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Hormonal underpinnings of status conflict: Testosterone and cortisol are related to decisions and satisfaction in the hawk-dove game

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ABSTRACT

A contribution to a special issue on Hormones and Human Competition. Testosterone is theorized to influence status-seeking behaviors such as social dominance and competitive behavior, but supporting evidence is mixed. The present study tested the roles of testosterone and cortisol in the hawk-dove game, a dyadic economic decision-making paradigm in which earnings depend on one's own and the other player's choices. If one person selects the hawk strategy and the other person selects the dove strategy, the player who selected hawk attains a greater financial pay-off (status differentiation). The worst financial outcome occurs when both players choose the hawk strategy (status confrontation). Ninety-eight undergraduate students (42 men) provided saliva samples and played ten rounds of the hawk-dove game with another same-sex participant. In support of the hypothesis that testosterone is related to status concern, individuals higher in basal testosterone made more hawk decisions — decisions that harmed the other player. Acute decreases in cortisol were also associated with more hawk decisions. There was some empirical support for the dual-hormone hypothesis as well: basal testosterone was positively related to satisfaction in the game among low basal-cortisol individuals but not among high basal-cortisol individuals. There were no significant sex differences in these hormonal effects. The present findings align with theories of hormones and status-seeking behavior at the individual level, but they also open up new avenues for research on hormone profiles at the collective level. Our results suggest that the presence of two or more high-testosterone members increases the likelihood of status confrontations over a limited resource that can undermine collective outcomes.

Status hierarchies are universal across human cultures and in many other social animals. Higher status provides benefits that promote survival and reproduction, such as preferential access to food and mates, making status attainment an attractive prospect (Ellis, 1994). Indeed, scholars have noted that the desire for status is a fundamental social motive (Anderson et al., 2015). One key behavioral mechanism for attaining higher rank in many species is through displays of dominance toward another conspecific — such as challenges and attacks — in socially competitive situations (Cheng et al., 2013). If the other conspecific engages in deference behavior and bows out of the conflict, then the dominance-displayer is granted the higher status position and in turn greater access to resources. But dominance can be risky because the other conspecific may also display dominance. In a scenario in which both competitors behave dominantly and neither is willing to defer to the other, fierce competition may ensue, leading to substantial losses for both competitors (e.g., injury, loss of resources to a third conspecific who is not engaging in a costly dominance battle). Thus, dominance has advantages because it leads to higher status if one's competitor backs down, but dominance also has a potential downside by fueling costly confrontations. It follows that deference is another viable strategy because it allows individuals to avoid costly conflicts over status. Inspired by evolutionary game theory, we examine hormones and decision-making in the hawk-dove game, a dyadic economic paradigm that is theorized to model dominance-deference strategies and the emergence of social hierarchy (Maynard-Smith, 1982). We test the hypothesis that individuals with higher testosterone concentrations are more likely to choose a dominance strategy (hawk) over a deference strategy (dove) in repeated interactions with another real player.

Prevailing theories propose that testosterone should influence behaviors implicated in the pursuit of status—such as aggressive, competitive, and dominant behaviors—especially during periods of social competition or challenge (Wingfield et al., 1990; Mazur and Booth, 1998; Archer, 2006). Evidence in support of this *challenge hypothesis*

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has emerged across a variety of non-human animal species (e.g., birds, Wingfield et al., 1990; mice, Trainor et al., 2004; fish, Oliveira et al., 2009). Research in humans also demonstrates connections between testosterone and status-seeking behavior (for reviews, see Mazur and Booth, 1998; Archer, 2006; Eisenegger et al., 2011; Hamilton et al., 2015). Both endogenous testosterone and exogenously elevated testosterone are positively related to markers of dominance motivation (van Honk et al., 2001; Schultheiss et al., 2005; Josephs et al., 2006; Hermans et al., 2008; Bos et al., 2012; Terburg et al., 2012; Terburg and van Honk, 2013; Goetz et al., 2014; Enter et al., 2014; Radke et al., 2015; Mehta et al., 2008; Zilioli and Watson, 2013; van der Meij et al., 2016), aggressive behavior (Carré et al., 2009; Carré and Olmstead, 2015), competitive behavior (Mehta and Josephs, 2006; Carré and McCormick, 2008; Mehta et al., 2008, 2009; Slatcher et al., 2011; Mehta et al., 2015b, 2015c; Reimers and Diekhof, 2015; Hahn et al., 2016; Eisenegger et al., 2016), and reduced prosocial behaviors including trust, perspective-taking, cooperation, and empathy (Hermans et al., 2006; Mehta et al., 2009; Bos et al., 2010; van Honk et al., 2011; Boksem et al., 2013; Wright et al., 2012; Ronay and Carney, 2013; Edelstein et al., 2014).

Whereas high-testosterone individuals strive for high status and find low-status positions aversive, low-testosterone individuals are uncomfortable in high-status positions and seem to prefer *lower* status as well as cooperative social contexts (Josephs et al., 2006; Newman et al., 2005; Mehta et al., 2008, 2009; Zyphur et al., 2009; Wright et al., 2012). These findings suggest that low-testosterone individuals may be especially sensitive to the costs of dominance and status pursuit, such as an increased likelihood of costly conflicts. As a result, low-testosterone individuals may enact deference behaviors as a strategy to avoid costly status battles (Mehta and Josephs, 2006; Wingfield et al., 1990; Josephs et al., 2006).

Despite evidence linking testosterone to social behavior and status motivation, many discrepant results have also emerged. For example, research results from studies of testosterone and human economic social interactions such as bargaining games have been highly inconsistent (Burnham, 2007; Eisenegger et al., 2009; Zak et al., 2009; Zethraeus et al., 2009; Mehta and Beer, 2010; Diekhof et al., 2014; Mehta et al., 2015a; Kopsida et al., 2016). The inconsistencies may arise because these prior studies on economic social decisions have failed to tap into the motivational processes critical for revealing testosterone's behavioral effects. New studies of testosterone and decision-making are needed that more closely model status competitions and the emergence of social hierarchies. Further, prior studies have generally examined anonymous one-shot social interactions with fictitious players. Real-world competitions typically occur over longer periods of time in repeated social interactions with an actual person. Experimental designs that examine status-based interactions using a series of repeated interactions with the same person may reveal clearer associations between testosterone and social decision-making.

The hawk-dove game is a dyadic decision-making paradigm that is theorized to model status interactions and hierarchy emergence (Maynard-Smith, 1982; Matsumura and Kobayashi, 1998; Neugebauer et al., 2008; van Vugt and Tybur, 2015). Each individual can adopt a dominance (hawk) or deference (dove) strategy, and each player's strategy has implications for the distribution of resources between the two players. This game is also known as the chicken game. The name chicken comes from a game in which two car drivers drive toward each other. One must swerve or both will crash. If one driver swerves and the other does not, the one who swerves is called the chicken (coward).

Fig. 1 shows the pay-offs associated with dominance (hawk) and deference (dove) strategies. If both players choose the dove strategy, then both players receive a moderate pay-off (upper left quadrant of Fig. 1). This outcome indicates that the two individuals chose to avoid a status confrontation and cooperate instead. If both players choose the hawk strategy, then this situation results in the worst possible

		Player 2: Dove	Player 2: Hawk
Player 1	Dove	2, 2	1, 4
	Hawk	4, 1	0, 0

Fig. 1. Pay-off matrix for hawk-dove game. Pay-offs depend on each player's decision. In each box, pay-off for player 1 is listed first followed by pay-off for player 2.

outcome (lower right quadrant of Fig. 1). This indicates a status confrontation that leads to losses for both parties. If one player selects the hawk strategy and the other the dove strategy, the player who chose the hawk strategy earns a much higher pay-off than the other player (upper right and lower left quadrants of Fig. 1). Ending up in either the upper right or lower left quadrants of Fig. 1 (a hawk-dove combination) signifies the best collective outcome (if one adds up the pay-offs of players 1 and 2) and indicates that the individual who chose the hawk strategy attains higher status than the other player (status differentiation, as indicated by unequal pay-offs). The hawk-dove combination is also the most beneficial outcome for each individual. That is, if player 1 expects that player 2 will adopt the hawk strategy, then player 1 achieves a higher pay-off by adopting the dove strategy (upper right quadrant of Fig. 1). But if player 1 expects that player 2 will adopt the dove strategy, then player 1 achieves a higher pay-off by adopting the hawk strategy (lower left quadrant of Fig. 1). The hawk-dove combination represents what is referred to as the game equilibrium and is akin to the formation of a social hierarchy because resources are distributed unequally (van Lange et al., 2013; van Vugt and Tybur, 2015).[2]

Through the lens of this game, an evolutionary analysis suggests that natural selection would have favored a mixed population of hawks and doves in many social species (Maynard-Smith, 1982). With too many doves in a population, hawks gain status and acquire more resources. And with too high a hawk population, costly competitions among hawks are rampant; doves thrive in such an environment by cooperating with other doves and avoiding competition with hawks. Supporting the advantages of a mixed hawk-dove population, empirical of hawk and dove tactics in many species. For example, male dung beetles (*Onthophagus taurus*) are dimorphic in their body types (Hunt and Simmons, 2001). "Major" males are larger, grow head horns, and have excellent fighting ability as a result. "Minor" males are smaller, remain hornless, and have poorer fighting ability. Major males fight for access to females, but minor males defer status to major males and mate with females by sneaking copulations. Evidence for different social tactics (e.g., hawk versus dove) is found in many other species as well, including earwigs, spiders, salmon, birds, and orangutans (Forslund, 2003; Fromhage and Schneider, 2005; Thomaz et al., 1997; Kokko et al., 2014; Harrison and Chivers, 2007).

The hawk-dove game also has relevance for understanding status interactions in humans and how these interactions impact individual and collective outcomes. According to the structure of the hawk-dove game, both players have incentives to establish a dominant-subordinate relationship (hawk-dove combination). Research in humans provides evidence in line with this core principle of the game. Humans are indeed

[2] If interactions settle into an equilibrium state and if each player assumes that the other player's strategy is set in stone, the interaction is likely to remain at this equilibrium state because neither player obtains a better outcome by switching to a different strategy. In game theory terminology, this is known as the Nash equilibrium.

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