman's competitiveness over mates appears to be influenced not only by her own cycle phase and the cycle phase of other women, but the two may also exert an interactive effect on her competitive behavior.

Despite this intriguing possibility, to our knowledge, no study has used a behavioral indicator of competition to examine whether women's intrasexual competitive behavior differs as a function of both their own fertility and the fertility of their potential competitors. The goal of the present study was to therefore explore this hypothetical interaction. In the present study, we used resource distribution in the dictator game to measure aspects of competitive behavior. During the dictator game, one participant determines how much of a cash reward another participant will receive. Strong fairness norms typically lead most respondents to give their opponents part of the cash reward (Engel, 2011). Consistent with prior research (c.f., Durante et al., 2014), we reasoned that giving a potential opponent less money may provide a woman with greater competitive advantage, and that as the need to compete decreases, women might give more generously. We predicted that fertile women would give less to fertile opponents than to non-fertile opponents, but that there would not be an effect of opponent's fertility on non-fertile women.

Methods

Participants

Women who reported that they experienced menstruation in the past 35 days, were not taking hormonal contraceptives, and had not been diagnosed with a hormonal disorder (*N* = 149, aged 18 – 40 years, *M* = 22.03, *SD* = 4.48) provided consent and participated in a University of Chicago IRB-approved study. Eligible participants were pre-screened from a larger population. Prescreening surveys included distractor questions to mask criteria relevant to the study.

Procedure

Participants engaged in a Dictator Game, ostensibly with another participant in a different room. To obscure study purpose, we photographed participants smiling, neutral-faced, and frowning before they began the study to suggest that the study was about emotion. We informed participants that we would share their picture with the other "participant". Participants learned that each participant pair would receive $5 and that participants would be randomly assigned to play the role of the "Proposer," who could allocate any portion of the money to the other participant, or the "Receiver," who would receive the money that the Proposer allocated to them (all participants actually played Proposers and received whatever money they kept from the Receiver as compensation for participating). Participants were randomly assigned to view a photograph of one of four women (the "Receiver") in either her late follicular ("fertile") or luteal ("non-fertile") phase (assessed via hormonal sampling). Stimuli demonstrated maximal deviations in attractiveness and in estrogen-to-progesterone ratio between fertile and non-fertile phases and were obtained from Puts et al., 2013[2]. In a free response box beneath the Receiver's photo, participants indicated how much money they wanted to share with her. After the Dictator Game, participants reported their demographic characteristics, start date of their last period, average cycle length, relationship status, and, if romantically involved, their partner's sexual attractiveness (Table 1). Post-hoc analyses on these latter two variables are included in Supplementary Material in Appendix F.

Determination of Fertility

Fertility was determined using the forward counting method (Wilcox et al., 2001). Counting methods rely upon the assumption that women exhibit regular cycles. As previously demonstrated, 95% of women (sample *N* = 2,316) exhibit average cycle lengths between 15-44 days (Chiazze, Brayer, Macisco, et al., 1968); thus we included only participants who reported average cycle lengths in this range (*N* = 127, 18-40 years, *M* = 21.81, *SD* = 4.29) in the primary

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[2] Stimulus selection procedure in Supplementary Material in Appendix F. Because our stimulus selection procedure confounded opponent attractiveness and fertility, and because opponent attractiveness influences the size of offers that participants provide in behavioral economics games (Rosenblat, 2008), we include opponent attractiveness as a covariate in analyses.

analyses. These participants' average cycle length was 28.92 days (*SD* = 3.27) (see Supplementary Material in Appendix F for more information regarding participants irregular cycle lengths). We identified days 10-15 inclusive (e.g., the five days before day of ovulation; Wilcox et al., 2001; Wilcox, Dunson, & Baird, 2000) as "fertile" (*N* = 30), where Day 1 corresponds with the onset of menstrual bleeding. Early follicular (*N* = 39) and luteal phases (*N* = 58) were categorized as "non-fertile".

Fertility was also determined using actuarial data from Wilcox et al. (2001) as a continuous measure of conception risk. Using only participants who reported regular cycle lengths, we first determined each participant's cycle day by subtracting the date of participation from the reported start date of her last menstrual period, which corresponds with Day 1. We referred to Wilcox et al. (2001) (Table 1, 2nd column) to determine conception risk (e.g., Day 13 would translate to 0.086 probability of conception). Because this method of determining fertility is continuous and thus introduces greater variability into our estimates of fertility, it was expected that this method of estimating fertility would have less power than a forward counting discrete-window method. However, should findings using this method be consistent with findings from our primary analyses, they would provide corroborating evidence that our effects are associated with fertility.

Finally, some participants (*N* = 92) opted to receive an email once a week for five weeks following the laboratory session, in which they reported whether menses began that week, and if so, the date that menstruation began. Of the 49 participants (53.26% of those contacted) who responded via email indicating when their next period began, only seven met our criteria for being classified as "fertile" using a discrete backward-counting method (see Supplementary Material in Appendix F), and only two of those were randomly assigned to view a fertile opponent in the Dictator Game. Therefore, although we had originally intended to assess fertility using a reverse-counting method as well, we did no further analyses with data regarding the start date of a participant's next menses due to low response rate and small cell sizes.

Results

Fertile and non-fertile participants did not significantly vary on any measure collected other than cycle day (Table 1.1), suggesting that differences between the groups are attributable to cycle day (which we have used to approximate fertility).

A 2 (participant fertility) x 2 (opponent fertility) analysis of variance, controlling for which stimulus woman served as the "Receiver", revealed a significant interaction between participant and opponent fertility on resource distribution in the Dictator Game, $F(1,120) = 6.18$, $p = 0.014$, $\eta^2 = 0.05$ (Figure 1.1). Fertile women gave marginally less money to fertile ($M = 1.67$, $SD = 0.92$) than to non-fertile opponents ($M = 2.30$, $SD = 1.03$), $p = 0.063$, $d = 0.65$, but non-fertile women exhibited a non-significant trend in the opposite direction, giving comparably to fertile ($M = 2.13$, $SD = 0.86$) and non-fertile ($M = 1.87$, $SD = 0.97$) opponents, $p = 0.142$, $d = 0.28$. No other effects were significant (*p*s > 0.298). When we instead controlled for opponent (stimulus) attractiveness, the interaction between participant and opponent fertility remained significant, $F(1,122) = 5.28$, $p = 0.023$, $\eta^2 = 0.04$. No other main effects were significant (*p*s > 0.267).

Using a continuous measure of participant conception risk and controlling for which stimulus woman served as the "Receiver", we found a significant interaction between participant conception risk and opponent fertility, $B = 13.41$, $SE = 5.91$, $t(120) = 2.27$, $p = 0.025$.

Decomposing the interaction by opponent fertility revealed that higher levels of participant conception risk were associated with giving less to fertile opponents, $B = -.7.80$, $SE = 3.83$, $t(62) = -2.04$, $p = 0.046$, but were unrelated to resource distribution to non-fertile opponents, $B = 5.92$, $SE = 4.70$, $t(55) = 1.27$, $p = 0.213$. A significant main effect of participant conception risk also emerged, $B = -20.29$, $SE = 9.19$, $t(120) = -2.21$, $p = 0.029$, such that participants gave less resources to their opponent as their conception risk increased, as well as a marginally significant main effect of opponent fertility, $B = -0.46$, $SE = 0.24$, $t(120) = -1.88$, $p = 0.062$, such that fertile opponents received greater rewards. Controlling instead for opponent attractiveness yielded a similar pattern of effects. The interaction between participant conception risk and opponent fertility remained significant, $B = 11.67$, $SE = 5.72$, $t(122) = 2.04$, $p = 0.044$, as did the main effect of participant conception risk, $B = -17.89$, $SE = 8.91$, $t(122) = -2.01$, $p = 0.047$. No other effects achieved significance (ps > 0.323).

Effects maintained when controlling for demographic variables as well as when removing all covariates (see Supplementary Material in Appendix F). Analyses on all participants (i.e., including those for whom assumptions of regular cycle lengths were violated) revealed the same pattern of effects (see Supplementary Material in Appendix F).

Discussion

The present study provides preliminary evidence that women differentially allocate resources as a function of their own and other women's fertility. Specifically, fertile women who were paired with a fertile opponent gave less money to their opponent than did fertile women paired with a non-fertile opponent, whereas how much money non-fertile women gave to their opponents appeared to be unaffected by opponent fertility. These data extend previous research which has demonstrated that women engage in greater intrasexual competition when they are near ovulation by considering the motivational states of the potential rivals against whom they are competing. We hypothesized that rivals who are more competitive for mates (specifically, other fertile women) may pose a greater threat to a woman near ovulation and therefore she may engage in more competitive behaviors toward such rivals. Our results suggest that fertile women may indeed compete differentially with other fertile women, who potentially most challenge their reproductive potential.

One limitation of this study is that we approximated participants' likelihood of conception using the forward counting method, which is an imperfect approximation of fertility. In forward counting, error that derives from imprecise estimates of cycle start date, potential anovulatory cycles, and variation in cycle length between- and within-women can be overcome by utilizing large sample sizes or within-subjects designs to achieve substantial statistical power (Gangestad et al., 2016). However, the present study, like much of the extant literature in this area, is likely underpowered, which could result in overestimated effect sizes (Button et al., 2013). Hence, although our results are strongly suggestive, they should be considered provisional and awaiting replication. This limitation is not unique to the present study – much of the empirical work which informs the present findings also utilized underpowered designs (e.g., small samples, between-subject comparisons, and self-report cycle data; c.f. Gonzales & Ferrer, 2015) and it is critically important that future research in this area strive to produce more robust estimates of how fluctuating levels of fertility influence female intrasexual behavior by utilizing more precise fertility estimation methods (e.g., hormonal sampling) and within-subject assessments of competition throughout a woman's cycle.

Additionally, participants viewed only one “rival” during the study, and it is therefore possible that our findings reflect women’s sensitivity to differences in mate-quality *between* rivals rather than to fluctuating mate-quality (i.e., fertility) *within* any given rival. Because we designed the present study to test a theoretical premise rather than the parameters of a population-level effect (c.f., Mook, 1983), only stimuli which demonstrated fluctuating attractiveness across the menstrual cycle (a potential signal of fertility status) were selected as opponents for the present study. Though this selection procedure strengthens our ability to test our theoretical premise, it also introduces the possibility that findings could be driven by differences in attractiveness, rather than fertility. To address these concerns, we controlled for opponent identity and attractiveness and importantly found that opponent fertility still significantly accounted for variance in resource distribution between fertile and non-fertile women. This suggests that an opponent’s fertility may be a key modulator of female competitive behavior at different phases in the menstrual cycle, and that while a rival’s fluctuating attractiveness may *signal* her fertility status, it cannot sufficiently explain the effect observed in the present study. Future research should examine which specific cues of opponent fertility women attend to when behaving competitively towards other women. Knowing which cues of a rival’s fertility motivate women’s competitive behavior will aid in determining the extent to which present findings generalize to a broader population, beyond the specific stimuli used in the present study.

Despite these limitations, the present study is the first to our knowledge to report that an opponent’s fertility may influence another woman’s behavior toward her differently at different points in the ovulatory cycle. Though Woodward et al. (2015) recently examined women’s responses to a survey measure of intrasexual aggression as a function of participants’ own hormones and cycle phase of a potential opponent and observed no significant interaction between opponent and participant fertility, we observed an interactive effect of opponent and participant fertility on competitive behavior. One potential explanation for these differing findings is that fertile women are not simply more competitive overall when other fertile women are present, but rather that they engage in competition only with rivals who are fertile, against whom winning a competition might be particularly advantageous. Alternatively, the aggressive behaviors examined in Woodward et al. (2015) may not map well onto resource distribution in the Dictator Game, where a more competitive response (giving fewer resources to an opponent) is also an objectively advantageous response (keeping more resources for oneself). We have operationalized competition as resource distribution in a behavioral economic game, but it is necessary to assess the extent to which our findings generalize to other competitive behaviors or face-to-face interactions with other women. Might there be social contexts or consequences (e.g., retaliation) which would make competition less favorable? To what extent does the outcome of a competition (e.g., access to material resources, access to a mate) moderate the likelihood of competing? Do these effects still emerge if other women fail to exhibit behavioral or physical cues to their fertility, and if so, by what mechanism? These questions are important, and the present findings are only the first in a promising line of research.

It is worth considering why women might have differentially competed with other women as a function of both women's fertility across evolutionary time, and how such competition may have been adaptive. One possibility is that women were in competition with other women over opportunities to mate with males who possessed "good genes," a tactic that would have been especially advantageous in the context of mixed mating strategies. Ancestral men's and women's proprietariness over mates, as well as time constraints imposed by women's relatively narrow fertile windows, likely made high-quality sires a limited resource. To the extent that having a sexual affair with a man constrained the ability of other women to have sexual affairs with him concurrently, this would have had the effect of forcing women with overlapping fertile windows into competition for high-quality sires. However, the competition observed in the present study was over material resources, not mating opportunities, and so the present study cannot speak directly to this possibility. Competition for material resources could reflect more general agonism between fertile women, for example, spurred by competition to acquire access to a high-quality sire. Because resources can be used for self-enhancement, they may indirectly aid in attempts to secure such a mate. Though it is certainly important to speculate on the ultimate mechanisms by which differential female competition for resources as a function of both competitors' fertility evolved, the present data cannot speak to the ways in which such a competitive strategy may have been advantageous for female fitness, and future work is necessary to disambiguate the motives for and benefits of such competition.

In sum, the present data indicate that variation in the fertility of a potential same-sex rival may moderate the extent to which fertile women distribute resources to her. These preliminary findings provide further evidence that, near ovulation, women may behave in ways that increase opportunities for conception. One way to increase conception likelihood may be to engage in intrasexual competition and out-compete same-sex rivals. The present study suggests that, near ovulation, women may compete selectively, attending to characteristics of potential competitors (e.g., proximate markers of fertility) and limiting access to resources among women who may most threaten their chances of successfully acquiring and securing a mate.

Appendix B: Table and Figure for Chapter 1

Table 1.1. Descriptive Statistics and Breakdown by Cell

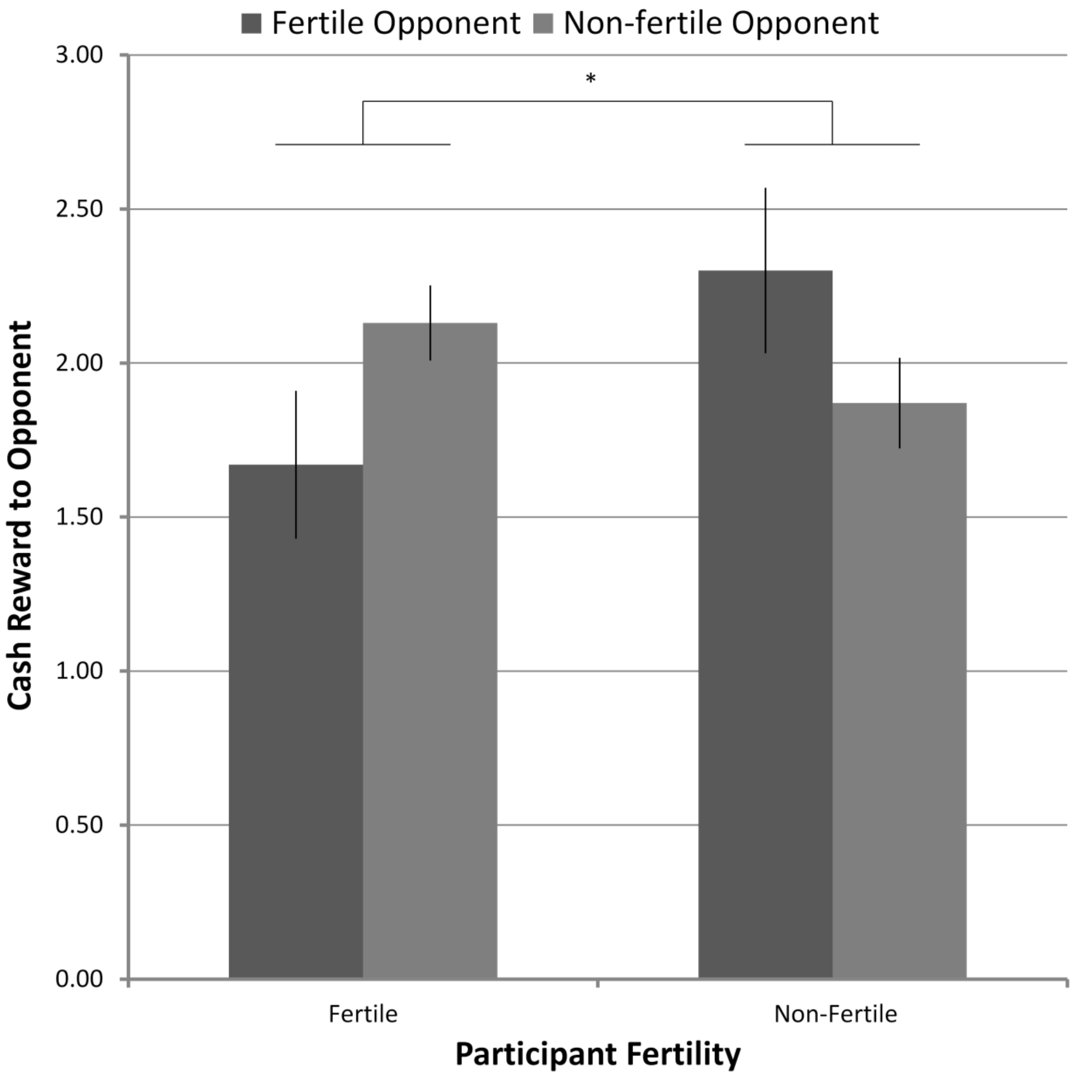
	Fertile		Non-Fertile		
Variable	*n*	*M* (*SD*)	*n*	*M* (*SD*)	*p*
Cycle Day	30	12.37 (1.85)	97	16.77 (10.47)	1.35E-4 *
Average Cycle Length	30	28.43 (2.32)	97	29.07 (3.51)	0.352
Demographic					
Age	30	21.82 (4.25)	97	22.77 (10.37)	0.627
Education	30	13.90 (1.50)	97	14.16 (1.75)	0.456
Marital					0.378
Married	0		2		
Cohabitating	0		4		
Separated	0		0		
Divorced	0		0		
Widowed	0		0		
Never Married	30		121		
Ethnicity					0.439
African American	3		23		
Asian/Pacific Islander	10		32		
Caucasian	10		28		
Hispanic	3		8		
Native American	0		1		
Other	4		5		

Table 1.1. Descriptive Statistics and Breakdown by Cell, Continued

	Fertile		Non-Fertile		
Variable	*n*	*M* (*SD*)	*n*	*M* (*SD*)	*p*
Sexual Orientation					0.789
Heterosexual	25		70		
Bisexual	2		12		
Homosexual	0		1		
Decline to label my sexuality	2		9		
Choose not to respond	1		5		
Romantic Relationship					0.562
Romantically Uninvolved	20		70		
Romantically Involved	10		27		
Partner's Sexual Attractiveness	10	18.70 (3.53)	26	19.38 (3.98)	0.637
Fertile Opponent	15		52		
Non-Fertile Opponent	15		45		

Note: *p*-values indicate the results of *t*-tests for continuous variables (which also include means and standard deviations) or of Chi-squared tests for categorical variables. The only difference between the fertile and non-fertile groups was cycle day. The numbers of fertile and non-fertile participants who were randomly assigned to view a fertile and non-fertile opponent are included in the bottom two rows.

Figure 1.1. Reward to Opponent by Participant and Opponent Fertility, Measured by Forward Counting.



Error bars represent standard errors. * $p < .05$

CHAPTER 2: STUDY 2

Introduction

How women attend to their environment varies across the menstrual cycle, in a manner which is seemingly consistent with fluctuating psychosocial motivations. When women's bodies are in the late follicular phase and their levels of estrogen and likelihood of conception are the highest, for example, they tend to demonstrate increased sexual desire (Bullivant et al., 2004; Roney & Simmons, 2013) and increased initiation of and engagement in sexual activity (Bullivant et al., 2004; Burleson, Trevathan, & Gregory, 2002). Concurrently, they also tend to exhibit an attentional bias towards attractive men (Anderson et al., 2010) and courtship language (Rosen & López, 2009). Given the congruence between women's fluctuating psychosocial behaviors and attention to these stimuli, attention is assumed to be motivationally relevant. That is, attending to something may make it easier to act upon motivations directed at the attended-to object (c.f., Smith & Semin, 2004). A woman who pays greater attention to men at a time when she more greatly desires them, for example, could reasonably be expected to have more success obtaining a partner than a woman who devotes less attention to her search.

Of course, there are many factors other than a woman's own motivations and attention which can influence her success in achieving some end-state. A woman's success in attracting a mate, for instance, depends not only upon how she behaves towards him, but also in part on his availability and interest in her, and whether he is currently involved with or distracted by another woman. The extent to which other women limit mating opportunities may influence women's engagement in intrasexual mating competition. Though preliminary, women do appear to be more likely to engage in behaviors which could be considered intrasexually competitive in nature at a time in their cycle when conception risk is highest, in the late follicular phase (Durante, Griskevicius, Hill, Perilloux, & Li, 2011; Piccoli, Foroni, & Carnaghi, 2013), and they may behave in ways which permit them to acquire status (e.g., to increase their own position relative to another woman; Durante, Griskevicius, Cantú, & Simpson, 2014; Lucas & Koff, 2013). Perhaps unsurprisingly, they are also more likely to have an attentional bias in this phase towards objects which convey or can be used to gain status (Lens, Driesmans, Pandelaere, & Janssens, 2012; Zhuang & Wang, 2014), a bias which is especially pronounced when other attractive women are made salient (Zhuang & Wang, 2014).

However, engaging in intrasexual competition can potentially lead women to overlook objectively better outcomes in favor of advancing their relative standing (Durante et al., 2014). Thus, women in their late follicular phase often compete selectively, preferentially engaging in what may be construed as competitive behaviors with women who present proximate threats to reproductive resources (Durante et al., 2014, 2011; Eisenbruch & Roney, 2016; Lucas & Koff, 2013), including other women who are also in the most probabilistically fertile (i.e., late follicular) phase of their cycle (Chapter 1; Necka, Puts, Dimitroff, & Norman, 2016). For example, Necka et al. (2016) observed that women in their fertile phase gave fewer monetary resources to other fertile women in a Dictator game, relative to patterns of resource distribution if either or both of the women were non-fertile, suggesting that fertile-phase women may uniquely avoid cooperating with another fertile women or that they may prefer retaining resources for themselves when they interact with another fertile woman. To the extent to which fertile women are more motivated to achieve status gains over other women, two women who are simultaneously in their fertile phase may be the most likely to compete with one another for such status. If women are more motivated to engage in competition with other women when they are in the late follicular (i.e., probabilistically fertile) phase of their cycle, we would expect that during this cycle phase they might exhibit increased sensitivity to other fertile-phase women who, by way of their similar motivations, would be most likely to oppose them in status or mating competitions.

Yet women need not be in their fertile phase to behave in ways which suggest that they discern a unique threat from fertile women. Even when probability of conception is low, women with higher levels of estradiol demonstrate an increased propensity to identify a fertile, relative to a non-fertile, woman as being likely to steal her date (Lobmaier, Bobst, & Probst, 2016). Further, partnered women report avoiding social interactions with women who are in their fertile phase, but not women who are in non-fertile phases (Krems, Neel, Neuberg, Puts, & Kenrick, 2016), presumably because fertile phase women would be more likely to mate-poach their partners. Though the extent to which fertile-phase women engage in mate-poaching has not, to the best of our knowledge, been measured, women do tend to behave in ways which attract male attention near the fertile phase of their cycle (Eisenbruch, Simmons, & Roney, 2015; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007; Miller, Tybur, & Jordan, 2007), and men tend to find fertile-phase women more attractive (Bobst & Lobmaier, 2012; Haselton & Gildersleeve, 2011) and may thus be more likely lured out of existing relationships. The possibility that women avoid fertile-phase women to protect their romantic relationships is bolstered by the finding that only women who have desirable partners who might be targeted by fertile-phase women avoided such women (Krems et al., 2016). Even among women without partners, sensitivity to other women's fertility status may be useful for refining a woman's expectations about her subsequent social interactions. Taken together, these findings argue that women may exhibit heightened sensitivity to fertile-phase women, regardless of their cycle phase.

Like men, women tend to identify women who are in their fertile phase as more attractive than women in their non-fertile phase (Roberts et al., 2004). Women's ratings of other women's attractiveness map onto reproductively relevant hormones: women's ratings of other women's attractiveness are inversely related to the progesterone levels of the woman being rated, such that women with probabilistically higher odds of conception (lower progesterone levels) tend to be rated as more attractive (Puts et al., 2013). These findings suggest that women are somewhat attuned to subtle visual cues to other women's fertility. To the extent to which women (aware or unaware) are indeed wary of fertile women as potential threats, be it threats to their likelihood of gaining social stature, successfully reproducing, maintaining their partners' commitment, or some other proximate cause, they may exhibit increased sensitivity to fertile women, regardless of their cycle phase.

We expect that women will demonstrate increased sensitivity to fertile women, sensitivity that will manifest as attentional and memory biases towards fertile women, and that they may do so more when they are in the probabilistically fertile phase of their own cycle. Visual attention tends to be value directed, such that stimuli which are motivationally relevant (and of either positive or negative valence) can capture attention even when such stimuli are task-irrelevant (Anderson, Laurent, & Yantis, 2011; Raymond & O'Brien, 2009). Further, visual attention plays a critical role in the encoding and maintenance of information in visual short term memory (Chun, 2011; Gazzaley & Nobre, 2012), such that attended items are better encoded (Gazzaley, 2011; Krawczyk, Gazzaley, & D'Esposito, 2007), transferred to visual working memory

(Schmidt, Vogel, Woodman, & Luck, 2002), and maintained (Towler, Kelly, & Eimer, 2015). Visual working memory is thus also enhanced for motivationally relevant stimuli (Krawczyk et al., 2007). Therefore, to the extent that fertile women are motivationally relevant to other women, we would expect that fertile women should better capture attention and be retained in memory, and that such biases will be responsive to differences in the motivational relevance of stimuli as a function of a woman's own fertility status.

Importantly, individuals with higher visual working memory are better able to control and direct their attention (Bleckley, Durso, Crutchfield, Engle, & Khanna, 2003; Conway & Kane, 2001; Engle, Kane, & Tuholski, 1999), and to resist prolonged attentional capture by salient, albeit task-irrelevant, stimuli (Fukuda & Vogel, 2009; 2011). Individual differences in visual working memory are also related to the extent to which individuals are susceptible to attentional capture by motivationally relevant stimuli (Anderson et al., 2011). Thus, we expect that women's visual working memory capacity will moderate the extent to which they display biases in attention and memory.

In sum, in the current research we tested two hypotheses regarding whether women preferentially attend to and remember other women. First, we hypothesized that women would preferentially attend to and remember the faces of fertile women, relative to non-fertile women. Second, we hypothesized that other women's fertility would differentially affect fertile-phase women, such that women's bias towards other fertile-phase women would be greatest when women themselves were in the fertile phase. Our overarching hypothesis is that individuals demonstrate increased sensitivity to those who may obstruct their ability to achieve motivated end-states, and that such increased sensitivity will be associated with attentional and memory biases.

Methods

Participants

Participants were prescreened from a larger population and selected for inclusion in the study if they reported that they were female, less than 40 years of age, and reported not currently using hormonal contraceptives. Prescreening surveys included distractor questions to mask criteria relevant to the study. Fifty nine participants (of 111 who initially met qualification criteria and were recruited) chose to participate in the study and provided written consent. Of these, one participant reported using hormonal contraceptives at the time that she participated in the study, one participant reported becoming pregnant between when she signed up for the study and when she participated in the study, and one participant reported having been diagnosed with an endocrine disorder; these three participants were therefore excluded. Analyses were thus conducted on 56 participants (mean age of 21.96 years, *SD* = 3.95 years, range 18-38 years), all of whom reported being premenopausal and not having used hormonal contraceptives in the three months preceding the study. The length of participants' menstrual cycles the cycle immediately preceding their participation was an average of 29.84 days long (*SD* = 4.69, range = 21- 44[1]).

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[1] Ninety-five percent of women exhibit average cycle lengths between 15-44 days (Chiazze, Brayer, Macisco, et al., 1968); thus we included only participants whose menstrual cycle immediately prior to participation in our study fell within this range. Using this inclusion criterion, we excluded no participants. However, a more conservative estimate of 23-35 days (Münster, Schmidt, & Helm, 1992), as recommended by Blake, Dixson, O'Dean, & Denson (2016), we exclude 7 participants. Patterns of results do not change with exclusion of these participants.

A-priori power analyses suggested that we would need at least 55 participants to achieve 80% power to detect a medium-sized effect (Gangestad et al., 2016); therefore, we recruited until we at least met this sample size.

Scheduling Protocol

Upon enrollment in the study, women reported the start date of their most recent menstrual period (R). Until the start of their next menstrual period, women received bi-daily emails which asked them to respond when they started their next period, at which point they were scheduled to participate in the study. When women responded to the email survey indicating that they had started their current menstrual period (C), a member of the research team calculated the duration of participants' last menstrual period ($D = C – R$) and used this to anticipate the expected start date of participants' next menstrual period (E) (e.g., $E = C + D$). Expected date of an LH surge (L) of the current menstrual cycle was calculated by subtracting 14 days (the approximate length of the luteal phase, c.f. Dixon, Schlesselman, Ory, & Blye, 1980) from the expected start date of the next menstrual period (e.g., $L = E – 14$).

Participants were scheduled to participate at two points in their cycle. All participants were scheduled to participate during their probabilistically fertile late follicular phase (e.g., approx. days -4 to 0, where 0 indicates the day of expected LH surge, L). Participants were also quasi-randomly assigned[2] to participate in one of two low-fertility phases: the early follicular phase (N = 29), or the mid-luteal phase (N = 27), where 0 indicates the day of the expected LH surge, L, the early follicular phase was defined as days -10 to -6, and the mid-luteal phase was defined as days 6 to 10.

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[2] Adjustment to random assignment was undertaken only in the case of scheduling difficulties.

Participants' sessions were an average of 7.94 days apart (*SD* = 2.91). Where possible, women were scheduled to participate at approximately the same time of day to control for diurnal fluctuations in hormone concentrations. For each session, we computed participants' adjusted probability of conception by estimating their cycle day on a 28-day cycle (as in Puts, 2006) and comparing values to actuarial data from Wilcox, Dunson, Weinberg, Trussell, and Baird (2001; Table 1, 3rd column).

Procedure

Data reported here are part of a larger study focusing on the relation between hormonal fluctuations across the menstrual cycle and social cognitive processes. Participants completed two one-hour sessions, during which they completed a number of cognitive tasks and survey measures. Participants were compensated $10 or 1.0 course credits per hour, plus an additional $5 or 0.5 course credits for completing both sessions. All cognitive tasks were presented using EPrime 2.0 and all surveys were presented through Qualtrics (Provo, UT, USA). ECG and impedance cardiography were collected continuously throughout each session using Ag/Cl electrodes in a standard Lead-II configuration (ECG) and spot electrodes (impedance cardiography; results to be reported elsewhere). Task order was pseudo-randomized between participants and remained consistent between sessions. Immediately following completion of the tasks, participants provided responses to a number of survey measures (to be reported elsewhere). Finally, participants rinsed their mouths with water and provided 1-2 mL of saliva via passive drool through a polypropylene plastic straw into polypropylene test tubes, which were then capped and frozen at -20°C for later analysis (to be reported elsewhere).

For all tasks presented here, participants saw stimuli from the same set of color photographs of the neutral faces of normally cycling women which were taken when the stimulus women were in their late follicular phase and their mid-luteal phase (Puts et al., 2013). Levels of estradiol and progesterone were measured in all stimulus women each time that their photograph was taken. All stimulus women were Caucasian (the dominant race of our participant pool). Stimuli have previously been normed on female- and male-rated attractiveness and flirtatiousness (Puts et al., 2013). To ensure that stimulus women were probabilistically fertile at the time when their late follicular photograph was taken, we selected stimuli from the larger stimulus set on the basis of their estradiol-to-progesterone (E:P) ratio, which is an approximate marker for ovulation (Baird, Weinberg, Wilcox, McConnaughey, & Musey, 1991). Only stimulus women whose E:P ratio in their late-follicular photograph was greater than the average of the sample of late-follicular photographs were included in the present study. For each stimulus woman, we obtained measures of E:P ratio and perceived attractiveness (ratings made by other, unacquainted women) at both ‘fertile’ and ‘non-fertile’ sessions. Control stimuli included pictures of neutral objects (chairs) against a white background.

Tasks

Visual Selective Attention Task. Participants completed a modified version of the exogenous cuing task (Posner & Cohen, 1984), as in Maner, Miller, Rouby, and Gailliot (2009) and DeWall, Maner, Deckman, & Rouby (2011), to assess biases in attention (see Figure 2.1A). In our task, each trial began with a presentation of a fixation cross in the center of the screen for 1000 ms. Following this, a stimulus (sized so that it subtended a 5.25° visual angle) appeared randomly on either the left or the right side of the computer screen 11.2° off center and was displayed for 500 ms. The stimulus was either the neutral face of a woman in her late follicular phase, the neutral face of a woman in her mid-luteal phase, or a neutral object. Immediately following the disappearance of the stimulus, a small probe (either a circle or a square; sized to subtend a .60° visual angle) appeared randomly and with equal frequency in either the same location (congruent trial) or the opposite location (incongruent trial) as the stimulus with equal frequency. Participants then identified as quickly and accurately as possible if the probe that appeared was a circle or a square by pressing the *a* or *k* key, respectively. Inter-trial intervals were 1500 ms. Participants completed three blocks of 24 trials each and stimulus type was randomized across trials within blocks. Participants completed eight practice trials before beginning the task and were reminded of which keys corresponded with each probe shape at the start of each block.

Incongruent trials require an attentional shift – participants are required to shift their attention away from the location where the stimulus was presented to the location where the probe is presented in order to identify the probe. In these trials, greater latency to respond can be interpreted as greater difficulty either disengaging from the stimulus or moving attention from a currently attended spatial location (c.f., Koster, Crombez, Verschuere, & De Houwer, 2004). Greater latency on incongruent trials thus suggests that 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[3]. Thus, in congruent trials, faster responding is interpreted as a greater attentional bias, that is, greater orienting toward or capture by the stimulus (c.f., Koster et al., 2004; Salemink, van den Hout, & Kindt, 2007).

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[3] Note that this effect is primarily observed at short stimulus-probe-onset intervals (e.g., <= 400 ms), whereas at longer intervals, responses to targets in previously attended locations are actually slowed (Posner & Cohen, 1984). However, the slowing may be due in part to participants' disengagement of attention from the task-irrelevant stimulus (Posner & Cohen, 1984). Further, for tasks which require participants to discriminate between, rather than simply detect, targets (e.g., as in our task, discriminating between a circle or a square), facilitation persists longer (e.g., up to 700 ms following the stimulus onset; Klein, 2000; Lupianez & Milliken, 1999).

Visual Working Memory Task. To assess visual working memory biases, participants completed a modified delayed-match-to-sample task with a visual search component (see Figure 2.1B). Each trial began with a presentation of a fixation cross in the center of the screen for 1000 ms. Following this, a stimulus (called the "sample" stimulus) was presented for 500 ms in the center of the screen, followed by an 8000 ms delay in which there were no stimuli present on the screen. After the delay, a diamond array of four stimuli (each stimulus subtended a 5.24° visual angle; vertical stimuli required a vertical shift of 15.11° from center and horizontal stimuli required a horizontal shift of 25.41° from center) was presented in which one of the stimuli was identical to the sample stimulus and the remaining three stimuli were comparison stimuli. The location of the sample stimulus (top, left, right, or bottom) was randomized across trials such that each location was equally represented. Participants' task was to identify as quickly and accurately as possible which image from the array matched the initial image that they saw using the arrow keys of the keyboard to indicate the position of the sample stimulus. Participants had 3000 ms to respond before the trial ended. Inter-trial intervals were 1000 ms. Participants completed two practice trials before beginning the task.

Participants completed three blocks of ten trials each, and the category of the sample stimuli varied by block. Sample stimuli were either the neutral face of a woman in her late follicular phase, the neutral face of a woman in her mid-luteal phase, or a neutral object. In each trial, the sample stimulus was randomly selected from a set of four stimuli which had been randomly (in the case of face stimuli) or pseudo-randomly (in the case of neutral stimuli) matched together prior to the experiment, and the other three stimuli were used as comparison stimuli for that same trial. For blocks in which the sample stimuli were faces, whether the comparison stimuli were of the same or opposite fertility status as the target varied between participants (but was consistent within sessions). This was included for exploratory purposes but was not a key variable of interest, and is included as a covariate in all analyses.

Participants also completed three additional social cognitive tasks which took an additional approximately 20 minutes to complete (to be reported elsewhere).

Data Analysis

Our data analytic strategy utilized mixed effects models, implemented in lmer v. 1.1.12 in R v. 3.2.2, which assessed participants' responses to individual stimuli as the level-1 observation. Mixed effects models are preferred when error terms are likely to be correlated because observations are not entirely independent of each other (e.g., each participants' response to a stimulus is not independent of their responses to other stimuli), and ignoring this structure can lead to biased estimation of standard errors (Hox, 2002; Raudenbush & Bryk, 2002). Linear mixed effects models were used for continuous dependent variables and binomial logistic mixed effects models were used for dichotomous outcomes (e.g., accuracy). For each analysis, we began by conducting log-likelihood tests of empty models to determine the best and most parsimonious random effects structure (as in Baayen, Davidson, & Bates, 2008). Once the random effects structure had been selected, we fit the structure with maximal random effects (e.g., correlated random intercept and random slopes of the highest order interaction) using maximum likelihood estimation and removed terms from the model in a stepwise fashion until the model converged, as in Barr, Levy, Scheepers, and Tily (2013). Parameter estimates were obtained using restricted maximum likelihood estimation, which provides less biased parameter estimates (Hox, 2002), and significance was tested using the Satterthwaite approximation for degrees of freedom (lmerTest v. 2.0.30 in R) for continuous outcomes and Wald chi square tests (car v. 2.1.1 in R) for dichotomous outcomes. Because observations can be outliers on one level while falling within the normal distribution of the other level(s) in mixed effects models, we do not presently exclude any data as outliers, opting to instead indicate the presence of particularly influential data where it exists (Langford et al., 1998; 1999; Nieuwenhuis et al., 2012). Equations for the mixed models from which significant parameters were obtained are reported in Supplementary Materials in Appendix G.

Because congruent and incongruent trials in the visual selective attention task assess different constructs (e.g., congruent trials assess attentional capture or orienting, whereas incongruent trials assess attentional holding or difficulty disengaging or moving attention), we analyzed responses to the two trial types independently (as in Dewall, Lambert, et al., 2011). Congruent and incongruent trials were presented with equal frequency to ensure equal power to test hypotheses regarding biases in both attentional capture/orienting (congruent) and attentional disengagement (incongruent). For all analyses of the visual selective attention task, we controlled for the visual field to which the stimuli were presented (left or right) and for probe-response congruency. Previous research has demonstrated that selective attention to the left and right visual fields may vary with cycle phase (Thimm, Weis, Hausmann, & Sturm, 2014), and thus it seemed pertinent to remove variance potentially attributable to this effect. Probe-response congruency was a measure of whether the location of the probe on the screen (left or right side of the screen) was congruent with the side of the keyboard where participants input their responses to the task (e.g., left to respond ‘a’ and right to respond ‘k’), and is distinct from trial congruency. Trials with probe-response incongruence could reasonably be expected require greater effort than trials for which probe location and key response were congruent, and thus could influence response times. For all analyses of the visual working memory task, we controlled for whether comparison stimuli (e.g., the stimuli in the array which did not match the sample) were of the same or different fertility status as the sample stimulus and the location on the screen where the correct stimulus was located (top, right, bottom, left).

Planned contrasts for session type compare responses in the early follicular phase to those in the late follicular phase and responses in the mid-luteal phase to those in the late follicular phase. Each planned contrast is thus a comparison of probabilistically fertile and low-fertile sessions within participants, where the first contrast examines differences across sessions within participants who participated during their early and late follicular phases and the second contrast examines differences across sessions within participants who participated during their late follicular and mid-luteal phases. Whereas each planned contrast examines a subset of the data, the omnibus test of the effect of session type includes data from all participants (i.e., session type is treated as a categorical variable with three levels: early follicular, late follicular, and mid-luteal) and is more powerful because it incorporates variance both within-participants (across fertile and low-fertile sessions) and between- participants assigned to different low-fertile cycle phases. Planned contrasts for stimulus type compare fertile stimuli to non-fertile stimuli and, where applicable, face stimuli to neutral object stimuli. For all other nominal predictors, deviation contrast coding was used. All continuous predictors were grand centered to aid in interpretation of coefficients.

After testing initial hypotheses, we also tested the robustness of these hypotheses by controlling for the demographic covariates of age, ethnicity (coded as Caucasian or non-

Caucasian to account for small *n*s in various non-Caucasian cells), sexual orientation (participants responded to a scale reported in Diamond (2007), but to account for small *n*s, we coded responses as heterosexual, non-heterosexual, or other), and whether participants were currently involved in a romantic relationship. Further, we also included potential mediators where possible (e.g., stimulus E:P ratio, stimulus attractiveness, and participants' adjusted estimated probability of conception) to examine the extent to which these variables share overlapping variance with our hypothesized effects and rule out potential alternatives[4].

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 (*p* = .573), race (*p* = .220), sexuality (*p* = .213), romantic relationship status (*p* = .240), the cycle day on which they participated in fertile session (*p* = .545), and cycle length the menstrual cycle prior to participating (*p* = .839). However, the cycle lengths of the cycle prior to participation fell outside of the recommended range of 23-35 days (Blake et al., 2016) for six participants who completed their low-fertile session during their mid-luteal phase, versus only one participant who completed their low-fertile session during their early follicular phase, *p* = .048.

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[4] For example, attractive women tend to capture female observers' attention more than less attractive women (Maner et al., 2003) and be better remembered and distinguished between than less attractive women (Becker, Kenrick, Guerin, & Maner, 2005; Maner et al., 2003). Given that progesterone is inversely associated with attractiveness (Puts et al., 2013) and progesterone levels vary between fertile-phase and non-fertile-phase stimuli, it is important to ensure that effects are robust to fluctuations in attractiveness to ensure specificity of the effect of stimulus fertility.

Visual Working Memory

Our measure of visual working memory was participants' accuracy on the control (i.e., neutral object) condition of the delayed match-to-sample task, which was computed for each session. We computed accuracy using the formula:

$$\frac{Number\ of\ Correct\ Responses}{Number\ of\ Correct\ Responses + Number\ of\ Incorrect\ Responses}$$

This measure of visual working memory excludes trials on which participants did not provide a response within 3000 ms, the point at which the trial timed out (2.95% of trials). Participants exhibited average accuracy of .92 (*SD* = .09) across both sessions. Accuracy on the visual working memory task did not vary by session type, *F*(2, 76.6) = 1.36, *p* = .260. Planned contrasts revealed no significant differences in visual working memory between when participants were in their early or late follicular phases, *B*= - .01, *SE* = .02, *t*(73.5) = -.58, *p* = .564, nor between when participants were in their late follicular or mid-luteal phases, *B* = .03, *SE* = .02, *t*(76.5) = 1.34, *p* = .184. Further, there were no differences in late follicular phase visual working memory between participants whose low-fertile session was in their early follicular phase and participants whose low-fertile session was in their mid-luteal phase, *t*(52.59) = -.54, *p* = .594, indicating no difference between participants as a function of random assignment to phase for their low-fertility session. Accuracy on this task was used as a moderator in all subsequent analyses, given that we expected attentional and memory biases to vary as a function of participants' visual working memory.

Attentional Bias

Prior to testing hypotheses, response times less than 200 ms and greater than 3 *SD* (1358 ms) were removed (1.43% of trials). Response times were then log-transformed for the purposes of analyses, though raw response times were used for the generation of figures. Incorrect responses were provided on only 3.46% of trials; these trials were excluded from analyses (though patterns of effects maintain even when including these trials). There were no differences in the late follicular phase response times, *p* = .433, or accuracy, *p* = .668, between participants whose low-fertile session was in their early follicular phase and those whose low-fertile session as in their mid-luteal phase.

Attentional Bias to Fertile Women. We first examined our hypothesis that women would preferentially attend to the faces of fertile women, relative to non-fertile women, an effect we expected to be moderated by visual working memory. We began with congruent trials, where shorter response times can be taken as evidence of an attentional bias. As predicted, a significant interaction between stimulus type and visual working memory emerged, *F*(2,194.6) = 4.19, *p* = .017. Planned comparisons revealed that visual working memory moderated responses to fertile versus non-fertile stimuli, *B* = .22, *SE* = .10, *t*(149) = 2.15, *p* = .034 (see Figure 2.2), such that when visual working memory was poorer, participants exhibited a greater attentional bias toward fertile stimuli, relative to non-fertile stimuli (i.e., were quicker to respond to a congruent probe). Using the computational tool for testing two-way interactions (Case 3) in multilevel modeling developed by Preacher, Curran, & Bauer (2006), we decomposed this interaction to examine the simple slopes of the association between stimuli type and response times among observations 1 *SD* higher and lower than the mean of visual working memory. Decomposition revealed that the simple slope was significantly negative among those lower in visual working memory capacity, *B* = -.04, *SE* = .01, *z* = -3.40, *p* = 7E-4, such that faster responses to fertile, relative to non-fertile faces, were observed, whereas the simple slope was nonsignificant among those higher in working memory capacity, B = 3E-4, SE = .01, z = -.03, p = .977. Our second planned comparison revealed a marginal interaction between visual working memory and the effect of face stimuli, relative to neutral object stimuli, on response times, B = .15, SE = .08, $t(328)$ = 1.82, p = .070.

Controlling for demographic covariates, a significant moderation of the effect of fertile relative to non-fertile stimuli on response times by working memory capacity maintained, B = .22, SE = .10, $t(147)$ = 2.15, p = .034. Importantly, the effect also maintained when controlling for the main effects of stimulus female-rated attractiveness and stimulus estrogen-to-progesterone ratio and their interactions with visual working memory, indicating that the interaction between visual working memory and stimulus fertility explained unique variance in response times, relative to effects from stimulus attractiveness or stimulus estrogen-to-progesterone ratio. Interestingly, the interaction between stimulus attractiveness and visual working memory was also a significant predictor of response times, B = .13, SE = .05, $t(2362)$ = 2.40, p = .016, such that participants with lower visual working memory responded quicker to congruent probes preceded by attractive stimuli.

However, neither stimulus type (p = .464) nor the interaction between stimulus type and visual working memory (p = .586) predicted response times on incongruent trials.

Attentional Bias to Fertile Women among Fertile Women. We next examined whether participants' cycle phase would moderate the attentional bias they were observed to exhibit towards fertile women in our first analysis. We began with congruent trials. The omnibus three way interaction between stimulus type, session type, and visual working memory, and three way interactions with session type's planned comparisons, were nonsignificant, all ps> .682. Interestingly, we did observe a significant interaction between session type and visual working memory, $F(2, 31.2)$ = 4.53, p = .019, such that participants responded more quickly in their late follicular phase relative to their mid-luteal phase when visual working memory was lower, relative to when it was higher, *B* = -.63, *SE* = .27, *t*(30) = 2.31, *p* = .028. However, as stated before, this effect was not moderated by stimulus type. Furthermore, no significant effects were observed on incongruent trials, all *p*s>.309. Thus, we observe no significant evidence that participants' cycle phase biases the time it takes them to respond to probes which immediately follow images of fertile, relative to non-fertile, women.

Memory Bias

We also expected that women may exhibit memory biases towards other women as a function of other women's fertility, their own fertility, or both. Each trial, participants were instructed to identify as quickly and as accurately as possible which of four faces matched the sample stimulus face that they had seen 8000 ms before; however, they knew that if they did not provide a response, the trial would time out and the next trial would begin. We would expect then that those participants who more accurately remembered the sample stimulus would identify the correct stimulus from the array, and that they would do so more quickly than participants who were less certain about their response. Thus, a memory bias can manifest as more accurate responding (i.e., a greater propensity to choose a correct response), or as quicker response times.

Because we were interested in the extent to which participants' memory bias specifically for women's faces would vary across levels of visual working memory capacity, we used their visual working memory scores (their accuracy on neutral object trials) as a moderator in all subsequent analyses, and used only face trials on which participants made responses (97.82% of trials) to compute our outcome variables. We computed accuracy on face trials for each session using the same formula we used to compute our measure of visual working memory. The average accuracy of all sessions was .97 (*SD* = .08), and average response time across all trials was 1303.38 ms (*SD* = 498.23). Neither accuracy nor response times in the late follicular phase differed as a function of participants' random assignment to low-fertility session type, $p = .600$ and $p = .158$, respectively. Though one can account for task accuracy and response time in a single measure (an inverse efficiency score), it is advisable to do so only in the case of high and linear positive correlations between the two measures (Bruyer & Brysbaert, 2011), which was not observed here, $r = .21$, $p = .459$. Given that participants exhibited minimal variance in accuracy rates, we instead focused on reaction times as our measure of memory bias[5]. As with the selective attention task, response times greater than 3 *SD* above the mean response time (2798 ms) were removed (no response times were less than 200 ms; 3.44% of trials removed). Response times were log transformed before analyses, though raw response times are presented in figures.

Memory Bias for Fertile Women. We first examined our hypothesis that women would preferentially remember the faces of fertile women, relative to non-fertile women, an effect we expected to be moderated by their visual working memory. We observed no significant interaction between visual working memory and stimulus fertility ($p = .924$), nor a significant main effect of stimulus fertility, ($p = .266$). Interestingly, we did observe a significant effect of comparison stimuli type, such that participants were slower to respond on trials for which the

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[5] In the face conditions of the memory task, used to assess a memory bias, accuracy was extremely negatively skewed, such that in 69.64% of sessions, participants performed at ceiling (i.e., a perfect score). While accuracy in the control condition (which is used as our measure of visual working memory capacity) was also negatively skewed, participants exhibited more variance in accuracy in the control condition, and performed at ceiling (i.e., a perfect score) in only 46.43% of sessions. Because our a priori plan was to analyze accuracy and we observed considerable spread in our accuracy measure in the control condition, we adhered to this a priori plan and used accuracy as our measure of visual working memory capacity, which is a moderator in all analyses. Note that using average response times in control trials instead of average accuracy in control trials as our measure of visual working memory capacity produces the same general pattern of effects, though alters patterns of significance.

comparison stimuli were of the same fertility status (e.g., fertile or non-fertile) as the sample stimulus, *F*(1, 68.9) = 9.61, *p* = .002.

Memory Bias for Fertile Women among Fertile Women. We next examined our hypothesis that cycle phase of participant and stimuli might interact to predict response times, such that fertile women would exhibit a memory bias for fertile women's faces, an effect we expected to be moderated by visual working memory. A significant three-way interaction between stimulus fertility, participant fertility, and visual working memory emerged, *F*(2, 2000.9) = 6.24, *p* = .002. As hypothesized, the three way interaction between our planned contrast comparing early to late follicular sessions, stimulus type, and visual working memory was significant, *B* = 1.42, *SE* = .45, *t*(2003) = 3.16, *p* = .002 (Figure 2.3A), as was the three-way interaction between our planned contrast comparing late follicular to mid-luteal sessions, stimulus type, and visual working memory, *B* = .76, *SE* = .32, *t*(2003) = 2.36, *p* = .018. Decomposition of these interactions revealed that when participants were in the early follicular phase of their cycle, they were faster to identify fertile faces stored in visual working memory when they had lower working memory capacity, *B* = .10, *SE* = .04, *z* = 2.24, *p* = .025, but not when they had higher working memory capacity, *B* = -.02, *SE* = .03, *z* = -.68, *p* = .497, whereas when participants were in the late follicular phase of their cycle, they were slower to identify fertile faces stored in visual working memory when they had lower working memory, *B* = -.06, *SE* = .03, *z* = -2.01, *p* = .044, but not when they had higher working memory, *B* = .04, *SE* = .03, *z* = 1.49, *p* = .136. There were no significant differences in response times to identify fertile and non-fertile faces as a function of working memory when participants were in the mid-luteal phase of their cycle (-1 *SD* working memory: *B* = .03, *SE* = .04, *z* = .73, *p* = .466, +1 *SD* working memory: *B* = -2.7E-3, *SE* = .04, *z* = -.07, *p* = .948)[6].

Consistent with previous analyses, a significant main effect of comparison stimuli type emerged, such that participants were slower to respond when comparison stimuli were of the same fertility status at the sample stimulus, *B* = .14, *SE* = .04, *t*(66.9) = 3.06, *p* = .003.

Controlling for demographic covariates, the significant three-way interaction between session type, stimulus type, and visual working memory capacity maintained, *F*(2, 2000.9) = 6.25, *p* = .002. Further, the effect maintained controlling for the main effects of stimulus female-rated attractiveness and stimulus estrogen-to-progesterone ratio, their interactions with visual working memory and session type, and the three-way interactions, and none of these effects were significant predictors of response times. Controlling instead for participants' probability of conception (based on Wilcox et al.'s 2001 actuarial data), both contrasts dropped below statistical significance though the same pattern of effects maintained, indicating that participants' probability of conception explained overlapping variance with that attributable to their assignment to fertile and low-fertile sessions. Neither probability of conception nor any interactive effects including probability of conception were significant predictors of response times.

Discussion

The present study suggests the fertility status of women may bias the attentional processes of other women, and that it may bias the memory processes of other women differentially across those other women's menstrual cycles. We demonstrate that women are

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[6] Analysis of influential cases revealed that one participant was particularly influential on the level of participants (Cook's Distance = 1.08). However, because Cook's Distance was nearly equal to one and only four of the participants' responses were influential on the level of trials, we opted to retain this participant in the analyses.

faster to respond in a selective attention task when a task-irrelevant image of a fertile-phase, relative to a non-fertile-phase, woman appears in the same spatial location where the task demands attention, but only when participants exhibit lower visual working memory capacity. We take this as evidence that when participants have poorer visual working memory, the neutral faces of fertile women capture their attention more than the neutral faces of non-fertile women, facilitating responding on tasks which require attention to the same spatial location as the picture. We also demonstrate that in the low fertile early follicular phase of the menstrual cycles, women with lower visual working memory are faster to identify the face of a fertile-phase woman maintained in visual working memory. Conversely, relative to their responses in the early follicular phase, women in the late follicular phase are actually slower to identify the face of a fertile-phase woman maintained in visual working memory when they have lower visual working memory capacity. Taken together, these results are consistent with the hypothesis that how women preferentially attend to and remember other women may be related to menstrual cycle phase. We discuss each of these effects in turn.

Like other mammals, female humans display characteristic changes in their physical appearance and behavior which may serve to signal their fertility status to others (Gangestad & Haselton, 2015; Gangestad & Thornhill, 2008; Haselton & Gildersleeve, 2011). Of relevance for the present study, in which static images of women’s neutral faces at different phases of their cycle were used, fertile-phase women’s faces tend to be rounder and redder (Bobst & Lobmaier, 2012; Jones et al., 2015, although see Burriss et al., 2015), though an integrated and exhaustive anthology of the visual cues in the face which fluctuate across the menstrual cycle has yet to be determined. Previous research has determined that women are likely sensitive to such cues in other women, and that they differentially judge other women as a function of the other women's fertility status or associated hormonal states (Krems et al., 2016; Lobmaier et al., 2016; Puts et al., 2013). However, the present study is the first, to the best of our knowledge, to demonstrate that such cues may shape attentional and memory processes.

For those with poorer visual working memory capacity, the neutral faces of fertile-phase women appear to capture attention more than the neutral faces of non-fertile-phase women, as evidenced by participants' quicker identification of probes which immediately replace the fertile faces. These effects persisted above and beyond differences attributable to the attractiveness of the stimuli. This may suggest that women find the faces of fertile-phase women particularly relevant to their behavioral goals, consistent with a theory of exogenous attentional control that proposes that stimuli are more likely to involuntarily capture attention if they congruous with the goals of a current task (Folk, Remington, & Johnston, 1992). Though the fertile faces were no more task-relevant than non-fertile faces, it is possible that fertile women are more relevant than non-fertile women for women's broader social goals (e.g., intentions to avoid social interactions with fertile-phase women, Krems et al., 2016), goals which are capable of directing attention even absent individuals' explicit awareness (Moskowitz, Li, & Kirk, 2004). Though the present data do not permit examination of the reasons why participants' attention might be captured by fertile-phase women, one possibility may be that fertile-phase women tend to seek status gains over other women (Durante et al., 2014) and that women are vigilant to the threat of a status loss which is posed by fertile-phase women. We expected that fertile-phase women would be most sensitive to this potential threat, consistent with their heightened motivations to maintain and gain status. However, we did not observe that participants' own fertility moderated their attentional biases, demonstrating that women's sensitivity to fertile-phase women remains relatively constant throughout their cycle and suggesting that any observed differences in women's behavior towards fertile-phase women as a function of their own fertility (i.e., Chapter 1; Necka et al., 2016) may reflect differential responses to, rather than differential attention to, fertile-phase women.

That we observe an attentional bias toward fertile women only when participants exhibit lower visual working memory is not surprising, given that those with higher visual working memory typically recover from attentional capture faster than those with lower visual working memory (Fukuda & Vogel, 2011). An open question for future research, however, is whether individuals with higher visual working memory might also experience greater attentional capture by fertile, relative to non-fertile, women's faces, albeit attentional capture that persists for only brief durations, shorter than those which would have produced a bias in the present study (i.e., the attentional capture lasts for less than 500 ms). Additionally, we assume here that faster responding on congruent trials following fertile faces indicates that fertile faces captured participants' attention and facilitated their subsequent performance on the task, as is typical in discrimination tasks which employ the stimulus-probe-onset intervals used here (c.f., Lupianez & Milliken, 1999). However, some evidence suggests that task performance is impaired when tasks demand attention to a spatial location to which participants have already attended (i.e., an inhibition of return; Posner & Cohen, 1984). Thus, an alternative interpretation of our finding is that participants' slower responses non-fertile faces could have resulted from an inhibition of return to these already attended locations; in other words, *non-fertile* faces could have more strongly captured participants' attention. If response times in congruent object trials were faster than response times in congruent non-fertile trials, this might lend some credence to the idea that non-fertile faces induced an inhibition of return (i.e., captured initial attention), because we would not expect neutral object trials to capture attention more than faces. However, response times on congruent object trials were comparable to response times on congruent non-fertile face trials. Taken together with the complex nature of our stimuli (e.g., faces, rather than simple changes in the luminance or color of shapes) and the demands of our task (e.g., discrimination rather than detection of a probe), we believe that it is unlikely that the present findings resulted from an inhibition of return effect (e.g., more attention to non-fertile faces). Nonetheless, either interpretation is compatible with the conclusion that the cycle phase of women differentially affects how other women attend to them.

It is perhaps surprising that we observe an effect of stimulus fertility only in congruent, but not incongruent, trials. The assumption underlying our selective attention task is that images which hold particular relevance for participants modulate response times, in keeping with work suggesting that threat-related words and images influence attentional processes in individuals with clinical and subclinical anxiety (c.f. MacLeod, Mathews, & Tata, 1986) and that goal- and threat-related words influence attentional processes in healthy individuals (Koster, Crombez, Damme, & Verschuere, 2004; Stolz, 1996; Vogt, Houwer, Moors, Damme, & Crombez, 2010). Though evidence is mixed, accumulating work suggests that threat-related stimuli tend to affect the disengagement of attention (i.e., slower responding in incongruent trials), rather than attentional orienting and capture (i.e., faster responding in congruent trials; Fox, Russo, Bowles, & Dutton, 2001; Koster, Crombez, Verschuere, et al., 2004), a pattern opposite to that observed here. The present data cannot explain why a bias was observed in trials typically thought to index attentional orienting, but not in those thought to index attentional disengagement.

However, one possibility is that stimulus fertility affected earlier stages of face processing (e.g., recognition of social categories and emotional expressions), increasing participants' alertness to the spatial location where the face appeared and speeding responses on congruent trials, but that fertility did not affect later stages of face processing (e.g., face name learning or identification; Puce, Allison, & McCarthy, 1999) which would be more likely to delay disengagement of attention from the spatial location where the face appeared and produce slower responding on incongruent trials. However, this is but one possibility for these findings, and it remains to be explicitly tested.

In the present study, we also observed that the time that it takes women to recognize a face maintained in visual spatial memory is modulated by both their own fertility and the fertility of the woman whose face they maintained, an effect which is robust even when controlling for differences in the attractiveness of the fertile and non-fertile stimuli. We expected that the greater motivational relevance of fertile-phase women among women in their late follicular (probabilistically fertile) phase would facilitate recognition of fertile-phase women, thereby reducing the time it takes to identify them. However, we actually observed the opposite: women in a probabilistically *non-fertile* phase of their cycle (i.e., the early follicular phase) were actually faster to respond to fertile-phase woman when they had lower visual working memory. One potential explanation for this observation relates findings from our visual working memory task to findings from our visual selective attention task. It has been suggested that information which is attended to involuntarily (as were the peripheral cues of fertile faces in our selective attention task) is selected for commitment to visual working memory (Prinzmetal, McCool, & Park, 2005; Schmidt et al., 2002), and in particular that faces which are attended to during encoding are better maintained in visual working memory (Towler et al., 2015). Fertile faces, which in our visual selective attention task captured more attention in women with lower visual working memory capacity than non-fertile faces, may capture greater attention for these women in the visual working memory task as well, thus improving their transfer to visual working memory and facilitating participants' ability to quickly recognize them in a subsequent visual search task. Though visual attention does not influence the integrity or accuracy of representations transferred to visual working memory (Prinzmetal et al., 2005; Schmidt et al., 2002), if fertile faces were more readily transferred to visual working memory or better maintained in visual working memory, participants may have been more certain that a face in the array matched the one maintained in visual working memory, speeding their response times. Consistent with this explanation, faster response times to fertile faces were observed only among low-fertile participants who had lower visual working memory (though this pattern of effects was only statistically significant for low-fertile participants in their early follicular phase), the same participants who exhibited an attentional bias towards fertile faces and for whom a boost in performance facilitated by attentional processes would be most apparent.

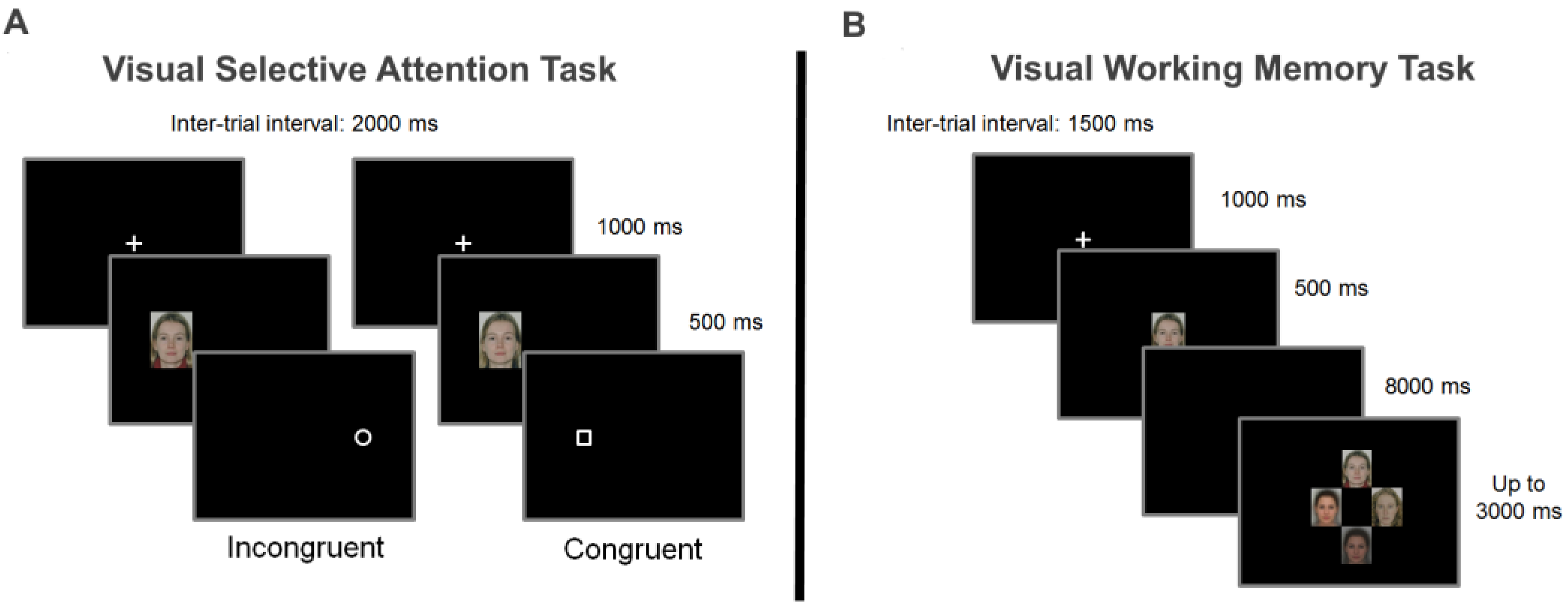
Yet the preceding explanation does not account for the moderating effect of participants' own cycle phase. The addendum to this explanation could be that in the late follicular phase of their menstrual cycle, women exercise more judiciousness when making judgments about fertile phase women, such that even though they may have better attended to and transferred fertile-phase women's faces to visual working memory, they exhibited slower, more cautious responding before selecting the target face (e.g., potentially disconfirming distractor faces before confirming the target face). Under this interpretation, two separate mechanisms can jointly account for women's responses in the visual working memory task: the perseverance of the internal representation of a face in visual working memory and the decision-making process guiding selection of a stimulus which matches one's internal representation. Whereas fertile-phase women's faces may be more privileged in terms of their representation in visual working memory (speeding their recognition), women's potentially more cautious responding to fertile-phase faces during their own fertile phase may eradicate any benefit gained from more privileged representation of these faces in visual working memory. Note the explanation of more careful responding in the late follicular phase is specific to responses to fertile-phase women's faces, potentially indicating greater sensitivity to and more calculated responding to these more formidable competitors. Though as a whole this is an attractive potential explanation, both this and alternative more parsimonious explanations remain to be tested, and the present data cannot speak to these possibilities.

An important feature of the present results is that in all cases, effects were observed only when women had lower levels of visual working memory capacity. Note that in all analyses, we treated women's visual working memory capacity as capable of fluctuating across the cycle, consistent with previous, albeit preliminary, evidence that some forms of working memory may fluctuate across the menstrual cycle (e.g., Phillips & Sherwin, 1992; Rosenberg & Park, 2002) or with levels of estradiol, one of the primary hormones which fluctuates across the menstrual cycle (e.g., Hampson & Morley, 2013; Hampson et al., 2015). We did not observe systematic differences in women's visual working memory capacity as a function of their menstrual cycle phase. However, our results suggest that within-woman fluctuations in attention and memory for other women may be more robust 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 their cycle. This, and 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 women across women's menstrual cycle, where other authors have failed to find differences (c.f., Anderson et al., 2010).

Taken together, the present findings suggest that women are sensitive to other women's fluctuating fertility, vigilant to it on the basis of static visual cues alone. Such sensitivities may ready women to respond to potential encounters with fertile-phase women. Yet women may be motivated to alter their behavioral strategies towards fertile-phase women only when they are in the probabilistically fertile phase of their own cycle, exercising more caution when making decisions with potential consequences for other fertile-phase women. These findings contribute to a broader literature suggesting that hormonal fluctuations may be related to attention and memory biases in ways congruent with individuals' psychosocial motivations, and links that work to broader cognitive theory by demonstrating that the presence of such biases may be modulated by individual differences in cognitive capacities.

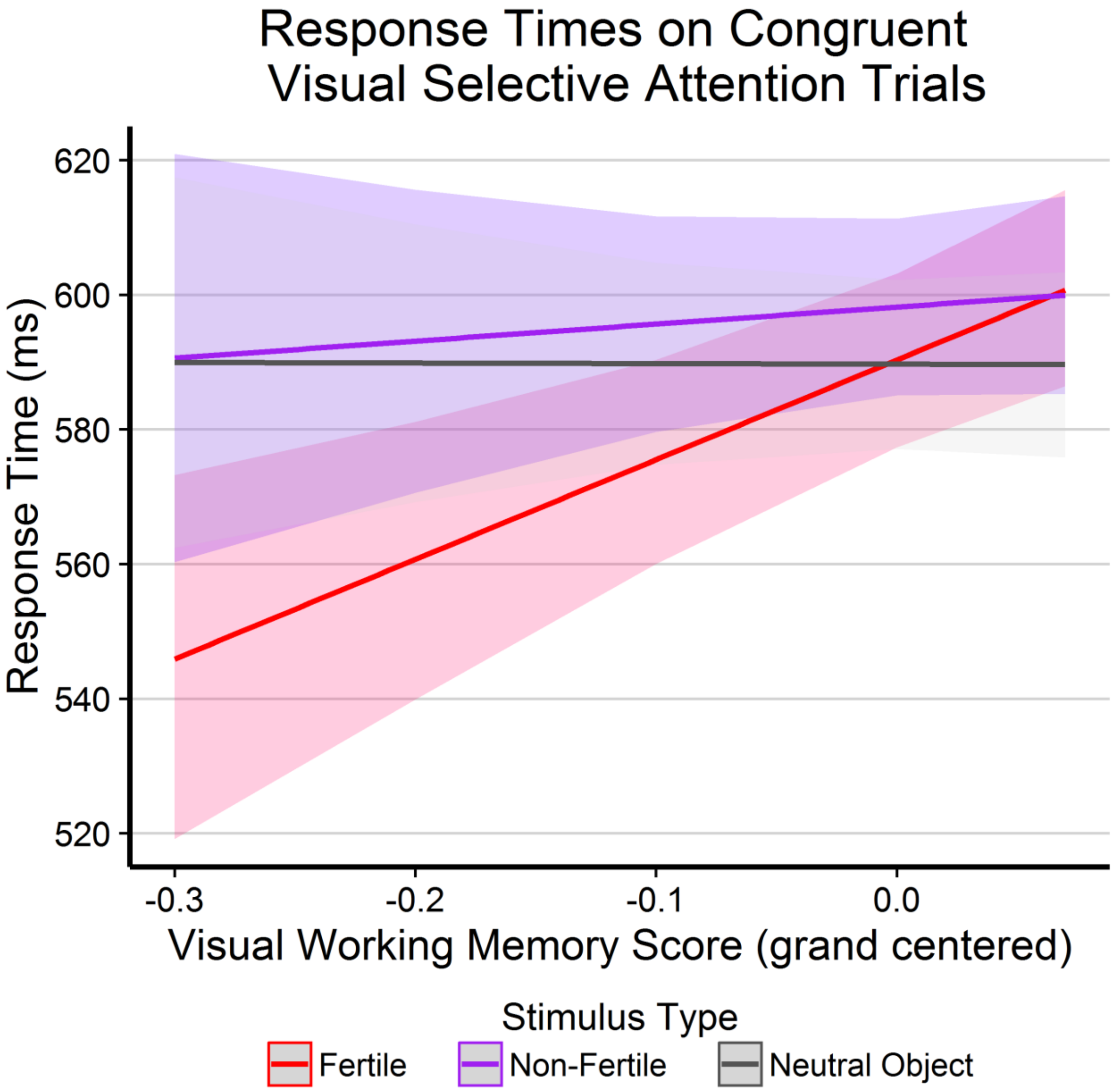
Appendix C: Figures for Chapter 2

Figure 2.1. 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 (congruent) or opposite location (incongruent) as the stimulus. Participants' task was to identify the shape of the probe as quickly as possible. (B) The visual working memory task. A 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 stimulus. Participants' task was to identify as quickly and as accurately as possible which image matched the one from the beginning of the trial. Note that we use example stimuli available in Roberts et al., 2004 & Bobst & Lobmaier, 2007 for illustrative purposes here.

Figure 2.2. Response Times on Congruent Dot Probe 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. Shaded regions indicate +/- 1 standard error.

Figure 2.3. 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. Visual working memory capacity is grand centered across all sessions within all participants, such that negative scores indicate less than average visual working memory capacity and positive scores indicate better than average visual working memory capacity. Participants were faster to recognize the neutral faces of fertile women than they were to recognize the neutral

Figure 2.3. Response Times in a Visual Working Memory Task, Continued
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; middle panel) and had lower visual working memory, they were slower to recognize the neutral faces of fertile women, relative to non-fertile women. No significant differences emerged when participants were their mid-luteal phase (right panel). Shaded regions indicate +/-1 standard error.

CHAPTER 3: STUDY 3

Introduction

Facial emotional expressions communicate a wealth of information about the psychological state and behavioral intent of the individual who conveys them (Fridlund & Russell, 2006; Parkinson, 2005), and can effectively motivate appropriate behavioral responses in one's social interaction partners (Niedenthal & Brauer, 2012; van Kleef, 2009). An individual's facial emotional expression of anger, for instance, conveys behavioral intentions to aggress against the target of one's anger (Horstmann, 2003; Yik & Russell, 1999), and can evoke confrontation from observers. Indeed, if approaching an individual can satisfy aggressive motivations, then observers are likely to respond to an individual who has an angry emotional expression with approach behavior, but not if approach is framed as an affiliative tactic (Krieglmeyer & Deutsch, 2013; Wilkowski & Meier, 2010). Yet humans' emotion recognition abilities are susceptible to environmental influences, and perceptions of emotions can vary based on the social norms, personalities, and goals of the observer (Hess & Hareli, in press). Stereotypes, social expectations, and observers' personalities can even lead them to see emotional expressions in faces where there are none (i.e., neutral faces; Adams, Nelson, Soto, Hess, & Kleck, 2012; Krems, Neuberg, Filip-Crawford, & Kenrick, 2015; Laser & Mathie, 1982; Suess, Rabovsky, & Rahman, 2013).

In a recent study, Krems and colleagues (2015) demonstrated that women are more likely to perceive anger on another woman's neutral face, but not on a male's neutral face. Women tend to suppress overt anger expressions (Evers, Fischer, & Manstead, 2011; Evers, Fischer, Mosquera, & Manstead, 2005), particularly when the target of a woman's anger is another woman. They report being equally likely to display an angry expression when they are angry with another woman as they are to display a neutral expression (Krems et al., 2015). Thus, one potential explanation for the bias observed by Krems et al. is that women expect that other women will not directly convey their anger, and such expectations influence their interpretations of the other women's emotional expressions. Krems and colleagues suggest that women's bias to see anger in the neutral faces of other women is a 'functional projection' which may increase their odds of detecting when other women are actually upset with them (Krems et al., 2015). It may be particularly advantageous for women to exhibit this bias towards other women, given that women are less likely than men to engage in direct aggression (Archer, 2004) and cultural norms may specifically encourage women's engagement in acts of indirect aggression (Campbell, 1999). Indirect aggression (sometimes referred to as relational or social aggression) includes tactics which are intended to reduce the target's social status, such as gossiping, ostracism, and rumor spreading (Archer & Coyne, 2005). Because indirect aggressive tactics can be covert (for example, a woman might not even know when she is the target of others' gossip), heightened sensitivity to other women's anger may improve a woman's odds of detecting when indirect aggressive behaviors may occur and ready her to respond more efficiently, even if it does this at the cost of increasing false alarms. Following this logic, we would expect that this bias should be greater when encountering women who are expected to exhibit more aggressive tendencies.

In the present study, we investigated women's tendency to perceive anger in the neutral expressions of other fertile- and non-fertile phase women. Across the menstrual cycle, women exhibit systematic fluctuations in competitive and cooperative behaviors (Anderl, Hahn, Klotz, & Rutter, 2015). When women are in the most probabilistically fertile phase of their cycle (i.e., near ovulation, with a high likelihood of conception from unprotected intercourse), they tend to be more likely to seek status gains over other women and to unevenly distribute resources in ways which advantage themselves over other women (Durante, Griskevicius, Cantú, & Simpson, 2014). Here, we construe competitive behaviors as those behaviors which are intended to improve a woman's status relative to other women, which can manifest as indirect aggressive behaviors. To the extent to which other women are wary of the competitive inclinations of fertile-phase women, they may be more biased to see anger in fertile-phase women's neutral faces. In addition to being associated with intention to directly aggress, angry emotional expressions convey behavioral intentions to oppose a social interaction partner and to act in an uncooperative manner (Van Doorn, Heerdink, & Van Kleef, 2012), types of indirect aggression. Thus, a bias to see anger on fertile-phase women's face may also prepare women for potential intrasexual competition.

Though it is unlikely that women can, without aid, explicitly classify another woman as being near ovulation, they may be able to detect subtle cues to other women's fertility, such as changes in women's physical appearance (e.g., facial skin redness, facial roundness, waist-to-hip ratio, and soft-tissue symmetry; Bobst & Lobmaier, 2012; Burriss et al., 2015; Jones et al., 2015; Kirchengast & Gartner, 2002; Manning, Scutt, Whitehouse, Leinster, & Walton, 1996; Scutt & Manning, 1996, but see Bleske-Rechek & Claire, 2011). Preliminary evidence suggests that other women may use such cues to inform the way that they behave towards and perceive fertile and non-fertile women. For instance, based on static images alone, women judge fertile-phase women as more likely to pose a threat to their romantic partnerships (Lobmaier, Bobst, & Probst, 2016), and they tend to distance themselves from fertile-phase women when their romantic partners are particularly desirable to such women, potentially as a way of limiting their partners' exposure to the fertile-phase women (Krems, Neel, Neuberg, Puts, & Kenrick, 2016).

Women's perception that fertile-phase women are more likely to threaten their social or relationship status may be related to an increased propensity to detect anger in the neutral facial expressions of fertile-phase, relative to non-fertile phase, women. A tendency to detect anger in fertile-phase women's neutral expressions would also potentially explain our recent finding that some women exhibit biased attentional processes toward fertile-phase women (Chapter 2), as angry faces tend to capture attention (Sawada & Sato, 2015; Shasteen, Sasson, & Pinkham, 2014). Because women do not try to suppress emotional expressions of anger directed towards men (Krems et al., 2015), we would not expect that male observers would be biased to differentially detect anger in the neutral expressions of fertile- and non-fertile-phase women.

However, it is possible that women are not explicitly aware that they are using cues of anger to distinguish between fertile- and non-fertile-phase women. That is, facial features which typically convey angry emotional expressions may capture women's visual attention more in fertile-phase women's faces than in non-fertile-phase women's face, but women may fail to overtly report any differences in fertile- and non-fertile-phase women's anger, unaware that they favored some regions of the face over others when visually inspecting fertile-phase women's faces. Though humans tend to process faces holistically (Behrmann, Richler, Avidan, & Kimchi, 2015), accumulating evidence suggest that eye movements may be functional for face-learning, face-recognition, and emotional recognition (Henderson, Williams, & Falk, 2005; Vaidya, Jin, & Fellows, 2014). Humans tend to preferentially use the nasion (e.g., the point between the eyes and above the nose) and the eyes to discern that an emotional expression is one of anger (Schurgin et al., 2014), and may also be biased to look for diagnostic information of angry emotional expressions in the upper nose region (Smith, Cottrell, Gosselin, & Schyns, 2005). Thus, if women do preferentially attend to regions which could convey cues of a fertile-phase woman's anger, then we would expect that they would preferentially fixate on the nasion and eye and potentially upper nose regions of the face when looking at fertile-phase women's neutral expressions. We do not expect men to be biased to see anger in the neutral expressions of fertile-phase women, and thus one possibility is that men may also attend to fertile- relative to non-fertile-phase women's faces in a comparable fashion, with no bias to look to regions which could convey anger. Alternatively, men may attend to cues of anger more in women's neutral faces, and specifically so in fertile-phase women, whom they expect would be more likely to go on a date with them (Bobst & Lobmaier, 2012). Evidence of cues that a woman is angry may be relevant for their decisions to court her, for example. Thus, we also tested whether participant sex would modulate the way that they attended to fertile- and non-fertile-phase targets' neutral faces.

Broadly, the present study examines the extent to which factors beyond the physical display of emotional expression in a face influence how the emotional expression in a face is perceived. Specifically, we test whether a woman's fertility status might modulate the emotions that observers perceive on her neutral face. Because women tend to be more intrasexually competitive when they are in the fertile phase of their cycle, and because women tend to suppress overt anger expressivity, particularly towards other women, we expect that women, but not men, may be biased to see anger on fertile-phase women's faces where none exists. We explore the extent to which a woman’s fertility may modulate observers’ tendency to look for visible hints of an angry expression on her neutral face.

Methods

Participants

Sixty-seven members of the University of Chicago campus community with normal or corrected-to-normal vision enrolled to participate in an eye-tracking study about “judging emotions and personalities in faces” in exchange for $10 cash compensation or course credit. Ten participants were excused from the study due to inability to calibrate the eye-tracker, one participant was inhibited from participating due to equipment malfunction, and one participant elected to suspend participation midway through the study due to sleepiness. Analyses were thus conducted on 55 participants (24 Caucasian, 18 Asian, 5 African American, 6 Hispanic, 2 other), aged 18 – 23 years old (*M*= 19.69 years, *SD* = 1.12 years). For one of these participants, eye-tracking data was lost due to equipment malfunction. Of the 36 female participants, 18 (50.00%) reported using hormonal contraceptives. Of those not currently using hormonal contraceptives, one reported being in a fertile-phase of their menstrual cycle (i.e., days 10-15, where 0 corresponds to the start of menstruation), whereas six reported being in the low-fertile early follicular phase of their menstrual cycle (e.g., days 1-9) and 11 reported being in the low-fertile mid-luteal phase of their menstrual cycle (e.g., days greater than 16 of the menstrual cycle)[1].

Procedure

Upon participants’ arrival to the laboratory, a researcher walked them through the study protocol, and all participants provided written consent. Participants then rested their forehead

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[1] Though we originally intended to examine if participants’ own fertility was a factor in any effects, we conducted no further analyses given that only one participant who was not using hormonal contraceptives was in the probabilistically fertile phase of her cycle.

and chin on the EyeLink 1000 (SR Research; Mississauga, ON) head/chin support, approximately 87 cm away from a video monitor (BenQ XL2420Z HD LED monitor, 60 Hz refresh rate, 1920 x 1080, 53 cm x 30 cm) to complete a 45 minute task during which their eye movements were tracked.

Participants completed an emotion and personality judgment task, as in Krems et al. (2015) and Maner et al. (2005). Participants were informed that they would view images of a number of individuals' (henceforth called 'targets') faces. Participants were told that the target individuals had been instructed to re-live events in their life which had evoked the emotions of anger, fear, happiness, or pride, and that we had then asked the targets to cover up their emotions by putting on a neutral facial expression before taking their photographs. Each target supposedly completed this procedure for each of the four emotions in a random order. In actuality, no targets participated in the emotion re-living procedure; all targets were told to simply assume a neutral facial expression before their photograph was taken. Participants were further told that emotions can often be detected even when people try to cover them with a neutral facial expression because other people subconsciously notice subtle expressions on people's faces, and that their task was to evaluate which emotion the targets had been assigned to re-live immediately prior to their photograph being taken. Participants were told that although each target was only instructed to re-live one emotion each time their photograph was taken, some of them reported experiencing multiple emotions. Thus, before they would indicate which emotion they thought the target had been assigned to re-live, they also reported how much they perceived that the targets actually experienced each of the four emotions immediately prior to their photograph being taken. Finally, participants were told that people's judgments of other people's personalities based on static images of their faces often correlate with their actual personalities, and that we would also ask them questions to gauge their perceptions of the targets' personalities. Participants were encouraged to use their gut responses, as we told them that judgments of emotions and personalities are particularly accurate when based on immediate gut reactions. To ensure comprehension, participants completed two instructional manipulation checks. In the event of an incorrect response, they received further instructional clarification.

Each trial began with a fixation cross in the center of the screen for 1000 ms. Following the fixation cross, a target image (650 x 650 pixels) subtending a visual angle of approximately 11.7° appeared randomly in one quadrant corner of the screen for 1600 ms [2]. After the image disappeared, participants were asked to judge the extent to which they believed that targets actually experienced the emotions of anger, fear, happiness, and pride in a random order using a 100-point visual analog scale ranging from "Not at all" to "Very Much". Then, they were asked to select which type of emotional experience they believed the target had been randomly instructed to re-live in a forced choice response type. Finally, they were asked to use a 100-point visual analog scale ranging from "Not at all" to "Very Much" to answer three questions about the target's personality (to be explored elsewhere). All responses were made using the mouse. Trials were randomized within blocks, and all participants completed three blocks (a total of 86 trials[3]), where stimulus type (e.g., fertile-phase women, non-fertile-phase women, men) varied between blocks. Block order was pseudo-counterbalanced – whether participants saw men or women first and whether they saw fertile or non-fertile women first was counterbalanced across participants of the same sex, but the two blocks of women were always presented consecutively

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[2] 1600 ms was chosen so as to index initial allocation of attention (c.f., Lischke et al., 2012).

[3] There were 29 stimuli in each of the female blocks, but only 28 photos for the block of male stimuli because only 28 of the stimulus men met male stimulus selection criteria.

and there was never a break between the two blocks of women so as to not draw attention to the fact that these blocks were different from each other.

Following the emotion and personality judgment task, participants provided demographic information and responses to a number of short surveys (see Measures). Participants then completed a funnel debriefing where they were debriefed about the task purpose and informed that the people in the photographs had not actually been instructed to re-live any emotional experience. Only two participants reported suspicion that the targets in the photographs had not actually completed the emotional re-living procedure. However, because these participants' average responses were within 1 *SD* of the grand mean of responses for each dependent variable, they were retained.

Finally, participants rinsed their mouths with water and provided approximately 2 ml of saliva via passive drool through polypropylene plastic straws into polypropylene tubes, which were then capped and frozen at -20°C for later analysis (to be reported elsewhere). All procedures were approved by the University of Chicago Institutional Review Board.

Stimuli and definition of areas of interest

Female stimuli for the current experiment were color photographs of the neutral faces of 29 regularly cycling premenopausal women who were not using hormonal contraceptives. Photographs were taken at two different points in stimulus females' menstrual cycle (Puts et al., 2013). Salivary estradiol and progesterone levels at the time each photograph was taken were measured and unacquainted females' ratings of stimulus women's facial attractiveness at each session were obtained. Photographs taken in their anticipated late follicular phase were considered to be photographs of the women in their "fertile" phase, and those taken at their anticipated mid-luteal phase were considered to be photographs of the women in their "non-fertile" phase. Male stimuli for the current experiment were color photographs of the neutral faces of 28 men, each of whom was photographed twice, approximately one week apart (Doll et al., 2014). All stimuli were Caucasian, to match the dominant race of our sample and to minimize the effects of cultural exposure on facial emotion recognition and looking patterns (Brielmann, Bulthoff, & Armann, 2014; Elfenbein & Ambady, 2003; Zebrowitz, Kikuchi, & Fellous, 2010).

Female stimuli used in the present study were selected from the broader stimulus set if their estradiol-to-progesterone (E:P) ratio, an approximate marker for ovulation (Baird, Weinberg, Wilcox, McConnaughey, & Musey, 1991), for their "fertile" phase photograph was greater than the average for all photographs, their E:P ratio for their "non-fertile" phase photograph was less than the average for all photographs, and their E:P ratio for their "fertile" session was greater than the E:P ratio for their "non-fertile" session. From this subset, women who were wearing jewelry or hair pieces were removed, and, in the case that more than one sibling from a sibling pair met inclusion criteria (stimulus women were originally recruited for a study on sibling relationships), only one sibling was randomly selected for inclusion in the present study's stimulus set. Male stimuli were considered for selection if ratings of the stimulus man's dominance (i.e., the likelihood that he would win in a physical fight against the average undergraduate male, as rated by unacquainted men) exhibited average stability across photographs (e.g., change in dominance ratings between photographs was within 1 SD of the mean). From this subset, approximately equal numbers of men whose standardized average dominance rating was high (+1 SD), average (-0.5 SD to +.5SD), and low (-1SD) were selected for inclusion in the present study, so as to equally represent men who might appear more and less threatening. We randomly selected photographs from men's first or second session. For each stimulus, 21 face regions were defined as areas of interest (AOIs), as in Schurgin et al. (2014); see Figure 3.1.

Measures.

Following completion of the eye-tracking portion of the study, participants completed a number of psychosocial survey measures. In particular, we measured participants' self-perceived sexual desirability, which has moderated women's likelihood to see anger on other women's neutral faces in prior research (Krems et al., 2015). Krems and colleagues have argued that sexually desirable women are more likely to be the targets of intrasexual aggression, and thus may be more attuned to other women's anger. Thus, as in Krems et al. (2015), we used the self-perceived mating success scale (Landolt, Lalumière, & Quinsey, 1995) to measure participant's self-perceived sexual desirability. Additional measures were also collected, but these were not of interest for the present research question and are thus explored elsewhere.

Apparatus and eye movement analyses

Eye position was noninvasively acquired using a table-mounted video-based eye tracker (Eyelink 1000; SR Research) at 500 Hz, and monocular data from the right eye were recorded. Prior to beginning the study, the eye tracker was calibrated to the participant using a nine-point calibration type. Calibration was considered successful if participants exhibited less than 1° of error in attending to all or all but one of the points in the calibration grid and if the EyeLink algorithm validated the calibration as "good" or "fair"; else, participants were thanked and excused from the experiment.

Any period during which the pupil was being tracked which was not defined as a blink or a saccade was denoted as a fixation. Saccades were defined as any period during which the eye exceeded a velocity of 30°/second or an acceleration of 8000°/second^2, and blinks were defined as any period for which the pupil position was not tracked or the pupil was partially occluded. Gaze position was determined by tracking pupil and corneal reflection, and samples were smoothed using the default algorithm for the Eyelink system (Stampe, 1993), set to levels which produce the lowest sample-to-sample artifact (SR Research, 2009). The manufacturer specified average accuracy for the desktop mounted system used here is 0.25° to 0.50°.

For each stimulus within each subject, we discarded fixations beginning prior to 1000 ms (i.e., the onset of the stimuli) and fixations which were immediately preceded or followed by a blink and lasted for 120 ms or less (as recommended by SR Research; c.f. Holmqvist et al., 2011)[4]. We used remaining fixations to create a duration-weighted 3-D Gaussian fixation map, or a "dwell map" (c.f., Wooding, 2002). For each fixation, we created a 220 x 220 pixel Gaussian mask centered at the fixation location using Matlab v. 2013b. Gaussian masks had a horizontal standard deviation of 55.01 pixels and a vertical standard deviation of 54.67 pixels (i.e., 2° visual angle, equivalent to the fovea, c.f., Henderson, 2003; Wooding, 2002) and a height proportional to the duration of that fixation (in ms). After submitting each fixation for a given stimulus within a given subject to this Gaussian kernel, we summed the Gaussian values for each pixel across all fixations to produce a single dwell map for each trial (that is, for each pixel, we obtained an estimate of the duration in milliseconds that pixel spent within focal attention across all fixations throughout the entire trial; see Figure 3.2), and summed across all pixels within each

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[4] Although all participants saw 86 stimuli, after data preprocessing, fixation maps for some stimuli for some participants were not available. On average, fixation maps were available for 83.85 stimuli (*SD* = 2.24) per participant.

AOI to determine the total time spent fixating to each AOI. We also computed fixation density for each AOI, or the number of times each AOI was fixated across the duration of the entire trial. Both total time spent fixating to a region and number of fixations to that region have been associated in past research on scene perception with elevated semantic importance of the region (Henderson & Hollingworth, 1999). We restrict analyses to the regions of the face which, on average, received the greatest number of fixations (as in Schurgin et al. (2014); see Table 3.1).

Data Analysis

We analyzed participants' responses for each stimulus using mixed effects models, implemented in lmer v. 1.1.12 in R v. 3.2.2. Utilizing mixed effects models allows us to model systematic variance on the level of the stimuli (e.g., target E:P ratio, target attractiveness) as well as on the level of the participants (e.g., participant sex), and to account for random variance at both levels (e.g., potential anovulatory cycles in targets, individual differences in participants' scan patterns when viewing faces; Mehoudar, Arizpe, Baker, & Yovel, 2014; Peterson & Eckstein, 2013). Mixed effects models are preferred when error terms are likely to be correlated because observations are not entirely independent of each other (e.g., each participants' response to each stimulus is not independent of their responses to other stimuli), and ignoring this structure can lead to biased estimation of standard errors (Hox, 2002; Raudenbush & Bryk, 2002). In all models, random intercepts were fit on the level of participants and targets. Parameter estimates were obtained using restricted maximum likelihood estimation, which provides less biased parameter estimates (Hox, 2002), and significance was tested using the Satterthwaite approximation for degrees of freedom (lmerTest v. 2.0.30 in R) and Wald chi square tests (car v. 2.1.1 in R) for dichotomous outcomes.

Multivariate mixed effects models were used to analyze participants' perception of targets' anger (e.g., while simultaneously analyzing their perceptions of targets' fear, happiness, and pride) and to analyze participants' dwell time and number of fixations to each AOI (e.g., simultaneously analyzing all AOIs). All dwell times were group mean centered within participants for ease of interpretation of coefficients. A series of binomial logistic mixed effects models were used for polytomous outcomes (e.g., how likely participants were to indicate targets were instructed to re-live anger, relative to each of the other emotions). In all analyses, we began by analyzing responses for only female participants, and then explored whether women's responses to fertile- and non-fertile-phase women differed from men's responses. In all analyses, we also controlled for potentially relevant demographic variables, including participants' ethnicity, relationship status, and sexual orientation. In the presence of significant effects of stimulus fertility, we tested whether using targets' E:P ratio or their attractiveness as predictors instead of their fertility status produced comparable effects.

Results

Perceiving Emotions on Neutral Faces – Behavioral Data

We first tested our hypothesis that women would be more likely to perceive anger on the neutral faces of fertile-phase women, relative to the neutral faces of non-fertile phase women. Multivariate mixed effects analysis of the effect of target fertility on female participants' perceptions of emotions on targets' neutral faces revealed no significant effects of target fertility (all *p*s > .085; see Table 3.2). Specifically, female participants were no more likely to indicate that the neutral face of a fertile-phase woman expressed higher levels of anger than they were to indicate that the neutral face of a non-fertile phase woman did, *B* = -.50, *SE* = .99, *t*(7930) = -.50, *p* = .614. Given past evidence that women who perceive themselves to be more sexually desirable are more likely to perceive anger on other women's neutral faces (Krems et al., 2015), we also explored a potential moderating effect of participants' self-reported sexual desirability, which did not interact with target fertility status to predict participants' likelihood of perceiving anger on targets' neutral faces, *B* = 1.11, *SE* = .82, *t*(7927) = 1.34, *p* = .179 (see Table 3.2). However, participants' sexual desirability did interact with target fertility status to predict participants' likelihood of perceiving pride on targets' neutral faces, *B* = 1.71, *SE* = .82, *t*(7927) = 2.08, *p* = .038, such that though participants generally perceived less pride on fertile-phase targets' faces, women with higher sexual desirability (+1 *SD*) saw marginally greater pride on fertile-phase targets' neutral faces than women with lower sexual desirability (-1 *SD*), *B* = 2.97, *SE* = 1.76, *z* = 1.68, *p* = .092, whereas for non-fertile-phase targets, there was no relationship between participants' sexual desirability and their tendency to see pride on targets' neutral expressions, *B* = 1.25, *SE* = 1.76, *z* = .71, *p* = .477 (Preacher, Curran, & Bauer, 2006). When we instead tested the univariate association between target estradiol:progesterone ratio and participants' sexual desirability on participants' perceptions of pride, the pattern of effect maintained with marginal significance, *p* = .077, whereas targets' female-rated attractiveness did not significantly interact with participants' sexual desirability to predict perceptions of pride, *p* = .236. Including target estradiol:progesterone ratio and female-rated attractiveness and their interactions with participants' sexual desirability as covariates, the interactive effect of target fertility status and participant sexual desirability dropped below statistical significance, *p* = .107, but the same pattern of effects maintained.

Including both male and female participants in the model, there was no participant sex by target fertility effect for any emotions (all *p*s > .582) and specifically, the target fertility by participant sex interaction for perceiving anger on neutral women's faces was non-significant, *B* = .16, *SE* = 1.81, *t*(12130) = .09, *p* = .928, indicating that men and women did not differentially perceive emotions on the faces of fertile and non-fertile women.

We also examined our hypothesis using participants' responses to a forced-choice question for which they had to indicate which emotion they thought the target had been instructed to re-live immediately prior to being photographed. To do so, we completed a series of multilevel binomial logistic regressions, comparing participants' likelihood of selecting 'anger' to their likelihood of selecting each of the alternative emotions. Female participants were no more likely to choose anger over happiness (*p* = .727), fear (*p* = .208), or pride (*p* = .605) as a function of the target's fertility, and their self-reported sexual desirability was not a significant moderator, (all *p*s > .123). Including both male and female participants in the model revealed no participant sex by target fertility effects (all *p*s > .395).

We also tested whether we replicated Krems et al.'s (2015) original findings that women exhibited a bias to see anger on the neutral emotional expressions of other women. To do so, we analyzed the interactive effect of target sex and participant sex on how much participants perceived each emotion on targets' neutral faces in a multivariate mixed effects model. Contrary to Krems et al. (2015), we found no interaction between participant and target sex in how angry participants perceived targets to be (*p* = .449), nor in how happy, fearful, or proud they perceived targets to be (all *p*s > .099), and participants' self-reported sexual desirability was not a significant moderator (all *p*s > .685)[5]. Analysis of forced-response data found no differences as a function of target sex and participant sex in participants' likelihood of selecting anger over fear (*p* = .976), happiness (*p* = .742), or pride (*p* = .685), and self-reported sexual desirability was again not a significant moderator (all *p*s > .685).

Perceiving Emotions on Neutral Faces – Eye Tracking Data

Though we did not find any evidence for an explicit bias to see anger on women's neutral faces as a function of their fertility status, we next examined whether fixation data from eye movements might reveal a biased tendency to look at areas of the face which may resemble or contain cues of angry expressions. We hypothesized that women might exhibit biased fixation patterns when looking at fertile-phase women's neutral expressions, dwelling longer on the nasion, upper nose, and eye regions of the faces of fertile-, relative to non-fertile, phase women. We restricted statistical analyses to AOIs which accounted for the most fixations, as in Schurgin et al. (2014). Here, we focus on the eyes, forehead, cheeks, nose, nasion, and upper lip, fixations to which together accounted for 88.80% of all fixations (see Table 3.1).

We first examined whether female participants differentially attended to any region of other women's faces as a function of the targets' fertility. We hypothesized that women would exhibit longer and more frequent fixations to regions of the face which may carry physical signatures of an angry expression, specifically the nasion, upper nose, and eye regions. Results of a multivariate multilevel analysis revealed that women's gaze

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[5] A mixed-effects ANOVA of the effect of participant sex and target sex on mean ratings of anger including no demographic covariates, replicating the statistical analysis conducted by Krems et al. (2015), also revealed no significant interaction, *F*(1, 104) = .039, *p* = .843, and self-reported sexual desirability was not a significant moderator, *F*(1,100) = .35, *p* = .558.

dwelled longer on fertile-phase women's foreheads than on non-fertile-phase women's foreheads, $B = 16.13$, $SE = 3.36$, $t(13550) = 4.81$, $p = 1.55E\text{-}6$, and less on fertile-phase women's women's cheeks than on non-fertile-phase women's cheeks, $B = -11.10$, $SE = 3.36$, $t(13550) = -$ $t(13550) = -3.31$, $p = .001$, see Table 3.3, though there were no differences in how frequently frequently women fixated to these regions (forehead: $p = .135$; cheeks: $p = .399$). Specifically, though women tended to look at targets' foreheads for a shorter duration than their average across other regions of the face, this effect was less strong when the target was a fertile-phase woman, though note the difference as a function of fertility was only approximately 16 ms. Whereas women tended to look longer at targets' cheeks than their average looking time to other regions of the face, they looked less long at fertile-phase women's cheeks, though note that this difference was only approximately 11 ms. Thus, though significant differences emerged, gaze patterns as a whole did not differ much as a function of target fertility (see Figure 3.2).

For all other regions, there were no differences as a function of target fertility in total dwell time (all ps > .124) or frequency of fixations (all ps > .135). Participants' self-perceived sexual desirability did not moderate how long they looked at any region as a function of fertility (all ps > .207), though it did moderate how frequently they looked at targets' upper nose region, $B = .15$, $SE = .05$, $z = 3.03$, $p = .002$. Participants tended to exhibit fewer fixations to the upper nose region in fertile-phase women, relative to non-fertile-phase women, but the effect of participants' sexual desirability on increasing their number of fixations to the upper nose region was nearly twice as large for fertile-phase targets, $B = .31$, $SE = .08$, $z = 4.05$, $p = 1.09E\text{-}4$, relative to non-fertile-phase targets, $B = .16$, $SE = .08$, $z = 2.14$, $p = .033$. When we instead tested the univariate interactions between target estrogen:progesterone ratio and participants' sexual desirability and between target female-rated attractiveness and participants' sexual desirability on participants' fixation density, comparable patterns of effects emerged, *p*s < .001, and controlling for each of these factors and their interactions with participants' sexual desirability, the interactive effect of target fertility status and participant sexual desirability maintained, *p* < .001.

Including both male and female participants, we observed no interactive effect of participant sex and target fertility on dwell times (all *p*s> .077) or on number of fixations (all *p*s>.177) for any region of the face.

Discussion

Hormonal fluctuations across the menstrual cycle are related to women's engagement in behaviors which could be construed as competitive or uncooperative in nature (Anderl et al., 2015; Durante et al., 2014), and other women may anticipate potential downstream consequences of interacting with fertile-phase women (Krems et al., 2016; Lobmaier et al., 2016). One product of such awareness may be that women expect fertile-phase women to be more likely to aggress against them, expectations which may bias their social perceptions. The present study tested whether women were biased to see anger on fertile-phase women's neutral expressions, as angry emotional expressions convey behavioral intent to aggress or act uncooperatively (Horstmann, 2003; Van Doorn et al., 2012; Yik & Russell, 1999). We found no evidence that a woman's fertility status influenced how likely other women were to attribute anger to her neutral facial expression, and also failed to find support for a bias more generally for women to perceive anger on other women's neutral faces, as observed in Krems et al (2015).

Interestingly, though we did not observe any differences in women's tendency to fixate to features of the face which in past research have been associated with discerning angry expressions (Schurgin et al., 2014; Smith et al, 2005) as a function of target fertility, we did observe that self-reported sexual desirability increased the frequency with which participants fixated to one of these regions, specifically the upper nose, more in fertile-phase women than in non-fertile-phase women. Previous work has suggested that sexually desirable women's increased victimization by other women (Vaillancourt & Sharma, 2011) may be related to an increased sensitivity to latent intrasexual threats and a bias to see emotional expressions associated with aggression where none exist (Krems et al., 2015). One possibility is that women who are more sexually desirable may more often come into conflict with fertile-phase women, particularly if they impede fertile-phase women's mating-related motivations. To the extent to which increased fixation density to a region indicates greater relevance of that region (c.f., Henderson & Hollingworth, 1999), one interpretation of our finding that sexually desirable women fixate to the upper nose in fertile-phase women could be that cues that a fertile-phase women is angry are more relevant for sexually desirable women, who are thus biased to look for such cues. Note, however, that the frequency of fixations to the upper nose was generally low, and the magnitude of the effect of sexual desirability was small, such that a one unit increase in self-desirability increased participant's frequency of looking to the upper nose region of fertile-phase women by less than one fixation. Though even small numbers of fixations are sufficient for face processing (Hsiao & Cottrell, 2008), the practical relevance of this small increase in fixation frequencies to the upper nose region is uncertain.

We observed that sexually desirable male participants exhibited a similar trend in their fixation frequencies to the upper nose region of fertile- and non-fertile-phase women (that is, we found no evidence for a moderating effect of participant sex). Although past work suggests that women do not mask their angry emotional expressions when they are directed at men (Krems et al., 2015), detecting whether women are angry may still be motivationally relevant for men, who are attracted to fertile-phase women (Bobst & Lobmaier, 2012). Information about a woman's emotional state which is conveyed in her upper nose region could be useful for sexually desirable men in the event that they decide to court her. But though humans tend use visual information conveyed in the upper nose region to discern angry emotional expressions (Smith et al., 2005), past work has failed to find evidence that they specifically fixate to this region longer or more frequently when judging if expressions are angry, relative to when judging other emotions, even when biased to expect anger on neutral facial expressions (Schurgin et al., 2014). Thus, greater fixations to the upper nose region may also reflect processes other than emotional search or detection. Initial fixations to faces tend to be to the nose (Hsiao & Cottrell, 2008), perhaps because maximal information acquisition, which facilitates holistic face processing, is possible when foveating to the nose. Under this interpretation, differential fixation frequencies to the upper nose region may reflect engagement in distinct face processing strategies as a function of the motivational relevance of the target face. Ultimately, however, explanation of this effect awaits further empirical investigation.

Our hypotheses in the present study were motivated by an expectation that individuals' increased sensitivity to other's angry expressions may increase their responsivity to corresponding competition or aggression, allowing perceivers to act effectively and mitigate the impact of any potential transgression. However, our assumption that anger is a veridical cue of a woman's more indirect, rather than direct, aggressive intentions against other women may be invalid. Though we find no differences between fertile- and non-fertile-phase targets in participants' perceptions of anger, we did find that participants' sexual desirability moderated their tendency to see pride on fertile-phase women’s neutral faces. Participants’ perceptions of pride in fertile-phase targets’ neutral faces were generally lower than their perceptions in non-fertile-phase targets’. However, more sexually desirable women (i.e., women who may be more likely to be the victims of fertile-phase women’s intrasexual aggression) perceived pride to a greater extent on fertile-phase women’s neutral faces than did less sexually desirable women, but sexual desirability did not affect participants’ perceptions of pride in non-fertile-phase women’s neutral faces. Could pride displays signal potential competitive intents? The emotional expression of pride (evident in both subtle facial cues and bodily postural expressions; Shariff, Tracy, & Markusoff, 2012; van der Schalk, Hawk, Fischer, & Doosje, 2011) is associated with high social status (Tracy, Shariff, Zhao, & Henrich, 2013). To the extent to which sexually desirable women are more attuned to fertile-phase women’s tendency to engage in status competition, they may be more biased to expect fertile-phase women to display emotional expressions associated with holding status. Yet this explanation does not account for the fact that participants in general tended to perceive less pride on fertile-phase women’s faces, relative to non-fertile-phase women’s faces, nor does it account for men’s comparable tendency to perceive pride in fertile-phase women’s neutral faces. Research into ‘pride’ as an emotional expression is still in its infancy, and future work which specifies the behavioral intent conveyed by pride in social contexts may help to clarify this effect.

More broadly, we did find distinct patterns of fixations to fertile-, relative to non-fertile-phase women’s faces. Across participants, we observed a tendency to look longer to the forehead of fertile-phase, relative to non-fertile-phase, women’s neutral faces and a tendency to look longer to the cheeks of non-fertile-phase, relative to fertile-phase, women’s neutral faces. However, though dwell patterns differed significantly between fertile- and non-fertile phase targets, the magnitude of such differences was small, and indeed the overall dwell maps for attention to fertile- and non-fertile-phase women's neutral faces were nearly identical (see Figure 3.2). Whereas fixations to the forehead may be important for learning new faces, potentially due to the strong individuating nature of features like hairline (Henderson et al., 2005), fixations to the cheek region may be more optimal for face recognition (Henderson et al., 2005; Peterson & Eckstein, 2012), potentially because they permit more holistic processing of the face. However, past research has demonstrated differences in attention to the forehead and cheeks proportionally at least three times the magnitude of those observed here (Henderson et al., 2005). Thus, though our results may point to differential social strategies when viewing fertile- and non-fertile women's faces, future research is necessary to determine the robustness of the present findings, and whether differences of such a small magnitude reflect meaningful differences in facial processing.

In the present study, we focused minimally on features of the participants which might bias their perceptions of emotions in other's neutral faces, examining only participant sex and participant self-reported sexual desirability as factors which could influence emotion perception. Yet emotion perception is not a uniform process; rather, individual observers are biased by their social milieu (Hess & Hareli, in press). Accumulating evidence also suggests that individuals' emotion recognition abilities may be biased or altered by their biological state - of particular relevance to the present study, by women's menstrual cycle phase and associated hormonal profiles. For instance, women in the follicular phase of their cycle are less likely to confuse angry emotional expressions with other expressions, relative to women in the luteal phase of their cycle

(Derntl, Kryspin-Exner, Fernbach, Moser, & Habel, 2008), and women in the early-follicular phase are better at recognizing anger than women in their late-follicular ovulatory phase and better at recognizing anger and fear than women in their luteal phase (Guapo et al., 2009). A woman's own cycle phase may also modulate the likelihood that she is the target of fertile-phase women's intrasexual competitive behaviors (Chapter 1; Necka, Puts, Dimitroff, & Norman, 2016). If cycle phase plays an important role in a woman's ability to accurately detect an emotional expression when it exists, it may also bias her tendency to overperceive emotions on neutral expressions. Further, if the tendency to overperceive emotions associated with intrasexual aggression or competition in other women's neutral faces depends in part on expectations of the other woman's aggressiveness or competitiveness, then a woman's own cycle phase or hormonal state may modulate the presence of such expectations and biases in emotional perceptions. A bias which is selectively present only when it is most needed, or most likely to effective reduce potential threats, would suppress unnecessary false alarms which might impair regular social interactions, and thus serving an adaptive function. Unfortunately, however, we could not examine cycle phase in the present study due to a small sample size of women not currently using hormonal contraceptives. Given our findings that individual differences which correspond to the likelihood of being targeted by intrasexual aggression modulate biased emotional processing, future work should investigate whether women's own cycle phase interacts with the cycle phase of female targets to influence emotion perception.

The present study is subject to a number of limitations. First, we did not measure participants' affective states prior to or during the emotion recognition task. There is evidence that observers tend to perceive moods in others which are congruent with their own affective state and have difficulty recognizing emotional expressions incongruent with their current mood

(Niedenthal, Halberstadt, & Margolin, 2000; Schmid & Mast, 2010), and preliminary evidence suggests that an observer's mood may modulate the strategies they use to visually inspect facial emotional expressions (Schmid, Mast, Bombari, Mast, & Lobmaier, 2011). In the present study, we are unable to account for potential emotional projection effects. Yet a straightforward emotional projection account cannot fully explain why more sexually desirable participants (who may feel higher in status or more prideful) selectively perceived pride on fertile-phase women's faces, instead of on all targets' faces. Still, our ability to interpret the substantial null associations we observed in the present study is inherently limited because we do not know participants' affective states during the task.

Perhaps more problematic is that we do not account for the fact that there may be observable and systematic physical differences between fertile- and non-fertile-phase women's neutral faces, differences which may influence perceptions of emotionality or aggression. Facial morphology is related to perceptions of trait aggressiveness, emotionality, and threat (Becker, Kenrick, Neuberg, Blackwell, & Smith, 2007; Carré, McCormick, & Mondloch, 2009; Oosterhof & Todorov, 2008; Said, Sebe, & Todorov, 2009). Though the specific ways in which a woman's facial appearance fluctuates across her menstrual cycle are under-researched, if facial structure changes (e.g., through fluctuations in soft-tissue symmetry; Manning et al., 1996; Scutt & Manning, 1996) in ways which bear more or less structural resemblance to certain emotional expressions, participants' judgments of targets' emotionality could be differentially influenced by objective cues in fertile- and non-fertile-phase targets' objective facial structure. Hypothetically, this could yield a result in which fundamentally different mechanisms produce equal perceptions of anger in fertile and non-fertile women's faces (as observed here), thereby masking any bias that exists. For instance, suppose non-fertile-phase faces resemble angry expressions more, on average, than fertile-phase faces. A bias to see anger in a fertile-phase woman's neutral face, then, could indeed result from expectations that she may exhibit intrasexual aggression, whereas a bias to see anger in a non-fertile-phase woman's neutral face may be a simple byproduct of the woman's facial structural resemblance to angry expressions. This is but one hypothetical, and until further research more clearly delineates how fertile- and non-fertile-phase faces physically differ, it is impossible to rule out. Future research should more comprehensively and precisely assess the physical differences in fertile- and non-fertile-phase women's faces, particularly those which observers use to behaviorally distinguish between them.

In sum, the present study suggests preliminary evidence that the ways in which individuals engage with and perceive the neutral faces of women may vary as a function of features of both the target and the observer. Specifically, consistent with past research which has shown that individuals exhibit biased attentional processes towards fertile-, relative to non-fertile phase women (Study 2), the present study suggests that patterns of looking at target women's faces may vary as a function of the targets' fertility. Importantly, individual differences in observers also modulate their tendencies to perceive emotions where none exist, such that individuals for whom fertile-phase women might be expected to be particularly relevant exhibit different responses than individuals for whom fertile-phase women might be less relevant. Yet such effects are small, and require additional exploration of their practical relevance for facial emotion processing. The present findings contribute to a broader literature suggesting that emotion perception is socially situated, and point to a role for visual cues of women's fertility in signaling socially relevant information.

Appendix D: Tables and Figures for Chapter 3

Table 3.1. Number of Fixations and Total Dwell Time for Each Region of the Face

Region	Number of Fixations	Maximum Number of Fixations	Total Dwell Time (ms)		Maximum Dwell Time
Right Cheek	0.87 (1.08)	6	218.09	(151.04)	904.49
Lower Nose	0.72 (0.91)	5	170.82	(103.20)	601.70
Upper Nose	0.55 (0.79)	4	98.27	(53.32)	319.03
Left Cheek	0.52 (0.81)	6	142.32	(116.18)	765.13
Upper Lip	0.44 (0.67)	5	84.20	(82.25)	469.23
Right Eye	0.42 (0.71)	4	66.69	(49.57)	331.64
Nasion	0.38 (0.69)	4	103.92	(66.73)	424.67
Forehead	0.36 (0.83)	7	116.86	(160.46)	1287.93
Left Eye	0.27 (0.59)	3	48.57	(43.89)	359.80
Right Brow	0.24 (0.55)	4	73.20	(59.92)	443.17
Left Brow	0.15 (0.43)	3	47.51	(46.17)	384.93
Lower Lip	0.13 (0.36)	2	30.18	(39.11)	261.47
Hair	0.09 (0.34)	4	29.75	(65.62)	977.32
Right Temple	0.06 (0.27)	3	16.77	(22.38)	185.42
Chin	0.05 (0.25)	3	28.26	(52.94)	473.43
Left Jowl	0.04 (0.25)	3	30.79	(54.01)	592.14
Right Jowl	0.04 (0.24)	4	29.45	(44.54)	487.90
Right Ear	0.02 (0.16)	4	6.37	(17.42)	238.49
Left Temple	0.02 (0.13)	2	8.24	(13.08)	135.45
Left Ear	0.00 (0.08)	3	1.80	(6.21)	212.77
Neck	0.00 (0.10)	5	3.60	(16.88)	725.16

Table 3.1. Number of Fixations and Total Dwell Time for Each Region of the Face.
Note: As in Schurgin et al. (2014), we proceeded with analysis on only the most attended regions of the face (regions listed in black). Consistent with Schurgin et al. (2014), this includes the eyes, nose, upper lip, and nasion. Additionally, we observed high fixation rates to the cheeks and the forehead. Note that we observe dominance in the right visual field in our fixation patterns, consistent with the fact that the left hemiface (i.e., left side of the face) is more dominant in conveying emotional expression (Borod, Haywood, & Koff, 1997). We also observe a tendency to focus on the cheeks. People tend to achieve optimal facial recognition when fixating just below the eyes (e.g., the cheeks; Peterson & Eckstein, 2012); thus, though participants were not instructed to engage in facial recognition processes, this may reflect an optimal facial viewing pattern. In the second column, the average number of fixations to each

Table 3.2. Number of Fixations and Total Dwell Time for Each Region of the Face, Continued

region across all stimuli and all participants is displayed, and the standard deviation is listed in parentheses. The minimum number of fixations to all regions was zero, and the maximum number of fixations is displayed in the third column. The average total dwell time to each region in milliseconds across all stimuli and all participants based on the Gaussian-smoothed dwell map is displayed in the fourth column, and standard deviations are listed in parentheses. The minimum dwell time to all regions was zero, and the maximum dwell time is displayed in the last column.

Table 3.2. Perceptions of Emotions on Targets' Neutral Faces

		A		B	
		B (SE)		B (SE)	
Anger	Intercept	48.00 (3.56)	***	41.18 (6.51)	***
	Target Fertility	-.50 (.99)		5.02 (4.23)	
	Participant Sexual Desirability			1.47 (1.21)	
	Target Fertility x Participant Sexual Desirability			-1.11 (0.82)	
Pride	Intercept	49.71 (4.12)	***	43.42 (9.74)	***
	Target Fertility	-1.71 (.99)		**-10.26 (4.23)**	*
	Participant Sexual Desirability			1.25 (1.76)	
	Target Fertility x Participant Sexual Desirability			**1.71 (0.82)**	*
Fear	Intercept	39.37 (3.70)	***	40.24 (7.16)	***
	Target Fertility	1.55 (0.99)		5.98 (4.23)	
	Participant Sexual Desirability			-0.17 (1.22)	
	Target Fertility x Participant Sexual Desirability			-0.89 (0.82)	
Happiness	Intercept	43.73 (4.59)	***	47.37 (9.58)	***
	Target Fertility	-1.64 (0.99)		0.06 (4.23)	
	Participant Sexual Desirability			-0.73 (1.68)	
	Target Fertility x Participant Sexual Desirability			-0.34 (0.82)	
Marginal R^2		0.02		0.02	
Conditional R^2		0.38		0.38	
AIC		74453		74453	

Table 3.2. Perceptions of Emotions on Targets’ Neutral Faces, Continued

Note: Results of a multivariate mixed effects model predicting female participants’ perceptions of emotions on female targets’ neutral faces, as a function of target fertility status and participant sexual desirability. Betas for each model are listed, with standard errors in parentheses. Note that all models also included demographic covariates, not shown here for sake of simplicity. Marginal R^2 explains the portion of variance explained from fixed effects, whereas conditional R^2 explains the portion of the variance explained including random effects. Models included random intercepts on the level of target and participant. Though we did not observe any effect of target fertility, participants’ sexual desirability, or their interaction on participants’ perceptions of anger, we did observe a significant effect on their perception of pride in targets’ neutral faces (indicated in bold). Significant predictors are bolded. * $p < .05$; *** $p < .001$.

Table 3.3. Total Dwell Time in and Fixations to Regions of the Neutral Face

		Dwell Time				Number of Fixations			
		A		B		A		B	
		B (*SE*)		*B* (*SE*)		*B* (*SE*)		*B* (*SE*)	
Eyes	Intercept	-45.13 (12.19)	***	-12.23 (26.04)		-.62 (.23)	**	-.71 (.50)	
	Target Fertility	3.22 (3.36)		-14.70 (14.60)		.11 (.09)		-.21 (.22)	
	Participant Sexual Desirability			-7.42 (5.35)				.02 (.10)	
	Target Fertility x Participant Sexual Desirability			3.56 (2.82)				.05 (.04)	
Nasion	Intercept	-34.75 (11.84)	**	-1.60 (31.96)		-1.15 (.36)	**	-.81 (.91)	
	Target Fertility	1.82 (3.36)		-.12 (14.60)		.06 (.13)		-.15 (.27)	
	Participant Sexual Desirability			-7.34 (6.56)				-.01 (.19)	
	Target Fertility x Participant Sexual Desirability			.38 (2.82)				.03 (.05)	
Upper Nose	Intercept	-52.85 (6.83)	***	-42.09 (18.87)	*	-.58 (.24)	*	-.85 (.63)	
	Target Fertility	-1.46 (3.36)		-5.86 (14.60)		-.10 (.10)		**-.76 (.25)**	**
	Participant Sexual Desirability			-2.34 (3.83)				.05 (.13)	
	Target Fertility x Participant Sexual Desirability			.87 (2.82)				**.15 (.05)**	**
Forehead	Intercept	-24.74 (4.14)		23.66 (112.81)		-1.94 (.40)	***	-1.12 (.97)	
	Target Fertility	**16.13 (3.56)**	***	18.37 (14.60)		.24 (.16)		.05 (.35)	
	Participant Sexual Desirability			-10.77 (23.23)				-.11 (.20)	
	Target Fertility x Participant Sexual Desirability			-.44 (2.82)				.02 (.07)	

Table 3.3. Total Dwell Time in and Fixations to Regions of the Neutral Face, Continued

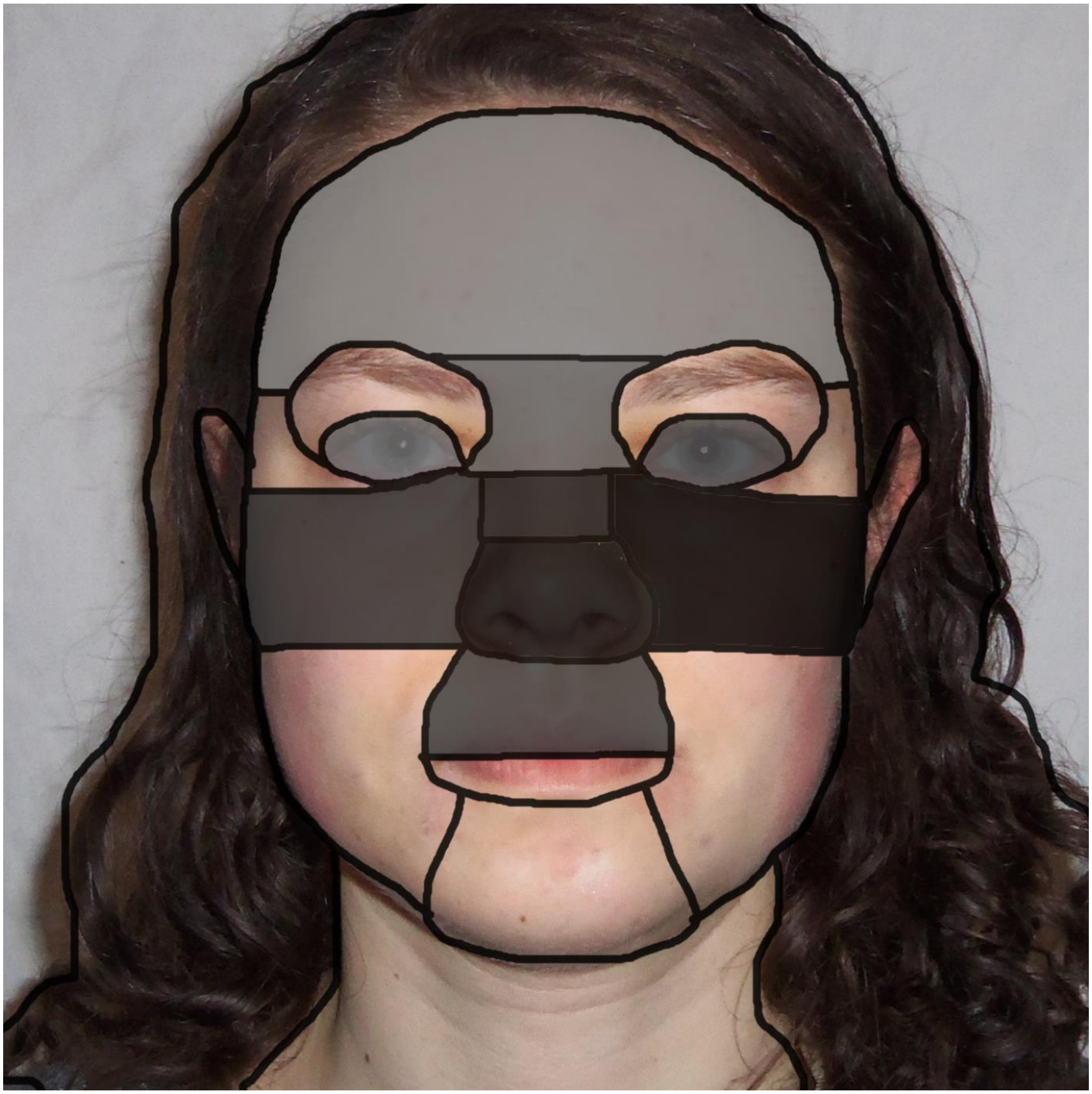
		Dwell Time				Number of Fixations		
		A		B		A	B	
		B (*SE*)		*B* (*SE*)		*B* (*SE*)	*B* (*SE*)	
Cheeks	Intercept	191.80 (27.16)	***	178.95 (73.39)	*	.22 (.17)	-.15 (.48)	
	Target Fertility	**-11.10 (3.36)**	*******	-25.88 (14.60)		-.06 (.08)	-.16 (.17)	
	Participant Sexual Desirability			3.02 (15.08)			.05 (.10)	
	Target Fertility x Participant Sexual Desirability			2.94 (2.82)			.03 (.03)	
Lower Nose	Intercept	11.29 (19.33)		-44.74 (51.32)		-.38 (.26)	-1.92 (.66)	***
	Target Fertility	-2.44 (3.36)		6.32 (14.60)		-.03 (.08)	.31 (.25)	
	Participant Sexual Desirability			12.33 (10.54)			**.32 (.14)**	*
	Target Fertility x Participant Sexual Desirability			-1.74 (2.82)			-.07 (.05)	
Upper Lip	Intercept	-57.75 (19.37)	**	-110.26 (52.39)	*	-.88 (.30)	-2.17 (.75)	
	Target Fertility	-5.17 (3.36)		12.30 (14.60)		.07 (.11)	-.52 (.32)	
	Participant Sexual Desirability			11.45 (10.78)			.28 (.15)	
	Target Fertility x Participant Sexual Desirability			-3.47 (2.82)			.11 (.06)	
Marginal R^2		.39		.39		.20	.21	
Conditional R^2		.72		.72		.57	.57	
AIC		160090		160110		25978	25911	

Note: Results of a multivariate mixed effects model predicting female participants' total dwell time in and fixations to regions of female targets' neutral faces, as a function of target fertility status and participant sexual desirability. Betas for each model are listed, with standard errors in parentheses. Note that all models also included demographic covariates, not shown here for sake of simplicity. Marginal R^2 explains the portion of variance explained from fixed effects, whereas conditional R^2 explains the portion of the variance explained including random effects. Models included random intercepts on the level of target and participant. All

Table 3.3. Total Dwell Time in and Fixations to Regions of the Neutral Face, Continued

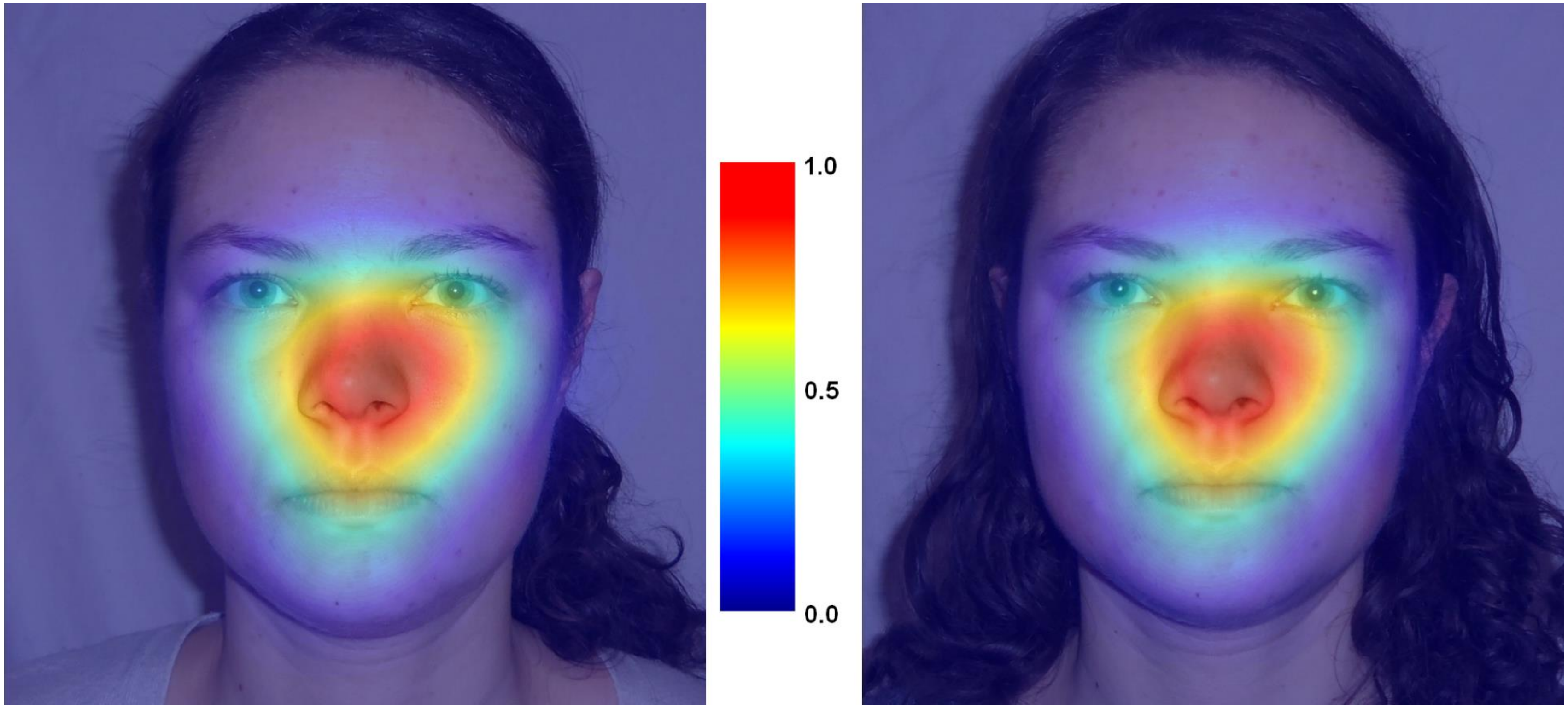
dwell times were centered within participants, such that more positive beta weights indicate that the participant dwelled longer in or fixated more frequently to that region than their average across the other regions presented here, whereas negative beta weights indicate that they did so less than average. Results indicate that participants dwelled longer on the foreheads of fertile-phase targets and less time on the cheeks of fertile-phase women, relative to non-fertile-phase targets. Further, participants higher in self-reported sexual desirability fixated more frequently to the upper nose region of targets' faces, particularly when targets were in their fertile-phase. Significant predictors are bolded. * $p < .05$; *** $p < .001$.

Figure 3.1. Illustration of Areas of Interest



Though we divided the face into 21 distinct areas of interest, shown here, we analyzed only those regions which received the greatest number of fixations, as in Schurgin et al. (2014). Regions which were included in analyses are shaded, such that darker shading indicates more frequent fixations on average to the region.

Figure 3.2. Average Dwell Maps to the Faces of Fertile- and Non-Fertile-Phase Women's Neutral Faces



For illustrative purposes, dwell maps were aggregated over all targets of the same fertility type and across female participants and are displayed here over prototypical fertile-phase (left) and non-fertile-phase (right) stimuli of the same target. Hotter colors (i.e., redder) indicate greater dwell time to the region, aggregated across the duration of the trial. Note that all analyses were conducted on dwell maps for individual stimuli within individual participants, rather than on aggregated data as visualized here. Though we observed a tendency for participants to look longer at the forehead region of fertile-phase women's neutral faces and to look longer at the cheek

Figure 3.2. Average Dwell Maps to the Faces of Fertile- and Non-Fertile-Phase Women's Neutral Faces, Continued
region of non-fertile-phase women's neutral faces, differences in time (in ms) were trivial (i.e., less than 20 ms out of 1600 ms of total looking time). Dwell maps are largely uniform across fertile- and non-fertile-phase women.

GENERAL DISCUSSION

Hormones are instrumental in the coordination of many of life's most basic processes, producing coordinated "concatenated interdependencies" (Beach, 1974), rather than sets of covariant one-to-one relationships. That is, rather than exerting specific effects on specific organs, hormones, via their release into the periphery, orchestrate harmonized responses from multiple downstream targets, which together tend to make the system more effective in meeting fitness demands and pressures. In addition to altering physiology, hormones are indirectly related to behavior, affecting the organism's sensitivity to internal and external influences and altering the probability that the organism responds to fitness-relevant stimuli in a fitness-enhancing manner (Nelson, 2010; Roney, 2016). In the present dissertation, I have studied how hormones in one organism potentially increase the relevance of that organism to its conspecifics, and how hormonal influences in the conspecific alter its sensitivity to the fitness-relevant organism and associated behavioral response.

More specifically, this dissertation has focused on behavioral fluctuations across the menstrual cycle that coincide with hormonal fluctuations supporting reproductive function in women and tested whether women's vigilance to other women varies as a function of either or both women's probabilistic fertility. Previous work has demonstrated that women tend to engage in behaviors towards other women which could be construed as competitive in nature when they are near the most probabilistically fertile phase of their menstrual cycle (Durante, Griskevicius, Cantú, & Simpson, 2014; Lucas & Koff, 2013; Piccoli, Foroni, & Carnaghi, 2013). To the extent to which fertile-phase women impede or otherwise thwart a woman's ability to achieve motivated end-states, vigilance toward them may be part of an adaptive coordinated response. Here, I have demonstrated **(a)** that women tend to be vigilant towards probabilistically-fertile phase women and **(b)** this vigilance is greater when women are in the probabilistically most fertile phase of their own cycle.

In **Study 1** (Necka, Puts, Dimitroff, & Norman, 2016), I showed evidence that fertile-phase women distribute resources more selfishly in a behavioral economic game with other fertile-phase women, whereas they are more egalitarian in interactions with non-fertile-phase opponents or when they are in the non-fertile-phase of their own menstrual cycle. I take this as indicative of women's behavioral vigilance towards fertile-phase women when women are in the probabilistically fertile phase of their own menstrual cycle. That is, **Study 1** demonstrates that when women are in the probabilistically most fertile phase of their cycle, they are watchful of their standing specifically relative to another fertile-phase woman and behave in ways which advantage themselves over her.

In light of evidence that women distinguish between fertile- and non-fertile-phase women when they themselves are in the probabilistically fertile phase of their own cycle, I then probed whether women's own fertility status and the fertility status of other women might impact early stages of social perception, focusing specifically on women's attention to and memory for other women. In **Study 2**, I demonstrated that women respond faster to an attentional probe when it is in the spatial location where an image of a fertile-phase woman appeared immediately before, and interpreted this as evidence that fertile-phase women captured the attention of other women, facilitating response times to the probe. Further, I demonstrated that women are faster to identify a fertile-phase woman's face maintained in visual working memory than a non-fertile-phase woman's face when they are in a non-fertile phase of their own cycle, but are slower to identify a fertile-phase woman's face when they are in the fertile-phase of their own cycle. At a minimum, this demonstrates that women's fertility is related to how they match their internal representations of other women to objective representations of those women, and that this relation varies as a function of the other woman's fertility. I suggest that heightened attention to fertile-phase women's faces facilitates their transfer to visual working memory and speeds recognition of internal representations, and that a woman's own fertility might bias her strategy for identifying fertile-, relative to non-fertile-, phase women, consistent with an interpretation that fertile-phase women are more vigilant to other fertile-phase women. Importantly, these effects emerge only when women have poorer visual working memory capacity, and can be presumed to be more susceptible to attentional capture. Thus, **Study 2** suggests that the fertility status of women, as conveyed by visual cues, may affect women's lower order social processing, and that women may engage in different judgment and decision strategies towards fertile-and non-fertile-phase women across their menstrual cycle.

What about a fertile-phase woman might capture a woman's attention, as demonstrated in Study 2, or motivate her to behave differentially toward a fertile-phase woman (as a function of her own fertility), as demonstrated in Study 1? Taken together, Studies 1 and 2 suggest that women perceive motivationally relevant cues in the faces of fertile-phase women. In **Study 3**, I tested whether perception of such cues might be evident in women's gaze patterns when inspecting the faces of fertile- and non-fertile women, focusing specifically on whether women would be biased to look for or see threatening emotional expressions on the faces of fertile-phase women when none exist. If women associate visual cues that another woman is fertile with heightened odds that the woman will transgress against her, a bias to interpret neutral expressions as threatening could be an effective motivator of behavior, enabling women to respond appropriately and mitigate the potential threat. I found no evidence that women were more likely to perceive anger on fertile-phase women's faces relative to non-fertile-phase women's faces, nor that they looked more for cues of angry emotional expressions on fertile-phase women's faces relative to non-fertile-phase women's faces. Participants' perceptions of their sexual desirability, however, modulated their responses, such that those participants who were more sexually desirable looked more frequently to regions of the face associated with anger and were more likely to perceive pride on women's neutral faces, an effect which was consistent across both male and female participants. However, most regularly cycling female participants in Study 3 were in non-fertile-phases of their menstrual cycle and thus the effect of women's own fertility on their perceptions was not assessed.

In light of Studies 1 and 2, one interpretation of the results obtained in **Study 3** could be that vigilance to fertile-phase women crucially depends on the motivational relevance of fertile-phase women. Specifically, for female participants, biased perceptions of and looking patterns at fertile-phase women's neutral faces were observed among those who may be more likely to come into direct competition with fertile-phase women (i.e., women who are sexually desirable). In Study 1, women exhibited vigilant behavior only when they and their opponent were both in their fertile-phase, and analogous fertility-associated motivations could have put them in direct conflict. In Study 2, though fertile-phase women captured other women's attention (when they had lower visual working memory capacity), memory processes were biased by both a woman's own fertility status and the fertility of other women. In Study 3, biased social perceptions were apparent only in women who might be more likely to attract male attention; that is, women who might thwart fertile-phase women's mating intentions. Though I was unable to test the effect of participants' own fertility status in Study 3, participants' fertility status may interact with the fertility status of other women, as in Studies 1 and 2, to predict women's emotion perception behavior, such that women would report seeing emotional observations which may signal threat on fertile-phase women's neutral faces when they are in the probabilistically most fertile phase of their own cycle. Future research might profit in further exploring the interactive effect of women's fertility and the fertility of their conspecifics in this context, and in other social cognitive phenomena.

Together, these three studies suggest that women's probabilistic fertility influences other women's perceptions of them. When other women are in the most probabilistically fertile phase of their own cycles (or are otherwise more likely to share motivated end states with fertile-phase women), women's fertility status evokes different behavioral responses in other women as well. However, there are limitations to the present dissertation. Importantly, the precise mechanism by which fertile-phase women elicit vigilant responses from other women, particularly fertile-phase women, is not established in the present work. Based on the results of Study 1 and other work (Durante et al., 2014; Lucas & Koff, 2013; Piccoli et al., 2013), I have interpreted women's vigilance for fertile-phase women as reflecting an implicit association between visual cues of fertility and increased odds of ensuing status competition (which may manifest as indirect aggression). Yet the robustness of the link I propose between fertility and status competition is unclear. Only recently have researchers begun to study the association between fertility and status competition in humans, and the nascent nature of this line of inquiry means that available evidence (and robust replication) in support of this relation is incomplete. Further, the indirect and covert nature of human female competition (e.g., gossip, social exclusion, and derogation) does not lend itself to a unified and concrete definition of what can be construed as competitive intrasexual behavior. Because it is the intents behind these behaviors, rather than the behaviors themselves, that make them competitive, the working definition of human female intrasexual competitive behavior used here (and in other research; c.f., Durante, Griskevicius, Hill, Perilloux, & Li, 2011) focuses on outcomes (status gains relative to other women). Yet outcomes can be achieved by many means (e.g., gains in one's objective status, gains in one's own status while inhibiting another's status gains, direct blows to another's status while maintaining one's own status constant, etc.), and the precise relation between each of these means and fertility, as well as the range of behaviors encapsulated in women's fertile-phase intrasexual competition, is underspecified.

The assumption that women associate visual cues of fertility with increased odds of ensuing status competition also depends on cues of women's fertility being systematic and traceable by other women. Though accumulating evidence suggests that there are changes in visual appearance across the menstrual cycle, such that women's attractiveness tends to be higher in the fertile-phase and lower when they have higher levels of progesterone (Puts et al., 2013; Roberts et al., 2004), research has tended to focus on changes in specific characteristics of the face, rather than on if such changes are coordinated or how they might alter holistic perception of the face. I have ruled out attractiveness as a potential alternative explanation – even though fertile-phase women tend to be rated more attractive than non-fertile phase women, women's fertility status explained systematic variance in other women's responses while controlling for attractiveness. An unexpected finding from Study 2 lends support to the idea that changes in women's facial appearance may be systematic: women seemed to have exercise more caution or experience more difficulty in identifying a face that matched their internal representation (as indexed by slower response times) when the face was surrounded by other faces of the same fertility status than when it was surrounded by faces of an opposite fertility status. Though this effect was unexpected, it persisted in every analysis conducted, and may suggest that changes in visual appearance across the menstrual cycle are systematic, such that fertile-phase women look more similar to each other than they do to non-fertile phase women and that non-fertile-phase women look more similar to each other than they do to fertile-phase women. This is an exciting avenue for future research, and emphasizes the importance of considering variations not only in specific facial characteristics but also of the face as a whole.

Though the present work points to differences in behavior which likely covary with women's neuroendocrine state across the menstrual cycle, I did not directly measure hormonal concentrations or their relation to any variable of interest in the present dissertation. Assessments of fertility based on participants' cycle phase are inherently noisy, stemming from inter- and intra-individual variation in cycle length and annovulatory cycles, among other factors (Gangestad et al., 2015), and do not permit examination of the precise hormonal mechanisms underlying observed effects. In Study 2, I divided participants' low-fertile sessions between two low-fertile phases of the menstrual cycle, the early follicular phase and the mid-luteal phase, as a way to isolate primarily estradiol- and progesterone-mediated processes. Specifically, effects of participant's fertility which emerged when comparing the early follicular to the late follicular session would suggest stronger evidence for estradiol-related processes, given the rise in estradiol across the follicular session, whereas effects which emerged when comparing the late follicular session to the mid-luteal session would suggest stronger evidence for progesterone-related processes, given the rise in progesterone levels in the mid-luteal phase, relative to the late follicular phase. I observed that participants' fertility moderated their response times to recognize fertile-phase women's neutral faces when their visual working memory was low, but decomposition of the interaction revealed significant differences in women's time to identify fertile- and non-fertile-phase as a function of participants' fertility only in the early follicular low-fertile phase of participants' menstrual cycle, and not in the mid-luteal low-fertile phase. This finding may point to a role for estradiol in discerning motivational relevance from visual cues of other women's fertility (as estradiol levels can reasonably be expected to have been higher when participants were in their late follicular phase, relative to their early follicular phase), which would be consistent with recent findings that estradiol predicts women's likelihood to choose a fertile-phase women as being more likely to steal their date (Lobmaier, Bobst, & Probst, 2016). Conversely, by increasing general sensitivity to social information in the luteal phase (Maner & Miller, 2014), progesterone may diminish specificity of vigilance to fertile-phase women. By testing women in multiple non-fertile phases of their cycles, Study 2 affords inferences about hormonal processes even in the absence of hormonal measurements, and helps derive clear predictions which can be tested in future work with hormonal assays. Study of the relation between estradiol and progesterone and women's intrasexual perceptions and behaviors can further an understanding of the broader coordinated changes that these hormones provoke.

Throughout this dissertation, I have suggested multiple ultimate and proximate mechanisms which may differentially motivate women's behavior across the menstrual cycle and modulate the motivational relevance of fertile-phase women. Most hormonally-mediated coordinated changes in physiology and behavior serve the ultimate purpose of increasing the system’s fitness. By this logic, hormonally-mediated changes in women’s intrasexual competitive behavior towards fertile-phase women across the menstrual cycle may be a necessary consequence of analogous mating-related motivations, and should serve to increase women’s likelihood of successful reproduction. However, I have not directly tested women’s mating motivations in any of the studies presented here, nor have I directly assessed any particular motivational account. Competitive behaviors towards other women across the menstrual cycle may indeed be driven by evolutionary pressures to secure access to high quality mates at a time when women are most likely to conceive. But they may also be an evolutionary vestige which is part of a broader set of hormonally-mediated behavioral processes which produce the general effect of increasing women’s intrasexual competitiveness when they are most probabilistically fertile. I suggest that particular vigilance towards other fertile-phase women may derive from learned associations between the visual cues of fertility in other women’s faces and an increased propensity to find oneself in competition with them, be it for mates or otherwise. Rather than focus on the ultimate motives guiding women’s behaviors, in the present studies, I have aimed to first establish that women are differentially vigilant to the fertility of other women, and that such vigilance varies across their menstrual cycle phases. Future research will be important for further investigating specific motivational accounts which may explain the effects observed here.

Taken together, the present studies suggest that individuals are sensitive to fluctuations in others’ hormonal states, and that their sensitivity may be heightened when their own hormonal state is congruous with their conspecifics’. The present studies demonstrate that visual features which are cues to another's biological state may convey important social information, and that the relevance of such information to observers can fluctuate in line with observers' own biological states. These results extend previous work on intrasexual vigilance in women as a function of fertility, which have demonstrated effects of either targets' or perceivers' fertility status on social outcomes, by identifying a previously unrecognized source of variance in women's perceptions of and behaviors toward other women: the congruence between perceivers' and targets' probabilistic fertility.

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Appendix E: Permission to Republish Copyrighted Materials

Chapter 1 of this dissertation has been published elsewhere and is reprinted here with permission of Elsevier. The original citation for this publication is:

Necka, E.A., Puts, D.A., Dimitroff, S.J., & Norman, G.J. (In Press). Other women's fertility moderates female resource distribution across the menstrual cycle. *Evolution and Human Behavior.* Advance online publication. doi:10.1016/j.evolhumbehav.2016.03.003

Appendix F: Supplementary Material for Chapter 1

Supplemental Methods

Stimulus Selection Procedure

Stimuli and standardized ratings of stimulus attractiveness were obtained from Puts et al., 2013. To maximize the power of our opponent fertility manipulation, we first verified which stimulus women actually demonstrated hormonal profiles indicative of high conception risk during the "late follicular" photograph session. First, we computed stimulus women's estrogen to progesterone (E:P) ratio for all stimulus women during their scheduled "late follicular" (i.e., "fertile") sessions and obtained a subset of only those women whose standardized E:P ratio was positive (that is, only stimulus women whose E:P ratio was greater than average). Next, we selected only women whose attractiveness fluctuation scores (female-rated facial attractiveness, based on ratings from Puts et al., 2013, at the scheduled "late-follicular" session minus female-rated facial attractiveness at the scheduled "luteal" session) were greater than average (i.e., standardized attractiveness fluctuation scores greater than 0). All of these women were judged to be more attractive in their "fertile" photograph, relative to their "non-fertile" photograph. Finally, because previous work has demonstrated that the presence of specifically attractive women increases consumption of appearance-enhancing products in women near peak fertility (Durante et al., 2011; Zhuang et al., 2014), we chose only stimulus women for whom female-rated attractiveness of "late-follicular" session photographs was at least one standard deviation above average to try to increase the likelihood that participants would engage in competitive tactics. From this subset, we selected Caucasian stimulus women, as this is the predominant ethnicity of our participant pool. This resulted in six stimulus women, of which we randomly chose four to use as stimuli (Table S1). This selection procedure limits generalizations from these stimuli but greatly increases our power to test the theoretical postulation that another woman's fertility (as indicated via visual cues) is capable of moderating female resource distribution across the menstrual cycle.

Determination of Fertility

Forward-counting Method. One potential limitation to our forward-counting approach to determining fertility is that early follicular and luteal phases were collapsed into a single "non-fertile" condition even though these phases are associated with different neuroendocrine profiles. There were no significant differences between the early follicular and luteal phase participants on any variables other than cycle day (p = 1.76E-37, all other ps > 0.243).

Exclusion of participants. Counting methods rely on the assumption that women exhibit normal cycle lengths. A number of publications have assessed typical cycle length and reported ranges as wide as 15-44 days (N = 2,316; Chiazze, Brayer, Macisco, Parker, & Duffy, 1968) or as narrow as 23-35 days (N = 1,526; Münster, Schmidt, & Helm, 1992). Because Chiazze et al. (1968) utilized a large sample and used prospective collection of at least ten cycles per woman, we chose to use this criterion to define regular cycle length. However, using this criterion could violate our assumption that days 10-15 are "fertile" if, for example, a woman reports a cycle length of 15 days. We had only one such participant who reported a regular cycle length of 15 days, but she participated on Day 1 of her cycle (squarely in a non-fertile phase) and including or excluding her did not change results. All other included participants reported regular cycle lengths of at least 23 days and no greater than 40 days. Using Münster et al.'s (1992) criterion of 23-35 days instead did not change results.

Twenty-two participants reported cycle lengths less than 15 days. Although instructions stated that subjects should report how many days are between the beginning of one menstrual period and the beginning of the next, and not the length of their menstrual bleeding, subjects may have accidentally reported the length of their menstrual bleeding rather than the length of their cycle. Even if this is the case, without an accurate response to this question we cannot discern whether these women regularly menstruate. Analyses were conducted on both the subset of participants who reported regular cycle lengths and on the full sample.

Follow-up Confirmation of Menses. For the 49 participants who provided the start date of their next menses (Puts, 2006), we identified cycle phase using the backward counting method. We identified reverse-count days 14-19 inclusive as “fertile”, where Day 1 corresponds with the last day before the onset of the next menstrual bleeding (e.g. the five days before and the day of ovulation). Women outside this phase were categorized as “non-fertile.” Only a small subset of participants (N = 36) met our inclusion criterion (typical cycle length between 15 and 44 days) and were categorized identically using both counting methods. Of these, only 2 fertile participants played against a fertile opponent and 5 fertile participants played against a non-fertile opponent. Although we had originally intended to analyze this subset, we did no further analyses with data regarding the start date of a participant’s next menses due to low response rate and small cell sizes.

Supplemental Results

Forward-Counting Method

Model excluding all covariates. The significant interaction between participant and opponent fertility on resource distribution in the Dictator Game maintained in a 2 (participant phase) x 2 (stimulus phase) ANOVA excluding all covariates, F(1,123)=5.37, p=0.022, η2= 0.04. No other effects were significant (ps> 0.349).

Demographic Covariates. In an ANCOVA model controlling for differences in participant age, ethnicity, education, marital status, and sexual orientation, the significant interaction between participant and opponent fertility remained significant, *F*(1,109)=5.59, *p*=0.020, η2= 0.04. Age and years of education also significantly predicted resource distribution, *F*(1,109) = 5.36, *p* = 0.022, η2= 0.04 and *F*(1,109) = 8.491, *p* = 0.004, η2= 0.06, respectively. Older participants (*B* = 0.06, *SE* = 0.02) and participants with less education (*B* = -0.17, *SE* = 0.06) gave more money to their opponents in the dictator game.

Post-hoc exploratory analyses. Including relationship status as a moderator on a model with no covariates revealed a trending three-way interaction between relationship status, participant fertility, and opponent fertility, *F*(1,119)=3.25, *p* =0.074, η2=0.03 (all other ps > 0.110). Single women exhibited a cross-over interaction similar to Figure 1.1, *F*(1,86)=7.94, *p*= 0.005, η2 = 0.01, and a trend towards a main effect of opponent fertility, *F*(1,86) = 2.81, *p* = 0.097, η2 = 0.01, but romantically involved women did not differentially allocate the cash reward as a function of either woman's fertility or the interaction, all *p*s > 0.205. Among romantically involved participants, perceptions of partner sexual attractiveness did not moderate any effects (*p*s > 0.211). However, given the post-hoc nature of these analyses, Bonferroni's correction for multiple comparisons reduces the alpha level to 0.025. At this alpha level, no effects should be considered trending towards significance.

Conception Risk

Model excluding all covariates. A significant interaction between participant conception risk and opponent fertility on resource distribution in the Dictator Game maintained, *B* = 11.44, *SE* = 5.71, *t*(123) = 2.01, *p* = 0.047. Additionally, marginally significant main effects of participant conception risk, *B* = -17.53, *SE* = 8.88, *t*(123) = -1.97, *p* = 0.051, and opponent fertility, *B* = -0.40, *SE* = 0.24, *t*(123) = -1.68, *p* = 0.096, were observed.

Demographic Covariates. In a regression model controlling for differences in participant age, ethnicity, education, marital status, and sexual orientation, the significant interaction between participant and opponent fertility remained significant, *B* = 11.95, *SE* = 5.97, *t*(109) = 2.00, *p* = 0.048. Age and years of education also significantly predicted resource distribution, *B* = .06, *SE* = .02, *t*(109) = 2.30, *p* = 0.024, and *B* = -.17, *SE* = .06, *t*(109) = -2.79, *p* = 0.006, respectively.

Analyses on full sample.

Analyses conducted on the full sample revealed the same pattern of effects observed in the subset who reported regular menstrual cycle lengths. In a 2 (participant fertility) x 2 (opponent fertility) model partialling out between-stimuli variance, a significant interaction between participant and opponent fertility emerged, *F*(1,142)=4.24, *p*=0.041, η2= 0.03, and no other main effects were significant (*p*s > 0.194). Partialling out between-stimuli variance in attractiveness instead, a marginally significant interaction between participant and opponent fertility emerged, *F*(1, 144)=3.51, *p*=.063, η2=0.02, and no other main effects emerged (*p*s > 0.193).

A model with no covariates revealed a marginally significant interaction between participant and opponent fertility, *F*(1,145) = 3.539, *p* = 0.062, η2= 0.02, and no other main effects were significant (*p*s > 0.254). In a model controlling for demographic covariates, the interaction between participant and opponent fertility was marginally significant, *F*(1,129)=3.86, *p*=0.052, η2= 0.03. As before, significant effects emerged only for age, $F(1,129) = 4.08$, $p = .045$, $\eta2 = 0.03$, and for education, $F(1,129) = 6.30$, $p = 0.013$, $\eta2 = 0.04$. No other main effects were significant (ps > .357).

Using conception risk instead as a measure of participant fertility while partialling out between-stimuli variance revealed a marginally significant interaction of participant conception risk and opponent fertility, $B = 11.61$, $SE = 5.92$, $t(142) = 1.96$, $p = 0.052$, as well as a marginally significant main effect of participant probability of conception, $B = -17.23$, $SE = 9.09$, $t(142) = -1.90$, $p = 0.060$. No other main effects emerged (ps > 0.115). Controlling instead for opponent attractiveness revealed a marginally significant interaction between participant conception risk and opponent fertility, $B = 10.19$, $SE = 5.78$, $t(144) = 1.76$, $p = 0.080$, and a marginally significant main effect of participant conception risk, $B = -15.23$, $SE = 8.90$, $t(144) = -1.71$, $p = 0.089$. No other main effects emerged (ps > 0.432). A model with no covariates revealed the same pattern of effects, including a marginally significant interaction between participant conception risk and opponent fertility, $B = 9.90$, $SE = 5.76$, $t(145) = 1.72$, $p = 0.088$, and a marginally significant main effect of participant conception risk, $B = -14.86$, $SE = 8.87$, $t(145) = -1.67$, $p = 0.096$. The main effect of opponent fertility was not significant, $p = 0.253$.

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Table S.1.1. Attractiveness of Stimuli Selected for Present Study.

Stimulus Attractiveness Scores

Stimulus	Cycle Phase		Average Attractiveness	Δ in Attractiveness
	Fertile	Non-Fertile		
A	4.07	2.80	3.44	1.27
B	4.47	4.20	4.34	0.27
C	4.60	3.13	3.87	1.47
D	4.13	3.60	3.87	0.53
Average	4.32	3.43	3.88	0.88
SD	0.26	0.61	0.37	0.57

Note: Attractiveness ratings were made on a seven-point Likert scale, with higher scores indicating greater attractiveness. Puts et al. (2013) obtained attractiveness ratings from both men and women. The ratings presented here (and used for stimulus selection) are from female raters.

Appendix G: Supplementary Materials for Chapter 2

Regression Equations for Mixed Models Reported in Chapter 2

Attentional Biases to Fertile Women

Level-1 model:

$$\begin{aligned} &\mathit{Log\ Reaction\ Time}_{ijk} \\ &= \beta_{0jk} + \beta_{1jk}\mathit{Stimulus\ Type}_{ijk} + \beta_{2jk}\mathit{Probe\ Response\ Congruency}_{ijk} \\ &+ \beta_{3jk}\mathit{Stimulus\ Location}_{ijk} + e_{ijk} \end{aligned}$$

Level-2 model:

$$\beta_{0jk} = \delta_{00k} + \delta_{01k}\mathit{Visual\ Working\ Memory\ Score}_{\ jk}$$

$$\beta_{1jk} = \delta_{10k} + \delta_{11k}\mathit{Visual\ Working\ Memory\ Score}_{jk} + u_{1jk}$$

$$\beta_{2jk} = \delta_{20k}$$

$$\beta_{3jk} = \delta_{30k}$$

Level-3 model:

$$\delta_{00k} = \gamma_{000} + v_{00k}$$

$$\delta_{01k} = \gamma_{010} + v_{01k}$$

$$\delta_{10k} = \gamma_{100}$$

$$\delta_{11k} = \gamma_{110}$$

$$\delta_{20k} = \gamma_{200}$$

$$\delta_{30k} = \gamma_{300}$$

Combined model:

$$\begin{aligned} &\mathit{Log\ Reaction\ Time}_{ijk} \\ &= \gamma_{000} + \gamma_{010}\mathit{Visual\ Working\ Memory\ Score}_{\ jk} + \gamma_{10k}\mathit{Stimulus\ Type}_{ijk} \\ &+ \gamma_{11k}\mathit{Visual\ Working\ Memory\ Score}_{jk}\mathit{Stimulus\ Type}_{ijk} \\ &+ \gamma_{20k}\mathit{Probe\ Response\ Congruency}_{ijk} + \gamma_{30k}\mathit{Stimulus\ Location}_{ijk} + v_{00k} \\ &+ v_{01k}\mathit{Visual\ Working\ Memory\ Score}_{\ jk} + u_{1jk}\mathit{Stimulus\ Type}_{ijk} + e_{ijk} \end{aligned}$$

where

$Log\ Reaction\ Time_{ijk}$ = Log Reaction Time for trial i in session j in subject k

and the effect of stimulus type is random on the level of session within subjects, the effect of visual working memory score is random within subjects, the intercept is random between subjects, and we assume no correlation between subjects' random intercept and their random slope of visual working memory score.

Note that the model was identical for congruent and incongruent trials, with one exception: for incongruent trials, the effect of stimulus type did not vary randomly on the level of session within subjects, as this model failed to converge. Therefore, a more parsimonious model which did not include a random slope of stimulus type was selected. This model successfully converged.

R code:

```
m1 <- lmer(log(RT)~StimType*DMTSScore.C + ProbeRespCong + StimLoc +
       (1|Subject) + (0 + DMTSScore|Subject) + (0+StimType|Subject:FertSess),
       data = data[data$TrialType=="Congruent"&data$ACC=="Correct",],
       na.action = na.omit, REML = T)
```

Memory Bias to Fertile Women among Fertile Women

Level-1 model:

$$Log\ Reaction\ Time_{ijkl}$$
$$= \beta_{0jkl} + \beta_{1jkl} Stimulus\ Fertility_{ijkl} + \beta_{2jkl} Comparison\ Stimlus\ Fertility_{ijkl}$$
$$+ \beta_{3jkl} Sample\ Location_{ijkl} + e_{ijkl}$$

Level-2 model:

$$\beta_{0jkl} = \delta_{00kl} + u_{0jkl}$$
$$\beta_{1jkl} = \delta_{10kl}$$
$$\beta_{2jkl} = \delta_{20kl}$$
$$\beta_{3jkl} = \delta_{30kl}$$

Level-3 model:

$$\delta_{00kl} = \gamma_{000l} + \gamma_{001l} Visual\ Working\ Memory\ Score_{00kl} + \gamma_{002l} Session\ Type_{00kl}$$
$$+ \gamma_{003l} Visual\ Working\ Memory\ Score_{00kl} Session\ Type_{00kl} + v_{00kl}$$
$$\delta_{10kl} = \gamma_{010l} + \gamma_{011l} Visual\ Working\ Memory\ Score_{00kl} + \gamma_{012l} SessionType_{00kl}$$
$$+ \gamma_{013l} Visual\ Working\ Memory\ Score_{00kl} Session\ Type_{00kl}$$
$$\delta_{20kl} = \gamma_{020l}$$
$$\delta_{30kl} = \gamma_{030l}$$

Level-4 model:

$$\gamma_{000l} = \varphi_{0000} + w_{000l}$$
$$\gamma_{003l} = \varphi_{0030} + w_{000l}$$
$$\gamma_{001l} \cdots \gamma_{030l} = \varphi_{0010} \cdots \varphi_{0300}$$

Combined model:

$$
\begin{aligned}
&Log\ Reaction\ Time_{ijk} \\
&\qquad = \varphi_{0000} + \ \varphi_{0100} Stimulus\ Fertility_{ijkl} \\
&\qquad + \ \varphi_{0010} Visual\ Working\ Memory\ Score_{00kl} \ + \varphi_{0020} Session\ Type_{00kl} \\
&\qquad + \ \varphi_{0030} Visual\ Working\ Memory\ Score_{00kl} Session\ Type_{00kl} \\
&\qquad + \ \varphi_{0110} Visual\ Working\ Memory\ Score_{00kl} Stimulus\ Fertility_{ijkl} \\
&\qquad + \ \varphi_{0120} SessionType_{00kl}\ Stimulus\ Fertility_{ijkl} \\
&\qquad + \varphi_{0130} Visual\ Working\ Memory\ Score_{00kl} Session\ Type_{00kl} Stimulus\ Fertility_{ijkl} \\
&\qquad + \ \varphi_{0200} Comparison\ Stimlus\ Fertility_{ijkl} \ + \ \varphi_{0300} Sample\ Location_{ijkl} \ + \ w_{000l} \\
&\qquad + w_{000l} Visual\ Working\ Memory\ Score_{00kl} Session\ Type_{00kl} + \ v_{00kl} + u_{0jkl} \\
&\qquad + \ e_{ijkl}
\end{aligned}
$$

where

$Log\ Reaction\ Time_{ijkl}$ = Log Reaction Time for trial *i* of stimulus *j* in session *k* in subject *l*

and the effect of the interaction between stimulus type and visual working memory is random within subjects, there are random intercepts on the level of subject, session within subject, and stimulus identity, and we assume no correlation between the random intercept and random slope on the level of subjects.

R code:

```
m2<- lmer(log(RTCorr)~StimFert*SessionType*WMC.C + CompType + SampLoc +
      (1|Subject) + (0 + SessionType:WMC.C|Subject) + (1|Subject:FertSess) +
      (1|StimID), data = data[data$StimType != "Object",], REML = T)
```