

Testosterone and human behavior: the role of individual and contextual variables

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The study of testosterone and aggression originated in experimental studies of animals, showing a direct causal link in some species. Human studies showed an overall weak correlation between testosterone and aggression. A theoretical framework ('the challenge hypothesis') enabled testosterone-behavior interactions in humans to be framed within a theory that emphasized hormonal responses to competition influencing subsequent aggressive behavior. The short-term administrations of testosterone to young women and to young men showed influences on behavioral and neural processes associated with aggression. Other findings are that testosterone influences aggression in high dominance men, and in those with low cortisol levels; and that testosterone can affect both aggressive and prosocial behavior, within the context of an experimental game.

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Introduction

Studies showing a link between testosterone and aggression have their origin in experimental studies of animals, first involving domestic fowl [1], and then house mice [2]. These were followed by correlational studies with humans, using a variety of measures of aggression and of testosterone. From the initial human study [3] to the early 2000s, a meta-analysis of 42 studies found an overall correlation of $r = 0.08$ between testosterone and measures of aggression [4^{*}], associations being greater for samples of younger men and for offenders. Other meta-analyses have found associations in boys, and in women [5^{**}].

There are three considerations that prevent the conclusion that there is a direct causal link between testosterone and aggression in humans, as there is in a range of vertebrates [6]. First, being successful in competitive situations, including those involving aggression, can lead to increased testosterone; this could accumulate over repeated successes to increase the testosterone levels of more competitive individuals. Second, there is evidence that levels of aggression do not increase at puberty in humans coincidental with rising testosterone levels [7]. Third, several controlled trials of the impact of long-term injections of testosterone on mood and behavior have produced null results overall [5^{**}], although studies of the short-term oral administration of testosterone to women show a range of changes, including features associated with aggression (*e.g.*, [8–10]), and with greater activity in brain regions associated with aggression [11–13].

The challenge hypothesis

Much of the existing evidence connecting testosterone and behavior in humans can be understood in terms of the evolutionarily-based 'challenge hypothesis', originally applied to birds [14,15]. The essence of this hypothesis is that since consistently high levels of testosterone have maladaptive consequences, such high levels should be restricted to times of high reproductive competition, particularly in species where there is bi-parental care, as in humans (see Ref. [16], for an update of its cope). The Challenge Hypothesis involves a number of predictions for humans: (1) there will be no increased aggression in males at puberty, despite the increased testosterone levels; (2) men will respond to sexual and competitive stimuli with increased testosterone; (3) increased testosterone will lead to more competitive aggression; (4) paternal care will lower testosterone levels. The evidence, first reviewed in the mid-2000s [5^{**}] and subsequently updated [17] broadly supports these predictions.

There is also considerable situational and individual variability, which can sometimes be predicted by the challenge hypothesis. Thus, paternal care is associated with lowering of testosterone levels [18,19]. There are also differences in the extent to which individual men prioritize parental or mating behavior, and this is correlated with their testosterone levels [5]. More recent evidence indicates considerable individual and situational variability in the testosterone-behavior link, indicating that this is more nuanced than expected solely from the challenge hypothesis.

Experimental studies of short-term effects of testosterone

A meta-analysis of the correlational studies of hormones and aggression [4] indicated considerable variation in the size of the hormone-behavior link. These earlier studies differed methodologically, and were restricted in several ways, for example reliance on self-reports, single measures of testosterone, and not taking into account context-dependent changes in testosterone. Subsequent experimental studies (for a review, see Ref. [17]) introduced greater control of both the behavioral measures and the manipulation of testosterone levels. However, they were limited in that they used young women as participants (the physiological protocol was only available for women at the time), and thus involved testosterone levels higher than the participants would experience from their endogenous levels. Recent studies have begun to overcome these limitations. It is now possible to investigate the extent to which single administrations of testosterone influence behavioral and neural processes in young men (*e.g.*, [20,21,22]). This research shows both contextual and individual differences in the links between testosterone and aggression.

Establishing the link between testosterone and aggression

Although there is inconsistent evidence for a link between trait-level (*i.e.*, baseline) testosterone and human aggression [4], a growing body of evidence suggests that acute changes in testosterone within the context of competition and/or social provocation may be more relevant for understanding individual differences in human aggression [23]. For example, two studies reported that acute changes in testosterone concentrations during competition were positively correlated with aggressive behavior measured on the Point Subtraction Aggression Paradigm, an established behavioral measure of reactive aggression in humans [24]. These findings occurred in men, but not women [25,26]. Another study demonstrated that a long-term intervention program designed to curtail antisocial behavior in 'at-risk' youth was successful, in part, because it dampened testosterone responses to social provocation [27]. This intervention was implemented in kindergarten, and the children assigned to the intervention condition received social-cognitive-behavioral therapy, whereas those assigned to the control condition received no such treatment. Twenty years after the intervention, participants were recruited for a laboratory session in which they performed the Point Subtraction Aggression Paradigm. The intervention group showed less aggression on the Point Subtraction Aggression Paradigm and decreased testosterone reactivity to social provocation than the control group. Notably, the association between assignment to the intervention condition and decreased aggression was statistically mediated by decreased testosterone reactivity to provocation [27]. Collectively, these findings are consistent with

experimental research in animals demonstrating that competition-induced changes in testosterone play a key role in modulating aggressive behavior [28,29]. This research has clearly established a causal role of testosterone in potentiating aggressive behavior.

Pharmacological challenge studies

During the past decade, pharmacological challenge studies indicate that a single dose of testosterone to healthy young women modulates various physiological (threat-related brain function) and behavioral (empathy, attention toward angry faces) processes relevant to human aggression (see Ref. [23] for review). Similar pharmacological challenge studies in men have only recently been conducted. In one study, a single application of testosterone to healthy men rapidly (within 90 min) increased amygdala, hypothalamus, and periaqueductal grey reactivity to angry facial expressions [21]. These findings are notable for several reasons: (1) similar effects of exogenous testosterone have been found in women [11,12]; (2) these subcortical brain structures are rich in both androgen and estrogen receptors [30–32]; and (3) these regions play a key role in potentiating reactive aggression in animals [33]. Studies outside the scanner have also yielded interesting effects of testosterone on social cognition and behavior. For instance, one study [34] found that a single application of testosterone increased men's perceptions of their own facial dominance. This finding suggests that the link between testosterone and human aggression in men may be due to testosterone's effects on a man's perception of his own physical formidability. In a more recent study [35], healthy young men ($n = 121$) perform the Point Subtraction Aggression Paradigm after receiving either testosterone or a placebo. Testosterone rapidly (within 60 min) increased aggression in men, but only to the extent that such men scored high on a self-report measure of trait dominance and/or low on a measure of trait self-control. This research is consistent with other experimental and correlational findings indicating that testosterone modulates competitive motivation [36] and aggressive behavior [25], but only among individuals relatively high in trait dominance.

Further evidence of the importance of trait dominance

The finding of an interaction between testosterone and trait dominance is highly consistent with other correlational and experimental work. For instance, one study reported that a rise in testosterone among male winners of a competitive interaction predicted increased aggressive behavior in a subsequent task—but only among men scoring relatively high in trait dominance [25]. In another study, individual differences in baseline testosterone concentrations were positively correlated with men's dominance behavior during mate competition, but only for men scoring high in trait dominance [37]. Administration of testosterone to women also increased their

competitive motivation after a victory, but only for those scoring high on trait dominance [36]. Collectively, this research highlights the importance of considering individual differences in personality when examining links between neuroendocrine function and human aggression.

Testosterone and the ultimatum game

Other correlational and pharmacological challenge studies examined the role of testosterone in modulating ultimatum game behavior. The ultimatum game is a behavioral economics task whereby a proposer is given a sum of money (*e.g.*, \$10) and has the opportunity to offer as much, or as little money to a receiver. Once the offer is made, the receiver has the choice to either accept or reject the offer. If the offer is accepted, both participants receive their split of the money. If the receiver rejects the offer, both participants leave with no money. Rejection behavior on the ultimatum game can be considered a form of aggressive behavior as its main function is to cause harm (*i.e.*, financial harm) to another individual, following what is considered an unfair offer. Two correlational studies have reported that men and women with relatively high baseline concentrations of testosterone are more likely to reject unfair offers [38,39]. In contrast, pharmacological challenge research in both men and women have not found these effects of testosterone on rejection behavior in the ultimatum game [40–42,22]. In a recent study [43], researchers investigated the effect of exogenous testosterone on men's punishment and reward behavior following unfair and fair offers in the ultimatum game. They found no effect of testosterone on rejection behavior in the ultimatum game. Nevertheless, men who received testosterone were more likely to pay money to punish proposers who made unfair offers, but at the same time, they were more likely to *reward* proposers who made fair offers [43]. This work indicates that testosterone can have both antisocial and prosocial effects on behavior depending on context. These findings suggest that rewarding fair proposers, and punishing unfair proposers in the ultimatum game, may be ways in which a person can maintain his or her social status and reputation—and that testosterone plays a key role in modulating status and reputational concerns (see Ref. [41]).

Testosterone–cortisol interactions

In addition to psychological and contextual moderators, a growing body of work suggests that individual differences in cortisol, the end product of the hypothalamic pituitary adrenal (HPA) axis, affects the degree to which testosterone influences variation in human aggression. In the first study to investigate the moderating role of cortisol [44], researchers found that salivary testosterone concentrations among male teenage inmates (17–18 years old) were positively correlated with severity of violent crimes committed, but this effect was only found among males with relatively low salivary cortisol concentrations. Similarly, testosterone concentrations of young adolescent males

(12–14 years old) were positively correlated with a self-report measure of overt aggression, but only among males scoring relatively low in cortisol concentrations [45]. Despite these findings, others have reported mixed results—some finding no moderating effects of cortisol [46,47], and others that testosterone positively predicts aggression and aggression-related phenotypes (*e.g.*, psychopathic traits), but only among those with *high* cortisol concentrations [48,49]. Consistent with the literature reviewed above, recent evidence suggests that trait dominance influences the degree to which testosterone and cortisol interact to predict human aggression. Specifically, testosterone positively predicted antisocial punishment, but only among individual scoring low in cortisol *and* high in trait dominance [50]. Clearly, more research on this topic will be necessary to determine the role that cortisol plays in moderating effects of testosterone on aggression.

Conclusions

Research on testosterone and human aggression has its roots in animal studies, some of which showed a straightforward causal link in animals, for example in the classic ablation-replacement studies using laboratory mice. Studies on humans followed from the 1970s onwards, when an overall weak association was found between testosterone and aggression, but no effect of long-term injections of testosterone in men. Recent work has progressed via a more subtle theory encompassing the testosterone–aggression link in humans and other animals (the challenge hypothesis) and through methodological advances enabling the short-term effects of hormones to be studied in the laboratory, first in women, and more recently in men. Overall these studies have shown subtleties in the testosterone–behavior relationship, so that it is now clear that this is subject to both individual difference and contextual variables, in particular: (1) testosterone influences aggression in high dominance men, and in those with low cortisol levels; and (2) studies with the ultimatum game show that testosterone can affect both aggressive and prosocial behavior.

Conflict of interest statement

Nothing declared.

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