

# Competition, testosterone, and adult neurobehavioral plasticity

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## Abstract

Motivation in performance is often measured via competitions. Winning a competition has been found to increase the motivation to perform in subsequent competitions. One potential neurobiological mechanism that regulates the motivation to compete involves sex hormones, such as the steroids testosterone and estradiol. A wealth of studies in both nonhuman animals and humans have shown that a rise in testosterone levels before and after winning a competition enhances the motivation to compete. There is strong evidence for acute behavioral effects in response to steroid hormones. Intriguingly, a substantial testosterone surge following a win also appears to improve an individual's performance in later contests resulting in a higher probability of winning again. These effects may occur via androgen and estrogen pathways modulating dopaminergic regions, thereby behavior on longer timescales. Hormones thus not only regulate and control social behavior but are also key to adult neurobehavioral plasticity. Here, we present literature showing hormone-driven behavioral effects that persist for extended periods of time beyond acute effects of the hormone, highlighting a fundamental role of sex steroid hormones in adult neuroplasticity. We provide an overview of the relationship between testosterone, motivation measured from objective effort, and their influence in enhancing subsequent effort in competitions. Implications for an important role of testosterone in enabling neuroplasticity to improve performance will be discussed.

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## Keywords

Competition, Motivation, Testosterone, Neuroplasticity, Winner effect

The focus of this review is on how competitions can be used to measure motivation, enhance motivation, and improve performance. We will describe the neurobiological mechanisms underlying motivation in competitions and we will provide insight into how sex hormones can enhance performance via their effects on neuroplasticity.

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## 1 COMPETITION AND MOTIVATION

Competition is essential for survival in virtually all-living organisms. Organisms compete to gain access to limited resources such as food, water, territory, protection, and sexual mates. In humans and nonhuman animals, competition is often a means to achieve and maintain a higher social status in a hierarchy that allows access to such valued resources. While nonhuman animals often compete by displaying aggression, in humans competitions are not only expressed in aggressive ways (ie, by causing physical harm to others through violence, for example; [Archer, 2006](#)) but often occur in nonaggressive forms, for instance, via personal achievements, performance or in negotiations. In humans, competition can be a powerful incentivizing tool. It enhances motivation and performance output across many domains such as in business, market economies, law, politics, education, and sports ([Deci et al., 1981](#); [Hirshleifer, 1978](#)).

Competition can be regarded as both an intrinsic and extrinsic incentive to perform. Sports tournaments are a good example to illustrate the distinction between the two incentives. Athletes need to be highly motivated to train long hours and perform to their maximum ability during competitions in order to outperform others and, for example, to achieve a higher position in the rankings, or win a prize (ie, external reward). On the other hand, athletes' motivation to work harder can also be prompted by the internal drive to challenge themselves to improve performance and thereby increase their competence and skills in the task. This is referred to as intrinsic motivation, which is the motivation to perform an action due to the enjoyment and self-determination resulting from the activity ([Deci et al., 1981](#)). The importance of intrinsic motivation has also been shown in anonymous competitions in the lab. Related to this is a study ([Kuhnen and Tymula, 2012](#)) where individuals had to compete against others in a math task (eg, solving as many equations as possible within an allocated time). It was found that the opportunity to privately compare own performance with the performance of the others significantly increased their motivation to exert effort in the subsequent rounds. Motivation was assessed from performance, that is, the number of correctly solved equations. The motivation to be able to compare own performance levels relative to the performance levels of other players is assumed to be driven by a desire to gain or maintain high self-esteem or feelings of competence ([Kuhnen and Tymula, 2012](#)). The increased self-esteem or competence from performing the task presumably intrinsically motivates them to exert more effort in the task. This suggests that the intrinsic value one can gain from the competitive activity is an important factor that incentivizes performance in

competition. In sum, in addition to the extrinsic incentives competition offers, it can also increase intrinsic motivation, which is relevant concerning the strong effects intrinsic motivation can have on behavior (Reeve and Deci, 1996). Both types of motivation influence the extent to which competitions can incentivize an individual's performance.

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## 2 EXPERIMENTAL APPROACHES TO MEASURE THE MOTIVATION TO COMPETE IN THE LABORATORY

Studies have assessed individuals' motivation to compete mostly in two ways. One approach is using choice preference as a measure of the motivation to compete (ie, competitiveness), by asking individuals to make a decision, for instance, between engaging into competition or rather performing an alternative task with no competitive element (eg, McGee and McGee, 2013; Mehta et al., 2015; Niederle and Vesterlund, 2007), or bidding at auctions where people have to decide between how much, if any, they want to bid on the target item (van den Bos et al., 2013). The other approach that is used by many studies is to assess individuals' motivation to compete directly from performance in real effort-based tasks. These real effort-based tasks can either require mostly cognitive effort, for example, solving mazes and puzzles (eg, Gneezy et al., 2003; Niederle and Vesterlund, 2007; Reeve et al., 1985), anagrams (Charness and Villeval, 2009), mathematical problems (Rutström and Williams, 2000), performing in trivia challenges (Hoffman et al., 1994), or playing videogames such as Tetris (Zilioli and Watson, 2014; Zilioli et al., 2014). In addition, there are numerous studies using real effort-based competitions where physical effort (ie, physical/motor tasks) is used as an index of competitiveness. These include, for example, cracking walnuts (Fahr and Irlenbusch, 2000), moving as many sliders to a fixed target as fast as possible (Gill and Prowse, 2012), performing a handgrip force endurance task (Cooke et al., 2013; Le Bouc and Pessiglione, 2013), or cycling in a head-to-head competition (Corbett et al., 2012). A meta-analysis by Stanne et al. (1999) using physical effort competitions found an overall enhancing effect of competition on performance.

Some studies have used both choice and real effort in the same design to assess individuals' motivation to compete. An influential study by Niederle and Vesterlund (2007) used a multistage competition design involving an incentivized cognitive effort task with monetary incentives (ie, payment was contingent on correctly adding up as many sets of five two-digit random numbers, within 5 min). In the first stage all players performed the effort task and received the same monetary reward for every correctly solved equation (noncompetitive piece rate payment). In the second stage participant performed a forced competition in groups of four and were only paid if they were the winner (tournament, involving fourfold higher payment for the winner). In the third stage of the experiment, participants were asked to decide according to which of the two payment schemes they wanted to perform the task. In men, an increased performance was found in the tournament condition relative to piece rate

condition, as well as in those who chose to compete again in the tournament condition in comparison to those who decided to perform in the piece rate condition (Niederle and Vesterlund, 2007). Together, these studies demonstrate that competitions can have motivation-enhancing effects, which can be measured in at least two fundamental ways, either by choice or by real effort. In addition to using dichotomous decisions (ie, to compete or not to compete), using a continuous measure such as real effort as an index of competitiveness is expected to receive increasing attention in competition research, as it provides a powerful measure of motivation and performance that might be more sensitive to pharmacological and context manipulations.

While much social and applied psychological as well as behavioral economics research has been devoted to further our understanding of the motivation-enhancing effects of competition, research on the underlying neurobiological mechanisms in humans has only recently begun. In the following part, we will describe the neurobiological basis of motivation in competition by relying on existing models from both animal and human research and discuss behavioral, psychopharmacological, and neuroimaging evidence in humans. We will show that testosterone is a key hormone involved in competition, and we will shed light on the mechanisms that could promote motivation in competition on longer timescales. Further, we will describe the neurobiological mechanisms underlying the so called “winner effect” in detail, which represents a particularly strong case of the motivation-enhancing effects of competition.

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### 3 NEUROENDOCRINOLOGICAL FACTORS THAT INFLUENCE COMPETITIVENESS

In addition to the modulating effects of psychological variables and social contexts on social behavior, neurotransmitters (eg, dopamine, serotonin, norepinephrine) and hormones (eg, testosterone, estradiol, oxytocin) have been found to play a crucial role in regulating behavior. These neuroactive hormones and neurotransmitters can regulate and adapt behavior by modifying neuronal dynamics, excitability, and synaptic function (Crockett and Fehr, 2014).

Research investigating human competition has shown an increasing interest in the role of neurotransmitters and hormones, of which primarily testosterone. The steroid androgen testosterone, a product of the hypothalamic–pituitary–gonadal axis, is produced in both men and women with approximately 95% of circulating testosterone in men produced by the Leydig cells of the testes, while in women approximately 50% of circulating levels are produced by the ovaries and placenta. The adrenal cortex also secretes testosterone; however, in men it contributes only 5% of circulating testosterone, while in women it accounts for roughly 50% of testosterone (Burger, 2002). Testosterone has an important role in the development of secondary sexual attributes, such as increased muscle tissue, bone mass, and body hair in males. Besides the developmental characteristics, testosterone also plays an important role

in socioemotional and decision-making behavior (Bos et al., 2012; Eisenegger et al., 2011). The substantial influence of testosterone on the brain in archetypical situations, such as fight, flight, mating, and the search and struggle for status, makes it an important variable in studying competition (Mazur and Booth, 1998).

In a broad number of animal species, including humans, testosterone secretion is modulated in the context of competitive interactions. So far, several models have described the relevance and function of androgen modulation associated with competition. The challenge hypothesis, which was originally postulated for birds (Wingfield et al., 1990), states that testosterone levels rise in males in response to challenges (eg, during the mating season), while they are low during periods of social stability. These fluctuations occur presumably to avoid the costs for keeping testosterone levels chronically high (Folstad and Karter, 1992). It also predicts that animal species were more likely to evolve the ability to increase androgens following a social dispute if such a response helped facilitate reproduction such as mate guarding, territory defense, and fighting ability during male–male competition. Whether the challenge hypothesis also applies to humans has been reviewed by Archer (2006). In humans, for instance, basal testosterone levels correlate positively with psychometric measures such as the self-reported willingness to win in competition (Suay et al., 1999; Williams et al., 1982; Zumoff et al., 1984), and betting strategies in auctions (van den Bos et al., 2013).

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#### 4 TESTOSTERONE LIKELY INFLUENCES COMPETITIVENESS VIA MODULATION OF DOPAMINERGIC FUNCTION

Accumulating evidence from animal research suggests that testosterone modulates the motivation to compete via actions on the mesocorticolimbic dopaminergic system (see Box 1). Work in animals has so far supported this assumption by identifying

##### BOX 1 THE LINK BETWEEN DOPAMINE, MOTIVATION, AND EFFORT

Integration of motivation and effort is assumed to be mediated primarily by the striatal dopamine system (Hosp et al., 2011; Salamone and Correa, 2002; Westbrook and Braver, 2016). Effort is often referred to as strenuous physical or mental exertion typically with the aim of achieving a desired outcome or goal. Thus, effort is generally considered costly, and if given a choice most animals will choose actions that are less effortful (Salamone et al., 2007). In rats, dopamine depletion decreases tolerance for effort (ie, increases effort costs), whereas drugs enhancing dopamine have the reverse effect (Salamone and Correa, 2002; Salamone et al., 2007). Evidence in humans also suggests that striatal dopamine is required to overcome costs when high levels of effort are necessary to obtain a desired goal (Botvinick et al., 2009; Kurniawan et al., 2010). Activity in the ventral striatum and midbrain correlates with the expected amount of reward, discounted by the amount of effort to be invested (Croxson et al., 2009). In addition, the anterior cingulate cortex might play a prominent role in the value of exerting effort for a potential reward. That is, dopamine in anterior cingulate cortex is posited to promote persistence of effort via its function in integrating action–outcome associations (see Kurniawan et al., 2011; Westbrook and Braver, 2016 for review).

the neurobiological pathways linking testosterone, and its primary metabolites  $5\alpha$ -dihydrotestosterone (DHT) and estradiol to several brain regions of the dopaminergic system (for more details on testosterone metabolization, see [Section 7.2](#)). For instance, fundamental neurobiological studies have demonstrated that dopamine neurons contain androgen receptors (ARs) ([Creutz and Kritzer, 2004](#)) and estrogen receptors alpha (ER- $\alpha$ ) and beta (ER- $\beta$ ) (for a recent review see, eg, [Almey et al., 2015](#)). In the substantia nigra of adolescent male rats, testosterone is also able to change—via direct action at ARs—the levels of dopamine receptors, and levels of the dopamine transporter protein, which regulates dopamine availability in the synaptic cleft ([Purves-Tyson et al., 2012, 2014](#)). Testosterone also appears to affect dopaminergic neurotransmission in prefrontal brain areas. Recent rodent research has shown that less than one quarter of the dopamine cells of the ventral tegmental area (VTA) that project to prefrontal cortex contain ARs ([Aubele et al., 2008](#)). However, all of the major afferent projections to the VTA—those arising from pyramidal cells of the prefrontal cortex itself, are by far the most AR enriched ([Aubele and Kritzer, 2011](#)).

Systemic manipulations of testosterone levels, for instance via castration, reduce the concentration of dopamine in the striatum in rodents, an effect that can be prevented by supplementation with testosterone, DHT, but also estradiol ([Alderson and Baum, 1981](#); [Mitchell and Stewart, 1989](#)). In rats, activity of tyrosine hydroxylase, which is the rate-limiting enzyme in dopamine biosynthesis, is reduced in the striatum following orchidectomy, and this reduction can be prevented by testosterone supplementation ([Abreu et al., 1988](#)). Moreover, administration of testosterone in gonadally intact adult male rats increases dopamine concentration ([de Souza Silva et al., 2009](#)) and dopamine turnover in the striatum ([Thiblin et al., 1999](#)). Furthermore, in rhesus macaques, circulating testosterone levels were found to correlate positively with concentration of striatal tyrosine hydroxylase ([Morris et al., 2010](#)). In sum, these studies highlight a close relationship between testosterone, including its metabolites, and the mesostriatal dopaminergic system.

Behaviorally, rodents can be conditioned with acute peripheral and intranucleus accumbens administration of testosterone and DHT, such that they show a place preference for where they received the hormone (for review see, eg, [Wood, 2008](#)). This effect has been localized to the nucleus accumbens shell ([Frye et al., 2002](#)), an important reward region in rodents ([Robbins and Everitt, 1996](#)) that corresponds to the ventral striatum in humans. Place preference for testosterone can be blocked by both D1 or D2 dopamine receptor antagonists (SCH23390 or sulpiride, respectively; [Packard et al., 1998](#)), which suggests that some of the rewarding effects of testosterone are mediated via the dopaminergic system. Not surprisingly, intracerebral testosterone self-administration protocols in rodents have shown that some animals overdose to lethal doses ([Wood et al., 2004](#)). Intriguingly, some of the general reinforcing effects of testosterone have been observed within time periods as short as 30 min poststimulus, suggesting that testosterone may have rapid effects on dopaminergic function ([Nyby, 2008](#)).



In humans, evidence is generally consistent with animal research. Clinically low testosterone levels as observed in hypogonadal men appear to be associated with apathy and lack of motivation (Bhasin et al., 2006). Single-dose testosterone administration in healthy female subjects increases motivation to engage in cued behaviors (Aarts and van Honk, 2009) and increases BOLD activation in the ventral striatum during reward anticipation, which is most pronounced in women with low appetitive motivation (Hermans et al., 2010). Together, this shows the tight neurobiological coupling between the androgen and the dopamine system and suggests that testosterone increases motivation to compete via activating selective dopaminergic pathways (see Box 1).

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## 5 HOW DO COMPETITION OUTCOMES MODULATE SUBSEQUENT COMPETITIVENESS?

Not surprisingly, competitiveness varies substantially as a function of prior experiences in competitions such as a previous victory or defeat. What is intriguing, however, is the observation that testosterone secretion varies with the outcome of competition. Specifically, in many species testosterone levels fluctuate as a function of whether the competition was won or lost, such that the winner experiences a surge of testosterone levels, while the loser experiences a drop of testosterone levels (bio-social model of status; Mazur, 1985). Work by Monaghan and Glickman (2001) illustrated this in rhesus monkeys, where they found that in a competition to establish rank the winning male emerged with a 10-fold increase in testosterone, while the loser experienced a drop to 10% of baseline levels within 24 h postcompetition, which persisted for several weeks. Similar results were observed in humans, for instance, in sports competitions testosterone levels increased before the contest started, and further increased after a win. These findings were found across a range of tournaments such as tennis (Booth et al., 1989), wrestling (Elias, 1981), and also non-physical contests such as chess (Mazur et al., 1992). Again, effects can be large; for example, athlete hockey players merely watching themselves win a match on video produced a 40% testosterone surge from baseline (Carré and Putnam, 2010). These changes occur relatively quickly, observed within approximately 15 min postoutcome in humans in most studies (for relevant reviews see, eg, Carré and Olmstead, 2015; Oliveira and Oliveira, 2014). However, not all studies in humans have consistently observed a testosterone surge following a win, and a drop of testosterone following a loss, as losers also often show an increase in testosterone levels (eg, Mehta and Josephs, 2006; Van Anders and Watson, 2007). The overall evidence in support of testosterone increases exclusively after wins in males appears to be small, albeit significant (Archer, 2006; Carré and Olmstead, 2015; Oliveira and Oliveira, 2014). In humans, this appears to be due to a large extent to moderating variables, such as the cognitive appraisal of the competition

(eg, whether it is experienced as a threat or as a challenge, mood, personality), but also variables like the physical location (eg, home versus away), which is evident in both humans and animals (Carré, 2009; Carré et al., 2006; Fuxjager and Marler, 2010; Oyegbile and Marler, 2005). If the extent of such moderating variables is being considered, the relationship appears to be more pronounced (reviewed in, eg, Carré and Olmstead, 2015; Salvador and Costa, 2009).

It is noteworthy that competition outcomes are often not clear cut—when there is no clear difference in performance between the winner and loser. The behavioral effects of such close outcomes have been well established for nonsocial contexts, where positive effects on motivation have been observed for outcomes that are experienced as “small” losses, or “near-misses” (ie, close but objective losses; Reid, 1986). Indeed, participants who nearly won in a gambling task, for instance, were more motivated to continue to gamble as compared to those who clearly lost (Berger and Pope, 2011; Clark et al., 2009). This phenomenon also extends to competitive contexts. A typical example is when an individual just ends up at second place with a small difference in performance compared to the winner, or in hierarchies that are not yet established or unstable. Recently, such situations have also been modeled in the laboratory (Zilioli et al., 2014). In this study, Zilioli and colleagues (2014) examined how victories and defeats in unstable hierarchies (ie, wherein participants experienced close victories and defeats, and where participants were uncertain of the competition outcome until the very end of the competition) can differently affect testosterone response in women (Zilioli et al., 2014). They found that participants who experienced a defeat in unstable hierarchies had larger increases in testosterone levels relative to participants who experienced a victory in unstable hierarchies. This testosterone surge has been interpreted as to boost motivation to increase performance on next encounters. Thus, close or unstable losses could increase individuals’ motivation to improve performance, also in competitive contexts. In short, competitive outcomes are an important moderator of individuals’ motivation to compete and are observed to have a bidirectional relationship with circulating testosterone levels.

What could be the function of these testosterone dynamics? Mazur and Booth (1998) have pointed toward a role of testosterone in guiding further status-seeking behavior. Specifically, that sustained testosterone increases motivation for subsequent status battles in winners, whereas when testosterone decreases it discourages such battles in losers. It has been shown that short-term fluctuations of testosterone correlate with a host of behavioral measures. For example, the extent of the testosterone surge has been shown to predict reactive aggression (Carré et al., 2013; Geniole et al., 2013). Importantly, the surge has also been shown to predict motivation in performance in subsequent competitions (Carré and McCormick, 2008; Mehta and Josephs, 2006). The precise role of these fluctuations remains to be further investigated. Interestingly, these behaviors were generally assessed shortly after the change in testosterone was detected (usually within 10–20 min) (Fig. 1A). In the following, we will focus on research showing how competition outcome, and acute fluctuations in testosterone can influence behavior long term.



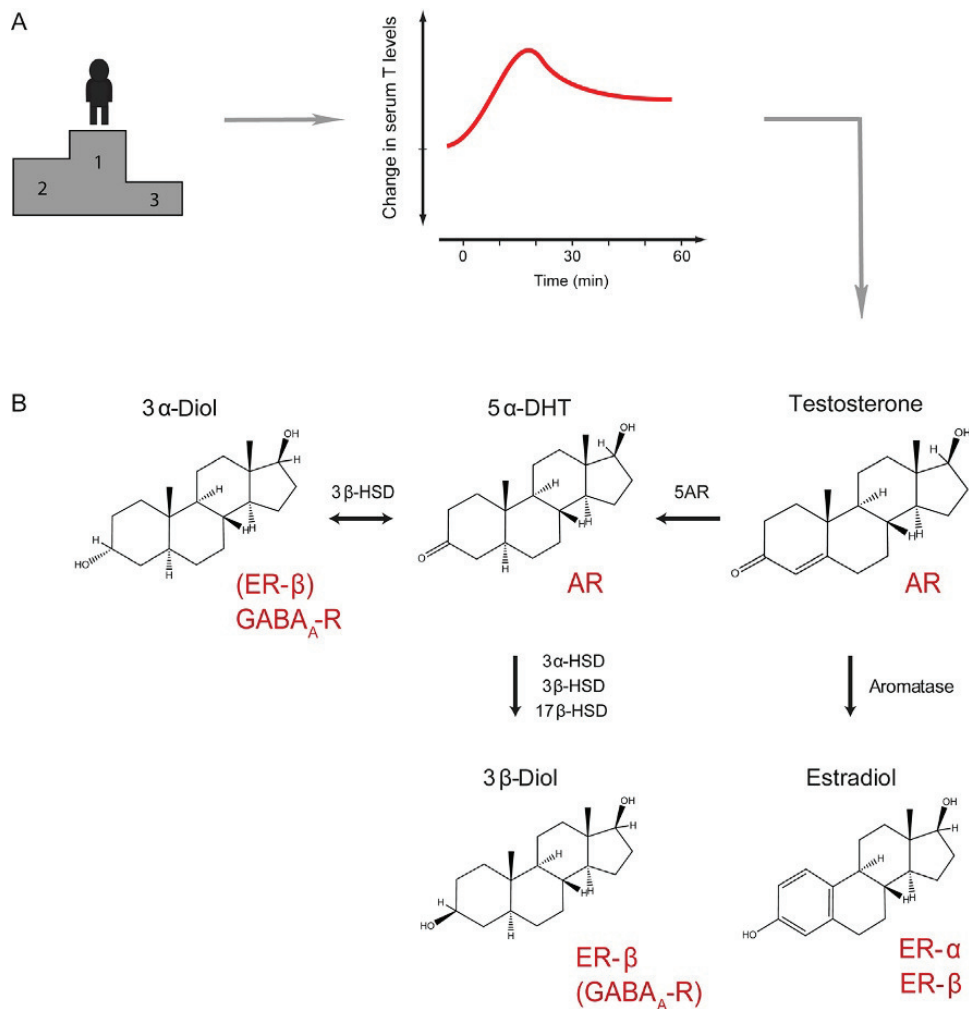
**FIG. 1**

Diagram depicting testosterone and its metabolites that may contribute to the winner effect in humans. (A) Illustration of a testosterone surge following victory. (B) The metabolization of testosterone that may take place in the central nervous system. Major receptor types for these metabolites are shown in red. Enzymes are shown in *italics*. *Single-sided arrow* depicts unidirectional catalysis, and *double-sided arrow* illustrates bidirectional catalysis. *3α-diol*, 5α-androstane-3α,17β-diol; *3β-diol*, 5α-androstane-3β,17β-diol; *3α-HSD*, 3α-hydroxysteroid-dehydrogenase; *3β-HSD*, 3β-hydroxysteroid-dehydrogenase; *17β-HSD*, 17β-hydroxysteroid-dehydrogenase; *5AR*, 5α-reductase; *AR*, androgen receptor; *ER-α*, estrogen receptor α; *ER-β*, estrogen receptor β; *GABA<sub>A</sub>-R*, gamma-aminobutyric acid receptor type A.

*Adapted from Handa, R.J., Pak, T.R., Kudwa, A.E., Lund, T.D., Hinds, L., 2008. An alternate pathway for androgen regulation of brain function: activation of estrogen receptor beta by the metabolite of dihydrotestosterone, 5alpha-androstane-3beta,17beta-diol. Horm. Behav. 53, 741–752. doi:10.1016/j.yhbeh.2007.09.012.*

## 6 LONG-TERM EFFECTS OF COMPETITION OUTCOMES ON COMPETITIVENESS

An interesting observation is that winning not only promotes further competitiveness, but that it enhances the probability of winning the next contest. This is referred to as the winner effect. In contrast, the loser effect refers to the observation that losing enhances the probability of losing a subsequent contest (Chase et al., 1994; Dugatkin, 1997). The influence of prior contest outcomes on winning or losing subsequent contests has been observed in many animal species, for instance in fish, rodents (Dugatkin, 1997; Fuxjager et al., 2011a; Gleason et al., 2009; Hsu et al., 2006; Oyegbile and Marler, 2005), and also humans (see Oliveira and Oliveira, 2014 for an overview).

Here, we will first focus on the psychological aspects that may underlie the winner effect. For instance, recent research indicates that human subjects who won in a competition provided more effort as measured by the number of mathematical equations solved in a laboratory task than subjects who lost in a prior competition. This effect was specific to the link between actual performance and outcome, as subjects who randomly won in a separate experimental condition did not invest more effort subsequently (McGee and McGee, 2013). Supporting this, on a cognitive effort task testosterone responded only to actual ability-determined competition outcomes, not to competition outcomes that were based on chance (Van Anders and Watson, 2007). This suggests that the experience of an actual achievement may be important for the motivation to compete and thus may be essential for the winner effect to emerge. In addition, in motor and cognitive tasks without a competitive element providing positive feedback about performance when participants chose to receive this feedback led to an increased performance compared to providing feedback at random times (Chiviacowsky, 2007; Chiviacowsky and Wulf, 2002). Together, these findings suggest that when performance feedback is perceived as real and can be attributed to the self (ie, is self-determined), it can intrinsically motivate behavior and positively affect learning (ie, a skill in subsequent competitions). This is in line with existing theories on motivation (Ryan and Deci, 2000), describing that not only the experience of perceived competence is important for motivating individuals to act, but specifically that their performance should also be perceived as self-determined.

While the above studies suggest that psychological variables such as perceived competence and personal achievement are important moderating factors of the winner effect, animal research has also shown changes in the neurobiology underlying the winner effect. It is thus important to scrutinize the nature of these neurobiological changes as they would allow building models on how to best harvest the beneficial effects of winning on subsequent motivation in humans.

So far, research in rodents has shown that testosterone surges observed after winning a competition increase the probability of winning a future competition (Oyegbile and Marler, 2005; Trainor et al., 2004). In those studies mice were castrated and implanted with testosterone, which maintains circulating testosterone at

levels typical of adult males but, in effect, prevents testosterone changes in response to social or environmental cues (Trainor et al., 2004). This procedure showed that a robust winner effect was evident if animals accumulate three separate victories in their home territory and receive additional testosterone injections after each of these contests. Mice form an intermediate winner effect when they accumulated the same number and type of victories but received postencounter saline injections (Fuxjager et al., 2011b). It has thus been proposed that postcompetition testosterone fluctuations represent a neuroendocrine substrate of the robust winner effect (Fuxjager and Marler, 2010; Oyegbile and Marler, 2005). This was also found in other animal species. For instance, in male tilapia, winners that were treated with an antiandrogen drug (ie, cyproterone acetate) were less likely to win a subsequent aggressive interaction (relative to controls) (Oliveira et al., 2009). However, the usual relationship of testosterone fluctuations and the winner effect has not always been observed (Hirschenhauser et al., 2008, 2013).

In humans, a recent study (Zilioli and Watson, 2014) found that a rise in testosterone during a laboratory competition predicted better performance 24 h later on the same competition. Concurring with the somewhat weak evidence for the existence of a “competition effect” (ie, where winners show an increase in testosterone following the competition, and losers show a decrease in testosterone) the positive relationship between reactivity of testosterone to the first competition and performance 24 h later was found in both winners and losers (Zilioli and Watson, 2014). Albeit that evidence in humans is still correlative, these findings suggest that testosterone may, in certain contexts, induce long-lasting changes in performance in competition.

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## 7 MECHANISMS MEDIATING LONG-TERM BEHAVIORAL EFFECTS FOLLOWING A TESTOSTERONE SURGE

It is well established that both short- and long-term modifications of behavior rely on changes of synaptic connections between neurons (Sweatt, 2016). Therefore, a likely mechanism by which testosterone surges might potentiate the winner effect is that the hormone affects synaptic and (more general) neuronal plasticity. Neuroplasticity refers to functional or structural changes that occur in the brain to adjust to changes in the external environment or internal milieu (May, 2011).

### 7.1 ROLE OF AR IN NEURONAL PLASTICITY

ARs are expressed in many different neuronal populations in the nervous system in both males and females (Choate et al., 1998; Simerly et al., 1990). Testosterone can either directly bind to ARs, or activate ARs after conversion to DHT, which is a more potent AR agonist than testosterone. The conversion of testosterone to DHT is catalyzed by the enzyme 5 $\alpha$ -reductase, which is expressed in the brain (Celotti et al., 1997) (see Fig. 1B).

There is accumulating evidence from animal research supporting a role of ARs in neuronal plasticity (Fester and Rune, 2015). In adult rats, castration results in massive reduction of spine synapses in the hippocampus and the prefrontal cortex that can be reversed by supplementation of both testosterone or DHT (see Hajszan et al., 2008 for review). Furthermore, changes in synaptic morphology in the hippocampus following castration in mice are associated with a decrease in levels of brain-derived neurotrophic factor (BDNF), a protein that is important for normal synaptic physiology. Such a reduction in BDNF levels can be both prevented and recovered by testosterone replacement (Li et al., 2012; for review see, eg, Pluchino et al., 2013). This is in line with *in vitro* studies of hippocampal preparations, showing that administration of androgens increases the number of dendritic spines (Hatanaka et al., 2009). Furthermore, there is evidence that ARs play a role in adult hippocampal neurogenesis promoted by physical exercise (Okamoto et al., 2012).

Importantly, it has been shown that genetically modified mice lacking ARs specifically in the nervous system show a deficit in long-term potentiation in the hippocampus as well as an impairment of memory consolidation (Picot et al., 2016). In rats, posttraining systemic injections of testosterone and DHT improve memory on tests performed 24 h later (Edinger et al., 2004; Frye and Lacey, 2001). Moreover, Edinger and Frye (2007a) demonstrated that intrahippocampal administration of the AR antagonist flutamide immediately after training impaired memory consolidation.

## 7.2 ROLE OF ER IN NEURONAL PLASTICITY

An alternative pathway for the action of testosterone involves its conversion to estradiol, which binds to ER- $\alpha$  and ER- $\beta$  (Fig. 1B) (Almey et al., 2015). Although estradiol is primarily known as a female sex hormone, the hormone controls many physiological and behavioral responses in both females and males (for review Cornil et al., 2012). The conversion of testosterone to estradiol is mediated by the enzyme aromatase, which is widely expressed in the human brain in both sexes (see Biegon, 2016 for review). The activity of the enzyme can be rapidly regulated via phosphorylation, resulting in fast changes in local estradiol concentrations. In addition, estradiol is assumed to fulfill all criteria for being classified as a neurotransmitter (for review, see Balthazart, 2010), which suggests that the indirect testosterone effects, via conversion to estradiol, may be tightly regulated by neuronal activity (Farinetti et al., 2015).

There is extensive literature on the role of ERs in neuronal plasticity. ERs seem to play a fundamental role in regulating neurogenesis, synaptogenesis, dendritic, and axonal growth (for recent reviews see, e.g., Fester and Rune, 2015; Frick et al., 2015). Similar to testosterone, posttraining systemic but also intrahippocampal administration of estradiol results in a “off-line gain” (ie, improvement) in memory performance on cognitive tests up to 24 h later (for review see, e.g., Packard, 1998). This is in line with the finding that posttraining administration of estradiol rapidly increases (ie, within minutes) dendritic spines in the hippocampus and the prefrontal cortex (Inagaki et al., 2010). In addition, administration of an estradiol antagonist

(bisphenol A) impairs memory consolidation, blocks the off-line enhancing effects of estradiol, and reduces dendritic spines in the hippocampus and the prefrontal cortex (for review see [Luine and Frankfurt, 2012](#)).

An alternative pathway by which ERs can be activated to affect off-line gains is via metabolites of DHT, which cannot be aromatized to estradiol ([Fig. 1B](#)). The DHT metabolites  $3\beta$ -diol and  $3\alpha$ -diol act on ER- $\beta$  and  $\gamma$ -aminobutyric acid type A (GABA<sub>A</sub>) receptors ([Frye et al., 2008](#); [Handa et al., 2008](#)). Similar to ER- $\beta$ , GABA<sub>A</sub> receptors have been associated with neuronal plasticity (for review, eg, [Pallotto and Deprez, 2014](#)).  $3\alpha$ -diol injected into the hippocampus following training in a memory task significantly increased task performance 1 day later ([Edinger and Frye, 2007b](#)). Furthermore, inhibiting the expression of ER- $\beta$ , but not ER- $\alpha$ , abolished the positive effect of  $3\alpha$ -diol ([Edinger and Frye, 2007b](#)).

Taken together, these studies demonstrate that testosterone may affect neuronal plasticity in various ways, at short timescales but with long-term consequences. Testosterone surges following a victory in competition may induce neuroplasticity via both ARs and ERs in several brain areas such as the hippocampus, prefrontal cortex, or striatum. These effects seem to occur fast enough to enhance memory consolidation and boost the behavior that led to victory in the first place. The winner effect can be modulated via the direct effects of testosterone onto ARs but also indirectly via its metabolites DHT and estradiol ([Fig. 1](#)). The reviewed literature supports the idea that estradiol might be involved in the neuroplasticity associated with the winner effect, and this might imply a potential role of aromatase in the winner effect in humans ([Fuxjager et al., 2011b](#)). An alternative pathway involves nonestrogen agonists of ER- $\beta$  ( $3\alpha$ -diol and  $3\beta$ -diol) in the winner effect. As of yet, the relative importance of these alternative pathways is not clear, and in humans the potential role of aromatase in the winner effect still needs to be investigated. The work reviewed in this section suggests that postcompetition activation of both ARs and ERs might in humans improve future winning ability by increasing motivation and enhancing skills via effects on neuroplasticity. Pharmacological models involving selective blockade of these receptor systems (eg, using flutamide to block ARs, and raloxifene to block ERs) may help to shed light on the relative weight these systems might have in shaping the winner effect in humans.

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## 8 DISCUSSION

Motivation to compete is a complex phenomenon that is influenced by psychological, neurobiological, as well as social contextual factors.

### 8.1 A CONCEPTUAL FRAMEWORK

In the following framework we summarize how competition influences motivation and performance. The framework is speculative and builds around existing models that describe the relationship between testosterone and the motivation to compete, as

well as describing how competition outcome, and psychological and cognitive variables interact with testosterone secretion (biosocial model of status: Archer, 2006; Mazur and Booth, 1998; Salvador and Costa, 2009; challenge hypothesis: Wingfield et al., 1990). To these models we added recent insights mostly stemming from animal research into how testosterone and estradiol might affect performance in competitive contexts in the laboratory on a longer-term basis via effects on neuroplasticity.

One way to illustrate competitiveness within this framework is as the *decision to compete or not to compete*. The decision to compete is assumingly based on an evaluation of the subjective benefit weighted against the subjective cost of competing (Croxson et al., 2009; Studer and Knecht, 2016). The subjective benefits associated with competition can be determined by an individual's *expectations* of winning (ie, probability) and the *subjective value* of winning a competition. The expectations of winning has also been described as the person's resource holding potential (Hurd, 2006). That is, an individual's physical or cognitive ability or skills that determine the ability to win a competition. The subjective value of engaging into a competition can thus be conceptualized as the expected subjective benefit of, for example, a gain in status plus the intrinsic value of competing. This could be the subjective benefit from winning a prize and the subjective benefit from the feeling of competence. A low subjective value of winning has, for instance, been suggested to explain why women relative to men are less motivated to compete in videogames, because these types of competitions may have low subjective value to women compared to other types of competitions (Niederle and Vesterlund, 2011). Furthermore, the expected benefit of winning needs to account for any potential expected disutility of losing a competition such as a loss in status, or perception of reduced competence. Finally, the effort (cognitive or physical) that has to be invested in the competition is conceptualized as the subjective costs to compete.

The other way, as reviewed here, indicates that the motivation to compete can also be measured in forced competition paradigms via real effort, and that the outcome of competition can map onto the subsequent motivation to compete. In reference to the above framework, this implies that for individuals who are engaged in a forced competition, the dependent variable of their motivation to compete is reflected in the effort they exert into the task (cf. Kuhn and Tymula, 2012). For example, in a forced real effort competition, an individual with a strong motivation to achieve or maintain high status will exert more effort because of the high subjective utility of winning. At the same time, effort can possibly also be motivated or enhanced by the high subjective disutility of losing. Here, testosterone might increase the subjective utility of winning *and* the disutility of losing, by its proposed effects on the motivation to seek and maintain social status (Eisenegger et al., 2011; Mazur and Booth, 1998). The hormone may also, by virtue of its acute effects on the mesostriatal and mesolimbic dopaminergic system, promote effort by reducing effort costs (see Box 1). In situations where effort can be directly inferred from performance, which is not limited by ability, higher effort will then increase the probability of winning (Wallin et al., 2015).



In humans it has been shown that a short-lived postcompetition testosterone surge positively correlates with performance more than 24 h postcompetition (Zilioli and Watson, 2014). The function of testosterone may in this context also be understood via its well-established role in promoting neuroplasticity within the dopaminergic reward system. Studies in rodents showed that repeated winning increased expression of ARs in the nucleus accumbens (Fuxjager et al., 2010) and potentiated the synthesis of catecholamines (Schwartz et al., 2013). This suggests that the winner effect involves an enhancement of dopaminergic neurotransmission and also a sensitization to androgens. This is significant also considering the established role of the dopaminergic system in memory consolidation of rewarding and reward predicting events (for review see, Miendlarzewska et al., 2015; Shohamy and Adcock, 2010). For instance, it has been demonstrated that rewards significantly increase off-line gains in long-term memory retention (Abe et al., 2011; Sugawara et al., 2012). In sum, these findings indicate that testosterone and dopamine may act in concert in inducing neuroplasticity that enhances both the consolidation of successful strategies and motivation to reach the desired goals.

Similarly, a reinforcement learning mechanism might be involved in the winner effect (see also Box 1). It is plausible, for instance, that winning a competition yields a pronounced positive reward prediction error (RPE), when the outcome is uncertain (Schultz, 1997). Recent evidence also showed that serum testosterone levels are positively related to RPEs in the ventral striatum of individuals performing a reinforcement learning paradigm, which suggests a role of the hormone in shaping RPEs in humans (Morris et al., 2015). However, in this study, testosterone was only related to positive RPEs, but not negative RPEs. Together, this suggests that a testosterone surge following a win might enhance the associated positive RPE that will increase the incentive motivation to perform in a subsequent competition. Incentive motivation entails a set of processes that translate higher expected rewards into higher effort exertion (Berridge, 2004). Although the relationship between expected reward and effort exertion is complex, recent findings in humans (Schmidt et al., 2012) provide insight for generating new hypotheses of how motivation in competition and competition outcome may promote effort in subsequent competitions. In this neuroimaging study different amounts of rewards were associated with effort in two domains, a physical and a cognitive domain. Schmidt and colleagues found that the ventral striatum reflected expected reward during both cognitive and physical effort exertion. Specifically they showed that the ventral striatum mediated these incentive effects through connections of the basal ganglia and midbrain dopamine neurons, boosting task-relevant brain regions and performance (ie, cognitive circuits for cognitive real effort and motor circuits for physical real effort tasks). Based on this research we can predict that a testosterone-enhanced RPE associated with winning would increase the expected reward of winning a subsequent competition. The higher expected reward then boosts effort invested via activation of dopaminergic pathways to the ventral striatum that map onto the task-specific circuits. Future studies could apply a reinforcement learning framework using a repeated competition design to address the complex relationship of motivation, real effort, competition, and testosterone levels.

There are motivational aspects of competition that are intriguing and powerful. For instance, what are the motivational incentives when humans compete with themselves? A motive that drives people to compete with themselves is the goal to improve skills in an activity, which can be classified as an extrinsic, though self-set and integrated, motive. However, intrinsic motivation might also play an important role in this, since a self-challenge might be enjoyable. Thus, self-competition is of particular interest because it has been shown that intrinsic motivation usually has a strong and longer-lasting influence on performance relative to extrinsic motivation (Reeve and Deci, 1996; Reeve et al., 1985). Prior research in the laboratory has shown that receiving performance feedback is a clear motivational incentive (Chiviakowsky and Wulf, 2002, 2005; Kuhnen and Tymula, 2012; Widmer et al., 2016), an effect that is likely driven by the feeling of competence and self-esteem. Furthermore, successful achievements of effortful challenges enhance motivation and increase the value of the achievement as reflected in the ventral striatum (Lutz et al., 2012).

An interesting and open question is the role of testosterone in such a self-competition. Evidence supports a role of the hormone in this by showing that individuals' level of self-efficacy, effort, and motivation are positively related to testosterone levels (Costa et al., 2016; van der Meij et al., 2010). The role of testosterone in individual challenges is elusive; however, some evidence showed that testosterone concentrations only rose in social competitions among individuals who self-reported to have shown good individual performance (Trumble et al., 2012). This suggests that in a real effort self-competition, there might be an increase in testosterone secretion following "wins," that is, when performance increases across several stages of self-competitions.

## 8.2 SUMMARY

We highlighted research showing that competition is a powerful incentivizing tool. These motivational effects can be segregated into extrinsic and intrinsic motivations. We have argued that real effort-based competitions have the advantage of providing an assessment of the motivation to compete that allows for higher variance in behavior, as opposed to measuring motivation to compete using dichotomous decisions. The reviewed work highlights testosterone as an important neuroendocrinological variable that promotes the motivation to compete. It further emphasizes the role of testosterone in the winner effect as representing a performance increasing effect that seems to persist for extended periods of time. Such effects critically require neuroplasticity, for which testosterone has been shown to play an important role. Furthermore, animal literature suggests that testosterone might enable neuroplasticity not only via direct action on ARs but also via indirect action on ERs following aromatization of testosterone to estradiol and the DHT metabolites  $3\beta$ -diol and  $3\alpha$ -diol. Testosterone or its metabolites may also induce neuroplasticity within the dopaminergic system and thus may have lasting effects on motivation to compete. The precise role of the different pathways of testosterone signaling in humans is still

elusive; however, psychopharmacological models could provide a better understanding of this. One approach would involve a blockade of the enzyme aromatase. Alternatively, there are also selective antagonists of both ARs and ERs available and approved for use in humans that may help to further specify effects. The use of increasingly sophisticated psychopharmacological approaches and behavioral paradigms will provide more insight into the neurobiological mechanisms that link testosterone, motivation, and competition in humans.

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