Adaptive attunement to the sex of individuals at a competition: the ratio of opposite- to same-sex individuals correlates with changes in competitors’ testosterone levels

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Initial receipt 4 January 2011; final revision received 16 May 2011

Abstract

Evolutionary theories (e.g., the challenge hypothesis) suggest that testosterone plays an important role in intrasexual competition. In addition, those theories suggest that testosterone responses during competition should depend upon the presence of potential, immediate mating opportunities associated with the competition. The current research tested the hypothesis that the sex composition of individuals at a competition (ratio of opposite-sex, potential mates to same-sex individuals) would influence changes in competitors’ testosterone levels. Consistent with our hypotheses, higher ratios of opposite- to same-sex individuals at an ultimate frisbee tournament were associated with greater increases in salivary testosterone among competitors. The relationship between sex ratio and increased salivary testosterone was observed for both male and female competitors and occurred regardless of whether competitors won or lost. Findings are consistent with the hypothesis that testosterone responses during competition are influenced by cues of potential, immediate mating opportunities.

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Keywords: Challenge hypothesis; Intrasexual competition; Hormones

In humans, as in many other mammals, individuals frequently compete with members of their own sex in order to gain reproductive access to opposite-sex partners (Buss, 1988; Walters & Crawford, 1994). Indeed, intrasexual competition has been a central driving force behind human evolution (Buss, 2007; Darwin, 1851, 1871). Consequently, competition is often accompanied by adaptive changes in basic physiological processes. In particular, a large literature implicates testosterone as a key hormone involved in competitive social situations (see Archer, 2006, and Salvador & Costa, 2009, for reviews).

To date, the vast majority of studies examining the links between testosterone and intrasexual competition have focused on changes in testosterone after winning or losing a competition. According to the biosocial status hypothesis (Mazur, 1985; Mazur & Booth, 1998), winning a competition is thought to promote increases in testosterone, thereby facilitating aggressive, dominant behaviors and displays of high status; in contrast, losing a competition is thought to promote decreases in testosterone, thereby eliciting submissive displays and a diminished tendency to fight. The overall evidence for this hypothesis has been mixed. Some studies have reported higher levels of testosterone among winners and lower levels of testosterone among losers (e.g., Booth, Shelley, Mazur, Tharp, & Kittok, 1989; Elias, 1981; Gladue, Boechler, & McCaul, 1989; Mazur, Booth, & Dabbs, 1992; Mazur & Lamb, 1980; McCaul, Gladue, & Joppa, 1992). Other studies have reported no differences in testosterone levels between winners and losers (e.g., Gonzalez-Bono, Salvador, Serrano, & Ricarte, 1999; Filaire, Maso, Sagnol, Lac, Ferrand, & Lac, 2001; Mehta & Josephs, 2006; Salvador, Simon, Suay, & Llorens, 1987; Suay et al., 1999; van der Meij, Buunk, Almela, & Salvador, 2010).

The large variability in findings across studies likely reflects the fact that the links between competition and testosterone are complex and not solely a function of winning or losing. Indeed, testosterone responses to competition...
depend upon a number of factors; the type of competition (Archer, 2006), characteristics of the opponent (e.g., van der Meij et al., 2010), and the psychological state and baseline hormone levels of the person competing (e.g., Maner, Miller, Schmidt, & Eckel, 2008; Mehta & Josephs, 2010; Schultheiss, Wirth, Torges, Pang, Villacorta, & Welsh, 2005) all play a vital role in shaping competition-based testosterone responses. Although this literature has uncovered several important variables predicting testosterone changes during competition, this literature has been limited to a certain extent by a tendency to neglect one important aspect of competition — variation in potential, immediate reproductive benefits associated with the competition.

Although an evolutionary perspective suggests that all intrasexual competitions serve reproductive purposes to some degree (Mazur & Booth, 1998), that same perspective also implies that different competitions have different levels of immediate reproductive importance. For example, whether the type of competition is valued by potential mates and whether potential mates are aware of the outcomes are likely to shape the degree to which winning leads to immediate mating-related benefits (e.g., attracting new romantic partners). Consequently, from an evolutionary perspective, competition-based testosterone responses (responses designed to promote successful intrasexual competition) should depend upon the extent to which the competition provides immediate access to potential mating opportunities.

This would be consistent with theories linking competition and testosterone in other animals. For example, the challenge hypothesis (Archer, 2006; Wingfield, Hegner, Dufty, & Ball, 1990), originally proposed to account for testosterone-aggression relationships in monogamous male birds, suggests that at the beginning of breeding seasons when males are motivated to seek new mates, male testosterone levels tend to rise. During periods of social instability or when challenges relevant for reproduction arise, testosterone levels rise further to facilitate mating-related intrasexual aggression (e.g., fights for territory or dominance). Indeed, across numerous species, males tend to display the highest levels of testosterone during breeding seasons when competition over female mates is crucial for reproductive success (e.g., Lynch, Ziegler, & Strier, 2002; Muroyama, Shimizu, & Sugiuara, 2007). Thus, similar to other animals, humans may display increased testosterone levels in challenging contexts that are immediately relevant for reproduction, thereby facilitating heightened mating motivation designed to promote successful competition over potential mates.

One factor that should increase the salience of potential, immediate reproductive benefit associated with competition is the presence of opposite-sex individuals (i.e., potential mates). Consequently, the sex of other individuals at a competition may have important consequences for changes in competitors’ testosterone levels. This would be consistent with several recent studies reporting that exposure to a potential mate elicits increases in testosterone in both men (Roney, Mahler, & Maestripieri, 2003, Roney, Lukaszewski, & Simmons, 2007; van der Meij, Buunk, van de Sande, & Salvador, 2008; see also Miller & Maner, 2010) and women (Lopez, Hay, & Conklin, 2009). In addition, testosterone increases and corresponding increases in risk taking have been observed among male athletes practicing in the presence of a female spectator (Ronay & von Hippel, 2010). Although informative, those studies did not examine testosterone responses to opposite-sex individuals during a formal competition in which individuals compete directly with intrasexual competitors. Moreover, previous studies have manipulated only the presence of a single same- or opposite-sex individual. In real-world arenas, the social context surrounding competitions can be complex and can include numerous individuals of both sexes. Thus, the purpose of the current research was to test for changes in testosterone during a competitive setting in which numerous individuals of both sexes were present.

In the current study, we examined changes in salivary testosterone among male and female competitors in an ultimate frisbee tournament. The mere presence of opposite-sex individuals has been shown to facilitate physiological and psychological processes reflective of heightened mating motivation (Roney et al., 2007, see also Miller & Maner, 2011). Thus, we expected that the presence of opposite-sex individuals at the tournament would act as a mating cue reflecting the immediate reproductive importance of the competition. Therefore, consistent with the challenge hypothesis, we predicted that competitors would display greater increases in testosterone as the ratio of opposite- to same-sex individuals increased (i.e., as the relative number of potential mates increased). We also probed for potential effects of winning/losing on changes in testosterone. As mentioned previously, there has been a lack of consensus in this area. Thus, we did not have any strong a-priori predictions relevant to winning or losing.

1. Methods
1.1. Participants

Members of the community-based coed Tallahassee Ultimate Frisbee League were e-mailed and asked to participate in a study involving competition and hormones. The Tallahassee Ultimate Frisbee League was composed of 105 members separated into 6 teams (11–12 men and 6 women per team) via a drafting process in which captains (elected by the Ultimate Frisbee League board members) each took turns picking players one at a time for their team. Forty-two members volunteered to participate. Six participants failed to provide at least one saliva sample. Thus, we were able to measure testosterone concentrations for 36 participants (20 male, 16 female; age range: 19–48 years). Although male and female participants differed in average age (male $M=27.1$, S.D.=6.8; female $M=22.6$, S.D.=3.2),
ancillary analyses revealed that age had no significant effect on any of the results.

1.2. Procedure

The study took place during the season’s final tournament. Six teams competed in 90-min single-elimination games. To avoid potential confounds associated with having competed in previous games that same day, we collected data only from each team’s first game of the tournament. Data were thus collected across four games (game 1: sixth seed vs. third seed; game 2: fifth seed vs. fourth seed; game 3: second seed vs. winner of game 1; game 4: first seed vs. winner of game 2). Although Games 3 and 4 included some players from the previous games, in each of those games, we only collected data from the players who had not played in a previous game (i.e., players on the first and second seeded teams). Games 1 and 2 occurred from 11:00 am to 12:30 pm; Games 3 and 4 occurred from 1:00 pm to 2:30 pm.

Approximately 10–20 min prior to their first game, participants completed consent paperwork and a brief questionnaire in which they indicated their age, sex and team. Participants then provided a pregame saliva sample by spitting into a collection vial (approximately 4 ml per sample). Approximately 5 min after the end of their first game, participants provided a postgame saliva sample. Each sample was placed in an ice cooler immediately after it was collected. After the last game, all samples were stored in a −20°C freezer.

At the beginning and end of each game, two research assistants independently counted the number of men and women in the nearby vicinity watching/playing the game. The research assistants agreed 87.5% of the time. In those cases in which their counts differed, the research assistants performed a recount and came to a mutual agreement. Before-game and after-game counts were then averaged to determine the average number of men and women at each game. On average, there were 22.4 (S.D.=4.2) men and 15.0 (S.D.=2.2) women at each game. After each game’s completion, we recorded which team had won and which had lost.

1.3. Hormone measurement

Saliva samples were frozen at −20°C. To precipitate mucins, samples were thawed and centrifuged at 4000 rpm for 10 min. The supernatant was stored in 500 μl aliquots at −20°C until assayed. A commercially available solid-phase Coat-A-Count125I radioimmunoassay kit (TKTT) provided by Siemens Medical Solutions Diagnostics (Los Angeles, CA, USA) was used to measure concentrations of testosterone. Tubes were incubated for 21 h after adding radiolabeled tracer. All samples were processed in duplicate using a high-throughput, automated gamma counter in a single assay. The intra-assay coefficient of variation was 11.02%. Mean baseline testosterone concentrations for men and women were 91.5 pg/ml (S.D.=37.1) and 19.1 pg/ml (S.D.=10.6), respectively.

2. Results

2.1. Changes in testosterone as a function of sex ratio

Change in testosterone (postgame minus pregame) served as our primary dependent measure. On average, both men and women displayed significant increases in testosterone over the course of the game (men: \(M=25.9\) pg/ml, S.D.=35.2, \(t(19)=3.29, p=.004\); women: \(M=10.28\) pg/ml; S.D.=14.9, \(t(15)=2.78, p=.02\)). Preliminary analyses confirmed that the raw score variability in testosterone change scores was greater in men than in women, Levine’s test: \(F(34)=11.73, p=.002\). Thus, consistent with previous research (Maner et al., 2008; Wirth & Schultheiss, 2007), we standardized testosterone change scores within men and women separately. Change in testosterone was unrelated to time of day, \(t(34)=.07, p=.95\).

Pre-to-post changes in testosterone concentrations were predicted from the ratio of female-to-male individuals at the game (a continuous between-subjects variable), the outcome of the game (won or lost; between-subjects), participant sex (male or female; between-subjects) and all interactions using a Mixed-Model Generalized Estimating Equation. All analyses were performed using a multilevel nested model with participants nested within team, teams nested within game, and games nested within time of day. Effect sizes were calculated using the following formula: \(r=\text{SQRT}(\chi^2/N)\). As predicted, we observed an interaction between sex ratio and participant sex, \(b=-18.5\), Wald \(\chi^2(1,N=36)=4.27, p=.039, r=.34\); all other effects were nonsignificant, all \(p’s>.50\).

Because no significant effects involving the game’s outcome (won vs. lost) were observed, this variable was dropped from the model and not considered further; the interaction between sex ratio and participant sex remained significant after dropping the outcome variable, \(b=-17.7\), Wald \(\chi^2(1,N=36)=7.87, p=.005, r=.47\).

To interpret the two-way interaction, we evaluated the simple effect of sex ratio among female and male participants separately. Among female participants, we observed an effect of sex ratio, \(b=-9.1\), Wald \(\chi^2(1,N=36)=3.77, p=.052, r=.32\), such that higher ratios of males to females at the game were associated with greater increases in testosterone. We also observed a significant effect of sex ratio among male participants, \(b=8.6\), Wald \(\chi^2(1,N=36)=4.13, p=.042, r=.34\), such that higher ratios of females to males were associated with greater increases in testosterone. Thus, as can be seen in Fig. 1, for both men and women, greater proportions of opposite- to same-sex individuals were associated with greater increases in testosterone.

2.2. Supplemental analyses

Another way of analyzing the data is to treat postgame testosterone levels as the dependent variable, while statistically controlling for pregame variability in testosterone levels. Thus, to provide another test of our hypotheses, we performed additional analyses in which
pregame testosterone, of change scores. In addition to a significant main effect of levels. Findings closely mirrored those from the analysis interaction, while controlling for pregame testosterone ratio of individuals at the game, participant sex and their postgame testosterone levels were predicted from the sex participant sex. For ease of interpretation, the figure depicts raw, unstandardized change scores.

Fig. 1. Men’s change in testosterone (solid line) from pregame to postgame was positively related to the ratio of female-to-male individuals at the game. Women’s change in testosterone (dotted line) was negatively related to the ratio of females to males (i.e., positively related to the ratio of males to females). Analyses were conducted using standardized change scores within participant sex. For ease of interpretation, the figure depicts raw, unstandardized change scores.

postgame testosterone levels were predicted from the sex ratio of individuals at the game, participant sex and their interaction, while controlling for pregame testosterone levels. Findings closely mirrored those from the analysis of change scores. In addition to a significant main effect of pregame testosterone, \( b=0.7, \) Wald \( \chi^2(1,N=36)=28.57, p<.001, r=.89 \), we observed the predicted interaction between sex ratio and participant sex, \( b=-13.1, \) Wald \( \chi^2(1,N=36)=7.81, p=.005, r=.47 \). Among women, sex ratio was a significant predictor of postgame testosterone levels, \( b=-7.8, \) Wald \( \chi^2(1,N=36)=5.15, p=.002, r=.39 \). Among men, sex ratio (marginally) predicted postgame testosterone levels, \( b=5.3, \) Wald \( \chi^2(1,N=36)=2.62, p=.10, r=.27 \). For both men and women, greater proportions of opposite-to same-sex individuals were associated with higher levels of postgame testosterone.

3. Discussion

The current study provides evidence that human endocrine responses during competition are sensitive to the sex composition of individuals at the competition. As the ratio of opposite- to same-sex individuals at an ultimate frisbee competition increased, so did competitor’s testosterone levels increase over the course of the competition. This was true for both male and female competitors and occurred regardless of whether competitors won or lost.

These results complement previous findings demonstrating that the presence of an opposite-sex individual can heighten testosterone levels in humans (e.g., Lopez et al., 2009; Ronay & von Hippel, 2010; Roney et al., 2003, 2007; van der Meij et al., 2010). The current research extends previous findings by providing evidence for testosterone changes in a competitive context in which numerous individuals of both sexes are present. As a whole, the findings suggest that the endocrine system is attuned not only to the presence or absence of a potential mate, but also to the mating-related composition of groups of individuals in a complex competitive social environment. These findings are consistent with the hypothesis that endocrinological responses to competition partially depend upon the potential, immediate reproductive benefits associated with that competition.

Compared to studies on men, relatively few studies have examined hormonal responses to competition among women (for exceptions, see Edwards, Wetzel, & Wyner, 2006; Kivlighan, Granger, & Booth, 2005; van Anders & Watson, 2007), and even fewer have examined how the presence of opposite- and same-sex individuals shape women’s testosterone responses. The current findings support the hypothesis that, similar to men, women display endocrine reactivity to the presence of potential mates at a competition. These findings may seem counterintuitive in light of previous research demonstrating that, across numerous species, males tend to compete with one another for access to potential mates to a relatively greater extent than females do (Smith, 1977; Trivers, 1972). Based on that literature, one might have expected sex differences in the degree to which opposite-sex individuals elicited endocrine responses reflecting competition for mates (Baker & Maner, 2008, 2009). However, there are many aspects of human mating that are different from other species. Indeed, although males of most species tend to compete over sexual access to females, there is evidence that human females compete over potential mates just as human males do (although perhaps not to the same extent) (Durante, Griskevicius, Hill, Perilloux, & Li, In press; Fisher, 2004).

Thus, the endocrinological responses of both men and women may be sensitive to the presence of potential, immediate reproductive opportunities (Lopez et al., 2009). Although the current findings support this hypothesis, it should be noted that our study focused on female athletes — a potentially unique population of women who presumably are relatively high in competitiveness; further investigation is needed to assess the generalizability of the current findings to other populations of women.

Similar to other studies (e.g., Gonzalez-Bono et al., 1999; van der Meij et al., 2010; Mehta & Josephs, 2006), we did not observe any effects of winning or losing on changes in testosterone. As mentioned previously, numerous factors can moderate the effects of winning and losing on endocrine responses. For example, some researchers have suggested
that testosterone responses depend more on perceived outcomes than real outcomes (Gladue et al., 1989; Gonzalez-Bono et al., 1999; Serrano, Salvador, Gonzalez-Bono, Sanchis, & Suay, 2000). Thus, the null findings with respect to the game’s outcome could reflect the fact that we collected data only during the first round of a multigame tournament (i.e., competitors had additional games to play, potentially downplaying any sense of winning). Nevertheless, the current findings do suggest that regardless of actual outcomes, competitors’ endocrine responses are sensitive to the sex of individuals at a competition. Future research may profitably extend these findings to controlled laboratory competitions and further examine potential interactions between sex ratios and perceived (rather than actual) outcomes.

Limitations of the current study provide valuable directions for future research. One limitation was that, due to our desire for high ecological validity (i.e., wanting to examine effects in a real-world setting outside of the laboratory), we were unable to control for or manipulate various factors that might have partially influenced the relationship between sex ratios and testosterone responses. For example, it is possible that, rather than the sex ratio of individuals at the game influencing competitor’s hormone levels, the direction of causality could have been the reverse; heightened testosterone levels among competitors may have influenced their behavior in such a way as to attract more opposite-sex individuals to the game. Alternatively, the direction of causality may have been as hypothesized (opposite-sex individuals produced heightened testosterone levels among competitors), but rather than being a direct effect, the effect may have been mediated by other variables not measured in the current study. For example, a large number of opposite-sex individuals could have prompted competitors to play harder and exert more physical energy, in turn leading to increases in testosterone.

It is also possible that the effects were influenced by confounding self-selection variables associated with participants’ dispositions. Only 40% of eligible players volunteered to participate. Because we described the research as a study on competition, this may have caused a self-selection bias such that players with relatively strong interests in competition selected into the study, whereas less competitive players may have chosen to avoid participation. One possible implication is that the effects we observed might apply primarily to individuals relatively high in their desire for competition. This would be consistent with previous research reporting competition-based testosterone changes only among individuals relatively high in implicit desires for power and dominance (Schultheiss et al., 2005).

It is also possible that the relationship between sex ratios and testosterone changes reflected considerations other than mating. That is, although we hypothesized that the sex ratios would reflect potential opportunities for mating, it is possible that sex ratios influenced testosterone responses for nonmating reasons. For example, men tend to be more physically athletic than women (Findlay & Bowker, 2009). Consequently, for women, high numbers of male competitors may have made the competition more athletically challenging, therefore requiring more physical exertion, in turn causing heightened levels of testosterone. By using controlled, laboratory experiments, future research may be able to address these issues and better elucidate the mechanisms underlying the relationship between the sex composition of people at a competition and competitors’ endocrine responses.

Another limitation involved the direct physiological mechanisms underlying changes in testosterone. Although changes in testosterone were observed among both male and female participants, the current study did not examine the biological structures responsible for those testosterone changes. Research indicates that the primary biological structures responsible for the release of testosterone are different in men and women. In men, testosterone is produced primarily by the gonads (the hypothalamic-pituitary-gonadal axis); in women, testosterone is produced primarily by the adrenal glands (the hypothalamic-pituitary-adrenal axis) (Jones & Lopez, 2006). Thus, although both men and women respond with heightened levels of testosterone when competing around opposite-sex individuals, the specific neuroendocrine pathways involved in this process may be different for the two sexes. This may have implications for the types of psychological and behavioral responses, as well as other endocrinological responses men and women display in response to opposite-sex individuals. For example, cortisol secretions are initiated primarily by activation of the HPA axis (Sapolsky, Romero, & Munck, 2000). If women’s testosterone responses to the sex ratio reflect activation of the HPA axis, this may suggest that women’s cortisol levels also change in response to the sex ratio of individuals at a competition. This remains an interesting question for future studies.

Another limitation is that we did not examine behavioral consequences of the observed changes in testosterone. From an evolutionary perspective, testosterone responses to opposite-sex individuals may function to facilitate success in intrasexual competition (e.g., enhancing athletic ability and desires to dominate same-sex rivals; Archer, 2006), or to promote courtship displays to opposite-sex individuals (e.g., enhancing behaviors that potential mates find attractive; Ronay & von Hippel, 2010) or to do both. Indeed, endocrinological sensitivity to the sex composition of individuals at a competition may lead to a host of behaviors serving multiple reproductive purposes. The current research provides a useful springboard for investigating those behaviors.

Another limitation involves the size and range of sex ratios observed in the current the study; female-to-male ratios ranged from 5.9 women to 7.4 women for every 10 men. The relatively small variation in sex ratios may account for some of the marginal effects observed in the current study. In addition, although higher proportions of women led men to experience heightened levels of testosterone, the total number of women was always smaller.
than the total number of men. Consequently, for men, there were always fewer potential mates than same-sex rivals. In settings in which there are more women than men, men may not have to compete as much for access to a potential mate (Kokko & Rankin, 2006). Thus, in such settings, variation in sex ratios may not influence men’s testosterone levels to the degree observed in the current study. Future research would benefit from exploring testosterone responses across a broad range of sex ratios.

Intrasexual competition is a driving force behind evolution by natural selection (Buss, 2007; Darwin, 1851, 1871). Thus, people possess adaptive physiological mechanisms that help them compete for access to mates (Archer, 2006). The current study suggests that, consistent with the challenge hypothesis (Wingfield et al., 1990), when people compete in the presence of a relatively large number of potential mates, they display heightened increases in testosterone. Thus, the sex composition of people at a competition may play an important role in shaping basic endocrinological processes.

References


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