Review

The role of testosterone in social interaction

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Although animal researchers established the role of testosterone as a 'social hormone' decades ago, the investigation of its causal influence on human social behaviors has only recently begun. Here, we review and discuss recent studies showing the causal effects of testosterone on social interactions in animals and humans, and outline the basic neurobiological mechanisms that might underlie these effects. Based on these recent findings, we argue that the role of testosterone in human social behavior might be best understood in terms of the search for, and maintenance of, social status.

Testosterone in context

Testosterone is one of the major sex hormones produced by the body, occurring in both men and women. In men, it is mainly produced by the Leydig cells of the testes, whereas the ovaries and placenta produce it in women. The adrenal cortex also secretes it in both sexes [1]. Testosterone has a well-known and important role in the development of secondary sexual attributes; for example, increased muscle, bone mass and body hair in men. However, it is also of special interest in the study of socio-emotional and economic behavior because it influences the brain in archetypical situations, such as fight, flight, mating and the search and struggle for status [2].

Three recent developments argue for a causal role of testosterone as a 'social' hormone. First, recent years have seen the advent of acute single-dose testosterone administration studies in humans. This methodological innovation is important because it enables the study of the effect of testosterone on complex social interactions between human subjects, rather than its impact on the more difficult to interpret behavioral repertoire of non-human animals. Moreover, testosterone administration studies can establish the causality of testosterone in facilitating particular motives and behaviors.

Second, the advent of sophisticated behavioral paradigms allows for the study of social emotional processes, such as threat vigilance, and affiliative behaviors, such as facial mimicry, emotion inference and trust. These paradigms not only make it possible to assess whether the hormone plays a role in modulating behavior, but also add to the understanding of the motives that might underlie human interactions. Third, the integration of experimental economic paradigms into the study of hormonal effects on behavior provides an opportunity to identify the precise channels through which testosterone affects social interaction in a controlled laboratory environment.

Together, these advances offer an exciting new opportunity to reassess the role of testosterone in driving behavior. Here, we summarize recent evidence using these approaches and argue that the role of testosterone in social interaction in humans might be best conceptualized as bringing motives for seeking social status to the fore. We also discuss the psychological and neurobiological channels that might underlie these effects.

Animal models of the role of testosterone in social interactions

Early evidence for the role of testosterone in social behavior suggested that it facilitates overt physical aggression (see Glossary) in social contexts. For instance, castrated rodents, which have little, if any, testosterone circulating in their blood, show a near-complete absence of physical fights; however, fights can be fully restored by providing testosterone supplementation to these animals [3].

Glossary

Aggression: behavior with the intent of inflicting physical or psychological harm on another individual.
Anti-predatory aggression: aggression in defense against predatory aggression.
Dominance aggression: aggression with the aim of achieving dominance over another individual; for example, during competing for food or valued resources, or in resisting control measures.
Dominance hierarchy: the organization of individuals in a group into those that are dominant and those that are submissive, as part of competition for resources. In rodents, competition is aggressive. In non-human primates, status is often allocated by non-aggressive, ritualized gestures, rather than by overt aggression.
Dominance: the motivation to achieve or maintain high social status; that is, to obtain power, influence, or valued prerogatives over another individual.
Irritable aggression: aggression directed towards an available target, living or non-living, induced by some sort of frustration event.
Predatory aggression: aggression aimed at chasing, catching and killing prey.
Proactive aggression: aggression carried out with a purpose in mind that extends beyond simply harming a victim. It tends to be 'calculated' and is characterized by low physiological arousal.
Reactive aggression: aggression as a defensive response to perceived or actual provocation. It involves retaliation and is characterized by anger and often accompanied by disinhibition, affective instability and high levels of arousal.
Territorial aggression: aggression between two conspecifics fighting for the right to claim prime hunting grounds, mating rights, or a safe place to rear young.

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However, the role of testosterone in facilitating aggression appears to be limited to specific social forms of aggression, such as territorial and dominance aggression (e.g. [1]). By contrast, it appears that testosterone is less involved in other non-social forms of aggression, such as predatory and anti-predatory aggression [4].

Conversely, physical aggression influences testosterone levels. This well-acknowledged fact is captured by the Challenge Hypothesis originally postulated for birds [5], which states that, perhaps owing to the costs of chronically elevated testosterone levels [6], testosterone levels rise only in response to challenges (e.g. during the mating season), whereas they are low during periods of social stability. (Note that testosterone decreasing as a result of losing challenges has also been reported in animals; however, we focus here on testosterone increases to prepare the ground for later discussion of the effects of exogenous testosterone increases through administration in humans.) Such challenge-induced rises in testosterone, in turn, can elevate the winning probability in subsequent conflicts (winner effect). Further experiments showed that the presence of testosterone is a necessary condition for this winner effect to occur [7].

Testosterone and human aggression

Does testosterone have the same aggression-related behavioral effects in humans as it appears to have in non-human animals? This question continues to generate substantial controversy in the literature. Two factors could be related to this.

First, studies on physical aggression in humans have been limited to researching the correlation between plasma hormone levels and observed aggressive behaviors in field studies. For instance, high testosterone levels in male prisoners have been linked to having a history of rape, murder and armed robbery, and relatively lower levels to a history of theft and drug abuse [8]. A similar pattern was observed in a study of female prison inmates [9]. However, the causality in these studies remains unclear: the higher levels of aggression might well have caused the higher testosterone levels, leaving open the question of whether testosterone is a causal factor driving this behavior.

The second problem in establishing the role of testosterone in driving behavior is the complexity of human aggression. In particular, human aggression often takes purely psychological or even economic forms, rather than being overtly violent. In addition, different motives might underlie these behaviors in humans; for example, offensive aggression primarily intended to achieve a goal, as opposed to reactive aggression (i.e. a defensive response to provocation) [10,11]. Moreover, aggression in humans is often measured by self-report and frequently emphasizes trait aggression at the expense of context-dependent aggression [11]. Not surprisingly, therefore, the existing evidence for a link between aggression and testosterone in humans is relatively weak, but positive [12]. Even if one accepts the fact that reactive aggression can be measured in a controlled laboratory environment, results are similarly inconclusive: recent studies found a positive relationship between baseline testosterone levels and laboratory measures of reactive aggression (reviewed in [11]), but others also reported null findings (in larger samples) [13]. Most importantly, however, a causal role for testosterone in forms of reactive aggression could not be confirmed, as neither long-term nor acute administration of testosterone had an effect [13,14].

In summary, although there is some evidence suggesting a role for endogenous testosterone levels in physical and non-physical forms of aggression, results are conflicting and inconclusive. In addition, there is no evidence for a direct causal link between testosterone administration and laboratory measures of non-physical aggression in humans.

Testosterone and social status

In contrast to the controversial role of testosterone in aggression, a mounting body of evidence in both animals and humans suggests that testosterone drives a more general repertoire of motivated behaviors, often subsumed under the concept of dominance behavior [1]. Dominance behavior refers to the motivation of an individual to achieve or maintain a high social status, which appears to be achieved non-aggressively in primates [15]. Thus, testosterone seems to influence an underlying motive rather than aggression per se. For instance, rhesus monkeys with high testosterone levels use stares, threats and displacements, rather than overtly aggressive interactions, to ascertain high social status [16]. In humans, status might be asserted in similarly subtle ways; for example, in face-to-face interactions by increased staring duration, speech duration and body postures displaying supremacy [15] (Figure 1). Nevertheless, physical violence might still be a component of status-seeking behavior in certain contexts [17] and it has been emphasized that one must control for whether the aggression displayed is suitable for improving the social status of a subject [18]. It is possible that this might ultimately reveal a more consistent positive relationship between adaptive aggressiveness in the context of status seeking and testosterone (Figure 1).

Baseline testosterone as a biomarker of social interactions

Do testosterone levels affect status-seeking behaviors? A first approach to this question is to ask whether baseline levels of testosterone correlate with these behaviors. Answering this question has recently become possible through the advent of valid tools for measuring bioactive steroid hormones in human saliva. Indeed, measurements of testosterone at a single time-point correlate positively with high dominance in both adolescents [19,20] and adults [21,22]. In addition, salivary testosterone levels correlate with implicit measures of power motivation [23] and increased vigilance for status threats [24,25]. As a result of these relationships, and the moderate stability of testosterone levels over time, some have suggested that baseline testosterone levels reflect a personality trait [26].

An alternative view, however, states that basal testosterone levels do not only correlate with particular behaviors, but also respond to the social environment. We discuss this evidence next.

Social modulation of testosterone

Do social interactions, in turn, also affect testosterone levels? An impressive example of context effects on

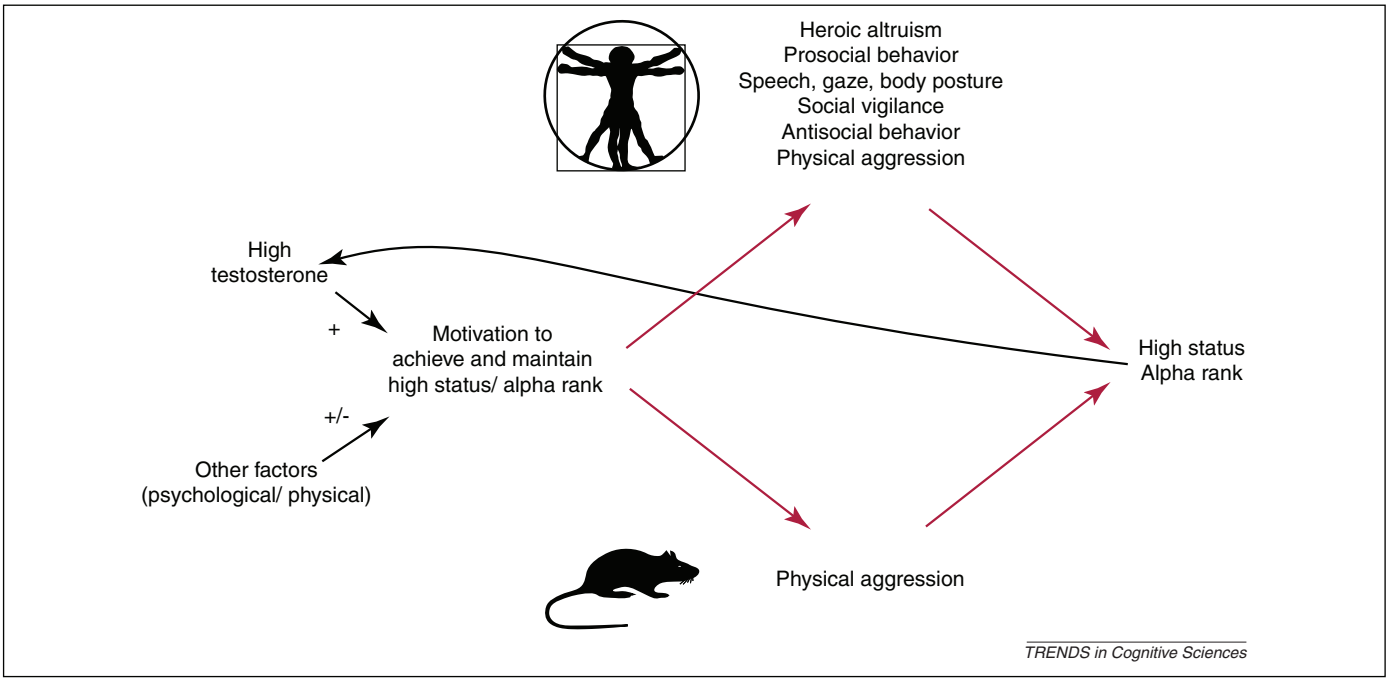

Figure 1. Illustration of the different means used by rodents and humans to achieve and maintain high status and/or alpha rank. High or acutely rising testosterone levels probably have a positive influence on the status motive, and achievement of a high status position might then increase testosterone further. Other factors (psychological or physical) might facilitate and/or inhibit this motivation independently of testosterone.

testosterone is the recent finding that men show a larger increase in testosterone when exposed to the scent of an ovulating woman compared with that of a non-ovulating woman or a control [27].

Apart from sexual social stimuli, which are reliable inductors of a testosterone response [28,29], social interactions outside a direct reproductive context have also been shown to induce a testosterone response [1]. In particular, testosterone levels rise within minutes in anticipation of both physical and non-physical competitive situations; for example, dyadic food competition in chimpanzees [30], or tennis, chess or domino tournaments in humans (reviewed in [31]).

Testosterone also reacts to contest outcomes [32], and not just to anticipation: for instance, stock traders show higher testosterone levels if their daily profits are above average, and winners of soccer matches show higher testosterone levels than do the losers [33]. One potential problem with these results is the question of causality, as winning a competition might be a consequence, not a cause, of higher testosterone levels. However, causal manipulation of social context (e.g. rigged contests) confirms a causal effect of winning situations on testosterone levels (e.g. [34–38]). These effects can be large; for example, merely watching oneself win a competitive interaction on video produces a 40% testosterone surge from baseline [37].

In sum, findings suggest that testosterone is both a cause and a consequence of competitive interactions. However, conclusive establishment of the direction of causality requires the exogenous administration of testosterone. As we show below, the recent development of clean methodological approaches for studying testosterone administration effects [39], combined with the recent development of new paradigms, allows a deeper insight into the causal effects of testosterone on a range of social–emotional behaviors that tend to increase the motivation and ability of an individual to acquire and defend social status.

Testosterone effects on social emotional behaviors in face-to-face interactions

In primates, status can be established and maintained through a series of short, face-to-face interactions [40]. Several recent studies suggest that testosterone facilitates particular social emotional mechanisms that tend to enhance the ability of an individual to achieve and maintain a high social status.

Processing of facial emotional expressions

An angry facial expression serves as an important threat signal in face-to-face dominance encounters [41]. In a comprehensive set of experiments, van Honk and colleagues established that individuals who generally have higher scores on self-reported dominance and higher basal levels of testosterone show vigilant responses to angry facial expressions (reviewed in [42]). Furthermore, exogenous administration of testosterone increases the sympathetic heart-rate response to angry, but not to happy facial expressions [43] (Figure 2). Although this could theoretically also reflect autonomic arousal as part of a fear response, testosterone has been shown to reduce fear [44], suggesting that dominant people perceive an angry face as a challenge.

Affiliative processes

Because humans are generally not inclined to affiliate with those with whom they expect to compete, a relative suppression of affiliative processes could benefit those who seek to improve their social status through competition

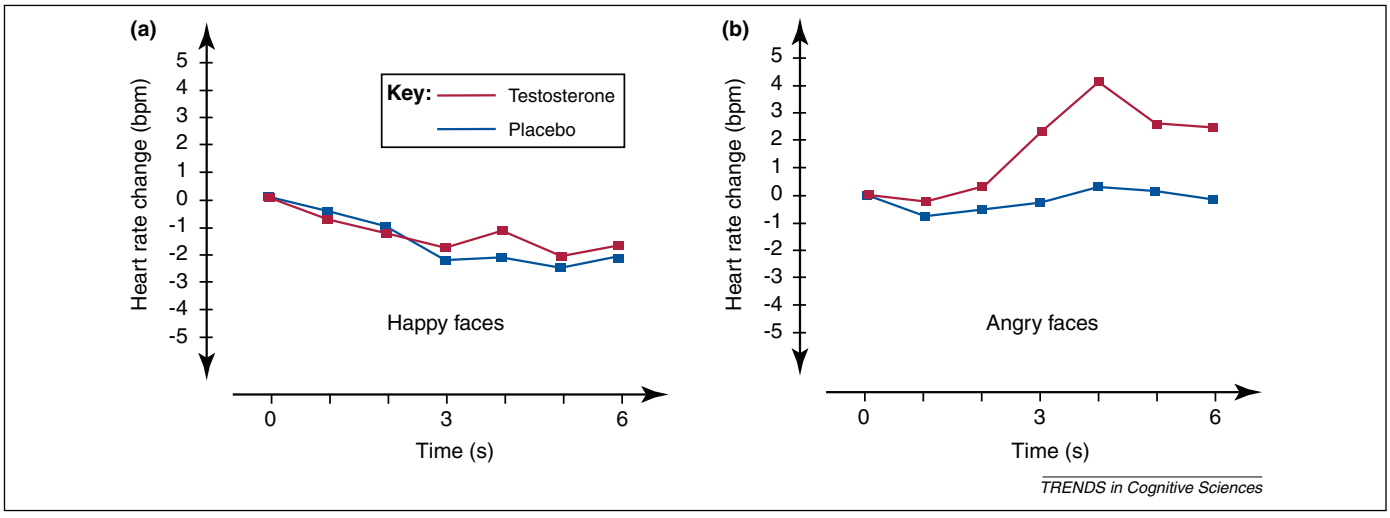

Figure 2. Mean heart rate change in beats per minute (bpm) from baseline (1 s before stimulus presentation) during the presentation of happy **(a)** versus angry **(b)** faces under testosterone (red) versus placebo (blue). Relative to placebo, testosterone administration induces a positive sympathetic response to the angry facial expressions **(b)**, an effect that is not observed in the happy faces condition **(a)**. Adapted from [43].

with others. Indeed, reduced facial mimicry, which is a precursor of empathy-related processes occurring automatically and without conscious awareness [45], has been observed when subjects face an explicit competition situation [46] and when they are subliminally presented with competition primes [47]. Notably, a recent testosterone administration study has shown that facial mimicry in response to emotional facial expressions is relatively suppressed after a single dose of testosterone [48].

Humans are generally aware of, and concerned with, the emotions of others. In the competition for status, however, this awareness might be detrimental, as it could boost concern for the other party at the expense of one's own status drive. Thus, if testosterone facilitates status seeking, it is conceivable that it might suppress emotion inference capacity. Indeed, it has recently been shown that a single administration of testosterone to young females leads to a significant impairment in the ability to infer emotions, intentions and feelings from the eye region of the face [49]. In addition, the same study established that subjects' second-to-:fourth digit ratio, which is thought to be a marker of prenatal testosterone exposure, is largely able to predict this effect and, thus, represents an important link between putative early androgen priming and testosterone challenge in the adult [49].

Finally, placing high trust in others in a dyadic competition is generally non-adaptive, as it might be easily exploited [50]. In line with this are findings of decreased trustworthiness ratings of facial photographs in subjects who received a single dose of testosterone [51]. Crucially, this effect was driven most strongly by those who trusted easily, suggesting that testosterone adaptively increases social vigilance in these trusting individuals to better prepare them for competition over status and valued resources [51].

Thus, testosterone appears to modulate a host of social–emotional processes that are relevant to status seeking in face-to-face interactions. In particular, it enhances sympathetic arousal in response to angry faces and suppresses facial mimicry, emotion inference and trust.

Because it is known that both humans and non-human primates use stares and eye aversion as important mechanisms for establishing and maintaining position in the status hierarchy of the group [40], a gaze aversion measure could be considered to be an ecologically valid measure of dominance in human face-to-face interactions. Recent results provide direct support for the hypothesis that speed of gaze aversion from masked facial anger depends on self-reported motives of dominance and submission [52]. Thus, future studies could ask whether testosterone also modulates this process.

Testosterone effects on economic interactions in anonymous settings

Status motives do not only affect behavior in face-to-face interactions [15], but can also play a role in anonymous interactions. It is possible, for example, to set up situations in which individuals compete for money [53] or can acquire a reputation [54] anonymously. Likewise, the proposer might perceive a rejection of her offer as aversive owing to status concerns in the ultimatum game [13]. The human motivation to form and maintain a good reputation [54] or the motivation to exercise authority (Fehr, E. *et al.* (2010) The lure of authority: motivation and incentive effects of power. A working paper; available from: http://www.hec.unil.ch/hec/hec_en_bref/evenements/deep/Herz%20-%20The%20Lure%20of%20Authority.pdf) are clearly related to status-seeking behavior. Status-related motives can thus even play an important role in anonymous settings, both in competitive and non-competitive environments.

The first study to use a causal testosterone administration procedure in an experimental economic setting did not find any effects on several economic social interactions [14]. Because the study used long-term administration of testosterone, this null finding might be due to secondary feedback effects on the neuroendocrine axis (i.e. suppression of endogenous testosterone production owing to chronic administration). In general, acute administration shows greater reliability in the production of both behavioral and neurophysiological effects (reviewed in [55]).

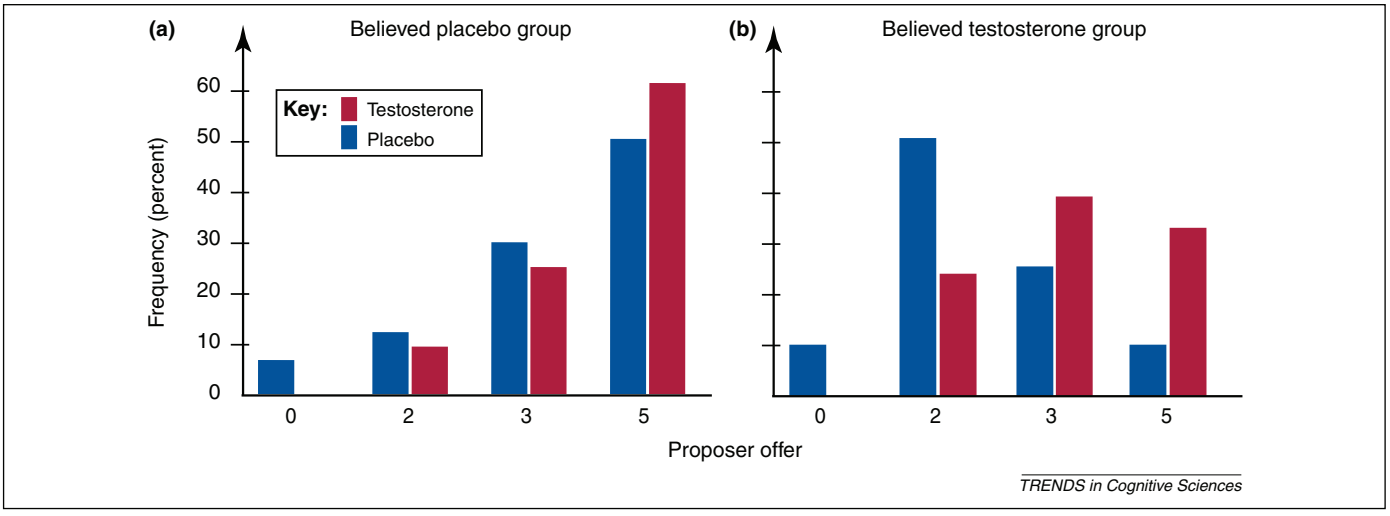

Figure 3. The frequency distribution of proposers' offers across treatments and beliefs in an ultimatum game under testosterone (red) versus placebo (blue). **(a)** The distribution of offers in the placebo and the testosterone group in those subjects who believed that they had received placebo. An overall left shift is observed in the frequency distribution of offers in the placebo and the testosterone group in those subjects who believed that they had received testosterone **(b)**. Adapted from [13].

What are the causal effects of testosterone administration on economic interactions when the administration procedure is acute rather than chronic? Folk wisdom holds that testosterone causes antisocial, egoistic, or even aggressive behaviors in humans. However, the correlational studies discussed above already suggest that this simple folk view probably requires revision [34,56]. A recent placebo-controlled testosterone administration study found support for the idea that the testosterone–aggression link might be based upon 'folk' views: individuals given placebo who believed they had been given testosterone showed less fair bargaining offers compared with those who believed that they had received placebo, thus confirming people's stereotypes about the behavioral effects of testosterone. More importantly, however, when statistically controlling for this belief of treatment assignment, one acute dose of testosterone in women increased the fairness of proposers' bargaining offers in an ultimatum game [13] (Figure 3). An important motive driving proposer behavior is to avoid the rejection of the offer. Thus, if testosterone increases the concern for status, subjects who received testosterone might have perceived a rejection as more aversive, inducing them to make fairer offers.

A caveat with respect to the findings in [13] is that beliefs about the treatment assignment were measured after the ultimatum game by self-report and, hence, the belief formation might have been endogenous (i.e. the behavior affected beliefs and not vice versa); future studies might therefore test whether a causal manipulation of beliefs about testosterone treatment allocation confirms this result. Another study [57] found that testosterone administration prior to an ultimatum game resulted in decreased generosity in a sample of healthy males if repeated measures were not controlled for. The results are insignificant, however, if the fact that the same subject participated in the ultimatum game several time is correctly controlled for statistically. Moreover, a recent study suggests that a low second-to-:fourth digit ratio (high prenatal testosterone exposure) is associated with unfair proposer offers if subjects had previously received an unfair offer when in the responder role [58]. Many possible spill-over effects can thus occur in a within-subject design such as that used in [57], where subjects repeatedly play as a proposer and a responder, rendering the interpretation of the results difficult.

In summary, recent evidence indicates that testosterone not only influences social behavior in face-to-face situations, but also in anonymous economic interactions. Future placebo-controlled testosterone administration studies could investigate the role of testosterone in reputation formation or the motivation to exercise authority. Furthermore, as testosterone has mostly been linked to competition in animals, an exciting prospect for future studies is the investigation of the causal effects of the hormone in zero-sum games.

Neurobiological mechanisms underlying the role of testosterone in social status hierarchies

Recent advances have focused on a distinctive set of psychological, neuroendocrinological and neurochemical processes that are modulated by testosterone and are relevant in the context of social status hierarchies. Maintaining a high status position requires an increased sensitivity for aversive events and impending social threats, particularly those that challenge the high social status of an individual. As we show below, testosterone appears to be able to influence such processes; in particular, it appears to confer high motivational drive, low fearfulness and high stress-resilience, either directly or via interactions with other hormones and neurotransmitter systems.

Amygdala and threat vigilance

Human neuroimaging findings have identified the amygdala and orbitofrontal cortex (OFC) in responding to angry facial expressions [59,60]. The amygdala is a brain structure that is rich in androgen receptors [61] and affected by circulating androgens [62]. Among healthy young men, the blood oxygen level-dependent (BOLD) response in the

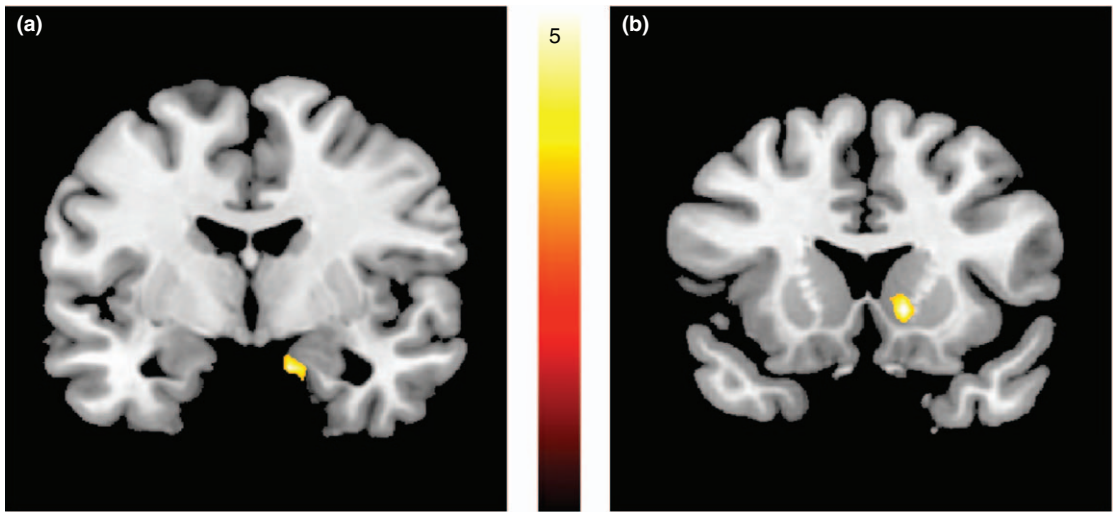

Figure 4. Testosterone-enhanced activation of the right amygdala in the contrast 'angry versus happy faces' **(a)**. Enhanced activity of the ventral striatum after testosterone administration in the contrast 'reward versus non-reward' trials **(b)**. Both images are overlaid on a canonical T1-weighted anatomical image. Adapted from [66] **(a)** and [82] **(b)**.

amygdala to fearful and angry faces co-varies positively with individual differences in serum testosterone concentrations ([63,64], but see [65]). Exogenous testosterone has been shown to activate the amygdala in young women viewing angry facial expressions [66] (Figure 4). A mechanism underlying these observations might be that testosterone induces a functional decoupling between OFC and amygdala activity [67,68].

An intriguing twist to the account above is the possibility that testosterone effects in the amygdala are not mediated by testosterone itself, but by its metabolite, the sex steroid estradiol, which is classically associated with the female neuroendocrine system. This metabolization is mediated by the enzyme aromatase, a protein that has recently attracted much interest [69]. Aromatase is expressed in the brain of all mammals and is found in areas implicated in the regulation of social behaviors [70]. Using the positron emission tomography (PET) ligand [11]C-vorozole, high binding affinity to aromatase *in vivo* was detected in the amygdala of rhesus monkeys [71] and humans [72]. Relevant in this context is also the fact that variants in the aromatase gene have been associated with different degrees of self-reported harm avoidance [73]. An exciting approach for future behavioral studies in humans might thus involve testosterone administration with a concurrent pharmacological inhibition of aromatase, and aromatase ligand–PET studies.

Reward and motivation

Another possible mechanism through which testosterone might promote status-seeking behavior is by a modulation of reward processing and motivational drive in the dopaminergic system, in particular in the striatum. Reward processing is considered to be a crucial element in social interactions [74] and social hierarchies [75] and has been shown to be influenced by testosterone. Rodents exhibit place preferences for testosterone administration [76]; this effect has been localized to the nucleus accumbens shell, an important reward region in rodents [77], and can be blocked by dopamine receptor antagonists [78]. Reward-based reinforcement effects in animals have been observed within short time periods (30 min) after systemic administration of testosterone [79], suggesting that a testosterone surge following a status-relevant social stimulus might reinforces any behavior that led to that testosterone response in the first place. In humans, patients who are hypogonadal (testosterone levels too low) show apathy and lack of motivation [80], whereas testosterone administration in healthy subjects induces motivation to act [81] and upregulates activity in the ventral striatum [82] (Figure 4).

As described above for threat vigilance, one intriguing possibility is that the reward-related effects of testosterone are mediated through its metabolite estradiol. For example, estradiol administration can increase striatal dopamine levels in rats, which were depleted following ovariectomy, and increases amphetamine-evoked dopamine release. In the amygdala, estradiol enhances electrically evoked dopamine release dose-dependently (reviewed in [83]). It is also readily self-administered [84]. Estradiol might also cause menstrual cycle-dependent modulation of activity in dopaminoceptive brain regions in healthy, premenopausal human females [85]. Thus, testosterone administration might influence motivational and reward processes either directly via androgen receptors, or indirectly via estradiol acting on estrogen receptors.

Anxiolysis and fear reduction

A further process that influences status-seeking behavior might be anxiolysis, as it might help to facilitate

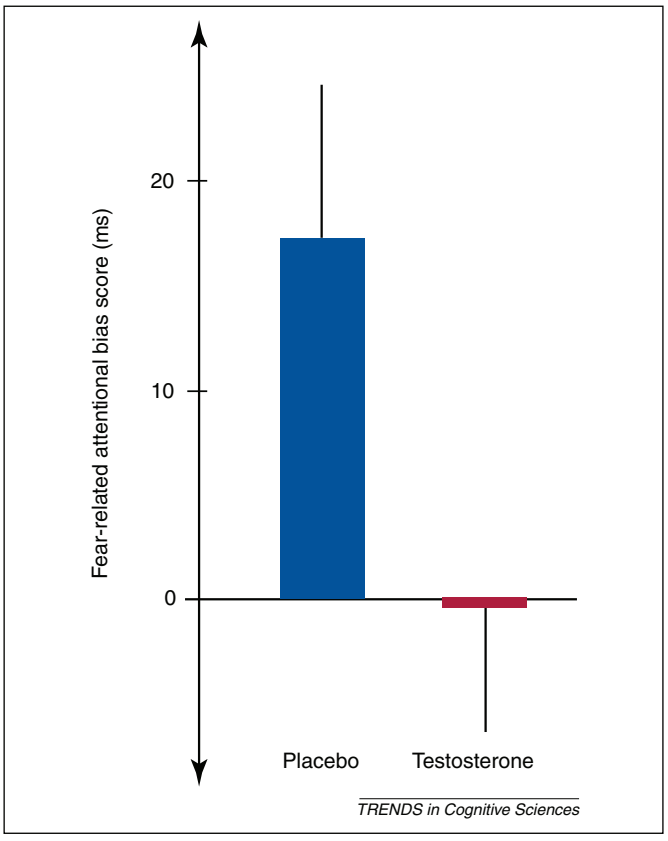

Figure 5. Mean fear-related attentional bias scores (i.e. response latencies for subliminally presented fearful faces minus response latencies for neutral faces) in ms under testosterone versus placebo. Testosterone administration abolishes the fear-related attentional bias. Vertical lines indicate standard errors of the mean. Adapted from [44].

engagement in a contest. Several studies have shown that testosterone administration reduces anxiety-like behavior in rodents in several behavioral paradigms, including the defensive burying test [86] and the elevated plus maze [87]. These effects have been shown to be gamma-aminobutyric acid A ($GABA_A$) receptor dependent [88] and the anti-androgen flutamide was shown to block the anxiolytic-like effect of testosterone in castrated male rats [86]. Aromatization to estradiol does not seem to be necessary for the anxiolytic effects in rodents [88]. In humans, single acute doses of testosterone have been shown to reduce subconscious fear (Figure 5) and fear-potentiated startle [44,89]. Together, these results suggest that testosterone takes its effects on status seeking through decreasing fear. In contrast to the mechanisms described above for threat vigilance and reward processing, aromatization to estradiol seems not to play a major role in mediating the fear-reducing effects of testosterone. However, future concurrent testosterone administration and aromatase inhibition studies in humans have yet to confirm this.

Stress resilience

In face-to-face interactions, individuals are assumed to compete for status in fairly well-defined contests, each trying to 'outstress' the other with verbal and facial cues, and the fact that low-ranked members show more stress symptoms than higher-ranked members during mutual interaction is a common feature of status hierarchies [40]. Stress probably also plays an important role in anonymous competition. Hence, stress resilience might enable an individual to cope with a challenge adaptively. Studies in animals have confirmed that testosterone downregulates the hypothalamic–pituitary–adrenal stress response [90]. It has also been shown to attenuate the sympathetically mediated stress response to aversive stimuli in humans [91].

In summary, testosterone seems to act at different neurobiological nodes that are important contributors to status-seeking and status maintenance behaviors. Studies in animals suggest that testosterone has anxiety-reducing properties. These effects are likely to be mediated via a non-genomic pathway and dependent on $GABA_A$ receptor signaling. Testosterone administration studies confirm that the hormone also has fear-reducing properties in humans. A further important function of testosterone is its role in motivation; animal models have shown a tight link with the dopaminergic system within striatal areas. Thus, together with the ability to reduce fear and buffer stress responses, testosterone might have a pivotal role in promoting upward movement in a status hierarchy by facilitating the engagement in a competition for status. By contrast, testosterone can promote threat vigilance, which enables an individual to not only detect potential status challenges, but also, as a consequence of, and facilitated through the mechanisms detailed above, act accordingly to defend its high status position. These effects might be mediated by the amygdala, possibly involving aromatization to estradiol.

Concluding remarks

Testosterone has been the focus of intensive research for decades. Whereas early studies pointed towards a role in physical aggression, recent evidence suggests that this simple view needs to be refined. In particular, it appears that testosterone promotes status-seeking and social dominance motives, and thus plays an important role in social status hierarchies. (Note, however, that most of these recent studies were conducted on Western student populations; it remains to be tested whether these findings generalize to other populations [92].) Most recently, several studies in humans have begun to test the causality of the link between social, emotional and economic interaction behavior through acute testosterone administration. These studies have confirmed that an account of testosterone as a simple mediator of aggression falls short of the truth; instead, testosterone appears to have a more subtle and complex role in driving behaviors that tend to increase an individual's motivation and ability to acquire and defend social status. The exact mechanisms by which testosterone has these effects remain elusive; however, recent research has suggested four plausible channels, namely threat vigilance, reward processing, fear reduction and stress resilience. The task of future studies will be to delineate the role of testosterone in social interaction more precisely and to test which of these candidate channels accounts for most of the observed behavioral variance (see also Box 1 for further outstanding questions).

Box 1. Outstanding questions

- How does winning or losing a contest interact with exogenously administered testosterone to determine future competitiveness in humans?
- Which effects on social interaction are mediated by estradiol and which by testosterone?
- Does testosterone influence learning effects in repeated (social) decision-making tasks?
- What are the effects of acute single doses of testosterone on social interaction in young men?
- Which animal models are useful for understanding testosterone effects in humans; which ones are not?

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