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SOCIAL NEUROENDOCRINOLOGY OF HUMAN AGGRESSION: EXAMINING THE ROLE OF COMPETITION-INDUCED TESTOSTERONE DYNAMICS

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Abstract—A large body of evidence indicates that individual differences in baseline concentrations of testosterone (T) are only weakly correlated with human aggression. Importantly, T concentrations are not static, but rather fluctuate rapidly in the context of competitive interactions, suggesting that acute fluctuations in T may be more relevant for our understanding of the neuroendocrine mechanisms underlying variability in human aggression. In this paper, we provide an overview of the literature on T and human competition, with a primary focus on the role of competition-induced T dynamics in the modulation of human aggression. In addition, we discuss potential neural mechanisms underlying the effect of T dynamics on human aggression. Finally, we highlight several challenges for the field of social neuroendocrinology and discuss areas of research that may enhance our understanding of the complex bi-directional relationship between T and human social behavior.

Key words: social neuroendocrinology, testosterone, competition, aggression.

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INTRODUCTION

Aggression, defined as any behavior directed toward another individual with the intent to cause harm (Baron and Richardson, 1994), evolved in the context of intraspecific competition for valued resources (e.g., food, shelter, mating opportunities, status). Thus, although aggression is widely regarded as a "negative" behavior – it is a quintessential component of our lives that can serve important adaptive functions. Despite progress in identifying some of the neurobiological factors associated with aggression (see Nelson and Trainor, 2007 for review), we know very little about the causal role of such factors in shaping variability in human aggression. Testosterone (T), a steroid hormone produced primarily by the gonads, is a prime biological candidate for mediating aggressive behavior within the context of human competition. The idea that T is related to human aggression comes from various sources: Men are generally more aggressive than women (Archer, 2009), have much higher T concentrations than women (Dabbs, 1990), and at a time when T concentrations are surging (e.g., ages 21–35), there is an increase in male-to-male aggressive behavior (Daly and Wilson,

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Abbreviations: ACC, anterior cingulate cortex; BMS, Biosocial Model of Status; GnRH, gonadotropin releasing hormone; HPG, hypothalamic–pituitary–gonadal; LH, luteinizing hormone; OFC, orbitofrontal cortex; PAG, periaqueductal gray; PSAP, Point Subtraction Aggression Paradigm; T, testosterone; UG, Ultimatum Game.

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1988). Despite T's clear association with aggression in animal models (see Simon and Lu, 2006) and its apparent link to human aggression, research indicates that individual differences in baseline levels of T are only weakly correlated with various indices of human aggression (r = .08, see Archer et al., 2005 for meta-analysis).

There are likely many reasons why the association between T and aggression is relatively weak in humans. First, it may be that only extreme, or supraphysiological concentrations of T are linked to aggression (see Pope et al., 2000), whereas normal variation in T is not. Second, it may be a measurement issue whereby human studies usually rely on self-report measures of aggression, which may not represent the most bias-free way to assess aggression. Notably, studies that use behavioral measures of aggression typically find stronger correlations between baseline levels of T and aggression (see Archer et al., 2005 for meta analysis). Third, researchers usually do not differentiate between reactive and proactive forms of aggression, which may in part underlie some of the inconsistencies observed in the literature. Reactive aggression is a defensive response to perceived or actual provocation and is characterized by anger, impulsivity, disinhibition, affective instability, and high levels of bodily arousal (Dodge and Coi, 1987). In contrast, proactive aggression occurs in the absence of direct provocation and is a goal-oriented behavior aimed at the acquisition of a valued resource (Dodge and Coi, 1987). Only a few studies have examined associations between individual differences in T and measures of reactive and proactive aggression. One study reported that baseline levels of T were positively correlated with reactive and proactive aggression in adolescent males (van Bokhoven et al., 2006), whereas another study found that baseline levels of T were positively correlated with reactive, but not proactive aggression (Olweus et al., 1988). Finally, many studies have relied on single measurements of T when examining correlations with self-report measures of aggression. This is quite problematic given that T concentrations are highly variable, fluctuating throughout the day (diurnal variation), the season, and in response to various social interactions. Indeed, a large body of work in both humans and non-human species indicates that competitive interactions rapidly potentiate T release (Wingfield et al., 1990; Archer, 2006; Oliveira, 2009; Oliveira and Oliveira, 2014). Thus, some have argued that acute fluctuations in T within the context of social competition may be more relevant to our understanding of individual differences in mating effort (including aggression) than baseline levels of T (McGlothlin et al., 2007). In this paper we review recent human work examining the relationship between T dynamics and competitive/aggressive behavior and draw comparisons to evidence from animal models. We also discuss recent neuroimaging work and speculate about a potential neural mechanism underlying links between T dynamics and human aggression. Finally, we highlight challenges to progress and suggest future research directions. Before reviewing the empirical work, we first present an overview of the 'Challenge Hypothesis' and the 'Biosocial Model of Status', two of the main theoretical models guiding current research on the bidirectional relationship between T and aggressive behavior.

TESTOSTERONE RESPONSES TO INTRA-SEXUAL COMPETITION

Challenge Hypothesis

The 'Challenge Hypothesis' was originally developed in an attempt to explain intra- and inter-species variation in T secretion in birds. Wingfield and colleagues (1990) noted that T concentrations fluctuate around three levels during the season: Level A, constitutive baseline; Level B, breeding baseline; and Level C, physiological maximum. In monogamous male birds that provide paternal care, T concentrations remain low during the non-breeding season (Level A). T increases (Level B) at the start of the breeding season as a means to initiate spermatogenesis, expression of secondary sex characteristics and the full display of male reproductive behavior. Finally, T may further increase (Level C) in response to intra-sexual competitive interactions as a means to facilitate territorial and aggressive behavior. When intra-sexual competition decreases, T concentrations return to Level A. It has been proposed that the costs associated with maintaining elevated T concentrations throughout the season (e.g., decreased paternal care, increased risk for physical injury/death, depressed immune function, increased energetic demands) may have led to a highly flexible endocrine system capable of modulating T concentrations in response to changes in the social environment (Wingfield et al., 2001). Although originally proposed to account for the trade-off between mating and parental efforts in birds, support for the Challenge Hypothesis has now been obtained in numerous taxa including fish (Oliveira, 2009), non-human primates (Bernstein et al., 1974; Sobolewski et al., 2013), humans (Archer, 2006), and insects (Tibbetts and Crocker, 2014).

Biosocial Model of Status

The 'Biosocial Model of Status' (BMS; Mazur, 1976, 1985; Mazur and Booth, 1998) is a conceptually similar theoretical model adopted primarily by researchers studying human competition and aggression. One important difference between the 'Challenge Hypothesis' and the BMS is that the latter makes the additional prediction that T concentrations during competition will vary as a function of the outcome of the competitive interaction with T concentrations increasing in winners and decreasing in losers. Although the BMS has mainly been studied within the context of human competition, its main predictions were guided by research in male rhesus monkeys. In a series of experiments, Rose and colleagues (1972, 1975) found that male rhesus monkeys successful in aggressive interactions (i.e., winners) experienced marked elevations in T, while unsuccessful males (i.e., losers) experienced decreased T concentrations. A number of studies have examined this 'winner/loser effect' in humans and have found elevated T concentrations in winners relative to