THE EFFECTS OF EXOGENOUS TESTOSTERONE AND MATING CONTEXT ON MEN'S PREFERENCES FOR FEMALE FACIAL FEMININITY

by

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Thesis submitted in partial fulfillment
of the requirement for the degree of
Master of Arts in Applied Psychology

Faculty of Graduate Studies
Laurentian University
Sudbury, Ontario, Canada

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THESIS DEFENCE COMMITTEE/COMITÉ DE SOUTENANCE DE THÈSE
Laurentian Université/Université Laurentienne
Faculty of Graduate Studies/Faculté des études supérieures

Title of Thesis Titre de la thèse	THE EFFECTS OF EXOGENOUS TESTOSTERONE AND MATING CONTEXT ON MEN'S PREFERENCES FOR FEMALE FACIAL FEMININITY
Name of Candidate Nom du candidat	Brian, Bird
Degree Diplôme	Master of Arts
Department/Program Département/Programme	Psychology
Date of Defence Date de la soutenance	June 20, 2016

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Abstract

Correlational research suggests that men show greater attraction to feminine female faces when their testosterone (T) levels are high. Men's preferences for feminine faces also seem to vary as a function of relationship context (short versus long-term). However, the relationship between T and preferences for female facial femininity has yet to be tested experimentally. This thesis examined the causal role of T in modulating preferences for facial femininity across both short and long-term mating contexts, using two separate experiments. Results of Experiment 1 (within-subject design, $n = 24$) showed that participants significantly preferred feminized versus masculinized versions of women's faces. Further, participants showed a stronger preference for feminine female faces in the short- versus the long-term context after they received T, but not after they received placebo. Post-hoc analyses suggest that this effect was driven by a lower preference for feminine faces in the long-term context when on T relative to placebo. Results from Experiment 2 (between-subject design, $n = 93$) were highly consistent with those of Experiment 1: men demonstrated a significant preference for feminized female faces in the short- versus the long-term context after T, but not after placebo administration, and this effect was driven by lower preferences for feminine faces in the long-term context when on T relative to placebo. Collectively, these findings provide the first causal evidence that T modulates men's preferences for facial femininity as a function of mating context.

Key Words: Testosterone; facial preferences; femininity; mate preferences; hormones; mating

Acknowledgements

First and foremost, I would like to thank my thesis supervisors, Dr. Justin Carré and Dr. Michael Emond. Dr. Carré, over the past several years, you have provided the foundational knowledge, the expert guidance, the medium, the opportunities, and the inspiration to make this thesis project come to life. Without your expertise in social neuroendocrinology, your steadfast dedication to research excellence, and your passion for helping students become the future's next influential researchers, I would not have been able to complete this project. Furthermore, your endless energy, creativity, and patience with the student learning process have truly afforded me the opportunities of a lifetime. Dr. Emond, similarly, you have been incredibly supportive over the journey of this thesis, providing moral support, methodological creativity, and helpful interpretation of the findings. Your prodigious attention to detail is something to aspire to. You were willing, quite early on, to collaborate between institutions, and to consider a project that involved pesky humans (versus those cooperative lab animals that do not have the capacity to talk back), and for this, I am very grateful. By the efforts of both of my incredible supervisors, I am happy to say that my journey through this thesis and my MA degree has been an absolute pleasure.

To my final committee member, Dr. Roy-Charland, and the other professors of the Psychology Department at Laurentian University (especially Dr. Joel Dickinson and Dr. Adèle Lafrance Robinson), I would like to thank you for your support through the various stages of this thesis and degree. You have been leaders within the department that I have relied on for support in a number of areas. Thank you so much for putting the students first, for believing that anything is possible, and for encouraging me to believe the same.

To the research coordinators (T. Ortiz, B. Moreau) and research assistants (B. Labine, N. Olmstead, Z. Root, E. Ruddick, S. Taylor and A. Videto) in Dr. Carré's lab at Nipissing University, thank you for your help with logistical organization and data collection.

To my family, including my Mom Sharon, my brother Steve, and my sisters Michelle and Heather, as well as my extended family, Marsha, Dave, Cari, and Carla, thank you for your incredible support throughout this process.

Lastly, to my beautiful wife, Bryanne: without your unwavering patience for the late nights of work, lengthy discussions about statistics (including being suddenly woken in the middle of the night to "see the new graphs"), full support of my life goals, and unconditional love, this project would not have been possible.

I would like to dedicate this thesis to my late father, Peter John Bird. Perhaps without realizing, he set the stage of my passion for learning about human behaviour. Undoubtedly, he would have been proud.

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CHAPTER 1: GENERAL INTRODUCTION

Introduction

Testosterone (T) is a sex hormone suggested to modulate behaviour in a number of evolutionarily-relevant domains. For instance, research in humans shows that men with higher testosterone are more likely to exhibit high status and dominance, to engage in more status seeking behaviour, or to pursue mates with greater effort (Archer, 2006; Carré, Putnam, & McCormick, 2009; Ehrenkranz, Bliss, & Sheard, 1974; Josephs, Newman, Brown, & Beer, 2006; Schaal, Tremblay, Soussigman, & Susman, 1996). Recent correlational findings implicate men's baseline testosterone levels as predictors of preferences for facial sexual dimorphism—secondary sexual characteristics influencing the degree of femininity or masculinity—in the faces of opposite sex individuals (Welling et al., 2008). However, given that testosterone can have a bi-directional relationship with behavioural outcomes (i.e., high or low T may influence behaviour, or behaviour may influence a rise or drop in T; Mazur, 2005; Mazur & Booth, 1998), the directionality of the association between T levels and preferences for facial sexual dimorphism cannot be fully understood without experimental methods. It is conceivable to think that men pursuing feminine women for short-term relationships would show acute increases in T, or that some third variable might account for noted positive correlations between T and preferences for femininity in the short-term context. To this end, the present study will use a double-blind, placebo-controlled, T-administration paradigm, in the pursuit of establishing a causal relationship between human male T levels, and their preferences for female facial femininity in short and long-term mating contexts.

Men's Preferences for Facial Femininity

In ancestral environments, determining the quality of a mate would have been crucial for avoidance of disease, and for successful reproduction (Buss, 2004). As such, it is proposed that humans have evolved cues that signal the phenotypic quality of potential mates (Arnocky, Bird, & Perilloux, 2014; Barber, 1995). For males seeking high-quality females, one such cue lies in the human face (Burriss, Marcinkowska, & Lyons, 2014; Little, Jones, & DeBruine, 2011) as it can provide information about a woman's health (Rhodes, Chan, Zebrowitz, & Simmons, 2003; Thornhill & Gangestad, 2006), and reproductive potential (Wheatley et al., 2014). Specifically, the degree to which a woman's face aligns with sex typicality (i.e., is more feminine) is thought to be one specific cue indicative of her health and/or fertility status, and may be used by men to help inform their decisions on whether to engage in sexual or romantic relationships. Feminine female faces (versus masculine female faces) are typically represented by specific features such as tall and wide eyes, full lips, small lower face area (e.g., small chin), thin eyebrows, and high cheekbones[1] (Cunningham, 1986; Cunningham et al., 1995; Johnston, 2006; Johnston & Franklin, 1993; Perrett, May, & Yoshikawa, 1994).

A large body of evidence suggests that men show a preference for women's faces that are more feminine (e.g., Cunningham, 1986; Lee et al., 2013; Little, Cohen, Jones, & Belsky, 2007; Marcinkowska et al., 2014; O'Connor, Fraccaro, Pisanski, Tigue, & Feinberg, 2013; Welling et al., 2008). For instance, in a landmark study by Perrett and colleagues (1998), advanced digital morphing techniques were used to allow the manipulation of female (and male) faces along a continuum of masculine to feminine (i.e.,

[1] See Figure 1 on page 61 for a comparison of a more feminine face versus a more masculine face of the same individual.

variation in sexual dimorphism). In part one of their study, male participants were asked to use a sliding continuum to morph a face more towards feminine or masculine, at their discretion, with the goal to stop the morphing at the point where they found the face most attractive. Results indicated that the female faces selected by male participants as most attractive were significantly feminized, and this was true for individuals rating faces of their own culture (i.e., Caucasians rating Caucasian faces), or of cross-cultural rating (i.e., Caucasians rating Japanese faces), although the effect was most pronounced among same-culture ratings. In part two of their study, facial morphs of females at 50% masculinization and 50% feminization were shown to a separate group of male participants in a forced-choice manner. Consistent with part 1, male participants selected significantly more feminized female faces as attractive than they did masculinized faces. This main finding has been replicated numerous times (e.g., Komori et al., 2009; O'Connor et al., 2013), suggesting that on the whole, men find feminized female faces more attractive than masculinized female faces.

Ubiquitous findings similar to those reported by Perrett and colleagues (1998) raise the question of why it is that men find feminine female faces attractive. Evolutionary psychologists propose that facial femininity may act as a cue to heritable fitness or other benefits, and thus may be seen as attractive to males (Perrett et al., 1998). Because facial femininity is influenced by exposure to hormones during puberty, and because estrogen may be an immunosupressing hormone to some degree, only females of the highest health status should be able to develop feminine features (Da Silva, 1999; Fink & Penton-Voak, 2002; Moore, Law Smith, Taylor, & Perrett, 2011). Indeed, research shows that women's circulating estrogen levels are positively related not only to

their feminine features, but also to judgments of attractiveness, femininity, and health, by opposite sex individuals (Law Smith et al., 2006; Röder, Fink, & Jones, 2013). Further, self-report and objective measures of health indices correlate positively with facial femininity and estrogen levels (Gray & Boothroyd, 2012; Thornhill & Gangestad, 2006; van Anders, 2010), and in cross-cultural examinations, preferences for facial femininity significantly correlate with the health of the nation, indicating that in hazardous environments, men may sacrifice fecundity for cues to resource holding potential (Marcinkowska et al., 2014). These findings align with other cultural preferences in that men migrating from resource-poor to resource-rich nations show a shift in larger body type preference to a thinner ideal (Tovée, Swami, Furnham, & Mangalparsad, 2006), suggesting that if survival is less of an immediate concern, preferences may shift towards cues of fertility. Collectively, these findings suggest that feminine female faces act as an honest signal of fertility and health status to men who are looking for high-quality mates.

If female facial femininity represents an honest and reliable cue to mate quality, it should be expected that men would prefer feminine female faces, regardless of mating context (i.e., engagement in short- or long-term partnerships). However, an emerging body of evidence suggests that the degree of attraction to femininity may actually vary as a function of strategic mating preferences that depend on these contexts (Little, Jones, Feinberg, & Perrett, 2013). Although feminine women are rated as more attractive, they are also rated as more intrasexually competitive, and more willing to engage in short-term mating relationships (Fink, Klappauf, Brewer, & Shackelford, 2014). Feminine women also become sexually active at an earlier age (Rhodes, Simsmons, & Peters, 2005), show a greater interest in unrestricted relationships (Boothroyd et al., 2008), are rated as having

lower parental suitability (Perrett et al., 1998), and are perceived as more likely to seek extra pair copulations (i.e., cheat on a partner) or be promiscuous (Brewer & Archer, 2007; Little et al., 2014). Therefore, it is not surprising that some men—typically those who perceive themselves as being attractive—prefer femininity in short-term, but not as much in the long-term relationships (Burriss, Welling, & Puts, 2011; Little, Connely, Feinberg, Jones, & Roberts, 2011; Little et al., 2014), as it may increase the likelihood of successfully reproducing with a healthy partner, while minimizing the potential for partner defection in a long-term relationship. Given that men may face uncertain paternity if a partner cheats, reducing this risk may be of increased importance for long-term relationships; therefore, somewhat less feminine women may be preferred in this context. Alternatively, preferences for femininity in short-term contexts may represent a tactic to maximize offspring phenotypic quality with mates who are likely to reciprocate sexual interest (Little et al., 2014)

Other research, however, shows contradictory findings in that facial femininity is preferred in long-term contexts, but not in short-term contexts (Cornwell et al., 2004; Fraccaro, Feinberg, DeBruine, Little, & Watkins, 2010; Jones et al., 2007). As noted in both Cornwell et al. (2004) and Fraccaro et al. (2010), the cause of the discrepancy between studies remains to be established, and further investigation is needed. Because researchers have suggested that men's variation in femininity preferences may be a function of their own testosterone levels and/or masculinity (Fraccaro et al., 2010), the present study may provide further insight into potential differences in context-dependent preferences for facial femininity by controlling men's testosterone concentrations, and by measuring femininity preferences across both short-term and long-term contexts.

Testosterone

Testosterone and human mating. Researchers argue that testosterone (T)—a widely studied sex hormone—has evolutionary relevance for human survival and sexual reproduction, and this appears to be especially true for men. For instance, research implicates baseline T, as well as acute changes in T, as a modulating factor in: human dominance and status seeking behaviour; decisions to compete with, or aggress against, same-sex individuals; resiliency to status threats; and mating behaviour—all of which have important implications for attracting mates, and fending off rivals (Archer, 2006; Carré & McCormick, 2008; Carré, Putnam, & McCormick, 2009; Caswell, Bosson, Vandello, & Sellers, 2014; Ehrenkranz, Bliss, & Sheard, 1974; Josephs, Newman, Brown, & Beer, 2006; Schaal, Tremblay, Soussignan, & Susman, 1996; Sellers, Mehta, & Josephs, 2006; Slatcher, Mehta, & Josephs, 2011).

If T is implicated in adaptive factors that theoretically lead to more successful reproduction, it should be expected that individuals higher in T would engage in, and benefit from, greater mating-related behaviours. Findings generally support this notion. For instance, in a study examining T concentrations associated with a simulated mating competition, Slatcher and colleagues (2011) found that among dominant men, levels of T were positively associated with competitive and dominance behaviours during the competition, and also a stronger belief that the participants "clicked" with the female with whom they were interacting and competing over. Correspondingly, Peters et al. (2008) measured the relationship between baseline salivary T levels and sexual history in a sample of undergraduate men. In controlling for lifestyle factors that may impact hormonal profiles, the authors found that T levels were positively and significantly

correlated with reported mating success (i.e., cumulative number of sexual partners). Similar positive associations between men's T levels, and also men's musculature (a direct result of increasing T at puberty: Griggs et al., 1989), and lifetime partners have been noted elsewhere (e.g., Frederick & Haselton, 2007; Lassek & Gaulin, 2009; Pollet, der Meij, Cobey, & Buunk, 2011). Previous findings also show that T can fortify traits associated with attractiveness and mating effort, such as the pursuit of status/social dominance (e.g., Archer, 2006) or the motivation to win a competition (Salvador, Suay, González-Bono, & Serrano, 2003). Other research examining paired (i.e., in committed and/or romantic relationships) versus non-paired (i.e., not in a committed relationship) men show differences in T levels in this predicted direction such that paired men have lower T; such findings have been shown repeatedly across both cross-sectional and longitudinal study designs (Burnham et al., 2003; Gettler, McDade, Feranil, & Kuzawa, 2011; Gray et al., 2004; Gray, Yang, & Pope, 2006). Because pair-bonding reduces the need to compete for mates, lower T levels may be a consequence, or alternatively, high T-levels may help facilitate mating for the most desirable mates. Taken together, these findings suggest that T plays a critical role in men's behaviour related to mating and reproductive success.

Testosterone and the brain. The mechanisms by which T can influence human preferences and decision-making have been the subject of investigation across multiple studies. Recent research suggests that both endogenous and exogenous T can enhance activation in brain areas that are important for emotions and associated decision-making, and particularly as related to information gleaned from human faces. One structure that appears particularly sensitive to T is the amygdala—a region rich in androgen receptors

(Rubinaw & Schmidt, 1996), and which functions to promote vigilance and arousal (Davis & Whalen, 2001). For instance, van Wingen et al. (2009) found that among healthy young women, endogenous levels of T were positively associated with amygdala activation, and for middle-aged women—with naturally lower levels of T—an administration of exogenous T rapidly increased amygdala reactivity to a level comparable to other women with naturally higher levels of circulating T. A separate study by Hermans et al. (2008) indicated that administration of exogenous T to healthy young women enhanced responsiveness to social threat (as indicated by angry facial expressions) in the amygdala, as well as the hypothalamus and orbitofrontal cortex. This latter finding has been conceptually replicated and extended in males, where Goetz and colleagues (2014) found that a single administration of T to healthy young men rapidly (within 90 minutes) increased amygdala, hypothalamic, and periaqueductal grey reactivity to angry facial expressions.

Other recent research suggests that the administration of T can induce reductions in trustworthiness evaluations from unfamiliar faces (Bos et al., 2010), and this reduction in perceived trustworthiness appears to be mediated by an increased activation in the amygdala, as well as a reduction in functional connectivity between the amygdala and the orbitofrontal cortex (Bos et al., 2012). Taken together, these findings suggest that T, at both circulating levels and following administration exogenously, can influence activation in various brain structures implicated in emotional reasoning and decision-making, which may be particularly relevant in studying the link between T and men's context-dependent preferences for opposite sex partners that vary on dimensions of facial sexual dimorphism.

Testosterone and preferences for facial femininity. Despite both the expansive literature showing T's association with mating-relevant behaviours, and that which suggests female facial femininity may represent a reliable cue to health and fertility (thus having important evolutionary implications for human mate choice and mating behaviour), surprisingly little research has explicitly examined the relationship between men's T levels and the associated preferences for female facial femininity.

A review of the extant literature revealed only one study that has directly examined how variation in men's T levels relates to their preferences for female facial femininity. In this study, Welling and colleagues (2008) transformed photos of both women and men to appear 50% more masculinized, or 50% more feminized (as was mentioned earlier in a study by Perrett and colleages in 1998), and were matched on other dimensions such as identity, skin color, and texture, in order to control for potential confounds. For their task, male participants were shown 20 pairs of male, and 20 pairs of female faces (each pair consisting of 1 masculinized, and 1 feminized version of the same individual). Next, they were asked to indicate which face they thought was more attractive, and by how much (slightly more attractive, somewhat more attractive, more attractive, or much more attractive). This task was performed twice, with two weeks between each session. Preceding each session, researchers collected a saliva sample for future analysis of hormone concentrations. After all measures were collected, participant data were split into a high T day, and a low T day. In other words, in completing the task twice, separated by two weeks, the day in which the participant had higher baseline T was deemed their "high T" day. Firstly, findings from this study showed that T concentrations were significantly higher for the "high T" day than the "low T" day, suggesting that

selecting the "high T" day and "low T" day effectively sorted the within subject T variable into meaningfully different groups. Secondly, results indicated that participants preferred the feminized female version (but not the feminized male version) significantly more often, regardless of T levels—a finding aligning with previous literature showing that men, on the whole, prefer feminine female faces. Interestingly, and most importantly, preferences for female facial femininity were significantly stronger on days where T was high, but only when rating women's faces, and not men's. As a whole, these findings provide evidence to support T's role in adaptively attuning attraction to females who may be healthy and fertile (Welling et al., 2008), and thus, would complement men's greater reproductive efforts that are associated with these higher levels in T.

The Present Study

Although studies investigating baseline T levels and facial preferences can provide important information about hormonal association with mating preferences, the correlational nature of these studies is an inherent limitation in the ability to establish relationship directionality; in other words, it is not clear whether T plays a causal role in men's shift in mating preferences, or whether these preferences for feminine faces during periods of higher T are perhaps simply a correlate of some unknown third variable. A potential solution to this directional problem may be found in manipulating human hormone concentrations via T administration—a relatively new, and potentially very fruitful, line of research (see Bos, Panksepp, Bluthé, & van Honk, 2012, for review). The discrepancy in the literature regarding preferences for femininity in short-term versus long-term mating contexts, coupled with the limited and strictly correlational research on

men's T levels in relation to their femininity preferences, calls for an experimental protocol. To this end, the present study will employ a repeated measures, double blind, placebo-controlled, T administration paradigm in order to temporarily elevate T hormone concentrations in healthy young men, and subsequently measure their preferences for facial femininity across both long- and short-term contexts. Such a design will allow causal inferences to be made, should similar associations be found.

CHAPTER 2: EXPERIMENT 1

Effects of Exogenous Testosterone and Mating Context on Men's Preferences for Female Facial Femininity

Introduction

Evidence indicates that humans prefer opposite sex faces that align with sex-typicality (i.e., men prefer feminine faces; women prefer masculine faces) for sexual relationships, where such preferences are thought to represent an adaptive strategy for securing mates with greater immunocompetence or fertility advantages (Gangestad & Scheyd, 2005; Lee et al., 2013; Little et al., 2007; Little et al., 2008; O'Connor et al., 2013; Wheatley et al., 2014). Other evidence suggests that facial preferences may also vary as a function of the perceiver's circulating hormone levels, perhaps helping to facilitate mating goals. For example, women show the greatest preferences for masculinity in men's faces when they are at peak fertility, and when their testosterone levels are high (Bobst et al., 2014; Little & Jones, 2012; Penton-Voak & Perrett, 2000; Welling et al., 2007, see Gildersleeve et al., 2014 for meta-analysis), which may function to increase offspring health through transmission of superior genes (Gangestad et al., 2004; Johnston et al., 2001).

In ancestral environments, the ability to determine the quality of a mate from physical appearance would have afforded survival or reproductive advantages to those who exploited these signals (Little et al., 2011; Little, 2014). The finding that men generally prefer feminine faces (e.g., Jones et al., 2007; Komori et al., 2009; O'Connor et al., 2013) and that facial femininity is correlated with judgments of attractiveness and health by opposite sex individuals (Law Smith et al., 2006; Röder et al., 2013) as well as certain health indices and/or estrogen levels (Gray & Boothroyd, 2012; Jones et al., 2015; Thornhill & Gangestad, 2006; van Anders, 2010), longevity (Henderson & Anglin, 2003),

and fertility (e.g., Jokela, 2009; Roberts et al., 2003) suggests that facial femininity may represent one such cue.

Recently, researchers have examined factors that map onto variability in men's preferences for facial femininity. For example, men scoring high on sensation seeking demonstrate greater preferences for feminine faces (Jones et al., 2007) and men who rate themselves as more attractive show a greater preference for femininity in short-term versus long-term mating contexts (Burriss et al., 2011). Other recent work has explored the role of men's endogenous testosterone (T) in modulating preferences for facial femininity. To the best of our knowledge, the only study that directly examined this relationship was conducted by Welling et al. (2008), whereby male participants entered the lab on two separate occasions for a facial preferences task, and provided saliva samples for the assessment of T. Each day, participants were asked to rate pairs of masculinized and feminized faces (1 masculinized and 1 feminized per pair) for their degree of attractiveness. Results showed that attractiveness ratings for the feminine female faces (but not feminine male faces) were highest on the day in which the participants had higher basal T-levels, suggesting that men may be more attracted to females who signal greater health or fertility when T-levels are high relative to low. One other study tacitly suggests that men's facial femininity preferences vary as a function of their T-levels: Welling et al. (2013) examined men's facial preferences following a competitive interaction, whereby participants were assigned to win or lose a first-person shooter video game against an unseen male confederate. Results revealed that winners showed an overall greater preference for feminine faces relative to losers. Additionally, for winners, femininity preferences in the short-term context were significantly higher

than for the long-term context, whereas this difference was not present among losers. Because T-levels typically rise in winners relative to losers (e.g., Archer, 2006; Carré & Olmstead, 2015), stronger preferences in winners may have been mediated by changes in their T-levels (Welling et al., 2013).

Effective mating strategies are also argued to depend on relationship context. Feminine women are rated as more attractive, more intrasexually competitive, and more willing to engage in short-term mating (Fink et al., 2014). Furthermore, they show a greater interest in unrestricted sexual relationships (Boothroyd et al., 2008), are perceived as more promiscuous (Brewer & Archer, 2007; Little et al., 2013) and as more likely to seek extra-pair copulations (i.e., cheat on a partner). Thus, differential preferences for feminine women across mating contexts (e.g., Burriss et al., 2011; Little et al., 2011; Little et al., 2013) may represent a trade-off between the likelihood of successfully reproducing with a healthy, feminine partner in a short-term relationship, while avoiding the potential for partner defection in a long-term relationship. However, the extent to which T-levels influence men's shifts in preferences for facial femininity across mating contexts remains untested.

Although studies investigating basal T-levels and facial preferences can provide important information about hormonal associations with mating preferences, the correlational nature of these studies eliminates the possibility of establishing causal relationships. This problem can be overcome by manipulating T levels via pharmacological challenge—a rapidly emerging line of research (reviewed in Bos et al., 2012). Evidence for varied partner preferences across mating contexts, coupled with the limited and strictly correlational research on men's T levels in relation to their femininity

preferences, calls for an experimental protocol. Thus, the present paper employed 2 experiments (Experiment 1: within-subjects; Experiment 2: between-subjects) in double blind, placebo-controlled T-administration paradigms, in order to temporarily elevate T-concentrations in healthy young men, and subsequently measure their preferences for female facial femininity across both short- and long-term mating contexts. Based on previously reviewed work suggesting that feminine faces are associated with judgments of health and fertility (e.g., Law Smith et al., 2006; Röder et al., 2013), as well as other work showing that T-levels are positively associated with mating success (e.g., Peters et al., 2008), and heightened attraction to feminine faces (Welling et al., 2008), men in the present experiments were expected to demonstrate a heightened preference for feminized female faces following T-administration, compared to the placebo condition. Additionally, the preference for feminine female faces in the T condition was expected to be more pronounced for contexts relating to short-term, rather than long-term relationships (Burris et al., 2011; Little et al., 2011; 2013), in light of the potential trade-off between attraction to a healthy and fertile partner who is willing to engage in short-term mating (i.e., more feminine face), and a faithful long-term partner who potentially poses less risk for partner defection (i.e., less feminine face).

Experiment 1

Methods

Participants. Our sample consisted of 30 healthy young men between the ages of 18 and 35 (M_{Age} = 21.21, SD = 2.19) who were part of a larger T-administration protocol at Nipissing University (n = 28 Caucasian, n = 1 Latin American, n = 1 First Nations/Aboriginal). Prior to enrolment in the study, each prospective participant was interviewed to determine his eligibility. Exclusion criteria for participants included the following: receiving prescription medication affecting hormone concentrations; taking performance enhancing substances; current diagnosis of a psychiatric disorder; diagnosed heart condition; and membership on a sports team or organization where T was a banned substance. Participants who qualified for the protocol consented to providing blood samples for future hormonal assay, as well as to having their T-levels temporarily manipulated. The study was approved by the Nipissing University Research Ethics Board under protocol #140609, and each participant provided informed consent prior to the commencement of the protocol. Because of the inherently heterosexual nature of this protocol (i.e., rating opposite sex faces for partner attractiveness), non-heterosexual participants were removed prior to analysis (n = 2). Finally, data for 4 participants were lost due to computer malfunction. Thus, our final sample size for analyses was n = 24.

Stimuli. In line with previous work investigating sexually-dimorphic face preferences (DeBruine et al., 2006; Jones et al., 2007; Welling et al., 2007, 2008, 2013), the present study used prototype-based image transformations in order to objectively manipulate sexual dimorphism of 2D shape in facial images, creating masculinized and feminized images of the same individual that are matched for other variables (e.g., skin

color, identity, texture: Rowland & Perrett, 1995). Briefly, prototype images (i.e., an average male face and an average female face) were created by averaging a group of male and a group of female images via widely-used computational methods in face perception studies (e.g., Jones et al., 2005; Penton-Voak et al., 1999; Welling et al., 2007). Once prototypes are established, individual stimuli are created by adding or subtracting a percentage of the differences in position between the prototype images from the corresponding points on a third face (for technical details see Rowland & Perrett, 1995; Tiddeman, Burt, & Perrett, 2001).

For the present study, 50% of the linear differences in 2D shape between symmetrized male and female prototypes were either added or subtracted from 20 young Caucasian female adults (M_{AGE} = 20.52 year, SD = 2.78), creating 40 images (i.e., 20 pairs, with each pair including one masculinized and one feminized version of the same individual). The resulting images were subjected to a manipulation check in previous work, and were rated by an independent group of observers as representing ecologically valid representations of feminine or masculine faces (Welling et al., 2007, 2008). See Figure 1 for an example of masculinized and feminized stimuli.

Procedure. Testing for the full protocol occurred across three separate days. Day 1 involved familiarizing participants with the experimental procedures, obtaining informed consent, as well as the administration of a number of self-report questionnaires as part of the larger protocol. Day 1 took approximately 1 hour to complete.

***Hormone and placebo administration*.** On day 2 of testing, a registered nurse drew 10 mL of blood from the antecubital area of the right arm. Next, participants either received 150 mg of AndroGel®—a topical gel commonly used for hypogonadal men—or

equivalent placebo (counter-balanced across participants). AndroGel® or placebo was applied to both upper arm and shoulder areas by a male research assistant blind to the drug condition (application site established based on the recommendations provided by AndroGel®). Additionally, blood samples were drawn at 60 and 120 min post drug administration, alternating between the right and left arms. After 120 min, participants then performed a series of computer-based tasks assessing social perception, cognition, and decision-making abilities over approximately two hours. Assessment of face preferences occurred approximately 3 h 15 min after gel application (M = 191.25 min, SD = 5.7 min). We chose this time-course for the assessment of face preferences as previous pharmacokinetic work indicates that T concentrations begin to rise 2 hours after gel application and peak concentrations occur 3 hours after application (Eisenegger et al., 2013). Moreover, recent evidence suggests that a single administration of T can rapidly (within 45 to 90 min) modulate brain function (see Goetz et al., 2014; van Wingen et al., 2008). Day 3 took place two weeks following Day 2 and was identical in nature to Day 2 described above, with the exception that participants received whichever drug they did not receive on their original testing day (AndroGel® or placebo). At the conclusion of Day 3 of testing, participants were asked whether they believed they received testosterone on the 2nd or 3rd day of testing. A binomial test indicated that participants were no better than chance at guessing which day they received testosterone (p = .10).

Prior to the facial femininity task, participants completed other tasks for hypotheses unrelated to the present study. These tasks included the Reading the Mind in the Eyes Task (Carré et al., 2015), 'Pick Your Own Face Task' (Welling et al., 2016), risk-

preference task, moral decision-making task (Arnocky et al., 2016), emotion recognition task, and selective visual attention tasks (inhibition of return)[2]

Face preferences task. Participants rated 20 pairs of female faces (each pair with one masculinized and one feminized version of the same individual) twice: once for attractiveness as a short-term partner, and once for attractiveness as a long-term partner. The 20 pairs were all rated for one context before moving on to the other. Randomization was used for each variable, including the order of context, the order of stimuli, and the side of the screen on which the masculine or feminine version of each pair was presented. Verbal instructions for each participant were as follows:

> "This task requires you to rate 20 pairs of faces for their attractiveness as a long- or short-term relationship. It's important that you understand what we mean by each, so please listen to these definitions. **Short-term relationship**: you are looking for the type of person that would be attractive in a short-term relationship. This implies that the relationship may not last a long time. Examples of this type of relationship would include a single date accepted on the spur of the moment, an affair within a long-term relationship, or a one-night stand. **Long-term relationship:** you are looking for the type of person that would be attractive in a long-term relationship. Examples of this type of relationship would include someone you may want to move in with, someone you may consider leaving a current partner to be with, or someone you may wish to marry (or enter a relationship on similar grounds as marriage). For each preference task, try not to think too long and hard about which face you're going to choose. We are most interested in your first impressions. The image pairs look very similar, but

[2] Statistically controlling for performance on these other measures did not alter the significance of any results.

they are subtly different. You will get one practice trial, and then you will proceed to the main rating task. Please read the instructions carefully on the screen at the beginning of the task prior to beginning. Do you have any questions?"

Following verbal instructions, participants could begin the task. Instructions on the screen prior to the first trial were as follows: "**Short-term relationship:** You will see 20 pairs of facial photographs of women. Please choose which of the two photographs you feel is most ATTRACTIVE for a SHORT-TERM RELATIONSHIP by clicking on the face you prefer. A short-term relationship refers to an uncommitted, purely sexual relationship such as a one-night stand." OR "**Long-term relationship:** You will see 20 pairs of facial photographs of women. Please choose which of the two photographs you feel is most ATTRACTIVE for a LONG-TERM RELATIONSHIP clicking on the face you prefer. A long-term relationship refers to a committed relationship, such as marriage."

Initial Processing of Data

Hormone assays. Blood samples were assayed for total-T concentrations using commercially-available enzyme immunoassay kits (DRG International). As standard procedure, all samples were assayed in duplicate, and the average of the duplicates were recorded for statistical analyses. The intra- and inter-assay coefficients of variation were 4.19% and 5.34%, respectively. The analytical sensitivity of the testosterone assay is .085 ng/mL.

Face preferences. For each participant, the number of trials in which the more feminine face from each pair was chosen, was calculated for each context (short- term vs. long- term) and drug (testosterone vs. placebo).

Results and Discussion

Testosterone Concentrations

A 3-Time by 2-Drug repeated-measures ANOVA on T-concentrations was performed [within-subject factors: Time (baseline vs. 60 min vs. 120 min) and Drug (Testosterone vs. Placebo)]. Results revealed main effects of Drug [$F(1, 23) = 29.44$, $p < .001$, $\eta^2_G = .20$][3] and Time [$F(2, 46) = 42.09$, $p < .001$, $\eta^2_G = .19$]. These main effects were qualified by a significant Drug by Time interaction [$F(2, 46) = 36.13$, $p < .001$, $\eta^2_G = .11$]. Post-hoc analyses indicated that T-concentrations were higher after Androgel® compared to placebo at 60 minutes post gel application [$t(23) = 5.38$, $p < .001$, Cohen's $D = 1.17$] and 120 post gel application [$t(23) = 6.94$, $p < .001$, Cohen's $D = 1.42$]. Overall, participants in the AndroGel® condition experienced an average increase of 56.39% in T from baseline to 120 mins. There were no differences in T-concentrations for Androgel® versus placebo prior to gel application [$t(23) = -.05$, $p = .96$] (See Figure 2).

Femininity Preferences

One sample *t*-tests comparing the number of times the feminine versions of the female faces were chosen against the chance value of 10 revealed that participants chose the feminine face as more attractive across both drugs (T-Day = Testosterone Day, P-Day = Placebo Day) and contexts: T-Day/Short-term [$t(23) = 10.39$, $p < .001$], T-Day/Long-term [$t(23) = 5.05$, $p < .001$], P-Day/Short-term [$t(23) = 12.31$, $p < .001$], P-Day/Long-term [$t(23) = 10.32$, $p < .001$].

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[3] Eta-squared (η^2) and partial eta-squared (η^2_p) are not particularly well suited for making comparisons across studies with different designs (e.g., within-subject design vs. between-subject design; Fritz, Morris & Richler, 2012). The generalized eta-squared (η^2_G) is a more appropriate measure of effect size for repeated measures and/or mixed factor designs and when one wishes to compare effect sizes across different experimental designs (Olejnik & Algina, 2003; Bakeman, 2005). Thus, we report η^2_G as an estimate of effect size for ANOVAs. We also report Cohen's *D* (Cohen, 1988) for simple group comparisons (paired sample t-tests and independent sample t-tests).

A 2-Drug by 2-Context by 2-Order of Drug Administration mixed ANOVA [within-subject factors: Drug (Testosterone vs. Placebo); Context (Short-Term vs. Long-Term); between-subject factor: Order of Drug Administration (T then P vs. P then T)] was conducted to test for differences in the frequency of trials in which the feminine face was selected as more attractive as a function of context and drug condition, and whether the order in which the drug was administered influenced the pattern of findings. Results revealed a main effect for Context [F (1, 22) = 7.21, p = .01, η^2_G = .04]. There was no main effect of drug condition [F(1, 22) = 2.88, p = .10, η^2_G = .017] or Order of Drug Administration [[F(1, 22) < .01, p = .99, η^2_G <.001]. However, there was a significant Drug by Context interaction [F(1, 22) = 5.28, p = .031, η^2_G = .013]; see Figure 3. Unexpectedly, we also observed a significant Drug by Context by Order of Drug Administration interaction [F(1, 22) = 14.01, p = .001, η^2_G = .033]. Analyses split by order of drug administration indicated that the Drug by Context interaction was specific to those receiving P on the first test session and T on the second test session [F(1, 11) = 13.32, p = .004, η^2_G = .17)]. Specifically, there was a stronger preference for facial femininity in the short-term mating context versus long-term mating context after T [t(11) = 3.54, p = .005, Cohen's D = 1.11), but not P (t(11) = -.12, p = .91, Cohen's D = -.03]. This effect was driven by a weaker preference for facial femininity in the long-term mating context for T (M = 13.50, SE = 1.27) relative to P (M = 16.75, SE = .85; t(11) = -2.81, p = .017, Cohen's D = -1.27). There was no Drug by Context interaction among those who received T on the first test session and P on the second test session [F(1, 11) = 1.66, p = .22, η^2_G = .01)]. See Figure 4. There was no Drug by Context interaction among

those who received T on the first session and P on the second session [$F(1, 11) = 1.66$, $p = .22$, $\eta^2_G = .01$)]. See Figures 4A and 4B.

Results of Experiment 1 indicate that 1) regardless of mating context, participants preferred feminine female faces significantly more than masculine female faces; 2) preferences for feminine female faces were significantly higher in the short-term context than the long-term context; 3) this effect was particularly robust after T administration; and 4) the effect of T on preferences for facial femininity in short-term versus long-term mating contexts was exclusively found among men who received P on the first test session, and T on the second test session.

Rationale For Experiment 2

Although there are considerable strengths associated with within-subject designs (e.g., increased power of having participants serve as their own control), there are also limitations, such as the Order of Drug Administration by Drug by Context interaction observed in the current study. The order effect was unexpected and is difficult to interpret in light of the relatively small sample size (n = 12 per order) and the absence of *a priori* hypotheses concerning the potential role of order of drug administration in modulating preferences for facial femininity. To address this limitation, we employed a second experiment using a between-subjects design to examine the extent to which the Drug x Context interaction is robust, while at the same time ruling out any potential order effects. Another limitation of Experiment 1 was that we did not take a blood sample directly before the facial femininity task. We based our timing of behavioral assessment on previous research indicating that a single 150 mg dose of Androgel® led to increased T

concentrations in healthy young men for up to 7 hours after drug administration (Eisenegger et al., 2013). Nevertheless, results from Experiment 1 indicate that T concentrations peaked more rapidly compared to previous work (60 mins vs. 180 mins; Eisenegger et al., 2013). In Experiment 2, we collected additional blood samples throughout the protocol, including a final blood draw immediately prior to the facial rating task to verify that blood serum levels remained significantly elevated directly before testing.

CHAPTER 3: EXPERIMENT 2

Experiment 2

Methods

Participants. Our sample consisted of 120 healthy young men between the ages of 18 and 35 (*Mage* = 25.27 years, *SD* = 4.98) who were part of a larger T-administration protocol run at a medical research facility in Sudbury, Ontario. Subjects were recruited from advertising on local media sites, through medical research participant databases, as well as through local colleges and universities. Prior to enrolment in the study, each prospective participant was interviewed to determine his eligibility. Exclusionary criteria were identical to Experiment 1. Participant ethnicities were self-reported as follows: 77.5% Caucasian, 13.1% First Nations/Aboriginal, 4.1% Asian, 1.7% Latin American, and 3.3% Other. Each participant provided informed consent prior to the commencement of the protocol. Because of the inherently heterosexual nature of this protocol (i.e., rating opposite sex faces for partner attractiveness), non-heterosexual participants were removed prior to analysis (n = 11). Additionally, individuals were removed who had femininity ratings more than 3.5 standard deviations below the mean (n = 2), did not complete the task (n = 3), or only rated faces for one of the two contexts (n = 11). Therefore, the final sample size for the present study was 93 (T n = 48; Placebo n = 45).

Stimuli

The feminine and masculine pairs were identical to those used in Experiment 1. The order of presentation of the stimuli and screen-side of presentation were randomized in a similar manner to that used in Experiment 1.

Procedure

Testing for the full protocol occurred in a single session. Participants reported to the laboratory at either 10:00am or 1:00pm. Upon arrival, participants completed informed consent and had the opportunity to ask any additional questions about the study. Following this introduction, participants completed a battery of online self-report questionnaires that were used for testing hypotheses unrelated to the present study.

Hormone and placebo administration. After the completion of the online questionnaires, participants received their initial blood draw, where one of two phlebotomists drew 10 mL of blood. This draw and subsequent blood samples were allowed to clot and then were centrifuged at 3000 rpm, after which serum samples were extracted and then stored in -60°C refrigeration until assayed. Next, participants were randomly assigned to one of two experimental conditions: 150 mg of AndroGel®, or equivalent placebo. Drug condition (AndroGel® or placebo) was fully randomized across participants. Regardless of drug condition, a male research assistant who was blind to the experimental condition applied topical gel to the upper arm and shoulder area. After gel application, participants rested for 1 hour, after which they received their second blood draw, and then performed a series of computer-based tasks assessing social perception, cognition, and decision-making abilities over approximately a one-hour span. The third and fourth blood draws were spread out over the rest of the protocol, with the final blood draw occurring directly before the facial femininity task that occurred at approximately 2 hours and 15 minutes post drug administration (M = 133.03 min, SD = 10.38 min). At the end of the protocol, participants were asked if they thought they had received T or

placebo. A binomial test indicated that participants were precisely at chance level (p = 1.0) for correctly identifying whether or not they had received T.

Prior to the facial femininity task, participants completed other tasks for hypotheses unrelated to the present study. These tasks included the 'Pick Your Own Face' task (Welling et al., 2016), Point Subtraction Aggression Paradigm (Carré et al., in press), Balloon Analogue Risk Taking task, a risk-preference task, and an emotion recognition task[4]

Facial preferences task. The tasks and instructions were identical in nature to those reported in Experiment 1. Briefly, participants rated 20 pairs of female faces (each pair with one masculinized and one feminized version of the same individual) twice: once for attractiveness as a short-term partner, and once for attractiveness as a long-term partner. Twenty pairs were all rated for one relationship context before moving on to the other context. As with Experiment 1, each variable was randomized, including the order of context, the order of stimuli, and the side of the screen on which the masculine or feminine version of each pair was presented.

Initial Processing of Data

Hormone Assays. Using commercially-available enzyme immunoassay kits (DRG International), blood serum samples were assayed for total T concentrations. All samples were assayed in duplicate, with the average of the duplicates being recorded for statistical analyses. The intra- and inter-assay coefficients of variation were 7.38% and 16.03%, respectively. The analytical sensitivity of the testosterone assay is .085 ng/mL.

[4] Statistically controlling for performance on these other measures did not alter the significance of any of the results.

Face preferences. As in Experiment 1, the number of trials in which the more feminine face from each pair was selected as attractive was calculated for each relationship context (short-term and long-term) and each experimental drug condition (T or placebo).

Results and Discussion

Testosterone Concentrations

A 4-Time by 2-Drug mixed-measures ANOVA on T-concentrations was performed **[**within subject factor: Time; between subject factor: Drug]. Results revealed main effects of Drug [$F(1,91) = 16.85$ $p < .001$, $\eta^2_G = .13$] and Time [$F(3, 273) = 30.80$, $p < .001$, $\eta^2_G = .06$]. These main effects were qualified by a significant Drug by Time interaction [$F(3, 273 = 21.55$, $p < .001$, $\eta^2_G = .04$]. Post-hoc analyses indicated that T concentrations were higher after Androgel® compared to placebo at blood sample 2 [$t(91) = 4.63$, $p < .001$, Cohen's $D = .97$], blood sample 3 [$t(91) = 4.59$, $p < .001$, Cohen's $D = .96$], and blood sample 4 [$t(91) = 4.36$, $p < .001$, Cohen's $D = .91$]. Importantly, blood sample 4 occurred directly before the femininity preferences task in order to confirm that blood serum T levels were in fact elevated prior to completing the task. Overall, participants in the AndroGel® condition experienced an average increase in T of 52.61% from baseline to 180 mins after administration, which is a relatively large effect size (Cohen's $D = 1.27$). As expected, there were no differences in T concentrations for Androgel® versus placebo prior to gel application [$t(91) = .52$, $p = .60$, Cohen's $D = .11$] (See Figure 5).

Femininity Preferences

One sample t-tests comparing the number of times the feminine versions of the female faces were chosen against the chance value of 10 revealed that participants chose the feminine face as more attractive across both drugs and contexts [T/Short-term ($t(47) = 17.74$, $p < .001$), T/Long-term ($t(44) = 11.64$, $p < .001$), P/Short-term ($t(44) = 14.01$, $p < .001$), P/Long-term ($t(44) = 14.28$, $p < .001$)].

A 2-Drug by 2-Context mixed measures ANOVA [between-subject factor: Drug (T versus Placebo); within-subject factor: Context (Short-Term versus Long-Term)] was conducted to test for differences in the number of trials in which the feminine face was selected as more attractive, as a function of drug and relationship context. Results revealed no main effect of Drug [$F(1, 91) = 1.48$, $p = .228$, $\eta^2_G = .014$], but a main effect of Context [$F(1, 91) = 4.48$, $p = .037$, $\eta^2_G = .007$], whereby participants demonstrated a stronger preference for feminine faces in the short-term relative to long-term mating context. This main effect was qualified by a significant Drug x Context interaction [$F(1, 91) = 9.89$, $p = .002$, $\eta^2_G = .014$]. Post-hoc analyses revealed that after T, participants showed a significantly higher preference for facial femininity in the short-term ($M = 16.77$, $SE = .43$) versus the long-term context ($M = 15.52$, $SE = .48$; $t(91) = 3.78$, $p < .001$, Cohen's $D = .49$). In contrast, participants in the placebo condition did not show a stronger preference for facial femininity in the short-term ($M = 16.76$, $SE = .44$) versus the long-term context ($M = 17.00$, $SE = .49$; $t(91) = .71$, $p = .48$, Cohen's $D = -.13$). Further analyses indicated that participants receiving T demonstrated a weaker preference for facial femininity in the long-term context ($M = 15.46$, $SE = .46$) compared to participants receiving placebo ($M = 17.00$, $SE = .49$; $t(91) = 2.18$, $p = .033$, Cohen's $D = -$

.46). In contrast, there was no difference in preference for facial femininity in the short-term after T relative to placebo [$t(91) = .03$, $p = .98$, Cohen's $D = .01$] (See Figure 6).

Results of Experiment 2 are remarkably similar to those reported in Experiment 1. Specifically, participants who received T significantly preferred feminine faces more in the short-term relative to the long-term context. Also, as in Experiment 1, this effect was driven by a lower preference for feminine faces in the long-term context. The finding that results from the second experiment—employing a between-subject design—are highly consistent with those from Experiment 1 (within-subject design) suggests that the initial effects found are not simply an artifact of order effects, but rather, are likely to be representative of true effects that would be found in the population.

In the next chapter, I provide a general discussion of findings from both experiments, explore similarities and differences to previous work, offer potential interpretations of the pattern of results, discuss limitations of the research, and suggest avenues for future explorations.

CHAPTER 4: GENERAL DISCUSSION

General Discussion

The experiments presented in Chapters 2 and 3 are the first to test the causal effects of exogenous T on men's preferences for facial femininity across both short- and long-term mating contexts. In both Experiment 1 and 2, initial face preference analyses suggested that regardless of short- or long-term mating context, participants preferred the feminine faces more than the masculine faces—an effect that aligns with previous findings showing that men indeed show a preference for feminine female faces versus masculine female faces (e.g., Jones et al., 2007; Welling et al., 2008, 2013). For the main analyses, results revealed that participants showed a weaker preference for feminine female faces in the long-term context versus the short-term context after T relative to placebo.

Although participants on T preferred feminine faces more in the short- than the long-term mating context, this effect appears to be driven by a smaller preference for feminine faces in the long-term context. This somewhat surprising finding requires consideration of a number of factors for interpretation. Given that T may increase interest in uncommitted sex (e.g., Puts et al., 2015), it is possible that an acute rise in T makes men less attuned to women in committed, long-term contexts, and thus women's characteristics in this context could be less salient. In other words, the smaller preferences for feminine faces in the long-term context by men who received T could represent a lower level of general *interest* in long-term mating, rather than a lower preference for femininity, per se. Should this be the case, it might be expected that men's preferences for feminine faces would be closer to chance level (i.e., 10 out of 20 faces) in the long-

term when they had received T; although femininity preferences in this case were indeed closer to chance, the results of one sample t-tests confirmed that the preferences for feminine faces were still *significantly* above chance, so this explanation may not tell the whole story.

Another possibility for the pattern of results is the presence of ceiling effects. Should participants have been given a greater range of morph percentages to rate (e.g., 15% feminized, 30% feminized), results might have shown that men receiving T preferred feminine faces significantly more so in the short-term versus the long-term context, but also significantly more so than preferences identified for either context when on placebo. In other words, if there are indeed ceiling effects present, the results found in the present study might actually be underestimated.

A third, but much more speculative possibility, is that T influences sensitivity to infidelity cues. Recent investigations have shown that near peak fertility, women's faces are not only rated as more attractive by observers, but are also characteristically more feminine in appearance (Oberzaucher et al., 2012; Puts et al., 2013; Roberts et al., 2004). Feminine female faces, both as composites and real faces, are accurately rated by men as having a more unrestricted sociosexuality (i.e., more likely to pursue short-term relationships; Boothroyd et al., 2011; Boothroyd et al., 2008; but see Campbell et al., 2009), and near ovulation, some women report a greater sex drive, as well as interest in, or fantasy about, extra-pair partners (Gangestad et al., 2002; Gangestad et al., 2010; Haselton & Gangestad, 2006; see Gangestad & Thornhill, 2008, for review). Further, men show an increase in jealous mate-guarding for women near ovulation (Gangestad et al., 2002), which is of evolutionary importance, given that ovulation reflects a period in

which a man's reproductive probability may be compromised by partner defection (Buss & Haselton, 2005). Although speculative, when considered in the context of this evidence, the present findings that men on T show a significantly greater preference for feminine female faces in the short-term versus long-term contexts (but no difference in context preference when on placebo) could suggest the possibility that T may increase men's sensitivity to infidelity cues, perhaps triggering careful decision-making regarding the trade-off between a healthy partner with good genes (i.e., feminine faces), and personality/potential for defection (i.e., a more masculine face offering reduced likelihood of cheating) when it comes to selecting a long-term mate. The present design did not allow a direct test of this hypothesis, so this remains entirely speculative as one of many possibilities for the pattern observed. Future research will be needed to ascertain whether men's perceptions of putative signals of infidelity risk vary as a function of their own T levels, and whether any such effects are predictive of men's preferences for feminine facial femininity. Moreover, any such hypothesis would need to be contrasted with other likely alternatives, such as men on T feeling more interest in short-term mating, and as such, less interest in long-term mating.

Of note is that the effects of Experiment 2 are highly consistent with those of Experiment 1, despite measurement occurring 1 hour earlier in Experiment 2 (Experiment 2 = ~2h15min post gel application versus Experiment 1 = ~3h15 min post gel application). Previous T administration studies have assessed behaviour around 3 to 4 hours following T administration (see Bos et al., 2013, for review). However, the current findings indicate that assessment of behaviour at 2 hours or 3 hours post T administration yields similar results. Thus, it appears that T may exert relatively rapid effects on face

perception within men. Whether assessment of behaviour at earlier time points (e.g., 1 hour post administration) would reveal similar findings is an important question for future investigations. Research in animal models indicates that T can exert rapid, likely non-genomic effects on brain function and behaviour (reviewed in Foradori, Weiser, & Handa, 2008), and therefore, the presence of face preference effects in humans earlier than 2 hours post administration is a possibility for investigation. Correlational evidence indicates that rapid changes in endogenous testosterone following a competitive interaction (measured approximately 15 minutes post task) map onto future behaviour such as aggression and risk-taking (reviewed in Carré & Olmstead, 2015) and recent T administration protocols show effects of Androgel® on aggression within 60 minutes of administration (Carré et al., under review).

The present findings show both similarities and differences to previous work. For instance, Welling et al. (2013) found that following a video game contest in which the outcome was unknowingly predetermined, winners (but not losers) showed significantly greater facial femininity preferences in the short-term versus the long-term contexts. As previously mentioned, there is evidence that winners of competitions experience a rise in T relative to losers (Archer, 2006; Carré & Olmstead, 2015). Although not directly tested, if the findings in Welling et al. (2013) were mediated by competition-induced T dynamics, then the present finding that feminine face preference was significantly higher in the short- versus the long-term context when participants were on T (but not placebo) aligns with their findings. However, the present study differs from Welling et al. (2013) in that there was no difference between short-term femininity preferences on T Day, relative to short-term femininity preferences on placebo day. One potential explanation

for this apparent discrepancy is that those winning the competition in Welling et al. (2013) may have not only experienced increased T levels, but may have also experienced increased perceptions of their own attractiveness or masculinity/dominance (Welling et al., 2013; Welling et al., 2016)—factors implicated in men's mating success (e.g., Rhodes et al., 2005). Indeed, recent evidence suggests that competition outcome can modulate self-perceptions on sexually-relevant dimensions (e.g., dominance: Watkins & Jones, 2012).

Welling et al. (2008) found that across two separate testing days, men showed greater preference for feminized versus masculinized faces on the day in which the men's T levels were higher. However, this study did not account for mating context (short- or long-term), which has since been shown to be an important consideration for men's facial preferences (e.g., Welling et al., 2013), and thus may partially account for the discussed differences. The present study provides further evidence to suggest that mating context is an important consideration for mate preference research—particularly with respect to hormonal influences—and thus should also be considered, where possible, in future studies.

Limitations and Future Directions

A number of important limitations to this study should be noted. Consistent with previous research, this study used a forced-choice paradigm whereby participants chose either a masculinized or a feminized version of a woman's face as their preference for either a short- or long-term partner. However, it is conceivable that some participants would prefer neither face if given the choice. The option to select neither face could provide more insight into the potential for T to reduce general interest for mating in long-

term contexts (e.g., if participants on T more often than not selected “neither” as their preference rather than a lower preference for femininity, it would provide some support for the view that T decreases general interest in long-term mating). In a similar respect, participants were not asked any questions about motivation for short- or long-term relationships, or given other tasks that address the broader topic of sexual motivation. To establish the mechanisms underlying the effects of the present study, future investigations will need to employ a wider variety of tasks, including those that measure participant interest and motivation to engage in each type of mating (short- or long-term partnerships), in addition to their preferences for facial femininity across these contexts.

Although Experiment 1 had a relatively small sample size, it was largely consistent with those used in previous single T-administration studies conducted in women examining effects on social, cognitive, and behavioural processes. For example, a recent review by Bos et al. (2013) showed that with the exception of one study with a relatively large sample size (Eisenegger et al., 2010; N = 121), previous T-administration studies have had an average of 18 participants, with a modal sample size of 16. Thus, the sample size and within-subject design in Experiment 1 made it a relatively powerful test of intra-individual variation in facial preferences. Experiment 2 bolstered these findings using a between-subjects design with a larger sample size of 93 men. It is possible that individual difference factors (e.g., personality traits) may play a role in the differences noted between the present research and previous findings. However, the inclusion of each potential moderator reduces statistical power (Hayes, 2013), which precluded the testing of further moderators with the sample sizes from the present study. Future T-administration studies may consider larger sample sizes in order to examine the extent to

which individual difference factors moderate effects of T on preferences for facial femininity. For instance, previous work indicates that people scoring relatively high on sensation seeking demonstrate greater preferences for feminine faces (Jones et al., 2007). Similarly, males rating themselves relatively high on attractiveness also demonstrate a stronger preference for feminine faces (Burriss et al., 2011). Therefore, T may have a strong effect on preferences for female facial femininity, but this may be reserved for those individuals who perceive themselves to be highly attractive, or who are high in trait levels of sensation seeking.

Future research employing substantial sample sizes might also consider the potential modulation effects of genetic variation. For instance, the trinucleotide CAG repeat polymorphism in the first exon of the androgen receptor (AR) gene could potentially play a role in T's influence on facial preferences. AR sensitivity appears to be negatively correlated with the length of CAG repeats, and as such, should produce larger phenotypic effects of androgens among those with relatively shorter CAG repeat lengths (Chamberlain et al., 1994; Choong et al., 1996). Indeed, recent evidence suggests that basal T concentrations are positively correlated with aggressive and non-aggressive risk-taking behaviour, but only among individuals with short CAG repeats (Vermeersch et al., 2008). Furthermore, positive correlations between T and impulsivity are only found among individuals with shorter CAG repeat lengths (Aluja et al., 2015). Therefore, the influence of T-administration on preferences for facial femininity across mating contexts may be strongest among those with relatively shorter CAG repeats, as they are most sensitive to any potential effects of androgens.

A separate study by Little et al. (2007) raises another potential consideration for future research. Little and colleagues investigated the influence of relationship context (short- or long-term) and hypothetical environmental harshness on participants' preferences for female facial femininity. Men and women were primed with one of two ecological scenarios—environmental safety or environmental harshness. In the environmental safe prime, participants were asked to imagine being a university-educated, single, gainfully employed individual with no children, who lives in a safe neighbourhood, and who has a supportive and cooperative family. In the harsh condition, participants were asked to imagine having left school at the age of 16, being recently unemployed, single, with no children, and a tumultuous relationship with parents and other family members (some of which was stemming from the disappointment of not finishing school and/or having a meaningful future), and living in a dirty, noisy, and unsafe neighbourhood, in an apartment that needs constant repairs. Consistent with other findings, these authors found that, on the whole, men preferred feminine female faces more so than masculine female faces. However, these authors also noted a mating-context by environmental condition interaction such that for the long-term mating context, men preferred more feminine faces in the safe condition than in the harsh condition (which may have been driven by a lowered preference for feminine faces in the harsh condition), but feminine ratings remained similar between safe and harsh conditions in the short-term context. Although this study did not measure hormones, it indicates that simply imagining living in a harsh or safe environment can influence context-dependent preferences for female facial femininity. A separate large-scale study across 28-countries confirmed that men's preferences are indeed positively correlated with the health of the

nation (Marcinkowska et al., 2013), although this particular study did not consider relationship context. Marcinowska and colleagues (2013) suggested that a somewhat lower preference for female feminine faces in harsher conditions may represent an adaptive switch to preferences for greater resource holding potential over fecundity. To the degree that T influences men's perceptions in the same way, or that T is correlated with similar cognitive processes happening under environmental harshness, will require future research. In investigating the influence of exogenous T on context-dependent facial preferences, it may be important for future research to consider variation in participants' typical environmental factors, such as socioeconomic status, or indices of health status.

Although facial femininity is an important consideration relating to the potential health, fertility, and overall attractiveness of a mate, so too are other aspects, such as a female's body. Some of the specific bodily features shown to be important for judgments of attractiveness include the waist-to-hip ratio (Henss, 1995; Singh, 1993; Streeter & McBurney, 2003), body mass index (Tovée, Maisey, Emery, & Cornelissen, 1999), and breast size (Furnham, Swami, & Shah, 2006; Furnham & Swami, 2007). Indeed, although there are correlated preferences between facial and bodily attractiveness, some studies have shown that the face and body still make independent contributions to ratings of overall attractiveness (e.g., Currie & Little, 2009; Peters, Rhodes, & Simmons, 2007). In a recent study by Confer and colleagues (2010), the relative importance of a woman's face and body—as a function of mating context—to men's attractiveness ratings were explored. Participants were assigned to imagine short-term or long-term mating conditions (similar to the present study), and were then asked to view an image of an opposite sex individual whose face and body were occluded by boxes—one on the face

and one on the body. Participants were tasked with removing either the face box or the body box, but not both, in order to help inform their decision about whether or not they would engage in a relationship with this female. Following their decision, participants were also asked to make quantitative judgments about the relative priority they placed on the image's face or body (i.e., indicate on a Likert scale if the face was more important, if the body was more important, or if they were equally important). Interestingly, men assigned to the short-term condition placed more emphasis on the woman's body than when they were in the long-term condition. In consideration of these findings, it is possible that administration of T could differentially affect how men prioritize women's faces or bodies when making mate preference choices that are dependent on short- or long-term contexts. Future research might consider examining men's prioritization of a woman's face or body, in addition to examining preferences for specific aspects of bodily attractiveness (e.g., variation in waist to hip ratio or breast size) as a function of receiving T or placebo. Findings from such studies may help establish whether the hormone influenced context-dependent preferences found for facial femininity in the present experiments map onto context-dependent preferences for different aspects of bodily attractiveness in similar ways.

Conclusion

The findings from both Experiment 1 and Experiment 2 provide the first evidence that a single administration of T can rapidly modulate preferences for female facial femininity in a mating-context dependent manner. Overall, men showed a decreased preference for feminine female faces in the long-term relative to short-term context when they were administered T, but this difference was not present when they were

administered placebo. While the experiments presented here prevented the confident identification of underlying psychological mechanisms, future studies can seek to extend the present findings and further contrast potential influences of T on general mating motivation across short- and long-term contexts.

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Figure Captions:

Figure 1. Example of feminized (left) and masculinized (right) stimuli.

Figure 2. Testosterone concentrations as a function of drug condition in Experiment 1. * $p < .001$ for difference between Androgel® and Placebo conditions.

Figure 3. Frequency of feminine faces selected across all trials as a function of drug and context in Experiment 1. Error bars represent the *SE*. * $p < .01$ ** $p < .05$

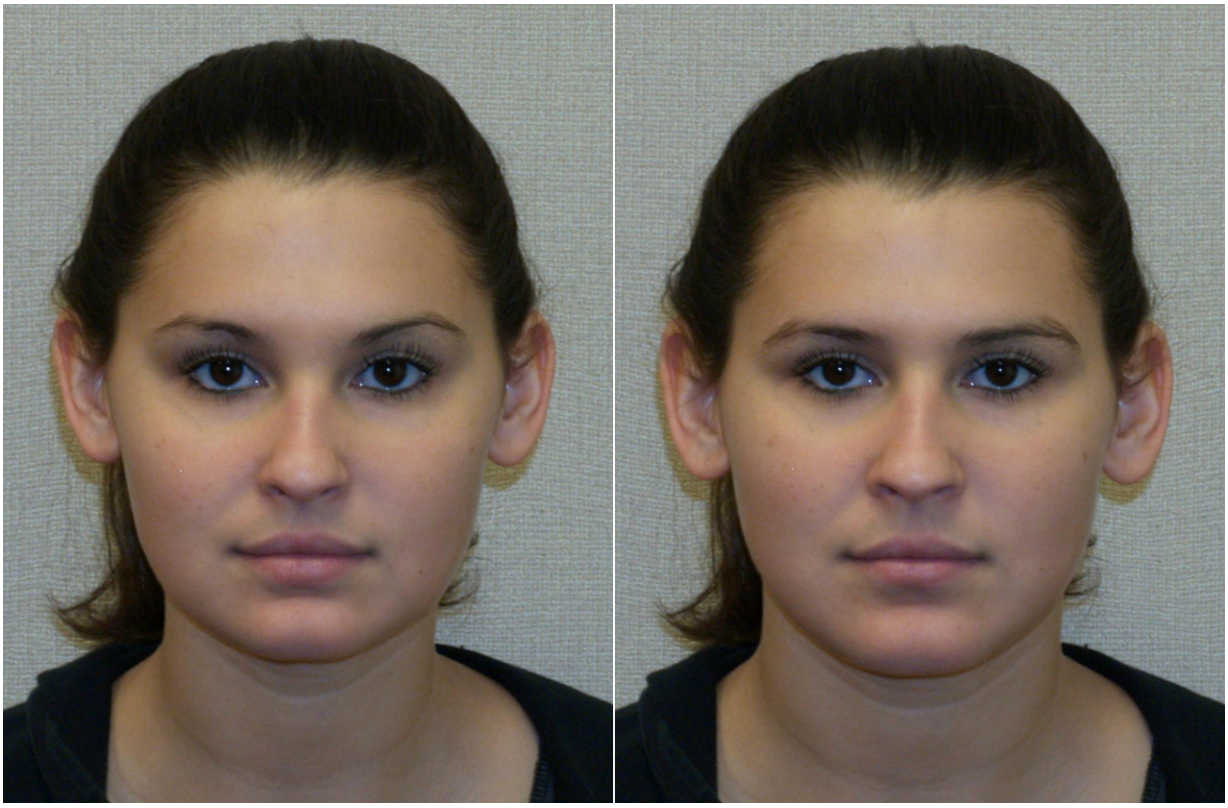
Figure 4A. Frequency of feminine faces across all trials as a function of drug and context for individuals who received Placebo on their first day of testing, and Testosterone on their second day of testing in Experiment 1. * $p < .01$ ** $p < .05$

Figure 4B. Frequency of feminine faces across all trials as a function of drug and context for individuals who received Testosterone on their first day of testing, and Placebo on their second day of testing in Experiment 1. No significant differences were found between conditions.

Figure 5. Testosterone concentrations as a function of drug condition. * $p < .001$ for difference between Androgel® and Placebo conditions in Experiment 2.

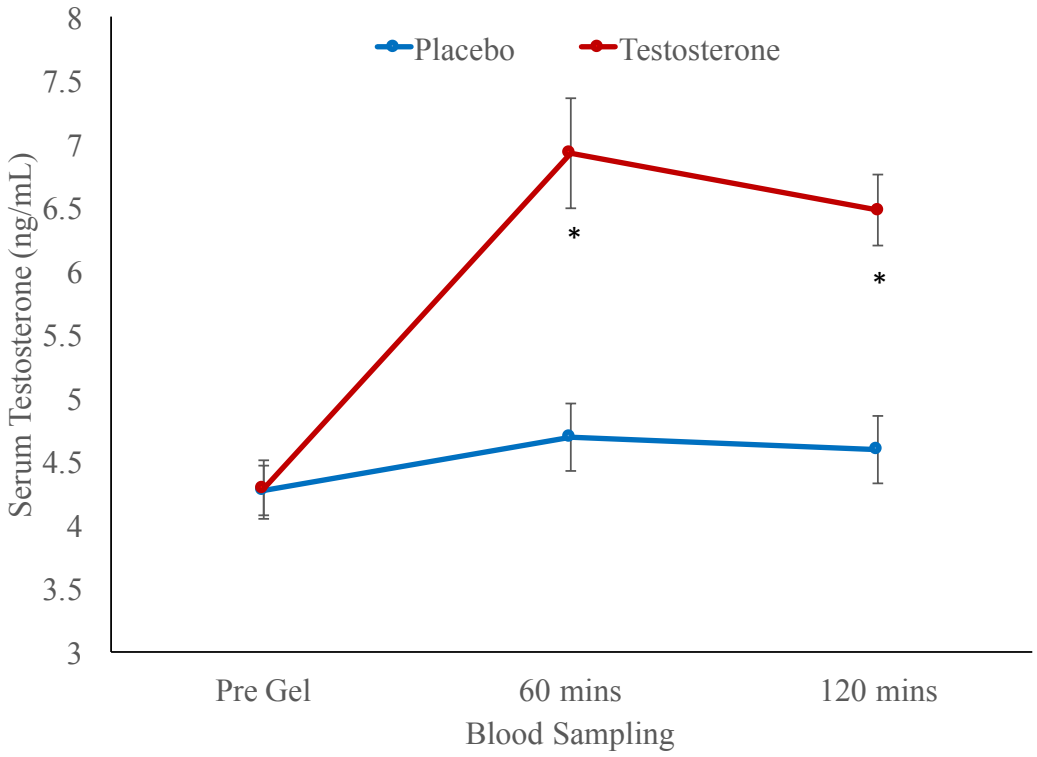
Figure 6. Frequency of feminine faces selected across all trials as a function of drug and context in Experiment 2. Error bars represent the *SE*. * $p < .01$ ** $p < .05$

Figure 1



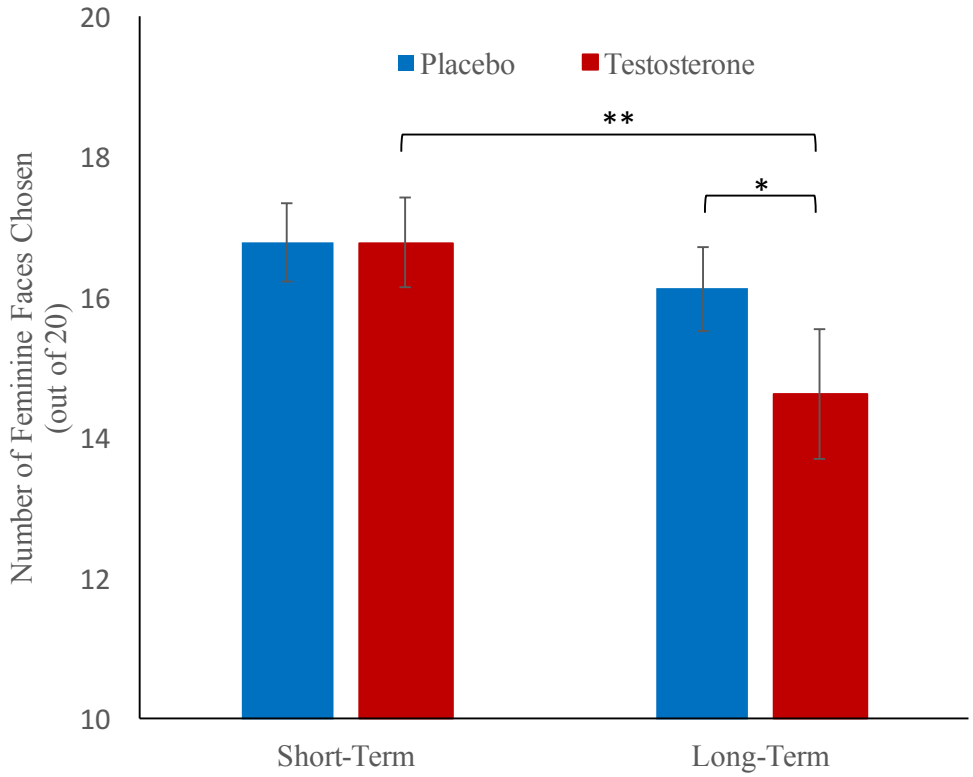
Example of feminized (left) and masculinized (right) stimuli.

Figure 2



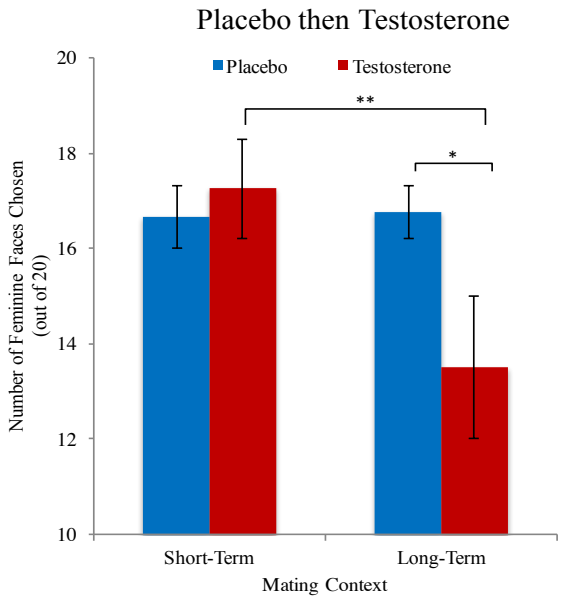
Testosterone concentrations as a function of drug condition in Experiment 1.
* $p < .001$ for difference between Androgel® and Placebo conditions.

Figure 3



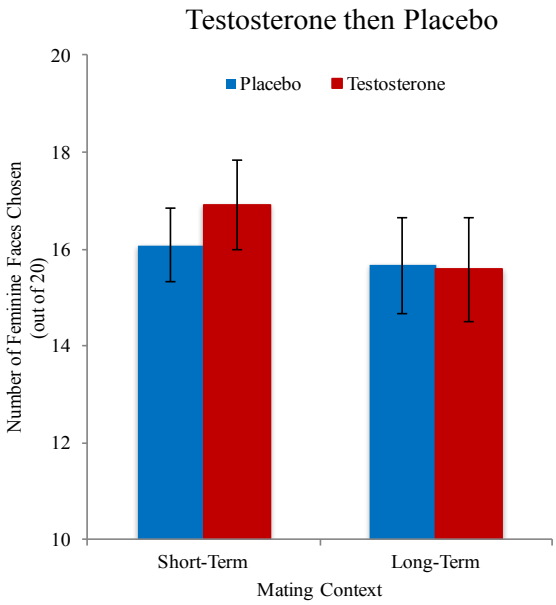
Frequency of feminine faces selected across all trials as a function of drug and context in Experiment 1. Error bars represent the *SE*. * p <.01 ** p < .05

Figure 4A



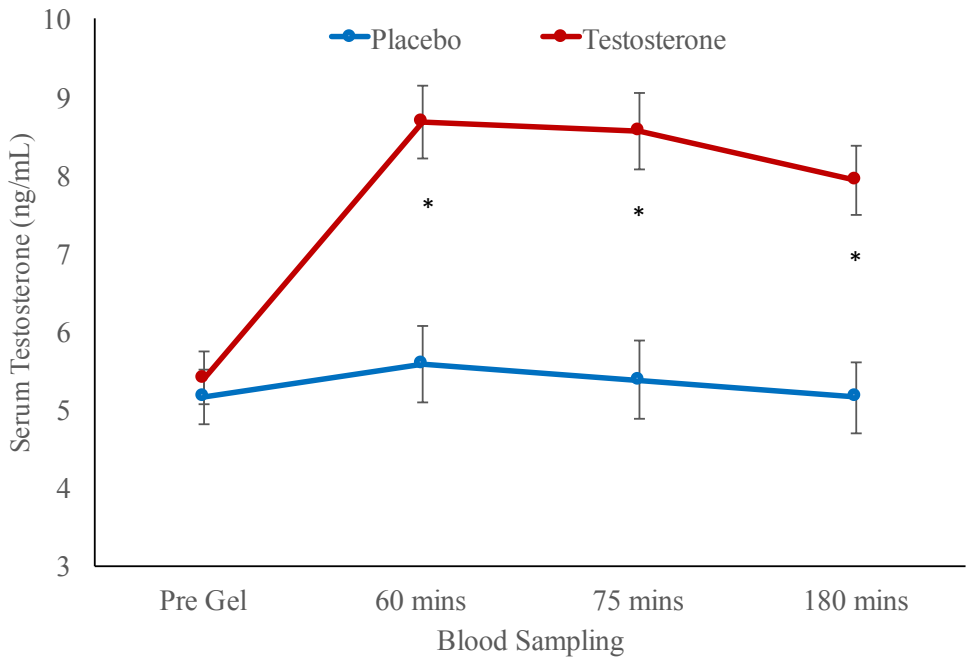
4A. Frequency of feminine faces across all trials as a function of drug and context for individuals who received Placebo on their first day of testing, and Testosterone on their second day of testing. * p <.01 ** p < .05

Figure 4B



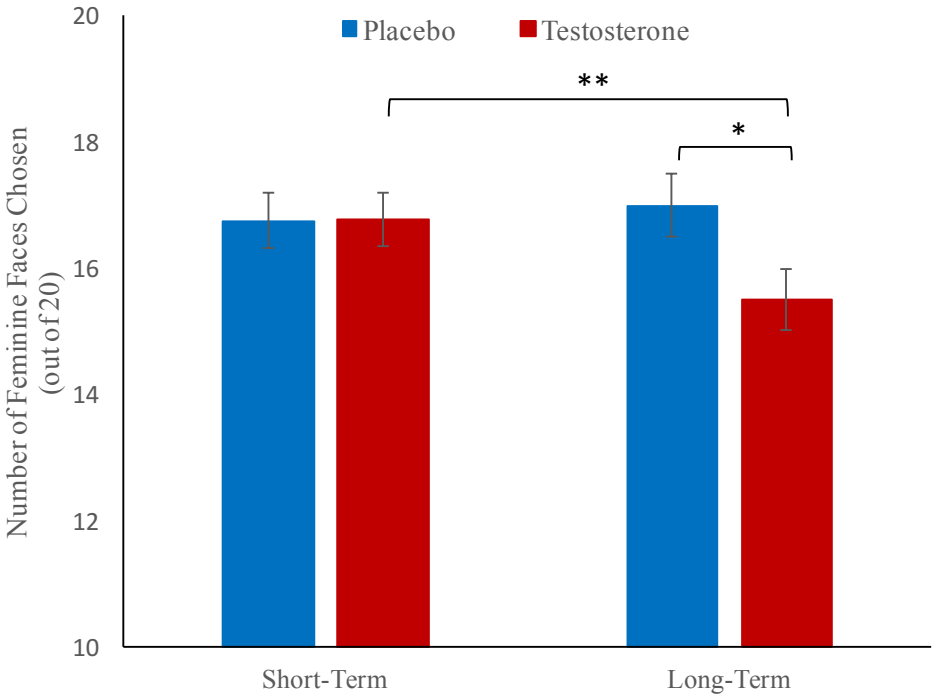
4B. Frequency of feminine faces across all trials as a function of drug and context for individuals who received Testosterone on their first day of testing, and Placebo on their second day of testing.

Figure 5



Testosterone concentrations as a function of drug condition. * $p < .001$ for difference between Androgel® and Placebo conditions in Experiment 2.

Figure 6



Frequency of feminine faces selected across all trials as a function of drug and context. Error bars represent the *SE*. * p <.01 ** p < .05