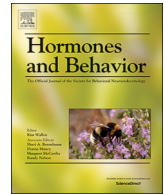




Contents lists available at ScienceDirect

## Hormones and Behavior

journal homepage: [www.elsevier.com/locate/yhbeh](http://www.elsevier.com/locate/yhbeh)

## Review article

## Human social neuroendocrinology: Review of the rapid effects of testosterone

Shawn N. Geniole<sup>a,b,\*</sup>, Justin M. Carré<sup>b,\*</sup><sup>a</sup> Department of Basic Psychological Research and Research Methods, Faculty of Psychology, University of Vienna, Liebiggasse 5, 1010 Vienna, Austria<sup>b</sup> Department of Psychology, Nipissing University, 100 College Drive, North Bay, Ontario P1B 8L7, Canada

## A B S T R A C T

It is well documented that testosterone concentrations change rapidly within reproductively relevant contexts (e.g., competition, mate-seeking). It has been argued that such rapid changes in testosterone may serve to adaptively fine-tune ongoing and/or future social behaviour according to one's social environment. In this paper, we review human correlational and experimental evidence suggesting that testosterone fluctuates rapidly in response to competition and mate-seeking cues, and that such acute changes may serve to modulate ongoing and/or future social behaviours (e.g., risk-taking, competitiveness, mate-seeking, and aggression). Some methodological details, which limit interpretation of some of this human work, are also discussed. We conclude with a new integrative model of testosterone secretion and behaviour, the Fitness Model of Testosterone Dynamics. Although we focus primarily on human aggression in this review, we also highlight research on risk-taking, competitiveness, and mate-seeking behaviour.

## 1. Introduction

Social cues relevant to reproduction and survival rapidly modulate approach or avoidance decision-making, and preferences for either of these responses are also dynamically updated with every relevant experience. One hormone that may be critical in mediating both of these processes, is testosterone. According to the Challenge Hypothesis (Wingfield et al., 1990), testosterone rises rapidly in response to cues of competition or social challenge in the environment and these changes in testosterone are functional in that they prepare the organism for competitive or aggressive interactions over resources important for survival and reproduction, especially during periods of social instability (e.g., when hierarchies, mates, or territories are being established). These transient surges are also thought to be more functional than sustained elevations given that elevations in testosterone may suppress immune function (Folstad and Karter, 2011; for review and meta-analysis, see Foo et al., 2017) and reduce parental care (e.g., Goymann and Flores Dávila, 2017), representing significant survival and reproduction costs. Therefore, testosterone fluctuations may govern dynamic trade-offs between parental and aggressive/competitive effort (Wingfield, 2017; Wingfield et al., 1990).

Although it was originally proposed to explain seasonal variation in testosterone concentrations in birds, the Challenge Hypothesis has since been applied to many taxa across different classes (for additional

review and meta-analysis, see Hirschenhauser and Oliveira, 2006). In European paper wasps, for example, removal of the colony's queen compared to a normal worker causes social instability and competition for the vacant queen position, leading to increases in juvenile hormone (a hormone that has similar effects on mating effort and may be functionally analogous to testosterone in vertebrates), with the greatest increases among those that become most dominant and aggressive (Tibbetts and Huang, 2010). In cichlid fish, 11-ketotestosterone and testosterone increase in anticipation of (Antunes and Oliveira, 2009), and 11-ketotestosterone increases in response to (Hirschenhauser et al., 2004), territorial intrusion, and both hormones also increase in response to viewing an agonistic bout between two other conspecifics (Oliveira et al., 2001). In California mice, testosterone rises after defeating a territorial intruder (e.g., Marler et al., 2005), and administration of testosterone increases subsequent aggression (e.g., Fuxjager et al., 2011). In male chimpanzees, the presence of an ovulating parous (but not nulliparous) female leads to an increase in testosterone and male-to-male competition (e.g., Muller and Wrangham, 2004) (for recent review of Challenge Hypothesis in non-human primates, see Muller, 2017).

Early work in humans revealed that baseline testosterone concentrations were elevated among men who self-reported being more (vs less) aggressive (e.g., Persky et al., 1971) and among female prisoners who were incarcerated for unprovoked compared to provoked (i.e.,

\* Corresponding authors.

E-mail addresses: [shawngeniole@gmail.com](mailto:shawngeniole@gmail.com) (S.N. Geniole), [justinca@nipissingu.ca](mailto:justinca@nipissingu.ca) (J.M. Carré).<https://doi.org/10.1016/j.yhbeh.2018.06.001>Received 17 February 2018; Received in revised form 12 May 2018; Accepted 2 June 2018  
0018-506X/ Crown Copyright © 2018 Published by Elsevier Inc. All rights reserved.

retaliatory) acts of violence (Dabbs et al., 1988). A meta-analysis of this and similar work on testosterone and aggression in humans suggested that testosterone shared a significant but rather weak association with aggression ( $r = 0.08$ ), with slightly stronger associations in women ( $r = 0.13$ ) than in men ( $r = 0.08$ ) (Archer et al., 2005). Also, meta-analyses suggest a positive association between basal testosterone and dominance in humans, with stronger links in women ( $r = 0.28$ ) than men ( $r = 0.12$ , Archer, 2006). Links between testosterone and human aggression may have been relatively weak given that much of this earlier work relied on self-report measures of aggression that captured one's trait-like or stable propensity for aggressive behaviour; conversely, the Challenge Hypothesis posits that links between testosterone and aggression are highly context-specific, with the strongest links existing during periods of social instability (Wingfield, 2017; Wingfield et al., 1990). Further, self-report measures may be more prone to response biases and inconsistent responding (e.g., Strang et al., 2013), and not always map onto actual behaviour (reviewed in Baumeister et al., 2007; Lobbstaal, 2015). As a consequence, behavioural measures of competition and aggression may be better suited to the investigation of hormone-behaviour relationships in humans, and thus produce stronger associations. Further, many of these studies employed baseline measures of testosterone, whereas testosterone fluctuates in response to social stimuli and behaviour, and such fluctuations (rather than baseline concentrations) are likely more relevant for driving mating effort (McGlothlin et al., 2007; for additional review, see Carré et al., 2011).

Here we review human research that supports the idea that testosterone fluctuates rapidly in response to a variety of social cues, contexts, and interactions, and that such fluctuations may function to modulate cognitive, behavioural, and neural function relevant to human mating effort – with a particular focus on human aggression (for additional reviews on testosterone and human social behaviour, see Archer, 2006; Carré et al., 2011; Carré and Olmstead, 2015; Eisenegger et al., 2011; Geniole and Carré, 2017; Goldey and van Anders, 2015; Knight and Mehta, 2014; Losecaat Vermeer et al., 2016; Oliveira and Oliveira, 2014; van Anders et al., 2011; van Anders and Watson, 2006; Zilioli and Bird, 2017).

## 2. Does testosterone rise in anticipation of, and in response to, social challenges and interactions relevant to reproduction?

### 2.1. Social challenges

Consistent with the Challenge Hypothesis, there is evidence in humans that testosterone rises in response to cues of social challenge and reproduction potential. In one study (Cohen et al., 1996), for example, participants who were shoulder bumped and insulted while walking down a hallway showed greater increases in salivary testosterone measured 10 min after the insult than did participants who were not bumped and insulted, an effect that was particularly robust among American participants who grew up in the south. In another study, a 15 min exposure to a strong cue of violence and aggression – a pellet gun that resembled a real handgun – caused a rise in testosterone greater than that caused by exposure to a children's toy (Klinesmith et al., 2006). Other studies have investigated anticipatory rises in testosterone leading up to competitive interactions, often sporting events, with meta-analytic summaries of this work providing evidence that testosterone does indeed increase prior to a competition (meta-analytic estimate:  $d = 0.27$ , after outlier removal, Archer, 2006). More recent investigations, not covered in this earlier meta-analysis, have also revealed similar anticipatory testosterone surges (e.g., Arruda et al., 2017; Cunniffe et al., 2015; T. Oliveira, Gouveia, & Oliveira, 2009; van der Meij, Almela, Hidalgo, et al., 2012; Arruda et al., 2017; Cunniffe et al., 2015; T. Oliveira, Gouveia, & Oliveira, 2009; van der Meij,

Almela, Hidalgo, et al., 2012; for recent review, see Casto and Edwards, 2016a).

Testosterone also changes during social challenges or competitive interactions. There is evidence, for example, that in more extreme social challenges, such as when soldiers are deployed to war zones, testosterone concentrations are elevated (Reijnen et al., 2015). Laboratory and field studies have also investigated testosterone responses to less extreme social challenges, such as those related to sport or other contests, with both men (e.g., Elias, 1981) and women (e.g., Bateup et al., 2002) showing increases in testosterone during the contests. Meta-analyses of this work indicate significant increases from pre- to post-competition ( $d = 0.16$ ), although effects are stronger in sport ( $d = 0.37$ ) compared to non-sport interactions ( $d = 0.06$ ), a difference likely driven by the additional influence of physical activity in sport-related contests (Archer, 2006). These changes may not be consistent in direction and magnitude across all contestants. According to the Biosocial Model of Status (Mazur, 1976, 1985; Mazur and Booth, 1998), winners and losers should experience divergent testosterone changes, with winners increasing and losers decreasing. These divergent responses are thought to facilitate subsequent dominance versus submissive behaviours, thus promoting further gains in or the protection of status in winners, and the prevention of further challenges and decreases in status in losers. This Biosocial Model of Status was based on earlier non-human primate studies in which male rhesus monkeys showed marked increases or decreases in testosterone (relative to baseline) depending on whether they were placed into a social hierarchy in which they assumed dominant versus submissive roles (Rose et al., 1975; Rose et al., 1972).

There are > 60 studies of this winner-loser effect in humans, with the contests varying on many important dimensions across studies (e.g., involving physical activity or not, playing in versus watching the competition, real world versus laboratory-based competitions). A recent meta-analysis of this work indicated that there was a significant effect of contest outcome on testosterone changes, with winners showing greater increases than losers ( $d = 0.20$ , with a 95% confidence interval of 0.10 to 0.31) (Geniole, Bird, Ruddick, & Carré, 2017). This estimate of the winner-loser effect is the most precise to date, and provides some support for the Biosocial Model of Status. The effect, however, was highly heterogeneous, and significantly larger for studies conducted outside of the lab (e.g., real sporting events and competitions:  $d = 0.43$ ) versus in the lab ( $d = 0.08$ ), perhaps because the outcomes of competitions that occur outside of the lab are more salient and meaningful to participants (Geniole, Bird, et al., 2017). For example, competitions outside of the lab are often public and have audiences, thus carrying greater social and reputational consequences. Contextual factors related to the composition of the audience (home versus away audience, Carré, 2009; ratio of opposite- to same- sex spectators, Miller et al., 2012) may further moderate these effects (see section below on additional moderators of these effects).

### 2.2. Cues or interactions relevant to reproduction

Testosterone also rises in anticipation of interactions relevant to reproduction. In a classic study, an anonymous author who spent weeks on an island in isolation – abstaining from sexual activity – noticed that his beard growth increased substantially on days leading up to his return to the mainland, where he would resume sexual activity (Anonymous, 1970). Because beard growth is promoted in part by testosterone (reviewed in Randall, 2008) and can thus be used as a proxy of androgenic activity, this study provided circumstantial evidence that testosterone may rise in anticipation of sexual activity. Women also appear to show an anticipatory testosterone surge to sexual activity: in one study that involved a within-subject design across multiple nights (van Anders et al., 2007), women showed greater

anticipatory testosterone surges leading up to sexual intercourse than to other control activities such as cuddling (controlling for physical contact) or exercise (controlling for physical activity) (for additional anticipatory effects, see [Hamilton and Meston, 2010](#)).

Testosterone also fluctuates in response to visual cues related to reproduction. For example, earlier studies suggest that viewing pornographic videos increases men's testosterone concentrations more than does viewing control videos (in serum within 10 min of exposure: [Stoléru et al., 1993](#); in saliva, within 15 min of exposure: [Hellhammer et al., 1985](#)). More recent studies employing larger samples also provide evidence that testosterone responds to these sexually explicit video stimuli in men (e.g., salivary changes within 12 min of exposure, [Ponzi et al., 2016](#)). In women, however, testosterone responses to sexually explicit video stimuli tend to be smaller and more variable (reviewed in [Goldey and van Anders, 2015](#)), with effects depending in part on the extent to which the women identify with the actors ([Goldey and van Anders, 2016](#)).

Testosterone concentrations also appear to fluctuate in response to subtler, less explicit cues or interactions relevant to reproduction (for reviews, see [Goldey and van Anders, 2015](#); [Roney and Gettler, 2015](#); [Zilioli and Bird, 2017](#)). For example, dancing with opposite-sex partners for 20 min caused a greater increase in testosterone in men and women than did dancing without the partners (salivary testosterone measured before and 25 min after initiation of the dance, [Quiroga Murcia et al., 2009](#)). Further, non-tactile, verbal interactions with women (for as little as 5 min) also increased men's testosterone concentrations more than did similar interactions with other men (changes detectable in saliva measured as early as 15 min from the beginning of the conversation, [Ronay and von Hippel, 2010](#); [Roney et al., 2007](#); [Roney et al., 2003](#); [Roney et al., 2010](#)). Finally, simply viewing photographs of opposite-sex faces posed in either angry or happy emotional expressions increased testosterone concentrations in both men and women more than did viewing same-sex faces posed in the same expressions (15 min viewing exposure, with detectable differences in saliva 40 min from the beginning of the face-viewing task, [Zilioli et al., 2014](#)). Testosterone concentrations also fluctuate in response to scents that may be relevant to reproduction. Specifically, testosterone concentrations are higher within approximately 15 min of the onset of exposure to olfactory cues of women near ovulation (high fertility) than to olfactory cues of women near menstruation ([Cerdeña-Molina et al., 2013](#); [Miller and Maner, 2010](#); but see [Roney and Simmons, 2012](#)). Therefore, testosterone concentrations increase relatively rapidly (within 15 to 20 mins) after brief and subtle exposures to cues that may be relevant for reproduction or mating.

One possibility is that the effects of these reproduction-relevant cues on testosterone are driven by explicit sexual thoughts that form in response to exposure to the cues. Nevertheless, studies that have investigated directly the influence of sexual thoughts on testosterone concentrations suggest that such thoughts have differential effects depending on the use of hormonal contraceptives in women – with decreases among women using, but increases among women not using, hormonal contraceptives ([Goldey and van Anders, 2011](#)) – and on the content of the imagined sexual thoughts in men – with larger testosterone increases as the imagined encounter had less versus more nurturance-related content ([Goldey et al., 2014](#)). These data in men are consistent with the Steroid/Peptide Theory of Social Bonds ([van Anders et al., 2011](#)), which posits that intimacy between partners may lead to divergent testosterone responses, depending on whether it is more sexual (aimed at reproduction or pleasure), which would increase testosterone, or more nurturant (aimed at establishing and enhancing loving and warm social bonds), which would decrease testosterone. Therefore, sexual thoughts may explain some of the cue-dependent and social interaction effects reviewed above, so long as they are low in nurturance-related content. This theory may also explain heterogeneity in testosterone responses within and across studies, with larger surges in testosterone expected as intimacy cues or interactions represent potential opportunities for sexual rather than nurturant intimacy.

### 3. How fast can testosterone surge?

To the extent that such rapid changes in testosterone are functional, either for survival or for reproduction, one might expect that such changes would map onto ongoing or future behaviours that serve these goals. Nevertheless, many decisions to approach or avoid must be made rapidly, within minutes or even seconds, whereas the fastest effects reviewed above occurred after approximately 10 min of the first exposure to the corresponding cue or interaction. One limitation of some of this work, at least with respect to capturing testosterone dynamics, is that salivary hormone measures were often used. These measures have a time-lag of approximately 10 min, relative to changes that are detectable in blood ([Riad-Fahmy et al., 1987](#)). This time-lag makes it difficult to establish the rapidity with which testosterone can fluctuate. Measuring blood concentrations of testosterone directly may thus better capture testosterone dynamics before, during, and after an exposure.<sup>1</sup> Using such measures in exercise physiology studies, for example, researchers have documented testosterone elevations immediately after the onset of intense exercise, increases which were greater than those obtained for less intense exercises matched for total workload ([Ježová et al., 1985](#)). In one study, there were significant elevations in testosterone over the course of 60 s, during which athletes completed a maximum force jumping exercise ([Bosco et al., 1996](#)). Therefore, blood measures may better capture rapid fluctuations in testosterone.

### 4. What systems drive these rapid testosterone surges?

Testosterone secretion is controlled, primarily, by the hypothalamic pituitary gonadal axis. To stimulate the secretion of testosterone into the bloodstream, the hypothalamus first releases gonadotropin-releasing hormone, which stimulates the anterior pituitary to release follicle stimulating and luteinizing hormones. Luteinizing hormone then stimulates the gonads which, in turn, lead to the synthesis and secretion of testosterone into the bloodstream. Because of the multiple steps required to trigger testosterone secretion, and the time delay required for each step (e.g., the last step alone, from luteinizing hormone release to testosterone release, is estimated to take 40–70 min based on pharmacological challenge studies in humans, [Veldhuis and Iranmanesh, 2004](#)), it is unlikely that the rapid changes in testosterone reviewed above are controlled by this axis (as pointed out by [Flinn et al., 2012](#); [Schultheiss et al., 2005](#)). Consistent with this idea, testosterone surges in some studies were found independent of surges in luteinizing hormones (i.e., the testosterone changes were not preceded or related to preceding surges in luteinizing hormone; e.g., in response to sexual cues, [Stoléru et al., 1993](#); in response to exercise, [Sutton et al., 1973](#)).

Some have suggested (e.g., [Carré and Olmstead, 2015](#); [Casto and Edwards, 2016a](#); [Schultheiss et al., 2005](#); [Stoléru et al., 1993](#); [Carré and Olmstead, 2015](#); [Schultheiss et al., 2005](#); [Stoléru et al., 1993](#)) that sympathetic catecholamines – specifically epinephrine and norepinephrine, which are released rapidly from the adrenal medulla during fight or flight responses – regulate these quick, dynamic fluctuations in testosterone. Leydig cells of the testis, for example, which are responsible for the synthesis and secretion of testosterone into the bloodstream, possess receptors for luteinizing hormone and for these catecholamines (e.g., [Rossi et al., 2018](#)). Epinephrine and norepinephrine also rise in response to the exercise, with the magnitude of the rise correlating strongly with that of the rise in testosterone (e.g.,

<sup>1</sup> Measuring hormones in blood, however, is more invasive and disruptive to the study protocol and procedures (making hormone measurement less flexible, especially for field studies). Some may have a strong aversion to needles as well, which could lead to heightened stress responses and a reduced willingness to participate. Therefore, it is important to weigh the temporal sensitivity of blood measures against the flexibility and reduced invasiveness of saliva measures (for more detailed review, see [van Anders, Goldey, & Bell, 2014](#)).



Ježová et al., 1985). Furthermore, blocking the adrenergic receptors to which these catecholamines bind, especially beta receptors (using the drug propranolol, for example), rapidly reduces testosterone (e.g., Lewis et al., 1981; Rosen et al., 1988) and abolishes the surge in testosterone that otherwise occurs in response to exercise (Ježová and Vigaš, 1981) (for similar catecholamine-dependent effects in non-human primates, see Sapolsky, 1986). Therefore, rapid surges in testosterone, induced by social interactions, cues, or exercise, are likely too quick to be controlled by the hypothalamic pituitary gonadal axis; instead, these surges may be driven by the rapid release of sympathetic catecholamines (for additional review of this slower versus faster system of testosterone secretion, see Casto and Edwards, 2016a).

## 5. Do rapid fluctuations in testosterone map onto social behaviours and cognitions relevant to survival and reproduction?

As mentioned above, if these rapid changes in testosterone are functional for survival and reproduction, these hormonal changes likely map onto behaviours, cognitions, and physiological responses that serve these goals. Many studies have established longer, more delayed effects of testosterone (e.g., 3–26 weeks of hormone replacement therapy are needed for changes in sexual interest and function, mood, and strength, reviewed in Saad et al., 2011), but if testosterone modulates rapid fight/flight or approach/avoid decision making, there should also be evidence for quicker effects.

Most human studies that have investigated the function of testosterone dynamics have employed correlational designs in which changes in testosterone were measured concurrently with ongoing behaviour or cognition. For example, across several laboratory studies, fluctuations in testosterone were correlated positively with concurrently measured anger (mixed-sex sample, Peterson and Harmon-Jones, 2012), aggression (in men: Carré et al., 2010; Carré and McCormick, 2008; Cote et al., 2013; Geniole et al., 2011) or punitive behaviour (marginal effects in men but not women, Prasad et al., 2017; in men: Inoue et al., 2017; but null effects in mixed-sex sample examining dominant or deferent economic decision making, Mehta et al., 2017; see Fig. 1a–b). Testosterone changes are also correlated with concurrently measured mate-seeking behaviours. For example, increases in men's testosterone were correlated positively with their talkativeness, extraversion, and attempts to impress women during conversations (Roney et al., 2003; Experiment 2 of Roney et al., 2007). Men may also attempt to impress or attract mates through risky behaviours, as a willingness to take risks may advertise qualities that are appealing to women [e.g., riskiness signals strength (Fessler et al., 2014), which women find attractive (e.g., Sell et al., 2017)]. In one study, men took more physical risks in a skateboard performance task, and had higher testosterone concentrations after the task, when their performance was being watched by a female compared to a male research assistant (Ronay and von Hippel, 2010). These post-task testosterone concentrations<sup>2</sup> were also correlated with the degree of risk taking. Therefore, results from these correlational studies suggest that rapid changes in testosterone may map onto ongoing behaviours relevant to competition and reproduction.

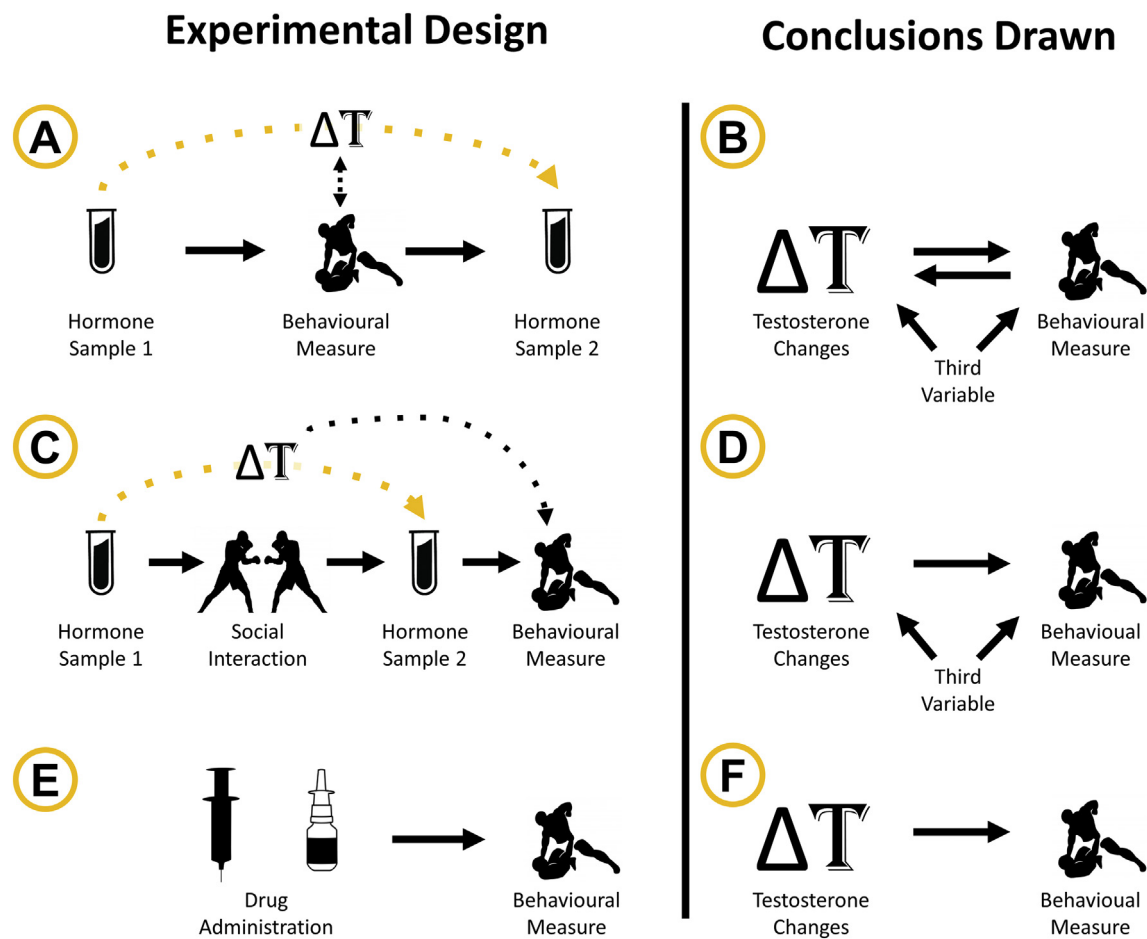
There are a few key limitations to this type of research design. First, the directionality of effects is obscured by the concurrent measurement of testosterone and behaviour. Rather than testosterone influencing behaviour, it may be that the behaviours influence testosterone, leading to the correlations. Also, it is possible that some third, unmeasured variable (e.g., state anger) is modulating both the rise in testosterone concentrations and the behaviour of interest. To better rule out the former possibility – that the behaviour is causing the testosterone surge – some researchers have examined behaviours measured after the testosterone changes occurred (reviewed in Geniole and Carré, 2017; see

Fig. 1c–d). From studies employing this approach, there is evidence that competition-induced testosterone changes predict decisions to compete in subsequent contests. This link, however, appears dependent on the outcome, decisiveness, and opponent in the competitions. When given the opportunity to play against the same opponent, testosterone changes positively predicted willingness to compete, but only among those who initially lost against the opponent (Mehta and Josephs, 2006). In this case, measurement of willingness to compete was assessed just 15 min after the post-competition saliva sample was obtained. Similarly, another study reported that a rise in testosterone in response to a competitive interaction with an ambiguous outcome predicted men's willingness to approach a subsequent competitive interaction just 10 min after the post-competition saliva sample was obtained (Carré and McCormick, 2008). When given the opportunity to play against a novel opponent, testosterone changes positively predicted willingness to compete (within 15 min of the post competition saliva sample), but only among those who won decisively (rather than non-decisively) against the opponent from the preceding contest (Mehta, Snyder, Knight, & Lassetter, 2015). Therefore, competition-induced fluctuations in testosterone may function to promote subsequent competitive decisions, perhaps aimed at regaining lost status (among those who lost), solidifying status (among those with ambiguous outcomes), or gaining additional status (among those who decisively won).

Fluctuations in testosterone also predict subsequent aggressive and antagonistic behaviours. For example, men, but not women, who experienced greater surges during competitions or social challenges were more likely to aggress towards others in the Point Subtraction Aggression Paradigm, a well-validated laboratory measure of aggression (reviewed in Geniole, MacDonell, & McCormick, 2017). In these studies, an increase in testosterone predicted subsequent aggression in men (Carré et al., 2013; Carré et al., 2014; Carré et al., 2009), but not women (Carré et al., 2009; Carré et al., 2013). In the latter studies, aggressive behaviour was assessed within 5–10 min after the post-competition saliva samples were obtained. In another study, participants were told they were the winners of a competitive interaction and were given the opportunity to determine the payout of their opponent. Testosterone surges during the competition in men, but not in women, predicted the amount given such that men who experienced greater surges in testosterone gave less money to the opponent (decisions were made 1–2 min after the post-competition saliva sample, Geniole et al., 2013). In other studies, testosterone surges predicted subsequent aggression when the surges occurred in response to cues of violence or aggression (a handgun) (male-only sample: Klimesmith et al., 2006), but not when they occurred in response to cues of nurturance (a baby crying) (male-only sample: van Anders, Tolman, & Jainagaraj, 2014), suggesting that the context in which testosterone surges occur may be important. In the former study, the increase in testosterone positively predicted subsequent aggression measured within 5 min of detecting the increase in testosterone. Together, this work suggests that testosterone surges, in response to competitions or cues of violence and aggression, predict subsequent aggressive or antagonistic behaviour in men, but not in women. In women, endogenous testosterone changes may even function to reduce aggression and promote prosocial behaviour: in one study, for example, competition-induced testosterone surges were correlated with women's self-reported willingness to reconcile with members of the team against which they just competed (Casto and Edwards, 2016b).

There is less work involving the extent to which endogenous testosterone changes predict other types of fitness-relevant behaviours (e.g., risk-taking, mate-seeking). Greater testosterone surges during competition predicted less risk aversion in men in one study (Apicella et al., 2014), but not in another (Smith and Apicella, 2017). Further, in a study on testosterone and mate-seeking, competition-induced surges in the hormone predicted more affiliative behaviours (e.g., smiling, talkativeness, eye contact) in men during their conversations with women, but not with other men (van der Meij, Almela, Buunk, Fawcett,

<sup>2</sup> Post-task testosterone concentrations may reflect changes during the task, although it is possible that the groups differed at baseline.



**Fig. 1.** (a) Correlational design in which changes in testosterone concentrations ( $\Delta T$ ) are measured concurrently with a social behaviour of interest (e.g., aggression); the researcher tests whether the change in testosterone is correlated with the ongoing behaviour (correlation represented by the dashed black line). (b) The direction of the relationship between change in testosterone and behaviour cannot be determined with this approach, nor can causal claims be made due to third variable problems. (c) Correlational design in which changes in testosterone concentrations are measured in response to a social interaction (e.g., competition) and assessment of behaviour is obtained after the change in testosterone is detected; the researcher tests whether the changes in testosterone predict the subsequent behaviour (correlation/prediction represented by the dashed black line). (d) Although this design enables one to rule out the role of behaviour in modulating testosterone concentrations, causal claims cannot be made due to third variable problems. (e) Experimental design in which testosterone concentrations are directly manipulated (e.g., through injections, nasal gels) and assessment of behaviour is obtained after the manipulation; the researcher tests whether the testosterone and placebo/control groups differ on the behaviour of interest. (f) This design removes the third variable problem and enables one to make causal claims about the role of testosterone in modulating behaviour.

& Salvador, 2012). Therefore, more work is needed on the relationship between fluctuations in testosterone and these other types of fitness-relevant behaviours, although current evidence suggests that increases in testosterone may promote mate-seeking behaviour in men.

## 6. How rapid are the effects of testosterone?

Although the studies reviewed above suggest that testosterone may promote behaviours relevant to competition and mate-seeking, salivary measures were often used, making it difficult to determine the rapidity with which these fluctuations can affect behaviour. Further, despite the temporal separation of testosterone changes and behaviour, and evidence that the preceding changes predicted the subsequent behaviours, it is still possible that third variables (e.g., state anger) cause an increase in testosterone and in competitive, aggressive, and mate-seeking behaviour, leading to the testosterone-behaviour associations. Without manipulating testosterone concentrations directly, it is difficult to establish causality and the time-course of the effects.

Several single-dose pharmacological challenge paradigms have been developed, which allow for identification of causal and time-course effects (for reviews of studies employing these designs, see Bos et al.,

2012; Zilioli and Bird, 2017). One of the most widely used challenge paradigms involves a single sublingual dose (0.5 mg) of testosterone. Because of initial validation work showing that the earliest physiological effects of this dose (as indexed by vaginal pulse amplitude, a marker of vaginal arousal) occurred 3–4.5 h after administration (Tuiten et al., 2000; for replication, see Tuiten et al., 2002), most studies use a similar delay. Such studies have provided evidence that testosterone increases threat-related neural activation (Hermans et al., 2008; for effects dependent on approach or avoidance, see Radke et al., 2015) and cardiac responses (van Honk et al., 2001), and reduces fear-potentiated startle (Hermans, Putman, Baas, Koppeschaar, & van Honk, 2006), empathy (indexed by facial mimicry, Hermans, Putman, & van Honk, 2006), and sensitivity to punishment (van Honk et al., 2004; also see Wu et al., 2016). Testosterone also decreased gaze aversion from, and physical avoidance of, angry faces (Enter et al., 2014; Terburg et al., 2012), especially among those with Social Anxiety Disorder (Enter, Spinhoven, & Roelofs, 2016; Enter, Terburg, Harrewijn, Spinhoven, & Roelofs, 2016; Terburg et al., 2016). Together, these studies suggest that within 4.5 h, testosterone can modulate physiology, cognition, and behaviour in a way that may promote mate-seeking, competition, and aggression.

Nevertheless, studies that have examined social behaviour more directly, using the same challenge procedure and time delay, suggest that testosterone increases competitive or antisocial behaviours in some circumstances, but prosocial or collaborative behaviours in others. For example,<sup>3</sup> in one study in which female participants could entrust money to another individual who could either exploit their trust or reciprocate, testosterone decreased the amount entrusted (Boksem et al., 2013). When the roles reversed, however, and participants had to decide whether to reciprocate in response to receiving money, testosterone increased reciprocity. In another study, female participants could split sums of money with other players who could either accept the offers (in which case both players received their corresponding payouts) or reject the offers, if they deemed them unfair (in which case both players received nothing). In this economic bargaining task, testosterone increased the amount offered to the other player (Eisenegger et al., 2010). In a game of bluff poker, in which the best strategy is to bluff randomly, even when you have a weak and disadvantageous hand (cold bluffing), testosterone decreased both random and cold bluffing in young women (van Honk et al., 2016). These seemingly discrepant findings may be explained by testosterone's role in increasing status promotion and protection, more generally (Eisenegger et al., 2011; Mazur and Booth, 1998). In these tasks, when status can be threatened – through having an offer rejected, trust exploited, a bluff called – testosterone promotes behaviours that, although superficially prosocial, primarily function to minimize this risk to status. Therefore, although testosterone promotes prosocial behaviour under some conditions, and antisocial behaviour under others, both of these behaviours may be outputs of a mechanism more generally geared towards status promotion and protection (Eisenegger et al., 2011).

Limitations of these single-dose administration studies reviewed above are that the studies involved exclusively female participants, the challenge paradigm increased concentrations of testosterone to a supraphysiological level (> 10 times the baseline endogenous concentrations in women; Tuiten et al., 2000), and only a single time lag has been used to assess effects on behaviour. To understand how fluctuations within a normal physiological range – that better mimic endogenous surges that occur in fitness-relevant contexts – regulate cognition and behaviour in men, researchers have recently validated an alternative single-dose pharmacological challenge paradigm, which boosts concentrations to the high-normal range within 30–120 min (e.g., see Carré et al., 2015; Eisenegger et al., 2013; Goetz et al., 2014). Results from studies employing this administration procedure, which also involved a wider range of time delays between administration and assessment of cognition and behaviour (0.5 h–3.5 h), generally converge with the results reported above. For example, testosterone increased threat-related neural activation (1.5 h delay; Goetz et al., 2014) and reduced personal distance from threatening stimuli (3.5 h delay; Wagels et al., 2017). In one study that directly compared shorter versus more delayed effects of testosterone, the drug increased self-perceptions of masculinity regardless of whether perceptions were measured 2.3 or 4 h after administration (Welling et al., 2016). Together, these results suggest that testosterone may exert similar effects across this time window, and similar effects in men and women, at least with respect to threat-related neural activation and approach/avoidance behaviours. Further, the consistency across these different paradigms and dose

types suggest that these effects may be particularly robust, and may alleviate potential concern regarding the generalizability of the findings from sublingual administration paradigms used in women.

Other studies that investigated decisions that were more directly related to mating and aggression have provided evidence that testosterone increases preferences for feminine faces for short- (vs long-) term relationships (Experiment 1: 3.25-h delay; Experiment 2: 2.25 h delay, Bird et al., 2016).<sup>4</sup> Testosterone also increased anger after a non-social provocation (an equipment failure in which a joystick stopped responding to pulls that were critical for successful performance), and the force with which participants yanked the joystick, a behaviour the authors used to index implicit aggression (3.5 h delay, Panagiotidis et al., 2017). In another study, however, involving an economic bargaining task and a mixed-sex sample,<sup>5</sup> testosterone reduced (non-significantly) costly retaliatory punishment (Kopsida et al., 2016). These heterogeneous effects of the hormone may be explained by variation in personality: testosterone appears to rapidly (within 1 h) potentiate costly aggressive behaviour, but only in men who are high in dominance and/or low in self-control (Carré et al., 2017). In the latter study, the main effect of testosterone on aggression was relatively weak, and not statistically significant ( $r = 0.15$ ). More recently, our laboratory has used a novel pharmacological challenge paradigm (intranasal testosterone gel), which increased testosterone to the high-normal range within just 15 min. In this work, we found that testosterone rapidly (within 30 min) increased aggressive behaviour in young men ( $n = 308$ ), an effect that was particularly pronounced among men with high-risk personality profiles (dominant, impulsive, independent) and fewer CAG repeats within the androgen receptor gene (Geniole et al., unpublished). Again, the main effect of testosterone on aggression was relatively weak, and not statistically significant ( $r = 0.11$ ). The time course of the effects of testosterone on aggression are consistent with correlational evidence in which acute rises in testosterone rapidly modulate subsequent competitive and aggressive behaviours (Carré et al., 2013, 2009; Mehta and Josephs, 2006). The latter findings also highlight the important interactive effects of drug condition, genetic polymorphism of the AR, and personality traits in rapidly potentiating aggressive behaviour in healthy young men (see below for more examples of individual difference and social/contextual moderators).

## 7. Situational and individual difference factors that moderate testosterone response to social cues, and its effects on behaviour and cognition

As mentioned above, testosterone responses to social cues and interactions, and testosterone effects on behaviour, are highly heterogeneous. A number of situation/context and individual difference moderators have been identified, that appear to account for some of this heterogeneity (for additional reviews, see Carré and Olmstead, 2015; Casto and Edwards, 2016a; Geniole and Carré, 2017; Zilioli and Bird, 2017). For example, with respect to mating contexts, cues, or interactions, testosterone increases when interacting with single women, but decreases when interacting with women who are paired with friends (Flinn et al., 2012); increases in response to sexually explicit stimuli, but especially among men with lower (vs greater) interest in babies (Zilioli et al., 2016); increases in response to imagining sexual interactions in women and men, but only to the extent that the men's imagined interactions contain little (vs much) nurturing content (reviewed in Goldey and van Anders, 2015); increases in response to interacting with women, but especially among men higher in aggressive dominance

<sup>3</sup> The focus of this paragraph was on a select set of studies conducted using the same challenge paradigm and a similar time delay, however there are additional studies using longer delays and other administration methods (e.g., Cueva et al., 2017; Dreher et al., 2016; Wibral, Dohmen, Klingmüller, Weber, & Falk, 2012), or that found effects dependent on other biological factors (e.g., prenatal hormone exposure as indexed by digit ratio, van Honk et al., 2012). The focus of this paragraph was on a select set of studies conducted using the same challenge paradigm and a similar time delay, however there are additional studies using longer delays and other administration methods (e.g., Dreher, Dunne, Pazderska, Prod, & Nolan, 2016; Wibral, Dohmen, Klingmüller, Weber, & Falk, 2012), or that found effects dependent on other biological factors (e.g., prenatal hormone exposure as indexed by digit ratio, van Honk, Montoya, Bos, van Vugt, & Terburg, 2012).

<sup>4</sup> This effect appears to be explained, primarily, by a reduction in preference for feminine faces as long-term partners, perhaps because feminine faces are perceived as less loyal or as more likely to cheat, thus representing a greater threat to status than less feminine faces.

<sup>5</sup> The dose increased testosterone concentrations to the high-normal range in men, and a supraphysiological level in women



(van der Meij et al., 2008), and who have fewer CAG repeats on exon 1 of the androgen receptor gene (a polymorphism associated with androgen receptor efficiency) and lower cortisol (Roney et al., 2010). With respect to competitive contexts, cues, or interactions, testosterone increases after competitions, but especially for men higher in skills relevant to the competition (Eisenegger et al., 2017) and who believe they performed well (Trumble et al., 2012); increases after victories, but especially for men with low basal cortisol and high basal testosterone (Zilioli and Watson, 2012), whereas for men with high basal cortisol testosterone may decrease after a victory if it is narrow (rather than decisive) (Wu et al., 2017). With respect to the link between endogenous fluctuations in, and pharmacologically manipulated, testosterone and affect, cognitions, and behaviour, this link appears stronger among individuals high in dominance (aggression: Carré et al., 2017, 2009 decisions to compete in winners: Mehta, van Son, et al., 2015; negative affect: Knight et al., 2017), independent self-construal (aggression: Welker, Norman, et al., 2017; risk taking, in winners of a competition: Welker, Roy, Geniole, Kitayama, & Carré, 2017), and lower in self-control (aggression: Carré et al., 2017). According to the dual-hormone hypothesis (Mehta and Josephs, 2010), testosterone's effects on behaviour are blunted by cortisol, such that stronger testosterone-behaviour links should be expected among those low but not high in cortisol. Whereas many studies have investigated this hormone interaction using baseline measures of testosterone and cortisol, few have examined whether rapid fluctuations in testosterone share stronger associations with behaviour among those low versus high in cortisol (reviewed in Mehta and Prasad, 2015). One set of studies demonstrated that increases in testosterone promote better financial bargaining outcomes when there is a concurrent decrease in cortisol, but worse outcomes when there is a concurrent increase in cortisol (Mehta, Mor, Yap, & Prasad, 2015), although there were no such interaction effects in a subsequent study involving a different financial decision making task (Mehta et al., 2017), or in the dominance or friendliness of participants during a negotiation exercise (Lozza et al., 2017).

Prenatal hormone concentrations may also be important moderators, priming the brain to be sensitive for later, rapid surges in testosterone. Along these lines, one putative marker of prenatal testosterone relative to estradiol exposure, the second-to-fourth digit-ratio (2D:4D ratios; lower 2D:4D ratios suggest higher prenatal testosterone to estradiol ratios), has been shown to moderate the effects of testosterone administration on behaviour and cognition in adulthood: Testosterone administration decreased cognitive empathy (in women: van Honk et al., 2011; but see null effects in Olsson et al., 2016; in men: Carré et al., 2015) and also reduced trust (in women: Buskens et al., 2016)<sup>6</sup> among those who had higher prenatal testosterone to estradiol ratios (i.e., lower second-to-fourth digit-ratios). Some effects of testosterone administration, however, were exaggerated among those with higher prenatal estradiol to testosterone ratios: testosterone increased the perceived permissibility of utilitarian decision-making in moral dilemmas in which harm was inevitable (e.g., killing a crying baby to prevent the hidden group from being detected by soldiers; the baby's death is inevitable, because it will also die if the hidden group is detected) (in women: Montoya et al., 2013; but see null effects, in men: Arnocky et al., 2017) and also increased financial contributions to a public good (van Honk et al., 2012), but only among those with higher prenatal testosterone to estradiol ratios. Some have proposed that this prenatal hormone ratio may influence the extent to which testosterone, later in life, is aromatised or not to estradiol (e.g., van Honk et al., 2012). If so, more exaggerated effects of testosterone among those who had higher prenatal estradiol to testosterone ratios (as indexed by

greater 2D:4D ratios) could indicate that the hormone is acting indirectly, through its aromatization to estradiol (see below for more on the role of estradiol). In any case, these interactive effects between digit ratios and testosterone administration suggest that early hormonal exposure may prime the brain for later effects of testosterone, although more direct measures of early testosterone exposure (e.g., umbilical cord blood concentrations) will likely be critical for providing stronger tests of this hypothesis.

## 8. Future directions

### 8.1. Identifying the mechanisms through which testosterone rapidly increases aggression

More research will be needed to elucidate the psychological/neural mechanisms through which testosterone modulates human aggression. One possibility is that testosterone increases one's sensitivity to threat-related cues in the environment, and this heightened sensitivity to threat may bias approach-related aggressive behaviour. One key brain region involved in processing threatening stimuli and mediating autonomic, neuroendocrine, and behavioural responses to such threat is the amygdala (for reviews, see Davis and Whalen, 2001; LeDoux, 2000). Pharmacological challenge experiments indicate that testosterone enhances amygdala reactivity to threat-related facial expressions (Goetz et al., 2014; Hermans et al., 2008; Radke et al., 2015; van Wingen et al., 2009) and decreases amygdala-OFC functional coupling during processing of such expressions (van Wingen et al., 2010). These findings are notable in light of research in animal models in which several interconnected cortical and subcortical structures are directly related to the expression of aggression (Nelson and Trainor, 2007). One prominent model suggests that the neural circuitry of reactive aggression consists of the medial amygdala, medial hypothalamus and periaqueductal grey (PAG) (Blair, 2010; Siegel et al., 2007). This model suggests that the medial amygdala provides excitatory input to glutamatergic neurons located within the medial hypothalamus, which exert excitatory drive on PAG neurons, ultimately mediating aggressive behaviour (Siegel et al., 2007). Importantly, androgen and estrogen receptors are widely distributed throughout the neural circuitry underlying reactive aggression (e.g., Donahue et al., 2000; Fernández-Guasti et al., 2000; Murphy et al., 1999; Newman, 1999; Roselli et al., 2001; Wood and Newman, 1999), suggesting that testosterone and/or its metabolites (e.g., estradiol) may directly modulate this circuitry by interacting with steroid hormone receptors in these regions. Such heightened threat-related neural function may ultimately increase anger in response to social provocation.

Another possibility is that testosterone modulates aggressive behaviour by increasing the reward value of aggression. Indeed, our most recent work indicates that testosterone's conditional effects on aggression were partly mediated by increases in feelings of reward associated with aggression (Geniole et al., unpublished). These findings are consistent with evidence in humans that aggression is rewarding, and that people regulate the degree/severity of aggression based on the extent to which they both self-report the behaviour to be rewarding (e.g., Ramírez et al., 2005) and show activation in reward-related brain regions (e.g., nucleus accumbens) during the decision to aggress (Chester and DeWall, 2016; Krämer et al., 2007; see Chester, 2017 for a recent review). Because testosterone increases sensitivity to reward (van Honk et al., 2004) and activity in the same brain regions (e.g., ventral striatum, which includes the nucleus accumbens, Hermans et al., 2010), it may upregulate subjective feelings of reward associated with retaliatory aggression. If testosterone regulates aggression by increasing the reward value of this behaviour, the dopaminergic system is most likely involved. In rodent models, the administration of testosterone enhances dopaminergic activity in reward regions of the brain within just 30 min (e.g., de Souza Silva et al., 2009), and testosterone's rewarding effects are abolished when dopamine receptor antagonists are

<sup>6</sup> People tend to entrust more money to others with whom they will have repeated compared to one-shot interactions, but this increased trust in repeated versus one-shot interactions was reduced after women with higher (but not lower) prenatal testosterone to estradiol ratios were administered testosterone (Buskens et al., 2016).

administered directly into the nucleus accumbens (Packard et al., 1998). The rewarding effects of aggression can be indexed more directly by having rodents exert effort (e.g., nose-pokes) to gain access to conspecific rivals; dopamine receptor antagonists, when administered to the nucleus accumbens, reduce this effort and, once access to the conspecific is eventually gained, reduce aggression during the bout (Couppis and Kennedy, 2008). Collectively, this work suggests that testosterone may modulate human aggression by upregulating the pleasure derived from – or anticipated in response to – aggression, with these effects mediated by the rapid regulation of dopamine (for additional review, see Losecaat Vermeer et al., 2016). Future studies would thus benefit from targeting this pathway directly by manipulating both dopamine receptor availability and testosterone concentrations to determine if effects of testosterone are abolished when these receptors are blocked (for additional review on the potential mechanisms underlying testosterone-driven mating effort, see Casto and Edwards, 2016a; Welker et al., 2015).

### 8.2. Sex differences/similarities in the relationship between testosterone and aggression, and the role of menstrual cycle phase, hormonal contraceptive use, and estradiol

A crucial area for future research is whether testosterone's effects on aggressive behaviour are sex-dependent. Previous work indicates that testosterone responses to competitive interactions positively predict subsequent aggression (Carré et al., 2013, 2009) and punitive behaviour (Geniole et al., 2013) in men, but not women. One difficulty in concluding that context dependent changes in testosterone do not modulate aggression in women is that it is difficult to accurately measure variability in testosterone concentrations in women using standard techniques (ELISAs), which may contribute to additional measurement error, ultimately obscuring hormone-behaviour relationships (e.g., Welker et al., 2016). Despite problems with measurement of testosterone in women, however, earlier studies provided evidence that links between baseline levels of testosterone and aggression (meta-analysis in Archer et al., 2005), dominance (meta-analysis in Archer, 2006), attention to anger (e.g., van Honk et al., 1999), and sensitivity to stereotype-threats (Josephs et al., 2003) were similar in magnitude between men and women, or even stronger in women. Also, despite using different drug administration protocols, neuroimaging work indicates that exogenous testosterone administration has similar effects on threat-related neural function in women (Hermans et al., 2008; van Wingen et al., 2009) and men (Goetz et al., 2014). Clearly, more work will be needed to determine the extent to which effects of testosterone on aggression are similar and/or different in men and women.

One possibility is that the relationships between testosterone dynamics and aggressive or antagonistic behaviour were only found in men because the measures used in these studies (Carré et al., 2013, 2009; Geniole et al., 2013) are more typical of male than of female aggression, which tends to be more relational or indirect (e.g., gossip, McAndrew, 2014). It is also possible that additional variability related to menstrual cycle and hormonal birth control obscures hormone-behaviour relationships in women; both factors have been shown to moderate the effects of hormones on dominance and aggression (e.g., Dougherty et al., 1997; Stanton and Schultheiss, 2007; Stanton and Schultheiss, 2007), or have had direct effects on antagonistic behaviour (e.g., Geniole et al., 2013) (for additional review on menstrual cycle and hormonal contraceptive effects, see Cobey and Hahn, 2017; Montoya and Bos, 2017).

The steroid hormone estradiol may also play a more important role than testosterone in regulating female mating effort, although findings have been rather inconclusive thus far: Estradiol (but not testosterone) was linked to implicit motivations for dominance (Stanton and Schultheiss, 2007; see also Stanton and Edelstein, 2009) and to self-reported (e.g., Stanton and Schultheiss, 2007) and behavioural measures of aggression (e.g., Geniole et al., 2013) in women, although the

direction of these relationships differed (positive with dominance, negative with aggression; for review of mixed evidence in female adolescents, see Balzer et al., 2015). Estradiol administration also increased aggression across some studies (e.g., in adolescents, Finkelstein et al., 1997) but not others (in postmenopausal women, using the Ultimatum Game as an index of reactive aggression, Zethraeus et al., 2009). Nevertheless, it remains possible that the rapid effects of testosterone administration observed in previous studies were indirect and mediated by its aromatization to estradiol. Estradiol rapidly modulates aggression in mice and birds (within 20 min of administration, reviewed in Heimovics et al., 2015), and testosterone administration increases concentrations of testosterone and estradiol in humans (e.g., Dreher et al., 2016), although one pharmacokinetic study suggests such estradiol increases may only be evident 4 h after the corresponding increase in testosterone (Eisenegger et al., 2013). Ultimately, to better identify the independent or synergistic effects of these hormones, it will be important to employ conditions in which testosterone is administered both alone and in combination with aromatase inhibitors (which would reduce testosterone's conversion to estradiol); If estradiol does mediate testosterone's rapid effects on mating effort, then such effects should be abolished with the co-administration of aromatase inhibitor. If, on the other hand, estradiol has no effects, then the co-administration of aromatase inhibitor should not change the effects of testosterone administration.

### 8.3. Pharmacogenetic approach

Testosterone's effects on cell function, and ultimately psychological and behavioural processes, is also mediated by testosterone itself, or its other metabolite, dihydrotestosterone, binding to the androgen receptor (AR). When activated by these androgens, ARs translocate to the cell nucleus where they ultimately have transcriptional control of androgen-dependent genes. Importantly, transcriptional potential of target genes by the AR is influenced by a relative expansion of a polyglutamine stretch in the N-terminal domain of the AR, which is encoded by a trinucleotide (CAG) repeat polymorphism of the AR gene. In vitro work indicates that the transcriptional efficiency of the AR is inversely related to the length of CAG repeats within the AR gene (i.e., fewer repeats confers a more 'efficient' AR; Chamberlain et al., 1994; Choong et al., 1996). Furthermore, in vivo work suggests that variation in the AR CAG repeat moderates the effect of testosterone replacement therapy on prostate volume growth. Specifically, testosterone increases prostate volume, but only among those individuals with relatively short CAG repeats within the AR (Zitzmann et al., 2003). Other research indicates that testosterone positively predicts amygdala reactivity to threat-related cues, but only among men with fewer CAG repeats within the AR gene (Manuck et al., 2010). More recently, we have found that administration of a single dose of testosterone rapidly increases aggressive behaviour, but only among men with relatively fewer CAG repeats within the AR gene (Geniole et al., unpublished). Although the above literature suggests that testosterone effects on such processes may be mediated via the AR, it is important to note that such studies are correlational. Future research will require combination manipulations, such as the concurrent use of testosterone administration with androgen receptor blockers and/or aromatase inhibitors. Such an approach may enable researchers to determine the extent to which testosterone's effects on behavioural processes are mediated by the AR, or other pathways (e.g., estrogen receptor).

### 8.4. Replicability of social neuroendocrine research

Despite substantial methodological advances in the field of social neuroendocrinology, challenges related to the replicability of social neuroendocrine research remain. For instance, the intra-nasal oxytocin literature exploded in the early 2000s with the publication of a landmark paper in the journal *Nature* demonstrating that a single dose of



oxytocin increased men's trust behaviour in an economic task (Kosfeld et al., 2005). Despite early excitement about the effects of oxytocin on human social behaviour, several recent replication attempts have failed, calling into question the robustness of some of the earlier findings (see Nave et al., 2015 for a review). Single dose testosterone administration studies have only started to be conducted over the past 5 years (but see Zak et al., 2009) and thus, it will be critical to replicate and extend some of the early promising findings (e.g., Carré et al., 2017; Nave et al., 2017; Welling et al., 2016) to determine the extent to which the effects are robust. In such replication attempts, it will be important to have well-powered studies, which will most likely require multi-laboratory collaborations to be able to detect relatively small-to-medium effects (especially when examining interactions between drug condition, personality traits, and/or genetic polymorphisms). In addition, pre-registration of study hypotheses will enable researchers to differentiate between confirmatory versus exploratory analyses (van't Veer & Giner-Sorolla, 2016). Replication efforts will also need to pay close attention to potential sex differences in the effects of testosterone, the testosterone dose administered, route of administration (e.g., intramuscular injection, transdermal gel, intra-nasal gel), the timing of behavioural assessment after drug application, personality traits, and genetic factors (e.g., CAG repeat within the AR gene) – all factors that may ultimately influence the effects of testosterone on the parameters assessed.

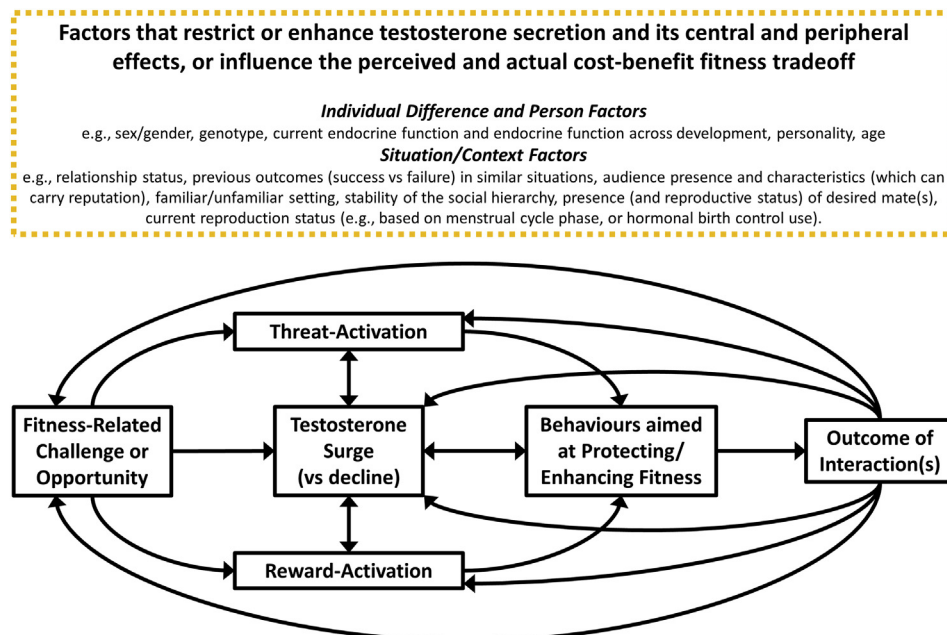
## 9. An integrative model of rapid testosterone secretion and human social behaviour

Based on this review of the literature and on models described elsewhere (e.g., Eisenegger et al., 2011; Mazur and Booth, 1998; Oliveira, 2009; van Anders et al., 2011; Welker et al., 2015; Wingfield et al., 1990; Zilioli and Bird, 2017), we propose the Fitness Model of Testosterone Dynamics (see Fig. 2). In this model, testosterone concentrations rise rapidly in response to cues of social challenge or opportunity that threaten or can enhance fitness (or resources and status/dominance important for fitness). These challenges and opportunities promote testosterone surges, in part, through the activation of neural and physiological systems related to the processing of threat (e.g., amygdala, sympathetic nervous system) and/or reward (e.g., mesolimbic dopaminergic pathway). These rapid testosterone surges then activate – implicitly and/or explicitly – a general fitness protection and

enhancement system, which generates behaviours (e.g., risk-taking, mate-seeking, competitive, and aggressive behaviours) that ultimately function to serve these fitness protection and enhancement goals, operating in part through the upregulation of threat and/or reward systems. Therefore, threat and reward systems mediate relationships both between social challenges/opportunities and testosterone surges, and between testosterone surges and behaviour. These behaviours and the corresponding outcomes (e.g., being successful/unsuccessful in risk-taking, mate-seeking, competition) feedback to further modulate testosterone such that more competitive (less nurturing) behaviours and more successful outcomes increase testosterone, whereas less competitive (more nurturing) behaviours and unsuccessful outcomes decrease testosterone. These outcomes also feedback to influence reward and threat activation (e.g., more successful outcomes increase reward processing) and the probability of encountering subsequent fitness-related challenges or opportunities (perhaps through regulation of approach/avoidance decision making, with successful outcomes increasing approach and decreasing avoidance behaviours).

These links involving testosterone, however, are not straightforward: they each depend on individual difference and situation/context factors that (1) restrict/inhibit or enable/increase testosterone secretion and its central and peripheral effects (e.g., androgen receptor availability and efficiency; hypothalamic pituitary adrenal axis activity; aromatase activity and efficiency) or; (2) determine the extent to which the challenge/opportunity is, or is interpreted as, costly versus beneficial with respect to fitness, or resources and status/dominance important for fitness. For example, individual difference factors such as trait dominance may make challenges or opportunities seem more promising or rewarding, and thus lead to bigger testosterone surges and a stronger correspondence between such surges and subsequent aggressive behaviour. Situational factors, such as the stability of a social hierarchy, the availability of a desired partner, the presence and composition of an audience, and previous outcomes in similar situations may also moderate testosterone responses to challenges or opportunities and influence the degree to which such surges lead to the subsequent behaviour. Again, however, these factors should only be important to the extent that they (1) restrict or enable testosterone secretion and its actions on the body and brain, and (2) influence the actual or perceived cost and benefits to fitness or resources and status/dominance important for fitness.

Note that although testosterone is posited to promote fitness



**Fig. 2.** Fitness Model of Testosterone Dynamics in which cues of social challenge or opportunity activate threat and reward systems which trigger testosterone release. These surges in testosterone then further regulate threat and reward systems that guide behaviours aimed at protecting or enhancing fitness (or resources and dominance/status important for fitness). These behaviours, and the result of the behaviours (i.e., the outcomes) further feedback to influence testosterone secretion. The outcomes also feedback to influence the probability of experiencing subsequent fitness-related challenges or opportunities. In the box above the model, we provide examples of potential moderators of these relationships, which are relevant to the extent that they restrict or enhance testosterone secretion and its central and peripheral effects, or influence the perceived and actual cost-benefit fitness tradeoffs.

enhancing or protection behaviours (those that increase survival, reproduction, or status/dominance and resources important for these goals), it likely decreases nurturance and parental investment (e.g., Kuo et al., 2016; for review, see van Anders et al., 2011), which may compromise overall fitness (e.g., by reducing offspring survival). The potential benefits of mate-seeking and competition (increased number of offspring) may, however, outweigh the costs of reduced parental effort (decreased offspring survival) for overall fitness. In any case, although not explicitly included in our model, another area that will require further work is examination of the extent to which testosterone may rapidly decline in response to fitness-related parental cues (e.g., presence of offspring), and the extent to which such rapid declines may promote fitness-enhancing parental behaviours (e.g., nurturance of offspring). For instance, van Anders et al. (2012) found that men given the opportunity to comfort a crying infant simulator (a doll designed to resemble a real baby) experienced rapid decreases in testosterone, with the largest decreases among the men who reported feeling more nurturance-related arousal and affect (e.g., pleasure, feelings of warmth, worry).

## 10. Conclusions

In summary, the evidence reviewed in this paper suggests that testosterone levels change rapidly in reproductively relevant contexts (e.g., competition, mating), and that such endocrine responses map onto ongoing and/or future social behaviours aimed at protecting or enhancing fitness, or resources and status or dominance important for fitness. These findings are consistent with evidence in animal models (e.g., Fuxjager et al., 2010; Gleason et al., 2009; James and Nyby, 2002; R. F. Oliveira, Silva, & Canário, 2009; Trainor et al., 2004) and suggest that context dependent changes in testosterone may enable organisms to rapidly adjust their behaviour according to the demands or opportunities in the current social environment.

## Acknowledgements

We would like to thank Caelan Mathers and Brittney Robinson for assistance with creating the figures. This project was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant (RGPIN-2014-06676) and Northern Ontario Heritage Fund Corporation (Project number 8510044) to JMC. SNG holds a Banting Postdoctoral Fellowship from the Social Sciences and Humanities Research Council (SSHRC) of Canada and is also supported by the Vienna Science and Technology Fund (WWTF VRG13-007).

## References

- van Anders, S.M., Watson, N.V., 2006. Social neuroendocrinology. *Hum. Nat.* 17 (2), 212–237. <http://dx.doi.org/10.1007/s12110-006-1018-7>.
- van Anders, S.M., Hamilton, L.D., Schmidt, N., Watson, N.V., 2007. Associations between testosterone secretion and sexual activity in women. *Horm. Behav.* 51 (4), 477–482. <http://dx.doi.org/10.1016/j.yhbeh.2007.01.003>.
- van Anders, S.M., Goldey, K.L., Kuo, P.X., 2011. The steroid/peptide theory of social bonds: integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrinology* 36 (9), 1265–1275. <http://dx.doi.org/10.1016/j.psyneuen.2011.06.001>.
- van Anders, S.M., Tolman, R.M., Volling, B.L., 2012. Baby cries and nurturance affect testosterone in men. *Horm. Behav.* 61 (1), 31–36. <http://dx.doi.org/10.1016/j.yhbeh.2011.09.012>.
- van Anders, S.M., Goldey, K.L., Bell, S.N., 2014a. Measurement of testosterone in human sexuality research: methodological considerations. In: *Archives of Sexual Behavior*. Springer, US. <http://dx.doi.org/10.1007/s10508-013-0123-z>. (February 27).
- van Anders, S.M., Tolman, R.M., Jainagaraj, G., 2014b. Examining how infant interactions influence men's hormones, affect, and aggression using the Michigan infant nurturance simulation paradigm. *Fathering* 12 (2), 143–160. <http://dx.doi.org/10.3149/ft.1202.143>.
- ANON, 1970. Effects of sexual activity on beard growth in man. *Nature* 226 (5248), 869–870. <http://dx.doi.org/10.1038/226869a0>.
- Antunes, R.A., Oliveira, R.F., 2009. Hormonal anticipation of territorial challenges in cichlid fish. *Proc. Natl. Acad. Sci.* 106 (37), 15985–15989. <http://dx.doi.org/10.1073/pnas.0900817106>.
- Apicella, C.L., Dreber, A., Mollerstrom, J., 2014. Salivary testosterone change following monetary wins and losses predicts future financial risk-taking. *Psychoneuroendocrinology* 39 (1), 58–64. <http://dx.doi.org/10.1016/j.psyneuen.2013.09.025>.
- Archer, J., 2006. Testosterone and human aggression: an evaluation of the challenge hypothesis. *Neurosci. Biobehav. Rev.* 30 (3), 319–345. <http://dx.doi.org/10.1016/j.neubiorev.2004.12.007>.
- Archer, J., Graham-Kevan, N., Davies, M., 2005. Testosterone and aggression: a reanalysis of book, Starzyk, and Quinsey's (2001) study. *Aggress. Violent Behav.* 10 (2), 241–261. <http://dx.doi.org/10.1016/j.avb.2004.01.001>.
- Arnocky, H.S., Taylor, S.M., Olmstead, N.A., Carré, J.M., 2017. The effects of exogenous testosterone on men's moral decision-making. *Adaptive Hum. Behavior Physiol.* 3 (1), 1–13. <http://dx.doi.org/10.1007/s40750-016-0046-8>.
- Arruda, A.F.S., Aoki, M.S., Carolina, A., Moreira, A., 2017. Salivary steroid response and competitive anxiety in elite basketball players: effect of opponent level. *Physiol. Behav.* 177, 291–296. <http://dx.doi.org/10.1016/j.physbeh.2017.05.017>.
- Balzer, B.W.R., Duke, S.-A., Hawke, C.I., Steinbeck, K.S., 2015. The effects of estradiol on mood and behavior in human female adolescents: a systematic review. *Eur. J. Pediatr.* 174 (3), 289–298. <http://dx.doi.org/10.1007/s00431-014-2475-3>.
- Bateup, H.S., Booth, A., Shirtcliff, E.A., Granger, D.A., 2002. Testosterone, cortisol, and women's competition. *Evol. Hum. Behav.* 23 (3), 181–192 ([http://doi.org/10.1016/S1090-5138\(01\)00100-3](http://doi.org/10.1016/S1090-5138(01)00100-3)).
- Baumeister, R.F., Vohs, K.D., Funder, D.C., 2007. Psychology as the science of self-reports and finger movements: whatever happened to actual behavior? *Perspect. Psychol. Sci.* 2 (4), 396–403. <http://dx.doi.org/10.1111/j.1745-6916.2007.00051.x>.
- Bird, B.M., Welling, L.L.M., Ortiz, T.L., Moreau, B.J.P., Hansen, S., Emond, M., ... Carré, J.M., 2016. Effects of exogenous testosterone and mating context on men's preferences for female facial femininity. *Horm. Behav.* 85, 76–85. <http://dx.doi.org/10.1016/j.yhbeh.2016.08.003>.
- Blair, R.J.R., 2010. Neuroimaging of psychopathy and antisocial behavior: a targeted review. *Curr. Psychiatry Rep.* 12 (1), 76–82. <http://dx.doi.org/10.1007/s11920-009-0086-x>.
- Boksem, M.A.S., Mehta, P.H., van den Bergh, B., van Son, V., Trautmann, S.T., Roelofs, K., ... Sanfey, A.G., 2013. Testosterone inhibits trust but promotes reciprocity. *Psychol. Sci.* 24 (11), 2306–2314. <http://dx.doi.org/10.1177/0956797613495063>.
- Bos, P.A., Panksepp, J., Bluthé, R.M., van Honk, J., 2012. Acute effects of steroid hormones and neuropeptides on human social-emotional behavior: a review of single administration studies. *Front. Neuroendocrinol.* 33 (1), 17–35. <http://dx.doi.org/10.1016/j.yfrne.2011.01.002>.
- Bosco, C., Tihanyi, J., Rivalta, L., Parlato, G., Tranquilli, C., Pulvirenti, G., ... Viru, A., 1996. Hormonal responses in strenuous jumping effort. *Jpn. J. Physiol.* 46 (1), 93–98. <http://dx.doi.org/10.2170/jphysiol.46.93>.
- Buskens, V., Raub, W., van Miltenburg, N., Montoya, E.R., van Honk, J., 2016. Testosterone administration moderates effect of social environment on trust in women depending on second-to-fourth digit ratio. *Sci. Rep.* 6 (1), 27655. <http://dx.doi.org/10.1038/srep27655>.
- Carré, J.M., 2009. No place like home: testosterone responses to victory depend on game location. *Am. J. Hum. Biol.* 21 (3), 392–394. <http://dx.doi.org/10.1002/ajhb.20867>.
- Carré, J.M., McCormick, C.M., 2008. Aggressive behavior and change in salivary testosterone concentrations predict willingness to engage in a competitive task. *Horm. Behav.* 54 (3), 403–409. <http://dx.doi.org/10.1016/j.yhbeh.2008.04.008>.
- Carré, J.M., Olmstead, N.A., 2015. Social neuroendocrinology of human aggression: examining the role of competition-induced testosterone dynamics. *Neuroscience* 286, 171–186. <http://dx.doi.org/10.1016/j.neuroscience.2014.11.029>.
- Carré, J.M., Putnam, S.K., McCormick, C.M., 2009. Testosterone responses to competition predict future aggressive behaviour at a cost to reward in men. *Psychoneuroendocrinology* 34 (4), 561–570. <http://dx.doi.org/10.1016/j.psyneuen.2008.10.018>.
- Carré, J.M., Gilchrist, J.D., Morrissey, M.D., McCormick, C.M., 2010. Motivational and situational factors and the relationship between testosterone dynamics and human aggression during competition. *Biol. Psychol.* 84 (2), 346–353. <http://dx.doi.org/10.1016/j.biopsycho.2010.04.001>.
- Carré, J.M., McCormick, C.M., Hariri, A.R., 2011. The social neuroendocrinology of human aggression. *Psychoneuroendocrinology* 36 (7), 935–944. <http://dx.doi.org/10.1016/j.psyneuen.2011.02.001>.
- Carré, J.M., Campbell, J.A., Lozoya, E., Goetz, S.M.M., Welker, K.M., 2013. Changes in testosterone mediate the effect of winning on subsequent aggressive behaviour. *Psychoneuroendocrinology* 38, 2034–2041. <http://dx.doi.org/10.1016/j.psyneuen.2013.03.008>.
- Carré, J.M., Iselin, A.R., Welker, K.M., Hariri, A.R., Dodge, K.A., 2014. Testosterone reactivity to provocation mediates the effect of early intervention on aggressive behavior. *Psychol. Sci.* 25 (5), 1140–1146. <http://dx.doi.org/10.1177/0956797614525642>.
- Carré, J.M., Ortiz, T.L., Labine, B., Moreau, B.J.P., Viding, E., Neumann, C.S., Goldfarb, B., 2015. Digit ratio (2D:4D) and psychopathic traits moderate the effect of exogenous testosterone on socio-cognitive processes in men. *Psychoneuroendocrinology* 62, 319–326. <http://dx.doi.org/10.1016/j.psyneuen.2015.08.023>.
- Carré, J.M., Geniole, S.N., Ortiz, T.L., Bird, B.M., Videto, A., Bonin, P.L., 2017. Exogenous testosterone rapidly increases aggressive behavior in dominant and impulsive men. *Biol. Psychiatry* 82 (4), 249–256. <http://dx.doi.org/10.1016/j.biopsycho.2016.06.009>.
- Casto, K.V., Edwards, D.A., 2016a. Testosterone, cortisol, and human competition. *Horm. Behav.* 82, 21–37. <http://dx.doi.org/10.1016/j.yhbeh.2016.04.004>.
- Casto, K.V., Edwards, D.A., 2016b. Testosterone and reconciliation among women: after-competition testosterone predicts prosocial attitudes towards opponents. *Adaptive Hum. Behav. Physiol.* 2, 220–233. <http://dx.doi.org/10.1007/s40750-015-0037-1>.

- Cerda-Molina, A.L., Hernández-López, L., de la O, C.E., Chavira-Ramírez, R., Mondragón-Ceballos, R., 2013. Changes in men's salivary testosterone and cortisol levels, and in sexual desire after smelling female axillary and vulvar scents. *Front. Endocrinol.* 4 (October), 1–9. <http://dx.doi.org/10.3389/fendo.2013.00159>.
- Chamberlain, N.L., Driver, E.D., Miesfeldt, R.L., 1994. The length and location of CAG trinucleotide repeats in the androgen receptor N-terminal domain affect transactivation function. *Nucleic Acids Res.* 22 (15), 3181–3186.
- Chester, D.S., 2017. The role of positive affect in aggression. *Curr. Dir. Psychol. Sci.* 26 (4), 366–370. <http://dx.doi.org/10.1177/0963721417700457>.
- Chester, D.S., DeWall, C.N., 2016. The pleasure of revenge: retaliatory aggression arises from a neural imbalance toward reward. *Soc. Cogn. Affect. Neurosci.* 11 (7), 1173–1182. <http://dx.doi.org/10.1093/scan/nsv082>.
- Choong, C.S., Kempainen, J.A., Zhou, Z.X., Wilson, E.M., 1996. Reduced androgen receptor gene expression with first exon CAG repeat expansion. *Mol. Endocrinol.* 10 (12), 1527–1535. <http://dx.doi.org/10.1210/mend.10.12.8961263>.
- Cobey, K., Hahn, A., 2017. The endocrinology of female competition. In: *The Oxford Handbook of Women and Competition*, pp. 371.
- Cohen, D., Nisbett, R.E., Bowdle, B.F., Schwarz, N., 1996. Insult, aggression, and the southern culture of honor: An “experimental ethnography.” *J. Pers. Soc. Psychol.* 70 (5), 945–960. <http://dx.doi.org/10.1037/0022-3514.70.5.945>.
- Cote, K.A., McCormick, C.M., Geniole, S.N., Renn, R.P., MacAulay, S.D., 2013. Sleep deprivation lowers reactive aggression and testosterone in men. *Biol. Psychol.* 92 (2), 249–256. <http://dx.doi.org/10.1016/j.biopsycho.2012.09.011>.
- Couppis, M.H., Kennedy, C.H., 2008. The rewarding effect of aggression is reduced by nucleus accumbens dopamine receptor antagonism in mice. *Psychopharmacology* 197 (3), 449–456. <http://dx.doi.org/10.1007/s00213-007-1054-y>.
- Cueva, C., Roberts, R.E., Spencer, T.J., Rani, N., Tempest, M., Tobler, P.N., ... Rustichini, A., 2017. Testosterone administration does not affect men's rejections of low ultimatum game offers or aggressive mood. *Horm. Behav.* 87, 1–7. <http://dx.doi.org/10.1016/j.yhbeh.2016.09.012>.
- Cunniffe, B., Morgan, K.A., Baker, J.S., Cardinale, M., Davies, B., 2015. Home versus away competition: effect on psychophysiological variables in elite rugby union. *Int. J. Sports Physiol. Perform.* 10, 687–694. <http://dx.doi.org/10.1123/jsspp.2014-0370>.
- Dabbs, J.M., Ruback, R.B., Frady, R.L., Hopper, C.H., Sgoutas, D.S., 1988. Saliva testosterone and criminal violence among women. *Personal. Individ. Differ.* 9 (2), 269–275 ([http://doi.org/10.1016/0191-8869\(88\)90088-8](http://doi.org/10.1016/0191-8869(88)90088-8)).
- Davis, M., Whalen, P., 2001. The amygdala: vigilance and emotion. *Mol. Psychiatry* 6, 13–34. Retrieved from: [www.nature.com/mp](http://www.nature.com/mp).
- van der Meij, L., Buunk, A.P., van de Sande, J.P., Salvador, A., 2008. The presence of a woman increases testosterone in aggressive dominant men. *Horm. Behav.* 54 (5), 640–644. <http://dx.doi.org/10.1016/j.yhbeh.2008.07.001>.
- van der Meij, L., Almela, M., Buunk, A.P., Fawcett, T.W., Salvador, A., 2012a. Men with elevated testosterone levels show more affiliative behaviours during interactions with women. *Proc. Biol. Sci. Royal Soc.* 279 (1726), 202–208. <http://dx.doi.org/10.1098/rspb.2011.0764>.
- van der Meij, L., Almela, M., Hidalgo, V., Villada, C., Ijzerman, H., van Lange, P.A.M., Salvador, A., 2012b. Testosterone and cortisol release among Spanish soccer fans watching the 2010 world cup final. *PLoS One* 7 (4), e34814. <http://dx.doi.org/10.1371/journal.pone.0034814>.
- Donahue, J.E., Stopa, E.G., Chorsky, R.L., King, J.C., Schipper, H.M., Tobet, S.A., ... Reichlin, S., 2000. Cells containing immunoreactive estrogen receptor- $\alpha$  in the human basal forebrain. *Brain Res.* 856 (1–2), 142–151. Retrieved from: <http://www.ncbi.nlm.nih.gov/pubmed/10677621>.
- Dougherty, D., Bjork, J., Moeller, F., Swann, A., 1997. The influence of menstrual-cycle phase on the relationship between testosterone and aggression. *Physiol. Behav.* 62 (2), 431–435. [https://doi.org/10.1016/S0031-9384\(97\)88991-3](https://doi.org/10.1016/S0031-9384(97)88991-3).
- Dreher, J., Dunne, S., Pazderska, A., Frodl, T., Nolan, J.J., 2016. Testosterone causes both prosocial and antisocial state-enhancing behaviors in human males. *Proc. Natl. Acad. Sci.* 113, 11633–11638. <http://dx.doi.org/10.1073/pnas.1608085113>.
- Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., Fehr, E., 2010. Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature* 463 (7279), 356–359. <http://dx.doi.org/10.1038/nature08711>.
- Eisenegger, C., Haushofer, J., Fehr, E., 2011. The role of testosterone in social interaction. *Trends Cogn. Sci.* 15 (6), 263–271. <http://dx.doi.org/10.1016/j.tics.2011.04.008>.
- Eisenegger, C., von Eckardstein, A., Fehr, E., von Eckardstein, S., 2013. Pharmacokinetics of testosterone and estradiol gel preparations in healthy young men. *Psychoneuroendocrinology* 38 (2), 171–178. <http://dx.doi.org/10.1016/j.psyneuen.2012.05.018>.
- Eisenegger, C., Kumsta, R., Naef, M., Gromoll, J., Heinrichs, M., 2017. Testosterone and androgen receptor gene polymorphism are associated with confidence and competitiveness in men. *Horm. Behav.* 92, 93–102. <http://dx.doi.org/10.1016/j.yhbeh.2016.09.011>.
- Elias, M., 1981. Serum cortisol, testosterone, and testosterone-binding globulin responses to competitive fighting in human males. *Aggress. Behav.* 7 (3), 215–224 ([http://doi.org/10.1002/1098-2337\(1981\)7:3 < 215::AID-AB2480070305 > 3.0.CO;2-M](http://doi.org/10.1002/1098-2337(1981)7:3 < 215::AID-AB2480070305 > 3.0.CO;2-M)).
- Enter, D., Spinhoven, P., Roelofs, K., 2014. Alleviating social avoidance: effects of single dose testosterone administration on approach-avoidance action. *Horm. Behav.* 65 (4), 351–354. <http://dx.doi.org/10.1016/j.yhbeh.2014.02.001>.
- Enter, D., Spinhoven, P., Roelofs, K., 2016a. Dare to approach: single dose testosterone administration promotes threat approach in patients with social anxiety disorder. *Clin. Psychol. Sci.* 4 (6), 1073–1079. <http://dx.doi.org/10.1177/2167702616631499>.
- Enter, D., Terburg, D., Harrewijn, A., Spinhoven, P., Roelofs, K., 2016b. Single dose testosterone administration alleviates gaze avoidance in women with social anxiety disorder. *Psychoneuroendocrinology* 63, 26–33. <http://dx.doi.org/10.1016/j.psyneuen.2015.09.008>.
- Fernández-Guasti, A., Kruijver, F.P., Fodor, M., Swaab, D.F., 2000. Sex differences in the distribution of androgen receptors in the human hypothalamus. *J. Comp. Neurol.* 425 (3), 422–435. Retrieved from: <http://www.ncbi.nlm.nih.gov/pubmed/10972942>.
- Fessler, D.M.T., Tiokhin, L.B., Holbrook, C., Gervais, M.M., Snyder, J.K., 2014. Foundations of the crazy bastard hypothesis: nonviolent physical risk-taking enhances conceptualized formidability. *Evol. Hum. Behav.* 35 (1), 26–33. <http://dx.doi.org/10.1016/j.evolhumbehav.2013.09.003>.
- Finkelstein, J.W., Susman, E.J., Chinchilli, V.M., Kunselman, S.J., D'Arcangelo, M.R., Schwab, J., ... Kulin, H.E., 1997. Estrogen or testosterone increases self-reported aggressive behaviors in hypogonadal adolescents. *J. Clin. Endocrinol. Metab.* 82 (8), 2433–2438. <http://dx.doi.org/10.1210/jcem.82.8.4165>.
- Flinn, M.V., Ponz, D., Muehlenbein, M.P., 2012. Hormonal mechanisms for regulation of aggression in human coalitions. *Hum. Nat. (Hawthorne, N.Y.)* 23 (1), 68–88. <http://dx.doi.org/10.1007/s12110-012-9135-y>.
- Folstad, L., Karter, A.J., 2011. Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* 139 (3), 603–622.
- Foo, Y.Z., Nakagawa, S., Rhodes, G., Simmons, L.W., 2017. The effects of sex hormones on immune function: a meta-analysis. *Biol. Rev.* 92 (1), 551–571. <http://dx.doi.org/10.1111/brv.12243>.
- Fuxjager, M.J., Forbes-lorman, R.M., Coss, D.J., Auger, C.J., Auger, A.P., Marler, C.A., 2010. Winning territorial disputes selectively enhances androgen sensitivity in neural pathways related to motivation and social aggression. *Proc. Natl. Acad. Sci. U. S. A.* 107 (27), 12393–12398. <http://dx.doi.org/10.1073/pnas.1001394107>.
- Fuxjager, M.J., Oyegbile, T.O., Marler, C.A., 2011. Independent and additive contributions of postvictory testosterone and social experience to the development of the winner effect. *Endocrinology* 152 (9), 3422–3429. <http://dx.doi.org/10.1210/en.2011-1099>.
- Geniole, S.N., Carré, J.M., 2017. Hierarchy and testosterone: how can testosterone promote upward mobility in status hierarchies? In: Welling, L.L.M., Shackelford, T.K. (Eds.), *Oxford Handbook on Evolutionary Psychology and Behavioral Endocrinology*. Oxford University Press, New York, NY.
- Geniole, S.N., Carré, J.M., McCormick, C.M., 2011. State, not trait, neuroendocrine function predicts costly reactive aggression in men after social exclusion and inclusion. *Biol. Psychol.* 87 (1), 137–145. <http://dx.doi.org/10.1016/j.biopsycho.2011.02.020>.
- Geniole, S.N., Busseri, M.A., McCormick, C.M., 2013. Testosterone dynamics and psychopathic personality traits independently predict antagonistic behavior towards the perceived loser of a competitive interaction. *Horm. Behav.* 64, 790–798. <http://dx.doi.org/10.1016/j.yhbeh.2013.09.005>.
- Geniole, S.N., Bird, B.M., Ruddick, E.L., Carré, J.M., 2017a. Effects of competition outcome on testosterone concentrations in humans: an updated meta-analysis. *Horm. Behav.* 92, 37–50. <http://dx.doi.org/10.1016/j.yhbeh.2016.10.002>.
- Geniole, S.N., MacDonell, E.T., McCormick, C.M., 2017b. The point subtraction aggression paradigm as a laboratory tool for investigating the neuroendocrinology of aggression and competition. *Horm. Behav.* 92, 103–116. <http://dx.doi.org/10.1016/j.yhbeh.2016.04.006>.
- Geniole, S.N., Procyshyn, T.L., Marley, N., Ortiz, T.L., Bird, B.M., Marcellus, A.L., Welker, K.M., Bonin, P.L., Goldfarb, B., Watson, N.V., Carré, J.M., 2018. Using a psychopharmacogenetic approach to identify the pathways through which and people for whom testosterone promotes aggression. (unpublished).
- Gleason, E.D., Fuxjager, M.J., Oyegbile, T.O., Marler, C.A., 2009. Testosterone release and social context: when it occurs and why. *Front. Neuroendocrinol.* 30 (4), 460–469. <http://dx.doi.org/10.1016/j.yfme.2009.04.009>.
- Goetz, S.M.M., Tang, L., Thomason, M.E., Diamond, M.P., Hariri, A.R., Carré, J.M., 2014. Testosterone rapidly increases neural reactivity to threat in healthy men: a novel two-step pharmacological challenge paradigm. *Biol. Psychiatry* 76 (4), 324–331. <http://dx.doi.org/10.1016/j.biopsych.2014.01.016>.
- Goldey, K.L., van Anders, S.M., 2011. Sexy thoughts: effects of sexual cognitions on testosterone, cortisol, and arousal in women. *Horm. Behav.* 59 (5), 754–764. <http://dx.doi.org/10.1016/j.yhbeh.2010.12.005>.
- Goldey, K.L., van Anders, S.M., 2015. Sexual modulation of testosterone: insights for humans from across species. *Adapt. Hum. Behav. Physiol.* 1 (2), 93–123. <http://dx.doi.org/10.1007/s40750-014-0005-1>.
- Goldey, K.L., van Anders, S.M., 2016. Identification with stimuli moderates women's affective and testosterone responses to self-chosen erotica. *Arch. Sex. Behav.* 45 (8), 2155–2171. <http://dx.doi.org/10.1007/s10508-015-0612-3>.
- Goldey, K.L., Avery, L.R., van Anders, S.M., 2014. Sexual fantasies and gender/sex: a multimethod approach with quantitative content analysis and hormonal responses. *J. Sex Res.* 51 (8), 917–931. <http://dx.doi.org/10.1080/00224499.2013.798611>.
- Goyman, W., Flores Dávila, P., 2017. Acute peaks of testosterone suppress paternal care: evidence from individual hormonal reaction norms. *Proc. R. Soc. B Biol. Sci.* 284 (1857), 20170632. <http://dx.doi.org/10.1098/rspb.2017.0632>.
- Hamilton, L.D., Meston, C.M., 2010. The effects of partner togetherness on salivary testosterone in women in long distance relationships. *Horm. Behav.* 57 (2), 198–202. <http://dx.doi.org/10.1016/j.yhbeh.2009.10.014>.
- Heimovics, S.A., Trainor, B.C., Soma, K.K., 2015. Rapid effects of estradiol on aggression in birds and mice: the fast and the furious. *Integr. Comp. Biol.* 55 (2), 281–293. <http://dx.doi.org/10.1093/icb/ictv048>.
- Hellhammer, D.H., Hubert, W., Schürmeyer, T., 1985. Changes in saliva testosterone after psychological stimulation in men. *Psychoneuroendocrinology* 10 (1), 77–81. [http://dx.doi.org/10.1016/0306-4530\(85\)90041-1](http://dx.doi.org/10.1016/0306-4530(85)90041-1).
- Hermans, E.J., Putman, P., Baas, J.M., Koppeschaar, H.P., van Honk, J., 2006a. A single administration of testosterone reduces fear-potentiated startle in humans. *Biol. Psychiatry* 59 (9), 872–874. <http://dx.doi.org/10.1016/j.biopsych.2005.11.015>.
- Hermans, E.J., Putman, P., van Honk, J., 2006b. Testosterone administration reduces empathetic behavior: a facial mimicry study. *Psychoneuroendocrinology* 31 (7),



- 859–866. <http://dx.doi.org/10.1016/j.psyneuen.2006.04.002>.
- Hermans, E.J., Ramsey, N.F., van Honk, J., 2008. Exogenous testosterone enhances responsiveness to social threat in the neural circuitry of social aggression in humans. *Biol. Psychiatry* 63 (3), 263–270. <http://dx.doi.org/10.1016/j.biopsych.2007.05.013>.
- Hermans, E.J., Bos, P.A., Ossewaarde, L., Ramsey, N.F., Fernández, G., van Honk, J., 2010. Effects of exogenous testosterone on the ventral striatal BOLD response during reward anticipation in healthy women. *NeuroImage* 52 (1), 277–283. <http://dx.doi.org/10.1016/j.neuroimage.2010.04.019>.
- Hirschenhauser, K., Oliveira, R.F., 2006. Social modulation of androgens in male vertebrates: meta-analyses of the challenge hypothesis. *Anim. Behav.* 71 (2), 265–277. <http://dx.doi.org/10.1016/j.anbehav.2005.04.014>.
- Hirschenhauser, K., Taborsky, M., Oliveira, T., Canário, A.V.M., Oliveira, R.F., 2004. A test of the “Challenge Hypothesis” in Cichlid fish: simulated partner and territory intruder experiments. *Anim. Behav.* 68 (4), 741–750. <http://dx.doi.org/10.1016/j.anbehav.2003.12.015>.
- van Honk, J., Tuiten, A., Verbaten, R., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., 1999. Correlations among salivary testosterone, mood, and selective attention to threat in humans. *Horm. Behav.* 36 (1), 17–24. <http://dx.doi.org/10.1006/hbeh.1999.1521>.
- van Honk, J., Tuiten, A., Hermans, E.J., Putnam, P., Koppeschaar, H., Thijssen, J., ... van Doornen, L., 2001. A single administration of testosterone induces cardiac accelerative responses to angry faces in healthy young women. *Behav. Neurosci.* 115 (1), 238–242. <http://dx.doi.org/10.1037/0735-7044.115.1.238>.
- van Honk, J., Schutter, D.J.L.G., Hermans, E.J., Putnam, P., Tuiten, A., Koppeschaar, H., 2004. Testosterone shifts the balance between sensitivity for punishment and reward in healthy young women. *Psychoneuroendocrinology* 29 (7), 937–943. <http://dx.doi.org/10.1016/j.psyneuen.2003.08.007>.
- van Honk, J., Schutter, D.J., Bos, P.A., Kruijt, A.-W., Lentjes, E.G., Baron-Cohen, S., 2011. Testosterone administration impairs cognitive empathy in women depending on second-to-fourth digit ratio. *Proc. Natl. Acad. Sci. U. S. A.* 108 (8), 3448–3452. <http://dx.doi.org/10.1073/pnas.1011891108>.
- van Honk, J., Montoya, E.R., Bos, P.A., van Vugt, M., Terburg, D., 2012. New evidence on testosterone and cooperation. *Nature* 485 (7399), E4–E5. <http://dx.doi.org/10.1038/nature11136>.
- van Honk, J., Will, G.J., Terburg, D., Raub, W., Eisenegger, C., Buskens, V., 2016. Effects of testosterone administration on strategic gambling in poker play. *Sci. Rep.* 6 (November 2015), 1–8. <http://dx.doi.org/10.1038/srep18096>.
- Inoue, Y., Takahashi, T., Burriss, R.P., Arai, S., Hasegawa, T., Yamagishi, T., Kiyonari, T., 2017. Testosterone promotes either dominance or submissiveness in the ultimatum game depending on players' social rank. *Sci. Rep.* 7 (1), 1–9. <http://dx.doi.org/10.1038/s41598-017-05603-7>.
- James, P.J., Nyby, J.G., 2002. Testosterone rapidly affects the expression of copulatory behavior in house mice (*Mus musculus*). *Physiol. Behav.* 75 (3), 287–294. Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/11897254>.
- Ježová, D., Vigaš, M., 1981. Testosterone response to exercise during blockade and stimulation of adrenergic receptors in man. *Horm. Res.* 15 (3), 141–147. Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/7338344>.
- Ježová, D., Vigaš, M., Tatár, P., Květnanský, R., Nazar, K., Kaciuba-Uścilko, H., Kozłowski, S., 1985. Plasma testosterone and catecholamine responses to physical exercise of different intensities in men. *Eur. J. Appl. Physiol. Occup. Physiol.* 54 (1), 62–66. <http://dx.doi.org/10.1007/BF00426300>.
- Josephs, R.A., Newman, M.L., Brown, R.P., Beer, J.M., 2003. Status, testosterone, and human intellectual performance. *Psychol. Sci.* 14 (2), 158–163. <http://dx.doi.org/10.1111/1467-9280.t01-1-01435>.
- Klinesmith, J., Kasser, T., McAndrew, F.T., 2006. Guns, testosterone, and aggression: an experimental test of a mediational hypothesis. *Psychol. Sci.* 17 (7), 568–571. <http://dx.doi.org/10.1111/j.1467-9280.2006.01745.x>.
- Knight, E.L., Mehta, P.H., 2014. Hormones and hierarchies. In: Cheng, J.T., Tracy, J.L., Anderson, C. (Eds.), *The Psychology of Social Status*. Springer, New York, pp. 269–302.
- Knight, E.L., Christian, C.B., Morales, P.J., Harbaugh, W.T., Mayr, U., Mehta, P.H., 2017. Exogenous testosterone enhances cortisol and affective responses to social-evaluative stress in dominant men. *Psychoneuroendocrinology* 85 (August), 151–157. <http://dx.doi.org/10.1016/j.psyneuen.2017.08.014>.
- Kopsida, E., Berrebi, J., Petrovic, P., Ingvar, M., 2016. Testosterone administration related differences in brain activation during the ultimatum game. *Front. Neurosci.* 10 (MAR), 1–11. <http://dx.doi.org/10.3389/fnins.2016.00066>.
- Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U., Fehr, E., 2005. Oxytocin increases trust in humans. *Nature* 435, 673–676.
- Krämer, U.M., Jansma, H., Tempelmann, C., Münte, T.F., 2007. Tit-for-tat: the neural basis of reactive aggression. *NeuroImage* 38 (1), 203–211. <http://dx.doi.org/10.1016/j.neuroimage.2007.07.029>.
- Kuo, P.X., Saini, E.K., Thomson, E., Schultheiss, O.C., Gonzalez, R., Volling, B.L., 2016. Individual variation in fathers' testosterone reactivity to infant distress predicts parenting behaviors with their 1-year-old infants. *Dev. Psychobiol.* 58 (3), 303–314. <http://dx.doi.org/10.1002/dev.21370>.
- LeDoux, J.E., 2000. Emotion circuits in the brain. *Annu. Rev. Neurosci.* 23, 155–184. Retrieved from. <https://www.annualreviews.org/doi/pdf/10.1146/annurev.neuro.23.1.155>.
- Lewis, M., Groom, G., Barber, R., Henderson, A., 1981. The effects of propranolol and acebutolol on the overnight plasma levels of anterior pituitary and related hormones. *Br. J. Clin. Pharmacol.* 12 (5), 737–742. <http://dx.doi.org/10.1111/j.1365-2125.1981.tb01298.x>.
- Lobbestael, J., 2015. Challenges in aggression assessment: the gap between self-report and behavior, and a call for new valid behavioral paradigms. *J. Socialomics* 5 (1), 5–6. <http://dx.doi.org/10.4172/2167-0358.1000141>.
- Losecaat Vermeer, A.B., Riečanský, I., Eisenegger, C., 2016. Competition, testosterone, and adult neurobehavioral plasticity. *Prog. Brain Res.* 229, 213–238. <http://dx.doi.org/10.1016/bs.pbr.2016.05.004>.
- Lozza, N., Spoerri, C., Ehler, U., Hubmann, P., Kesselring, M., Farahmand, F., ... La Marca, R., 2017. Predicting social behavior: basal and dynamic joint effects of testosterone and cortisol. *Adapt. Hum. Behav. Physiol.* 3 (3), 255–274. <http://dx.doi.org/10.1007/s40750-017-0069-9>.
- Manuck, S.B., Marsland, A.L., Flory, J.D., Gorka, A., Ferrell, R.E., Hariri, A.R., 2010. Salivary testosterone and a trinucleotide (CAG) length polymorphism in the androgen receptor gene predict amygdala reactivity in men. *Psychoneuroendocrinology* 35 (1), 94–104. <http://dx.doi.org/10.1016/j.psyneuen.2009.04.013>.
- Marler, C.A., Oyegbile, T.O., Plavicki, J., Trainor, B.C., 2005, September. Response to Wingfield's commentary on “A continuing saga: the role of testosterone in aggression.”. *Horm. Behav.* <http://dx.doi.org/10.1016/j.yhbeh.2005.05.010>.
- Mazur, A., 1976. Effects of testosterone on status in primate groups. *Folia Primatol.* 26 (3), 214–226. <http://dx.doi.org/10.1159/000155752>.
- Mazur, A., 1985. A biosocial model of status in face-to-face primate groups. *Soc. Forces* 64 (2), 377–402.
- Mazur, A., Booth, A., 1998. Testosterone and dominance in men. *Behav. Brain Sci.* 21 (3), 353–363. Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/10097017>.
- McAndrew, F.T., 2014. The “sword of a woman”: gossip and female aggression. *Aggress. Violent Behav.* 19 (3), 196–199. <http://dx.doi.org/10.1016/j.avb.2014.04.006>.
- McGlothlin, J.W., Jawor, J.M., Ketterson, E.D., 2007. Natural variation in a testosterone-mediated trade-off between mating effort and parental effort. *Am. Nat.* 170 (6), 864–875. <http://dx.doi.org/10.1086/522838>.
- Mehta, P.H., Josephs, R.A., 2006. Testosterone change after losing predicts the decision to compete again. *Horm. Behav.* 50 (5), 684–692. <http://dx.doi.org/10.1016/j.yhbeh.2006.07.001>.
- Mehta, P.H., Josephs, R.A., 2010. Testosterone and cortisol jointly regulate dominance: evidence for a dual-hormone hypothesis. *Horm. Behav.* 58 (5), 898–906. <http://dx.doi.org/10.1016/j.yhbeh.2010.08.020>.
- Mehta, P.H., Prasad, S., 2015. The dual-hormone hypothesis: a brief review and future research agenda. *Curr. Opin. Behav. Sci.* 3, 163–168. <http://dx.doi.org/10.1016/j.cobeha.2015.04.008>.
- Mehta, P.H., Mor, S., Yap, A.J., Prasad, S., 2015a. Dual-hormone changes are related to bargaining performance. *Psychol. Sci.* 26 (6), 866–876. <http://dx.doi.org/10.1177/0956797615572905>.
- Mehta, P.H., Snyder, N.A., Knight, E.L., Lasseter, B., 2015b. Close versus decisive victory moderates the effect of testosterone change on competitive decisions and task enjoyment. *Adapt. Hum. Behav. Physiol.* 1, 291–311. <http://dx.doi.org/10.1007/s40750-014-0014-0>.
- Mehta, P.H., van Son, V., Welker, K.M., Prasad, S., Sanfey, A.G., Smidts, A., Roelofs, K., 2015c. Exogenous testosterone in women enhances and inhibits competitive decision-making depending on victory – defeat experience and trait dominance. *Psychoneuroendocrinology* 60, 224–236.
- Mehta, P.H., Lawless DesJardins, N.M., van Vugt, M., Josephs, R.A., 2017. Hormonal underpinnings of status conflict: testosterone and cortisol are related to decisions and satisfaction in the hawk-dove game. *Horm. Behav.* 92, 141–154. <http://dx.doi.org/10.1016/j.yhbeh.2017.03.009>.
- Miller, S.L., Maner, J.K., 2010. Scent of a woman: Men's testosterone responses to olfactory ovulation cues. *Psychol. Sci.* 21 (2), 276–283. <http://dx.doi.org/10.1177/0956797609357733>.
- Miller, S.L., Maner, J.K., McNulty, J.K., 2012. Adaptive attunement to the sex of individuals at a competition: the ratio of opposite- to same-sex individuals correlates with changes in competitors' testosterone levels. *Evol. Hum. Behav.* 33 (1), 57–63. <http://dx.doi.org/10.1016/j.evolhumbehav.2011.05.006>.
- Montoya, E.R., Bos, P.A., 2017. How oral contraceptives impact social-emotional behavior and brain function. *Trends Cogn. Sci.* 21 (2), 125–136. <http://dx.doi.org/10.1016/j.tics.2016.11.005>.
- Montoya, E.R., Terburg, D., Bos, P.A., Will, G.-J., Buskens, V., Raub, W., van Honk, J., 2013. Testosterone administration modulates moral judgments depending on second-to-fourth digit ratio. *Psychoneuroendocrinology* 2012. <http://dx.doi.org/10.1016/j.psyneuen.2012.12.001>.
- Muller, M.N., 2017. Testosterone and reproductive effort in male primates. *Horm. Behav.* 91, 36–51. <http://dx.doi.org/10.1016/j.yhbeh.2016.09.001>.
- Muller, M.N., Wrangham, R.W., 2004. Dominance, aggression and testosterone in wild chimpanzees: a test of the “Challenge Hypothesis.”. *Anim. Behav.* 67, 113–123. <http://dx.doi.org/10.1016/j.anbehav.2003.03.013>.
- Murphy, A.Z., Shupnik, M.A., Hoffman, G.E., 1999. Androgen and estrogen (alpha) receptor distribution in the periaqueductal gray of the male rat. *Horm. Behav.* 36 (2), 98–108. <http://dx.doi.org/10.1006/hbeh.1999.1528>.
- Nave, G., Camerer, C., McCullough, M., 2015. Does oxytocin increase trust in humans? A critical review of research. *Perspect. Psychol. Sci.* 10, 772–789.
- Nave, G., Nadler, A., Zava, D., Camerer, C., 2017. Single-dose testosterone administration impairs cognitive reflection in men. *Psychol. Sci.* 28 (10), 1398–1407. <http://dx.doi.org/10.1177/0956797617709592>.
- Nelson, R.J., Trainor, B.C., 2007. Neural mechanisms of aggression. *Nat. Rev. Neurosci.* 8 (7), 536–546. <http://dx.doi.org/10.1038/nrn2174>.
- Newman, S.W., 1999. The medial extended amygdala in male reproductive behavior. A node in the mammalian social behavior network. *Ann. N. Y. Acad. Sci.* 877 (1 ADVANCING FRO), 242–257. <http://dx.doi.org/10.1111/j.1749-6632.1999.tb09271.x>.
- Oliveira, R.F., 2009. Social behavior in context: hormonal modulation of behavioral plasticity and social competence. *Integr. Comp. Biol.* 49 (4), 423–440. <http://dx.doi.org/10.1093/icb/icp055>.



- Oliveira, G.A., Oliveira, R.F., 2014. Androgen responsiveness to competition in humans: the role of cognitive variables. *Neurosci. Neuroecon.* 3 (August), 19–32. <http://dx.doi.org/10.2147/NAN.S55721>.
- Oliveira, R.F., Lopes, M., Carneiro, L.A., Canário, A.V.M., 2001. Watching fights raises fish hormone levels. *Nature* 409 (6819), 475. <http://dx.doi.org/10.1038/35054128>.
- Oliveira, R.F., Silva, A., Canário, A.V.M., 2009a. Why do winners keep winning? Androgen mediation of winner but not loser effects in cichlid fish. *Proc. Biol. Sci. R. Soc.* 276 (1665), 2249–2256. <http://dx.doi.org/10.1098/rspb.2009.0132>.
- Oliveira, T., Gouveia, M.J., Oliveira, R.F., 2009b. Testosterone responsiveness to winning and losing experiences in female soccer players. *Psychoneuroendocrinology* 34 (7), 1056–1064. <http://dx.doi.org/10.1016/j.psyneuen.2009.02.006>.
- Olsson, A., Kopsida, E., Sorjonen, K., Savic, I., 2016. Testosterone and estrogen impact social evaluations and vicarious emotions: a double-blind placebo-controlled study. *Emotion* 16 (4), 515–523. <http://dx.doi.org/10.1037/a0039765>.
- Packard, M.G., Schroeder, J.P., Alexander, G.M., 1998. Expression of testosterone conditioned place preference is blocked by peripheral or intra-accumbens injection of  $\alpha$ -flupenthixol. *Horm. Behav.* 34 (1), 39–47. <http://dx.doi.org/10.1006/hbeh.1998.1461>.
- Panagiotidis, D., Clemens, B., Habel, U., Schneider, F., Schneider, I., Wagels, L., Votinov, M., 2017. Exogenous testosterone in a non-social provocation paradigm potentiates anger but not behavioral aggression. *Eur. Neuropsychopharmacol.* 27 (11), 1172–1184. <http://dx.doi.org/10.1016/j.euroneuro.2017.07.006>.
- Persky, H., Smith, K.D., Basu, G.K., 1971. Relation of psychologic measures of aggression and hostility to testosterone production in man. *Psychosom. Med.* 33 (3), 265–278. <http://dx.doi.org/10.1097/00006842-197105000-00007>.
- Peterson, C.K., Harmon-Jones, E., 2012. Anger and testosterone: evidence that situationally-induced anger relates to situationally-induced testosterone. *Emotion* 12 (5), 899–902. <http://dx.doi.org/10.1037/a0025300>.
- Ponzi, D., Henry, A., Kubicki, K., Nickels, N., Wilson, M.C., Maestripietri, D., 2016. Autistic-like traits, sociosexuality, and hormonal responses to socially stressful and sexually arousing stimuli in male college students. *Adapt. Hum. Behav. Physiol.* 2 (2), 150–165. <http://dx.doi.org/10.1007/s40570-015-0034-4>.
- Prasad, S., Narayanan, J., Lim, V.K.G., Koh, G.C.H., Koh, D.S.Q., Mehta, P.H., 2017. Preliminary evidence that acute stress moderates basal testosterone's association with retaliatory behavior. *Horm. Behav.* 92, 128–140. <http://dx.doi.org/10.1016/j.yhbeh.2016.10.020>.
- Quiroga Murcia, C., Bongard, S., Kreutz, G., 2009. Emotional and neurohumoral responses to dancing tango Argentina: the effects of music and partner. *Music Med.* 1 (1), 14–21. <http://dx.doi.org/10.1177/1943862109335064>.
- Radke, S., Volman, I., Mehta, P., van Son, V., Enter, D., Sanfey, A., ... Roelofs, K., 2015. Testosterone biases the amygdala toward social threat approach. *Sci. Adv.* 1 (5), e1400074. <http://dx.doi.org/10.1126/sciadv.1400074>.
- Ramírez, J.M., Bonniot-Cabanac, M.C., Cabanac, M., 2005. Can aggression provide pleasure? *Eur. Psychol.* 10 (2), 136–145. <http://dx.doi.org/10.1027/1016-9040.10.2.136>.
- Randall, V.A., 2008. Androgens and hair growth. *Dermatol. Ther.* 21 (5), 314–328. <http://dx.doi.org/10.1111/j.1529-8019.2008.00214.x>.
- Reijnen, A., Geuze, E., Vermetten, E., 2015. The effect of deployment to a combat zone on testosterone levels and the association with the development of posttraumatic stress symptoms: a longitudinal prospective Dutch military cohort study. *Psychoneuroendocrinology* 51, 525–533. <http://dx.doi.org/10.1016/j.psyneuen.2014.07.017>.
- Riad-Fahmy, D., Read, G.F., Walker, R.F., Walker, S.M., Griffiths, K., 1987. Determination of ovarian steroid hormone levels in saliva. An overview. *J. Reprod. Med.* 34 (4), 254–272.
- Ronay, R., von Hippel, W., 2010. The presence of an attractive woman elevates testosterone and physical risk taking in young men. *Soc. Psychol. Personal. Sci.* 1 (1), 57–64. <http://dx.doi.org/10.1177/194850609352807>.
- Roney, J.R., Guttler, L.T., 2015. The role of testosterone in human romantic relationships. *Curr. Opin. Psychol.* 1, 81–86. Retrieved from. <http://www.elsevier.com/authorrights%5Cnhttp://dx.doi.org/10.1016/j.copsyc.2014.11.003>.
- Roney, J.R., Simmons, Z.L., 2012. Men smelling women: null effects of exposure to ovulatory sweat on men's testosterone. *Evol. Psychol. Int. J. Evol. Appr. Psychol. Behav.* 10 (4), 703–713. Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/23089078>.
- Roney, J.R., Mahler, S.V., Maestripietri, D., 2003. Behavioral and hormonal responses of men to brief interactions with women. *Evol. Hum. Behav.* 24 (6), 365–375. [http://dx.doi.org/10.1016/S1090-5138\(03\)00053-9](http://dx.doi.org/10.1016/S1090-5138(03)00053-9).
- Roney, J.R., Lukaszewski, A.W., Simmons, Z.L., 2007. Rapid endocrine responses of young men to social interactions with young women. *Horm. Behav.* 52 (3), 326–333. <http://dx.doi.org/10.1016/j.yhbeh.2007.05.008>.
- Roney, J.R., Simmons, Z.L., Lukaszewski, A.W., 2010. Androgen receptor gene sequence and basal cortisol concentrations predict men's hormonal responses to potential mates. *Proc. R. Soc. B Biol. Sci.* 277 (1678), 57–63. <http://dx.doi.org/10.1098/rspb.2009.1538>.
- Rose, R.M., Gordon, T.P., Bernstein, I.S., 1972. Plasma testosterone levels in the male rhesus: influences of sexual and social stimuli. *Science* 178 (4061), 643–645. Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/4628711>.
- Rose, R.M., Berstein, I.S., Gordon, T.P., 1975. Consequences of social conflict on plasma testosterone levels in Rhesus monkeys. *Psychosom. Med.* 37 (1), 50–61.
- Roselli, C.E., Klosterman, S., Resko, J.A., 2001. Anatomic relationships between aromatase and androgen receptor mRNA expression in the hypothalamus and amygdala of adult male cynomolgus monkeys. *J. Comp. Neurol.* 439 (2), 208–223. Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/11596049>.
- Rosen, R.C., Kostis, J.B., Jekels, A.W., 1988. Beta-blocker effects on sexual function in normal males. *Arch. Sex. Behav.* 17 (3), 241–255. <http://dx.doi.org/10.1007/BF015417>.
- Rossi, S.P., Walenta, L., Rey-Ares, V., Köhn, F.-M., Schwarzer, J.U., Welter, H., ... Mayerhofer, A., 2018. Alpha 1 adrenergic receptor-mediated inflammatory responses in human testicular peritubular cells. *Mol. Cell. Endocrinol.* <http://dx.doi.org/10.1016/j.mce.2018.01.027>.
- Saad, F., Aversa, A., Isidori, A.M., Zafalon, L., Zitzmann, M., Gooren, L., 2011. Onset of effects of testosterone treatment and time span until maximum effects are achieved. *Eur. J. Endocrinol. Eur. Fed. Endocrine Soc.* 165 (5), 675–685. <http://dx.doi.org/10.1530/EJE-11-0221>.
- Sapolsky, R.M., 1986. Stress-induced elevation of testosterone concentrations in high ranking baboons: role of catecholamines. *Endocrinology* 118 (4), 1630–1635. <http://dx.doi.org/10.1210/endo-118-4-1630>.
- Schultheiss, O.C., Wirth, M.M., Torges, C.M., Pang, J.S., Villacorta, M.A., Welsh, K.M., 2005. Effects of implicit power motivation on men's and women's implicit learning and testosterone changes after social victory or defeat. *J. Pers. Soc. Psychol.* 88 (1), 174–188. <http://dx.doi.org/10.1037/0022-3514.88.1.174>.
- Sell, A., Lukaszewski, A.W., Townsley, M., 2017. Cues of upper body strength account for most of the variance in men's bodily attractiveness. *Proc. R. Soc. B Biol. Sci.* 284 (1869), 20171819. <http://dx.doi.org/10.1098/rspb.2017.1819>.
- Siegel, A., Bhatt, S., Bhatt, R., Zalman, S.S., 2007. The neurobiological bases for development of pharmacological treatments of aggressive disorders. *Curr. Neuropharmacol.* 5 (2), 135–147. Retrieved from. <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2435345&tool=pmcentrez&rendertype=abstract>.
- Smith, K.M., Apicella, C.L., 2017. Winners, losers, and posers: the effect of power poses on testosterone and risk-taking following competition. *Horm. Behav.* 92, 172–181. <http://dx.doi.org/10.1016/j.yhbeh.2016.11.003>.
- de Souza Silva, M.A., Mattern, C., Topic, B., Buddenberg, T.E., Huston, J.P., 2009. Dopaminergic and serotonergic activity in neostriatum and nucleus accumbens enhanced by intranasal administration of testosterone. *Eur. Neuropsychopharmacol.* 19 (1), 53–63. <http://dx.doi.org/10.1016/j.euroneuro.2008.08.003>.
- Stanton, S.J., Edelstein, R.S., 2009. The physiology of women's power motive: implicit power motivation is positively associated with estradiol levels in women. *J. Res. Pers.* 43 (6), 1109–1113. <http://dx.doi.org/10.1016/j.jrp.2009.08.002>.
- Stanton, S.J., Schultheiss, O.C., 2007. Basal and dynamic relationships between implicit power motivation and estradiol in women. *Horm. Behav.* 52 (5), 571–580. <http://dx.doi.org/10.1016/j.yhbeh.2007.07.002>.
- Stolér, S.G., Ennaji, A., Cournot, A., Spira, A., 1993. LH pulsatile secretion and testosterone blood levels are influenced by sexual arousal in human males. *Psychoneuroendocrinology* 18 (3), 205–218. [http://dx.doi.org/10.1016/0306-4530\(93\)90005-6](http://dx.doi.org/10.1016/0306-4530(93)90005-6).
- Strang, E., Peterson, Z.D., Hill, Y.N., Heiman, J.R., 2013. Discrepant responding across self-report measures of men's coercive and aggressive sexual strategies. *J. Sex Res.* 50 (5), 458–469. <http://dx.doi.org/10.1080/00224499.2011.646393>.
- Sutton, J.R., Coleman, M.J., Casey, J., Lazarus, L., 1973. Androgen responses during physical exercise. *Br. Med. J.* 1, 520–522.
- Terburg, D., Aarts, H., van Honk, J., 2012. Testosterone affects gaze aversion from angry faces outside of conscious awareness. *Psychol. Sci.* 23 (5), 459–463. <http://dx.doi.org/10.1177/0956797611433336>.
- Terburg, D., Syal, S., Rosenberger, L.A., Heany, S.J., Stein, D.J., van Honk, J., 2016. Testosterone abolishes implicit subordination in social anxiety. *Psychoneuroendocrinology* 72, 205–211. <http://dx.doi.org/10.1016/j.psyneuen.2016.07.203>.
- Tibbetts, B.A., Huang, Z.Y., 2010. The challenge hypothesis in an insect: juvenile hormone increases during reproductive conflict following queen loss in *Polistes* wasps. *Am. Nat.* 176 (2), 123–130. <http://dx.doi.org/10.1086/653664>.
- Trainor, B.C., Bird, I.M., Marler, C.A., 2004. Opposing hormonal mechanisms of aggression revealed through short-lived testosterone manipulations and multiple winning experiences. *Horm. Behav.* 45 (2), 115–121. <http://dx.doi.org/10.1016/j.yhbeh.2003.09.006>.
- Trumble, B.C., Cummings, D., von Rueden, C., O'Connor, K.A., Smith, E.A., Gurven, M., Kaplan, H., 2012. Physical competition increases testosterone among Amazonian forager-horticulturalists: a test of the "challenge hypothesis". *Proc. R. Soc. B Biol. Sci.* 279 (1739), 2907–2912. <http://dx.doi.org/10.1098/rspb.2012.0455>.
- Tuiten, A., van Honk, J., Koppeschaar, H., Bernaards, C., Thijssen, J., Verbaten, R., 2000. Time course of effects of testosterone administration on sexual arousal in women. *Arch. Gen. Psychiatry* 57 (2), 149–153. Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/10665617>.
- Tuiten, A., van Honk, J., Verbaten, R., Laan, E., Everaerd, W., Stam, H., 2002. Can sublingual testosterone increase subjective and physiological measures of laboratory-induced sexual arousal? *Arch. Gen. Psychiatry* 59 (5), 465. <http://dx.doi.org/10.1001/archpsyc.59.5.465>.
- van't Veer, A.E., Giner-Sorolla, R., 2016. Pre-registration in social psychology—A discussion and suggested template. *J. Exp. Soc. Psychol.* 67, 2–12.
- Veldhuis, J.D., Iranmanesh, A., 2004. Pulsatile intravenous infusion of recombinant human luteinizing hormone under acute gonadotropin-releasing hormone receptor blockade reconstitutes testosterone secretion in young men. *J. Clin. Endocrinol. Metab.* 89 (9), 4474–4479. <http://dx.doi.org/10.1210/jc.2004-0203>.
- Wagels, L., Radke, S., Goerlich, K.S., Habel, U., Votinov, M., 2017. Exogenous testosterone decreases men's personal distance in a social threat context. *Horm. Behav.* 90, 75–83. <http://dx.doi.org/10.1016/j.yhbeh.2017.03.001>.
- Welker, K.M., Gruber, J., Mehta, P.H., 2015. A positive affective neuroendocrinology approach to reward and behavioral dysregulation. *Front. Psychiat.* 6 (July), 1–13. <http://dx.doi.org/10.3389/fpsy.2015.00093>.
- Welker, K.M., Lasseter, B., Brandes, C.M., Prasad, S., Koop, D.R., Mehta, P.H., 2016. A comparison of salivary testosterone measurement using immunoassays and tandem mass spectrometry. *Psychoneuroendocrinology* 71, 180–188. <http://dx.doi.org/10.1016/j.psyneuen.2016.10.020>.

- 1016/j.psyneuen.2016.05.022.
- Welker, K.M., Norman, R.E., Goetz, S., Moreau, B.J.P., Kitayama, S., Carré, J.M., 2017a. Preliminary evidence that testosterone's association with aggression depends on self-construal. *Horm. Behav.* 92, 117–127. <http://dx.doi.org/10.1016/j.yhbeh.2016.10.014>.
- Welker, K.M., Roy, A.R.K., Geniole, S., Kitayama, S., Carré, J.M., 2017b. Taking risks for personal gain: an investigation of self-construal and testosterone responses to competition. *Soc. Neurosci.* 1–15. <http://dx.doi.org/10.1080/17470919.2017.1407822>.
- Welling, L.L.M., Moreau, B.J.P., Bird, B.M., Hansen, S., Carré, J.M., 2016. Exogenous testosterone increases men's perceptions of their own physical dominance. *Psychoneuroendocrinology* 64, 136–142. <http://dx.doi.org/10.1016/j.psyneuen.2015.11.016>.
- Wibral, M., Dohmen, T., Klingmüller, D., Weber, B., Falk, A., 2012. Testosterone administration reduces lying in men. *PLoS One* 7, e46774.
- van Wingen, G.A., Zylicz, S.A., Pieters, S., Mattern, C., Verkes, R.J., Buitelaar, J.K., Fernández, G., 2009. Testosterone increases amygdala reactivity in middle-aged women to a young adulthood level. *Neuropsychopharmacology* 34 (3), 539–547. <http://dx.doi.org/10.1038/npp.2008.2>.
- van Wingen, G.A., Mattern, C., Jan, R., 2010. Testosterone reduces amygdala-orbitofrontal cortex coupling. *Psychoneuroendocrinology* 35, 105–113. <http://dx.doi.org/10.1016/j.psyneuen.2009.09.007>.
- Wingfield, J.C., 2017. The challenge hypothesis: where it began and relevance to humans. *Horm. Behav.* 92, 9–12. <http://dx.doi.org/10.1016/j.yhbeh.2016.11.008>.
- Wingfield, J.C., Hegner, R.E., Dufty, A.M., Ball, G.F., 1990. The “Challenge Hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* 136 (6), 829–846.
- Wood, R.I., Newman, S.W., 1999. Androgen receptor immunoreactivity in the male and female Syrian hamster brain. *J. Neurobiol.* 39 (3), 359–370. Retrieved from. <http://www.ncbi.nlm.nih.gov/pubmed/10363909>.
- Wu, Y., Liu, J., Qu, L., Eisenegger, C., Clark, L., Zhou, X., 2016. Single dose testosterone administration reduces loss chasing in healthy females. *Psychoneuroendocrinology* 71, 54–57. <http://dx.doi.org/10.1016/j.psyneuen.2016.05.005>.
- Wu, Y., Eisenegger, C., Zilioli, S., Watson, N.V., Clark, L., 2017. Comparison of clear and narrow outcomes on testosterone levels in social competition. *Horm. Behav.* 92, 51–56. <http://dx.doi.org/10.1016/j.yhbeh.2016.05.016>.
- Zak, P.J., Kurzban, R., Ahmadi, S., Swerdloff, R.S., Park, J., Efremidze, L., ... Matzner, W., 2009. Testosterone administration decreases generosity in the ultimatum game. *PLoS One* 4 (12), e8330. <http://dx.doi.org/10.1371/journal.pone.0008330>.
- Zethraeus, N., Kocoska-Maras, L., Ellingsen, T., von Schoultz, B., Hirschberg, A.L., Johannesson, M., 2009. A randomized trial of the effect of estrogen and testosterone on economic behavior. *Proc. Natl. Acad. Sci. U. S. A.* 106 (16), 6535–6538. <http://dx.doi.org/10.1073/pnas.0812757106>.
- Zilioli, S., Bird, B.M., 2017. Functional significance of men's testosterone reactivity to social stimuli. *Front. Neuroendocrinol.* <http://dx.doi.org/10.1016/j.yfrne.2017.06.002>.
- Zilioli, S., Watson, N.V., 2012. The hidden dimensions of the competition effect: basal cortisol and basal testosterone jointly predict changes in salivary testosterone after social victory in men. *Psychoneuroendocrinology* 37 (11), 1855–1865. <http://dx.doi.org/10.1016/j.psyneuen.2012.03.022>.
- Zilioli, S., Caldbick, E., Watson, N.V., 2014. Testosterone reactivity to facial display of emotions in men and women. *Horm. Behav.* 65 (5), 461–468. <http://dx.doi.org/10.1016/j.yhbeh.2014.04.006>.
- Zilioli, S., Ponzi, D., Henry, A., Kubicki, K., Nickels, N., Wilson, M.C., Maestripieri, D., 2016. Interest in babies negatively predicts testosterone responses to sexual visual stimuli among heterosexual young men. *Psychol. Sci.* 27 (1), 114–118. <http://dx.doi.org/10.1177/0956797615615868>.
- Zitzmann, M., Depenbusch, M., Gromoll, J., Nieschlag, E., 2003. Prostate volume and growth in testosterone-substituted hypogonadal men are dependent on the CAG repeat polymorphism of the androgen receptor gene: a longitudinal pharmacogenetic study. *J. Clin. Endocrinol. Metab.* 88 (5), 2049–2054. <http://dx.doi.org/10.1210/jc.2002-021947>.