



Review article

What can animal research tell us about the link between androgens and social competition in humans?



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ABSTRACT

A contribution to a special issue on Hormones and Human Competition. The relationship between androgenic hormones, like testosterone (T), and aggression is extensively studied in human populations. Yet, while this work has illuminated a variety of principals regarding the behavioral and phenotypic effects of T, it is also hindered by inherent limitations of performing research on people. In these instances, animal research can be used to gain further insight into the complex mechanisms by which T influences aggression. Here, we explore recent studies on T and aggression in numerous vertebrate species, although we focus primarily on males and on a New World rodent called the California mouse (*Peromyscus californicus*). This species is highly territorial and monogamous, resembling the modern human social disposition. We review (i) how baseline and dynamic T levels predict and/or impact aggressive behavior and disposition; (ii) how factors related to social and physical context influence T and aggression; (iii) the reinforcing or “rewarding” aspects of aggressive behavior; and (iv) the function of T on aggression before and during a combative encounter. Included are areas that may need further research. We argue that animal studies investigating these topics fill in gaps to help paint a more complete picture of how androgenic steroids drive the output of aggressive behavior in all animals, including humans.

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## 1. Introduction

Research on competition and hormones with non-human animals can illuminate exploration of this relationship in humans. Within animals, we can use precise manipulations and control variables, such as prior experience, and have a significantly greater ability to identify neural mechanisms. Within humans, researchers can delve into cognitive issues more easily and address significantly more complex social factors. Here, we explore some issues to help identify areas that may foster the exchange of ideas between animal and human research on androgens and competition.

When introducing the topic of testosterone (T) and aggression in animals, it is common to describe how this androgenic sex hormone increases during the breeding season and functions to increase the probability that aggression is expressed in response to provocation. This in turn, increases the energy and effort invested in garnering resources to support reproductive effort (Fuxjager et al., *in press*). Such a perspective relies primarily on the view that baseline androgen levels change in a way that represents stable and lasting elevations in T in the absence of acute environmental challenges. However, a more nuanced view of the relationship between T and aggression emerged through the research of Wingfield et al. (1990) and has been extended to a variety of species (e.g. review by Hirschenhauser and Oliveira, 2006); this relates to functions of T surges or pulses encompassed by the “Challenge Hypothesis” that explains pulses or surges that occur in T in males in response to challenges from other males as a result of differences in mating systems and level of parental care. These pulses are transient and return to baseline. It has been demonstrated across taxa, with abundant evidence in humans (reviews by Hirschenhauser and Oliveira, 2006; Carré and Olmstead, 2015; Casto and Edwards, 2016). Because T pulses occur in males in response to interactions with females as well, the T pulses may more generally allow adaptations to changing social conditions related to reproduction (Gleason et al., 2009). From a mechanistic perspective, we need to understand the physiological and neural pathways through which both T baseline levels and these T pulses influence aggression. Complicating this scenario are the findings that context can greatly influence the interactions between testosterone and aggression, including social context and physical context (e.g. familiar versus unfamiliar opponent; home territory versus novel location) as described below. Embedded within these complexities is another layer that involves the reward-like effects of testosterone and aggression that also display plasticity. The emerging story described below is one of even greater plasticity in behavior and mechanisms influencing functions of T pulses than originally proposed in the “Challenge Hypothesis”. The functions of these rapid fluctuations in T extend well beyond the classical view of T’s ability to increase aggression over a season.

The majority of research we describe focuses on the function and mechanisms of T pulses in males that occur after social encounters. It is important to be aware that both the timing of T pulses and temporal pattern in which individuals experience the T pulses likely have a significant impact on behavior because the effects of T pulses can be cumulative (e.g. Trainor et al., 2004) and timing of T pulses, such as before, during or after a social interaction may be critical in shaping the behavioral responses. Yet another layer to be added is that the effects of T may be either rapid, within seconds or minutes, or long term, working through changes in gene expression expressed within hours or days. From an adaptive perspective, we can think of T release as a mechanism for the brain to cue in on that reflects both short and long-term sampling of the environment.

For this review, we chose to identify four areas that focus primarily on the agonistic aspects of competition with an emphasis on sex steroid hormones: (1) a comparison of the associations and causal relationships between baseline levels of T and T responsiveness as related to aggression; (2) the importance of the social and physical context in which the competition takes place; (3) the rewarding effects of androgens on behavior; and (4) the timing of androgen release, before, during or after a social interaction.

We focus primarily on the California mouse (*Peromyscus californicus*), which has emerged as an important mammalian model system for examining the function of these transient pulses in T in response to male social interactions. This rodent is monogamous, biparental and territorial (e.g. review by Marler et al., 2008; Gubernick and Alberts, 1987; Gubernick and Teferi, 2000; Gubernick and Nordby, 1993; Ribble, 1991; Ribble and Salvioni, 1990), lending itself to studies that reflect aspects of human behavior. While typical rodent aggression occurs in California mice – as measured by latency to attack, chases, and wrestles that result in biting – we can also assess how this behavior drives larger events, including the “winner effect” (Hsu et al., 2006; Fuxjager and Marler, 2010). In animal behavior research, the winner effect refers to the finding that winning aggressive disputes can enhance future ability to win contests and can be viewed as an increase in winning ability through integration of multiple winning experiences: a topic just beginning to be explored in humans (e.g. Zilioli and Watson, 2014). On a quantitative level a winner is defined as an individual that initiated three consecutive attacks that elicits freezing behavior (loser behavior) from the opponent such as occurs in male California mice (e.g. Fuxjager et al., 2009). The effect of post-encounter T pulses on future ability to win is referred to as the “Winner-Challenge Effect” (Oyegbile and Marler, 2005). From a mechanistic standpoint, the causal link between post-victory T pulses and the winner effect can be tested by administering injections of T, which mimic the natural changes in this hormone’s circulation that otherwise occur after a fight (a transient T increase that is approximately 3–5× greater than baseline and that lasts for approximately 10 min).

Below, we integrate research from California mice with a variety of other species, including humans, to explore this relationship between T and competition, with the caveat that there is species variation in hormonal control of behavior across species.

## 2. Baseline testosterone (T)

Testosterone has long been considered to be an important hormone for promoting aggressive behaviors in males and in some cases females (Duque-Wilckens and Trainor, *in press*). In many species, removal of the testes reduces or eliminates male aggression and T implants restore aggression (Soma, 2006; Trainor et al., 2009; Fuxjager et al., *in press*). However, there are a number of studies illustrating that castration in some species has no effect on male aggression (Caldwell et al., 1984; Demas et al., 1999; Goymann et al., 2007; Trainor and Marler, 2001), indicating that the relationship between T and aggression is not always linear. The link between baseline T levels and aggression in human literature has been inconsistent: some studies have identified positive relationships between T and aggression, while many other studies report no association (Archer, 1991; Salvador and Costa, 2009; Carré and Olmstead, 2015). Recent discoveries suggest that this inconsistency is less about reproducibility and more about factors associated with short-term changes in T and/or the actual context in which aggressive responses are studied (Archer, 2006; Carré and Olmstead, 2015). The maturation of the “Challenge Hypothesis” generated a focus on changes in T in response to social interactions (Wingfield et al., 1990). These ideas provided new perspectives on the relationship between T and aggression across species, including humans (Archer, 2006). Moreover, studies that examine dynamic T that corresponds with competitive interactions have revealed important relationships between T and aggression that cannot be detected with analyses of baseline T.

## 3. Transient testosterone (T) levels

An important component of the Challenge Hypothesis was an analysis of how T levels rapidly increased during aggressive interactions when baseline T was otherwise low, such as during the non-breeding season. Indeed, comparative studies across multiple vertebrate taxa suggest that an ability to increase T during aggressive encounters is

evolutionarily conserved (Hirschenhauser and Oliveira, 2006; Wingfield, 2005), which suggests that mechanisms that regulate T levels in response to aggressive interactions is important to optimize and/or balance reproduction and survival. Yet, the functional significance of competition-induced T secretion has only recently been studied.

The California mouse is an interesting case of a species in which castration does not reduce male aggressive behavior (Trainor and Marler, 2001). However, male California mice that win a single aggressive encounter exhibit a significant increase in T levels that peaks about 45 min after the encounter is over (Marler et al., 2005). The time course for this increase is slower than that observed in some avian species (e.g. 10 min in song sparrows; Wingfield and Wada, 1989); however, the slow ramp up of T is similar to that found in house mice and rats (Amstislavskaya and Popova, 2004). It may be that, in mammals, the effects of post-encounter increases in T are more long-term (hours or days) after the aggressive encounter concludes. This was tested in male California mice that were castrated and given T implants that produced a baseline T level that was similar to baseline T levels in intact males (Trainor et al., 2004). Each male was tested in a resident-intruder test and then injected with either saline or T 30 min after the test. Injections of T produced an increase in T that peaked at 45 min post-encounter, matching the T profile observed in intact individuals. Males injected with T were more aggressive in subsequent resident-intruder tests days later, suggesting that a function of the post-encounter T pulse is to increase aggression in future encounters. Interestingly, the white footed mouse (*Peromyscus leucopus*), a promiscuous species, does not exhibit a post-encounter increase in T and does not show a significant winner effect unless administered a post-encounter increase in T (Fuxjager et al., 2011a). Testosterone pulses could increase aggression and future ability to win in a number of ways, including by increasing an individual's attachment to the location of the winning experience (as discussed in the section on endogenous reward) or by inducing long-term plasticity in neurobiological circuits that control aggression. Nevertheless, it is likely that these mechanisms, and potentially others as well (see Marler et al., 2005; Wright et al., 2012), contribute to the long lasting effects of T and winning experiences on behavior.

One of the most important effects of winning experiences is to increase effectiveness in aggressive contests, most likely through more intense aggressive behavior (Fuxjager et al., in press). Intact male California mice that win aggressive encounters are more likely to induce submissive behavior in a larger intruder in later aggressive encounters (Oyegbile and Marler, 2005). Interestingly, a T injection alone is sufficient to increase aggressive behavior, but this effect is stronger when paired with winning an aggressive encounter (Fuxjager et al., 2011b). Many behavioral effects of T in male California mice have long-term influences on aggression, although short-term effects also occur under other circumstances such as rapid inhibition of ultrasonic vocalizations (within 20 min) towards unfamiliar females in pair bonded but not single males (Pultorak et al., 2015).

More direct evidence for rapid effects of T on aggression is found in men (although not women; review by Geniole et al., 2016). For example, in the Point Subtraction Aggression Paradigm (PSAP), participants compete against an opponent (usually a computer) in which they can earn points or take points from their partner. The latter (taking points from the partner) is associated with rapidly increasing T levels during the task (Carré et al., 2011, 2014). Other researchers have developed a novel approach to further examine the relationship between T and neural activation in response to threat-related stimuli (van Wingen et al., 2010; Goetz et al., 2014; Zilioli and Watson, 2014; Mehta et al., 2015; Carré et al., in press). In one of these studies, they gave healthy men a gonadotropin releasing hormone antagonist, which normalized T concentrations to low baseline levels. These men were then randomly assigned to receive treatment with T or placebo and tested in a face-matching task while undergoing fMRI. Men treated with T had greater increases in reactivity in the amygdala and hypothalamus to angry

faces compared to men treated with placebo (Goetz et al., 2014). In a subsequent study, exogenous T increased self-perceptions of physical dominance in men (Welling et al., 2016), with these effects of T on brain function and behavior occurring within 2 h of T administration. Indeed, the rapid effects of T extend beyond humans and are found in fish, birds, and mammals (Remage-Healey and Bass, 2004, 2006; Mangiamele and Thompson, 2012; Cornil et al., 2013; Fuxjager et al., 2015; Pultorak et al., 2015), suggesting that these effects are an important mechanism for T effects on aggression across vertebrate taxa. Some of this work has even begun to show that such rapid T effects are the result of estradiol acting through nongenomic mechanisms to control aggression behavior (Heimovics et al., 2015; Laredo et al., 2014).

#### 4. Mechanisms underlying behavioral effects of dynamic testosterone (T)

In male California mice, winning territorial disputes increases the number of androgen receptor (AR) positive cells within the nucleus accumbens (NAcc), ventral tegmental area (VTA), and dorsal-lateral bed nucleus of the stria terminalis (dIBST) (Fuxjager et al., 2010). Increased AR expression is also observed in the NAcc of dominant male C57Bl6 mice, compared to subordinates, when social status is determined via aggressive outcomes (Greenberg et al., 2014). Together, these data suggest that brain regions that are part of the mesolimbic dopamine (DA) system and social behavior network become more sensitive to androgen. Thus, winning competitive contests likely induces long-term changes (at least on the order of days) in mechanisms by which androgenic hormones, like T, can mediate neural circuits that help control behavioral motivational and social interactions (O'Connell and Hofman, 2012; Goodson, 2005).

Currently, the mechanisms through which winning experiences drive changes in brain and behavior are not well understood. Intriguingly, in male California mice, aromatase inhibitors, which prevent the conversion of testosterone to estradiol, can increase baseline levels of aggression that mice ordinarily show in a male–male contest, but not the actual positive change in aggression that otherwise occurs in response to the acquisition of prior agonistic experiences, such as a decrease in attack latency (Trainor et al., 2004; Villalon Landeros et al., 2012). This suggests that estrogenic pathways (i.e., via estrogen receptor) and androgenic pathways (i.e., via AR) may control baseline and experience-induced plasticity in aggression, respectively. This is an exciting idea that needs further investigation because there has not been a clear-cut division or theoretical framework regarding baseline versus such experienced-induced change in aggression at a mechanistic level. Yet, understanding the mechanisms underlying these differences will allow us to explore whether there is feedback between changes in these two aspects of aggressive phenotype, and which components can be manipulated. Interestingly, experience induced changes can also be blocked using DA blockers post-encounter (Becker and Marler, 2015), suggesting a link between AR and DA (DA is discussed further in the section on endogenous reward).

Testosterone is also known to promote vasopressin (AVP) synthesis (Wang and De Vries, 1993; Rood et al., 2013). During social encounters, male AVP immunoreactivity in the PVN decreases and blood AVP levels increase (Steinman et al., 2015), suggesting AVP release. In addition, central infusion of a V1a receptor antagonist reduces male aggression (Bester-Meredith et al., 2005). A missing link is whether a transient increase in T would be sufficient to increase AVP production, as previous studies examining the effects of T on AVP have used long-term manipulations on baseline hormone levels. Interestingly, in Syrian hamsters, AVP1a receptor binding increases in brain areas in response to repeated aggressive encounters (Cooper et al., 2005).

Another potential mechanism of experience-induced changes in aggression could be activation of cyclic AMP response element binding protein (CREB). Phosphorylation leads to activation of CREB, allowing it to bind to cAMP response elements and regulate gene expression.

Winning an aggressive encounter reduces phosphorylated CREB positive cells within frontal cortex, lateral septum, anterior hypothalamus, medial amygdala and periaqueductal gray (Trainor et al., 2010). Dephosphorylation of CREB can reduce its effectiveness as a transcription factor, so even short term changes in CREB phosphorylation could lead to long-term changes in protein expression. To our knowledge, no study has examined the effects of T on CREB phosphorylation in the brain. However, in Sertoli cells T acts rapidly to phosphorylate CREB (Fix et al., 2004), which would suggest that aggression-induced decreases in CREB might not be directly mediated by T. Still, even indirect effects of T on CREB could potentially induce long lasting changes in gene expression that could in turn affect aggressive behavior in future encounters.

### 5. Effects of context on the interaction between testosterone (T) and aggression

A fight's context can profoundly influence the relationship between T and aggression. This idea is well established and historically viewed through the lens of seasonal effects on T and aggression. For example, classic field studies in song sparrows (*Melospiza melodia*) show that males are aggressive throughout much of the year, and will even protect territories well outside of the breeding season (Wingfield and Hahn, 1994). In these birds, however, T influences aggression only during the summer breeding periods, whereas other mechanisms control aggression during the winter when individuals are not actively mating (Wingfield and Soma, 2002). Similar results are found in mammals, like the dusky-footed wood rat (*Neotoma fuscipes*), where castration decreases aggression during the breeding season, but has no impact on aggressive behavior during other times of the year (Caldwell et al., 1984). These studies therefore show that animals may maintain their aggressive repertoires across much of the year, but T only influences these repertoires in certain sexual contexts.

More recent work shows that context has a large effect on dynamic T levels, and thus helps determine whether an animal mounts a T response to a fight. In cichlid fish (*Oreochromis mossambicus*), for instance, males normally show a large post-victory surge in 11-ketotestosterone (11-KT), which is the main androgen in fish (Hirschenhauser et al., 2004). However, if males are presented with a mirror and therefore forced to fight against their own reflection, they subsequently do not experience a transient rise in 11-KT once the contest is over (Oliveira et al., 2005). A similar effect is described in quail, where individuals fighting against their own mirror images fail to show any post-contest change in T (Hirschenhauser et al., 2008). It is thought that the males may perceive these encounters as a tie or draw, since they are unable to resolve the “fight,” because their opponents never show signs of submission or defeat in response to an attack (Oliveira et al., 2005; Hirschenhauser et al., 2008). Although researchers have questioned this interpretation (Desjardins and Fernald, 2010), the data suggest that an appraisal of a fight's context, as opposed to the output of aggressive behavior, determines whether androgens are released after the dispute ends. Importantly, the view that the perception of a win or loss dictates subsequent hormonal responsiveness is largely consistent with work in humans, which shows that non-combative competitions (Apicella et al., 2014; see Casto and Edwards, 2016 for a review) can elicit post-encounter T pulses. This, of course, implies that the physical act of fighting is not in and of itself necessary to trigger the release of T following a competition (e.g., Salvador et al., 1999).

Context also affects the ability of T to influence the formation of the winner effect. In adult California mice, males that accrue three separate victories in their home cage show an increase in future winning ability, while males that accrue three separate victories in a series of unfamiliar cages do not (Fuxjager and Marler, 2010). Thus, the saliency of the location in which a mouse fights its opponents mediates whether the experiential factors associated with the outcome of the battle are likely integrated at the level of the brain to shape future aggression. From a

physiological standpoint, this study also suggests that these effects are regulated through context-dependent modulation of post-victory T. Males, for example, that acquire a win at home experience a transient surge in T after the encounter, while males that win in an unfamiliar location do not (Fuxjager and Marler, 2010). This likely means that environmental context determines whether T levels rise after a fight, and this T surge then regulates whether future winning ability is enhanced. Interestingly, this framework is consistent with what we know about the home advantage in humans, whereby male athletes experience a T spike after victories at “home games,” but not after victories at “away games” (Carré, 2009; Casto and Edwards, 2016).

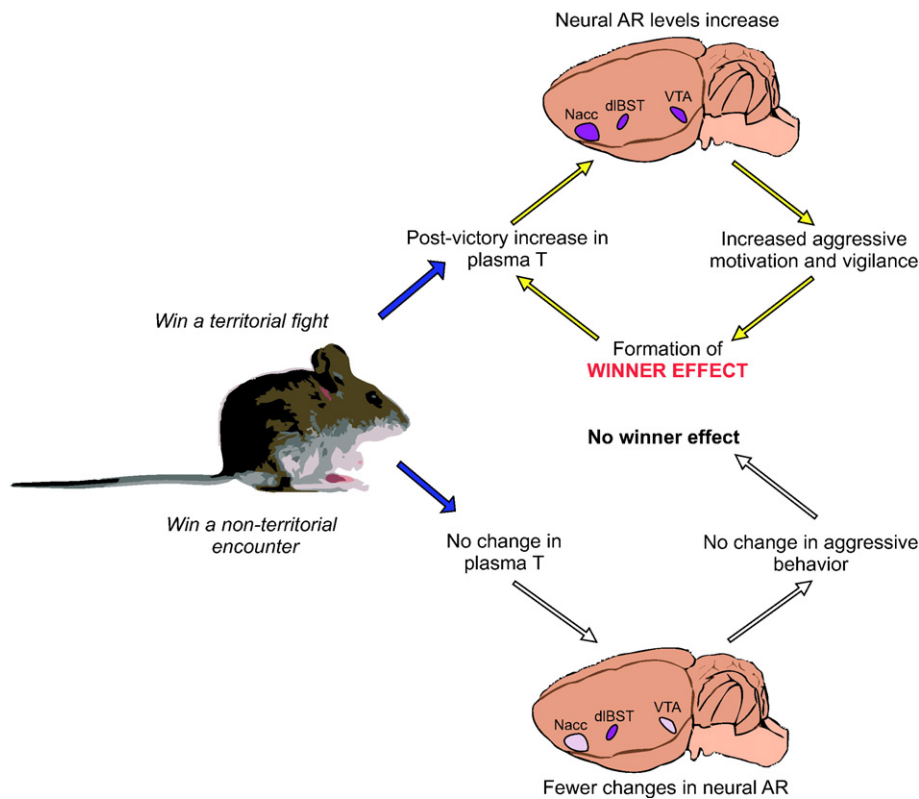
The link among context, T and the winner effect can be traced back to the brain. As we describe above, studies in California mice show that acquiring prior wins increases AR levels in the NAcc, VTA, and dBST (Fuxjager et al., 2010). This same study shows that these effects largely depend on where a win occurs. That is, if mice acquire wins in unfamiliar environments, AR levels increase only in the dBST, and not in the NAcc and VTA (Fuxjager et al., 2010). This finding indicates that winning modifies the androgenic phenotype of the brain in a context-dependent manner. Furthermore, levels of AR-immunoreactivity specifically in the NAcc and VTA are positively associated with winning behavior during bouts of clear territorial defense, whereas this relationship does not exist in the dBST. The ability of androgens to act within the NAcc and VTA is therefore likely related to an individual's aggressive repertoire in a way that predicts whether or not he wins future territorial or ‘home’ fights. Thus, by gating whether AR levels increase in these two regions of the mesolimbic reward system, environmental context may regulate whether individuals form a winner effect as a result of accrued winning experiences (Fig. 1).

### 6. Testosterone (T) and endogenous reward

Above, we alluded to the fact that androgenic effects on aggression are tightly linked to endocrine and brain-level systems that underlie reward and reinforcement, and it is therefore unsurprising that aggression itself is a “rewarding” behavior. Numerous studies have shown that male rodents with prior aggressive experiences will seek out future agonistic encounters with conspecifics (de Almeida et al., 2005; Fish et al., 2002), and other work implies that these effects are the product of mesolimbic dopaminergic activity (Couppis and Kennedy, 2008). For instance, microdialysis studies reveal that DA levels in the NAcc rise during and after a fight with a conspecific (van Erp and Miczek, 2000, 2007). Furthermore, blocking dopaminergic activity in this brain nucleus using a D1 and D2 receptor antagonist blunts the reinforcing effects of these aggressive experiences (Couppis and Kennedy, 2008).

Other work has begun to explore the role of DA in modulating the winner effect and plasticity in aggression. In male Syrian hamsters (*Mesocricetus auratus*), the accumulation of multiple winning experiences that lead to a strong winner effect is positively associated with substantial increases in tyrosine hydroxylase positive cells in NAcc, BST, and lateral septum (LS) (Schwartz et al., 2013). As tyrosine hydroxylase is the rate-limiting enzyme in the DA synthesis pathway, these data suggest that winning experience enhanced the ability of select brain regions to produce DA. Work in California mice further suggests that any build-up of DA in these brain regions is likely functional, with respect to its impact on aggression. That is, if male California mice are given a DA receptor antagonist after they win a fight, then they fail to develop a strong winner effect (Becker and Marler, 2015). It is notable, however, that these mice still behave aggressively, suggesting that their ability to participate in competition is not completely abolished. Taken together, this work suggests that dopaminergic systems are involved in experience-induced plasticity in competitive behavior, possibly by altering the motivational properties that underscore reinforced aggression-seeking behavior.

How do androgens influence this connection between aggression and the winner effect? Answering this question is difficult, as there



**Fig. 1.** Schematic representation of how the winner effect works in California mice. Males that accrue wins while defending their territory (upper figure) experience a post-victory testosterone (T) surge, as well as increased expression of androgen receptor (AR) in the nucleus accumbens (NAcc), dorsal lateral bed nucleus of the stria terminalis (dlBST), and the ventral tegmental area (VTA) (denoted by dark purple coloration of the nuclei). These changes in neural phenotype are associated with increased future winning ability, and thus underlie a positive feedback loop between winning experience, post-encounter T, and expression of brain-level AR. By contrast, males that accrue the same number and type of wins in novel, unfamiliar locations (lower figure) do not experience a post-victory T surge, nor do they experience an increase in AR expression within the NAcc and VTA (denoted by light purple coloration of the nuclei). Thus, these males fail to form a winner effect.

may be subtle species differences in the endocrine mechanisms that underlie plasticity in a male rodent's aggressive behavior in response to its prior social experience. Nonetheless, certain work on androgens and reinforcement suggest that T acts within select parts of the mesolimbic system to mediate the actions of DA. This idea is supported by the fact that T itself is a rewarding stimulus; indeed, exogenous T not only induces a conditioned place preference (Alexander et al., 1994; Arnedo et al., 2000; Packard et al., 1997), but also is voluntarily self-administered in operant conditioning tests (Wood, 2002; Wood et al., 2004). Importantly, studies also suggest that T exerts its reinforcing effects by acting on neural target cells that influence the release of DA in the NAcc (DiMeo and Wood, 2006; Packard et al., 1997). Social victory may therefore stimulate the release of endogenous T, which in turn strengthens aggressive motivation. This model is likely adaptive from an ethological perspective, as territorial individuals that win fights while protecting their home likely stand to benefit from the resulting increase in territorial fidelity and vigilance. Indeed, territorial fidelity may come to animals in the form of a conditioned place preferences for certain sites within a territorial range, whereas territorial vigilance may come to animals in the form of a persistent desire to pursue and evict unwanted intruders.

However, there are additional factors to consider when evaluating the efficacy of this model. In some species, for example, regions of the reward system express few, if any, AR (Wood and Newman, 1995; 1999). This would suggest that there is little substrate within the mesolimbic reward system on which T or its androgenic metabolites can act to modulate dopaminergic control of behavioral reinforcement. This is corroborated by recent work in Long-Evans rats that shows that T does not enhance motivation for aggression (Wood et al., 2013). This

study also reports that T decreases measures of behavioral impulsivity and has no effect on tyrosine hydroxylase protein levels in NAcc, VTA, and prefrontal cortex. Although these results may seem difficult to resolve with work that highlights clear and robust connections between androgens, reward systems, and aggression (see above), we suspect that factors related to social experience or context may explain discrepancies among studies. We know, for example, that repeated winning experience in ecologically salient environments modifies the ability of androgens to act within various parts of the brain, including the NAcc and VTA. Thus, low levels of AR in these (or other) brain regions or the inability of T to increase aggressive motivation may be due to a lack of "experiential priming" of androgenic systems within the brain. Such effects are evident in California mice, as T reinforces a conditioned place preference in sexually naive males, but not pair-bonded males (Zhao and Marler, 2014). This indicates that experiences associated with the formation of a sexual pairing re-shape the neuroendocrine systems that govern the rewarding properties of T. Other work in humans also suggests that plasticity that can be found in the reward-related systems. Studies are now needed to assess how context interacts with androgenic and reward systems to modulate behavior and the level of plasticity within these reward systems.

## 7. Temporal pattern of testosterone (T) pulses

Thus far, we have focused on research examining T release after or during a contest. However, because T release can also occur before a competition, it is also important to focus on T's functions prior to and during a competitive encounter (Marler et al., 2005). There are two issues that become particularly relevant during these time periods: the

anticipatory T release and the rapid effects of T before and/or during a social encounter. We already touched on rapid effects of T (see above), but here we focus on the anticipatory increases in T. Implicit in this anticipatory rise is the existence of predictability in the competitive social environment. Through Pavlovian conditioning, male blue gouramies (*Trichogaster trichopterus*; a freshwater fish) can be induced to prepare for an aggressive encounter, which leads to early aggressive display behavior and more aggression during an encounter (Hollis, 1984). Following this, Antunes and Oliveira (2009) demonstrated in the cichlid fish (*Oreochromis mossambicus*) that males learn to predict an oncoming male-male competition (via a light cue) and release anticipatory 11-KT, as measured after the time when an encounter would have occurred. In another example, prior to territorial patrolling in chimpanzees, which occurs every seven to nine days, there is a rise in T that is based on unknown cues, although social factors are likely involved (Sobolewski et al., 2012). Detection of an opponent's pheromones may also prime individuals through an increase in androgens in advance of an aggressive interaction, such as in mangrove rivulus fish (*Kryptolebias marmoratus*) (Garcia et al., 2015). These studies demonstrate that anticipatory T can be released in nonhuman animals and that as a result of some cue(s) in the environment the timing potentially can be conditioned. What is unclear is whether the specific timing of T release in relation to the behavioral encounter is important, and without experimental manipulations of androgens, we do not know cause and effect for androgen release and changes in behavior. Moreover, as Seyfarth and Cheney (2013) point out, we know little about the advantages of the ability to anticipate social changes, which presumably involve theory of mind to some extent (ability to attribute state of mind to others) that applies not only to affiliative behavior, but also, we speculate, to aspects of competitive behavior in non-human animals. Another potential area of animal research is to better investigate both the advantages of predictability and an ability to assess the intent of others (group competition) in anticipation of a individual or group encounters/competitions, both in and of themselves, as well as when linked to anticipatory increases in T.

In contrast to non-human animals, there are a number of studies with humans illustrating a pre-competition or sporting event causes a rise in T (Booth et al., 1989; Mazur et al., 1992; Neave and Wolfson, 2003; Suay et al., 1999; but see Salvador et al., 2003 for individual variation). These studies suggest that T has a preparatory or anticipatory function, potentially involving a higher motivation to win and can be related to the home advantage (Carré et al., 2006). Consistent with this is evidence that positive coach feedback to a team can increase T levels prior to a game; higher T levels in turn are linked with better performance in the game (Cook and Crewther, 2012). In a group competition there is also support for the idea that individuals are assessing the emotions of others; T can increase attention towards angry faces (e.g. van Honk and Schutter, 2007). Predictability also allows individuals a level of control over a situation that may significantly reduce the stress of a competitive encounter.

On a mechanistic level, the changes in T may be related to anticipatory changes in DA that increase before an aggressive encounter (Ferrari et al., 2003). Male Long-Evans rats exposed to encounters at a specific time on days 1–10, display increased DA before, during and after an encounter even in the absence of an encounter on day 11 at that same specific time. The interactions of T with this DA pattern (and a drop in post-encounter serotonin in the same study) have not been investigated to our knowledge. As described earlier, T can have an excitatory effect on the DA system and may therefore amplify an aggressive response or influence the rewarding aspects of T or an aggressive encounter, making this an interesting area of study.

## 8. Conclusion

Our review illustrates that there is potential for cross-exchange between animal and human research to germinate new ideas or

approaches for understanding interactions between androgens and competition. We know little about how variation in temporal pattern of T release impacts competitive and aggressive behavior and are just beginning to understand how the rapid and long-term effects of T impact behavior before, during, and after competitive encounters in both humans and animals. The rewarding aspect of T found in rodents is potentially important because learning in the form of place preference conditioning can occur in the development of addiction to drugs of abuse (review by Huston et al., 2013). In humans, plasma T has important effects on activity of the ventral striatum (containing the nucleus accumbens) during learning, and the midbrain contains abundant androgen receptors (Morris et al., 2015). These observations are consistent with the distribution of androgen receptors in rodents, although dependent on past experience (as described earlier). So far it is unclear whether increased ability to win a competition at “home” is mediated by the rewarding effects of T on dopamine signaling in either animals or humans. In our review of social and physical context, we illustrated how critical context can be for the behavioral effects of T in rodents. In humans, the physical context is also important, as illustrated by the link between T and the home advantage (Carré, 2009; review by Casto and Edwards, 2016). Recently it has been suggested that the effect of T on sexual behavior in animals and humans is also context dependent (review by Goldey and van Anders, 2015).

We further illustrated more variation in function of T pulses through animal studies, demonstrating that past reproductive experience can impact the functions of T pulses through conditioned place preferences such as whether a male has pair bonded or not (Zhao and Marler, 2014, 2016). The effect of pair bonding on T levels has been extensively demonstrated in humans and indirectly linked to competition associated with reproduction as well (review by Goldey and van Anders, 2015). The most well documented similarities between rodents and humans that we described is the interaction between T and sports competitions, but T increases in response to many other competitive situations in humans (Archer, 2006; Carré and Olmstead, 2015; Casto and Edwards, 2016). Because winner and loser effects may contribute to dominance hierarchies (Bergman et al., 2003; Dugatkin and Druen, 2004), the influence of winner effects and the associated T links may also extend beyond what we describe in this review.

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