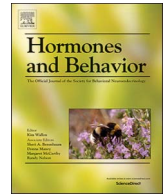


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Women's preferences for men's beards show no relation to their ovarian cycle phase and sex hormone levels

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ABSTRACT

According to the ovulatory shift hypothesis, women's mate preferences for male morphology indicative of competitive ability, social dominance, and/or underlying health are strongest at the peri-ovulatory phase of the menstrual cycle. However, recent meta-analyses are divided on the robustness of such effects and the validity of the often-used indirect estimates of fertility and ovulation has been called into question in methodological studies. In the current study, we test whether women's preferences for men's beardedness, a cue of male sexual maturity, androgenic development and social dominance, are stronger at the peri-ovulatory phase of the menstrual cycle compared to during the early follicular or the luteal phase. We also tested whether levels of estradiol, progesterone, and the estradiol to progesterone ratio at each phase were associated with facial hair preferences. Fifty-two heterosexual women completed a two-alternative forced choice preference test for clean-shaven and bearded male faces during the follicular, peri-ovulatory (validated by the surge in luteinizing hormone or the drop in estradiol levels) and luteal phases. Participants also provided for one entire menstrual cycle daily saliva samples for subsequent assaying of estradiol and progesterone. Results showed an overall preference for bearded over clean-shaven faces at each phase of the menstrual cycle. However, preferences for facial hair were not significantly different over the phases of menstrual cycle and were not significantly associated with levels of reproductive hormones. We conclude that women's preferences for men's beardedness may not be related to changes in their likelihood of conception.

1. Introduction

Evolution by sexual selection occurs when morphological or behavioral characters result in variation in reproductive success among individuals (Andersson, 1994). Female choice has shaped the evolution of male ornaments and status signals in many species (Kokko et al., 2003), including humans (Dixon, 2009). Some sexually selected traits are physiologically costly to maintain and only sustainable by individuals of high genetic quality (Kokko et al., 2003). Female preferences for males bearing well developed secondary sexual traits can evolve via indirect sexual selection, wherein traits indirectly signal genetic quality (i.e. 'good genes') that enhance offspring fitness (Kokko et al., 2003). Ornaments can also evolve under direct selection, whereby secondary sexual characters are associated with competitive ability that enhance female and offspring fitness via material benefits (Wong and Candolin, 2005).

Women's preferences for exaggerated facial sexual dimorphism in men are argued to reflect sexual selection for both underlying genetic quality (Little et al., 2011) and direct benefits (Puts, 2010). Androgens play organizational roles in shaping masculine facial features, including a prominent jawline, brow ridge and midface in men (Whitehouse et al., 2015; Geniole et al., 2015). Facial masculinity is positively associated with male physical strength (Fink et al., 2007; Windhager et al., 2011), health at adolescence (Rhodes et al., 2003) and adulthood (Thornhill and Gangestad, 2006). However, androgens may impact on immune response (Muehlenbein and Bribiescas, 2005), so that only high quality males can maintain androgen-dependent traits and indirectly signal genetic qualities to mates (Foo et al., 2017). There is some evidence that testosterone is positively correlated with men's immune response and facial attractiveness (Rantala et al., 2012). However, not all studies have found that facial masculinity is associated with health (Boothroyd et al., 2013) and whether facial masculinity reflects

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immunocompetence remains controversial (Scott et al., 2013). Recently, Phalane et al. (2017) reported that facial masculinity and facial muscularity were associated with men's immunity and women's judgments of male health and attractiveness, highlighting a complex relationship between facial masculinity, immunity and male facial attractiveness.

In addition to facial masculinity, androgens promote facial hair growth in men (Randall, 2008). However, the androgenic processes underpinning beard growth differ from those for facial masculinity. Beard hair follicles are activated when testosterone is converted to dihydrotestosterone via 5 alpha reductase enzymes in the dermal papillae of hair follicles (Randall, 2008). Sexual dimorphism in facial hair first appears around 10 years of age (Trotter, 1922) and continues to develop in boys throughout adolescence, becoming fully developed at adulthood (Hamilton, 1958). The extent to which androgens exert their effects on facial hair are due to shared genetic background, so that beard pattern and density is identical in monozygotic twins, variable among dizygotic twins and highly variable among non-twin brothers (Hamilton, 1964). While facial hair appears to bear no cost to survival and is not related to proficiency in hunting or horticulture, beards enhance ratings of male sexual maturity and masculinity (Dixon, 2016). This suggests facial hair plays a role in intra-sexual signaling (Puts, 2010); accordingly, beards consistently enhance ratings of men's social status, dominance and aggressiveness (Dixon and Vasey, 2012; Muscarella and Cunningham, 1996; Neave and Shields, 2008; Saxton et al., 2016; Sherlock et al., 2017). Success in male-male competition can lead to higher status and signal resource holding potential and protection, so that beards likely signal direct rather than indirect benefits to women (Dixon et al., 2017a).

Given their associations with indirect and direct benefits, women may prefer masculine facial features and beards in partners. Although men's mating success is positively associated with facial masculinity (Hill et al., 2013; Rhodes et al., 2005) and beardedness (Barber, 2001), women's preferences for both traits are highly variable (Dixon et al., 2016). Some studies reported a greater preference for full beards among women (Pellegrini, 1973; Dixon et al., 2016; McIntosh et al., 2017), while others found that clean-shaven faces (Dixon and Vasey, 2012; Muscarella and Cunningham, 1996), or stubble (Dixon and Brooks, 2013; Dixon et al., 2013; Neave and Shields, 2008) were the most attractive. Similarly, mixed results are also reported for women's preference for craniofacial masculinity (Rhodes, 2006), and beards enhance ratings of male facial masculinity (Dixon et al., 2017a).

These inconsistencies in women's preferences are thought to reflect a paradoxical role of masculine traits in human mate choice decisions. On the one hand, phenotypic masculinity may reflect biological quality, while on the other hand, masculine traits are also associated with negative personality traits and potentially reduced paternal investment (Dixon, 2016). For instance, masculine men report stronger preferences for and engage more often in short-term than long-term relationships (Boothroyd et al., 2007, 2008; Rhodes et al., 2005), and women accurately judge male sexual infidelity using facial masculinity from photographs (Rhodes et al., 2013). Beardedness is positively associated with men's self-reported masculinity (Wood, 1986) and support of traditional masculine gender roles (Oldmeadow and Dixon, 2016a, 2016b), as well as their serum testosterone (Knussman and Christiansen, 1988), which is negatively associated with paternal investment (Gettler, 2014). Thus, women may face costs when choosing a masculine partner, which may explain why facial masculinity reduces paternal investment ratings (Kruger, 2006; Perrett et al., 1998).

Based on the possible trade-off between heritable biological quality and parental quality, women's preference for masculine traits could be greater in circumstances where these benefits are more likely to be realised (Gangestad and Simpson, 2000). Previous research reported women's preferences for masculine traits were strongest when judging short-term mates (Little et al., 2011), and particularly during the peri-ovulatory phase of the menstrual cycle (Gangestad and Thornhill,

2008). Ovulatory shifts have been found for masculine facial shape (Little et al., 2008; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000), deeper vocal pitch (Puts, 2005), and greater height (Pawlowski and Jasienska, 2005). However, this interpretation has recently been questioned (Dixon et al., 2017b; Scott et al., 2014), and is not supported by recent genetic evidence (Lee et al., 2014; Zietsch et al., 2015). Additionally, unsuccessful attempts to replicate ovulatory shift effects (Harris, 2011, 2013; Harris et al., 2013; Zietsch et al., 2015) and conflicting results from two separate meta-analyses (Gildersleeve et al., 2014a; Wood et al., 2014) has sparked debate regarding the robustness of ovulatory shift effects and highlighted issues of sampling techniques, statistical analyses, and methodologies (Gildersleeve et al., 2014b; Harris et al., 2014; Wood and Carden, 2014). One recurring methodological issue in tests of the ovulatory shift hypothesis concerns estimating fertility indirectly via questionnaires asking participants to recall the onset, length, and regularity of their menstrual cycles. These techniques are not only inaccurate owing to participant's memory and knowledge of their menstrual cycles (Jukic et al., 2008; Small et al., 2007), and variability in cycle physiology (Jasienska and Jasienska, 2008), but also result in unreliable estimates of current fertility (Blake et al., 2016; Gangestad et al., 2016). Further, studies often used small sample sizes and between-subject designs, which further reduce the likelihood of identifying robust effects (Gangestad et al., 2016). Thus, whether women's preferences for masculinity shift with ovulation remains contentious.

Women's menstrual cycles last, on average, 28 days (Popat et al., 2008) and the peri-ovulatory period is characterised by a surge in luteinizing hormone (LH) and an increase followed by a drop in estradiol levels (Lipson and Ellison, 1996). Studies using within-subject designs in concert with validating the peri-ovulatory phase via the LH surge and the drop in estradiol provide robust and statistically powerful tests of the ovulatory shift hypothesis (Blake et al., 2016; Gangestad et al., 2016). However, only a minority of studies have used these approaches. Peters et al. (2009) reported no significant within-subject differences in masculinity preferences from high and low fertility phases when the peri-ovulatory phase was validated via LH surges. Using within-subject designs, Feinberg et al. (2006) reported stronger preferences for vocal masculinity at the peri-ovulatory phase, particularly among women with low estradiol, while Roney et al. (2011) reported stronger facial masculinity preferences at the peri-ovulatory phase that were positively associated with estradiol. One cross-sectional study measuring women's reproductive hormones and their facial masculinity preferences reported positive associations between preferences and estradiol levels (Roney and Simmons, 2008) while two others did not (Escasa-Dorne et al., 2017; Marcinkowska et al., 2016). Previous studies investigating menstrual cycle shifts in women's preference for beards have found no evidence of a positive association (Dixon and Brooks, 2013; Dixon et al., 2013; Dixon and Rantala, 2016, 2017). However, these studies relied on inaccurate counting methods generated from self-report, using between-subject designs with small sample sizes. Therefore, it is unclear whether these null results are representative or reflect an inability to detect a true effect due to methodological issues.

The current study tests whether the attractiveness of men's beards shifts across the menstrual cycle where participant menstrual cycle phase was verified by daily measurements of sex hormone levels and LH tests. Preferences data were collected from 52 heterosexual women during the follicular, peri-ovulatory and luteal phases of their menstrual cycles. We also collected daily saliva samples for measurements of estradiol and progesterone at each phase of the cycle in order to test the hormonal associations underpinning potential cycle effects. Our sample size of 52 women and within-subject design at three targeted points of the menstrual cycle has 80% power to detect a medium effect size of $d = 0.5$ (Gangestad et al., 2016). Prior studies used natural facial stimuli to test women's preferences for men's facial hair that, although high in ecological validity, likely vary on several dimensions, including craniofacial masculinity, that influence women's preferences for beards

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