The effects of exogenous testosterone on economic decision making and executive functioning

by

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Abstract

A small body of correlational work suggests that the steroid hormone testosterone may play an important role in economic decision-making, although mixed findings have raised questions about the nature of these relationships. Very few studies have featured the experimental control of testosterone that would be needed to establish causal relationships between testosterone and decision-making, and it remains unknown whether causal effects are modulated by important contextual or individual difference variables. A further gap exists in understanding if, and how, testosterone influences executive functions—the higher order cognitive mechanisms that are germane to purposeful behaviour, including economic choice. This dissertation sought to address these gaps in three experiments that employed double-blind, placebo-controlled, testosterone administration paradigms. Experiment 1 examined the effects of testosterone on economic decisions in a one-shot public goods game, with participants randomized to make their decision under time-pressure or after time-delay. Results from Experiment 1 indicated that testosterone (1) abolished a prosocial time-pressure effect among men low in a personality risk factor for testosterone-induced antisociality, and (2) fully reversed a prosocial time-delay effect among men high in personality risk. Replicating and extending this work, results from Experiment 2 indicated that (1) testosterone reduced prosocial economic decisions among high risk (but not low risk) men when there was no game observer; (2) when the game observer was a man perceived as relatively more (vs. less) attractive, testosterone increased prosocial economic contributions among participants with restricted sociosexualities (long-term mating orientations) but decreased contributions among those with unrestricted sociosexualities (short-term mating orientations); and (3) when the game observer was a woman perceived as relatively less (vs. more) attractive, testosterone reduced prosocial contributions most prominently for participants with unrestricted sociosexualities. Experiment 3 examined the effects of testosterone on executive functioning, and economic decision-making on the Iowa Gambling Task (IGT). Results from Experiment 3 indicated that testosterone (1) down-regulated task planning ability and inhibition, and (2) produced null effects for economic decisions on the IGT. The experiments herein are discussed within the context of evolving theoretical models that link rapid increases in testosterone to context-dependent, reproductively-relevant behaviours.

Keywords: Testosterone; Social Heuristic Hypothesis; Challenge Hypothesis; Economic Decision Making; Executive Functioning; Executive Functions; Public Goods Game; Iowa Gambling Task

Dedication

This dissertation is dedicated to Bryanne and Jamie.

Their endless patience, support, encouragement, and ability to create and appreciate humour, made all of this possible and worthwhile.

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Chapter 1.

General Introduction

Human decision-making, and particularly economic decision-making involving cost-benefit trade-offs for self and/or others, is a sophisticated enterprise driven principally by cognition, along with various modulatory inputs from physiology and the environment. Considerable research efforts have been spent identifying the contribution of certain variables within some of these domains, such as personality traits (Zaleskiewicz, 2001; Zhao & Smillie, 2015), social preferences (Fischbacher & Gachter, 2010), and emotions (Bechara & Damasio, 2005; Naqvi et al., 2006). Less is known, however, about the role that key physiological signals play in decision making—most notably endocrine factors, which can track environmental cues, and may subsequently influence cognitive programs. Androgens can function as one such signal, yet few studies have focused on androgens and economic decision-making, and most have done so using correlational study designs, placing limits on our understanding of potential directional relationships.

The steroid hormone testosterone, in particular, has received little attention, yet may represent a critical biological mechanism that independently, or through interaction with contextual and/or individual difference variables, predicts human economic decisions. There are several reasons for this proposition. First, testosterone has been implicated in a host of other human behavioural domains that involve risk-benefit trade-offs, such as competition and aggression, mating and parenting, and trust (for reviews, see Bos et al., 2012; Carré & Olmstead, 2015; Geniole & Carré, 2018; Gray et al., 2019; Zilioli & Bird, 2017). Second, testosterone has been found to modulate neural processing relevant to risk-taking and decision-making (Goetz et al., 2014; Hermans et al., 2010; Op de Macks et al., 2011; Rudebeck et al., 2006; Tobiansky et al., 2018). Third, some recent work using correlational designs has indicated that testosterone may indeed play a role in economic decision-making, such as findings that circulating levels of testosterone positively correlate with risk-taking in a laboratory investment task (Apicella et al., 2008) (see Apicella et al., 2015 for review). Nevertheless, it remains unclear to what extent testosterone plays a causal role in such decision-making, resulting partly from a lack of studies, study design limitations (e.g., correlational versus experimental),

restricted populations of study (e.g., exclusively women), and mixed findings (Stanton, 2017).

1.1. Economic Decision-Making

1.1.1. Interdependent contexts and intuitive choice

In the context of decisions that depend not only on one's own choice but also the choice of others (i.e., interdependent or social contexts), there has emerged one particularly influential approach to explain human decision making—the *dual process framework*. Dual process approaches to human decision-making have attempted to understand the conditions under which human decisions are intuitive versus deliberative, and whether such decisions are prosocial/cooperative or selfish/antisocial in nature. The dual-process approach to decision-making suggests that human choices are the result of tradeoffs between two cognitive systems—one that is automatic, fast, rigid, relatively effortless, and intuitive, and another that is deliberate, slow, flexible, effortful, and controlled (Bear & Rand, 2016; Kahneman, 2003; Sloman, 1996; Stanovich & West, 1998; Zaki & Mitchell, 2013).

Emerging from the dual process framework is the *social heuristic hypothesis*, which posits that human intuitions determine if our default response is selfish or cooperative, with the suggestion that such intuitions are shaped by our daily experiences (Bear & Rand, 2016; Rand et al., 2014). Willingness to cooperate, coordinate, and act in prosocial ways, it is argued, is advantageous in daily life because in our repeated interactions with others, our reputational status is at stake, accompanied by the possibility of consequences for good or bad behaviour. Thus, individuals can successfully navigate these social interactions by cooperating. Some experiments attempting to manipulate intuitive or deliberative decision-making have produced results consistent with the social heuristic hypothesis, such that when individuals are primed to make an intuitive decision (i.e., to make a decision under time pressure), they contribute more money to a one-shot public goods game than they do when primed to deliberate about their decision (Rand et al., 2012; e.g., Rand, 2016a)[1].

1 The proposals of the social heuristic hypothesis have not gone unchallenged. The primary finding in Rand et al.'s original article (2012)—that individuals contribute more when under time pressure than time delay—was specific to those who followed task instructions. A recent multi-lab

The dual process approach and related social heuristic hypothesis can be contrasted with a separate, value-based decision-making framework, which suggests that cognitive processes involved in economic decision-making and cooperative behaviour are not fixed, but instead hinge on individual differences (Hackel et al., 2020; Levy & Glimcher, 2012). Specifically, it suggests that individuals with more prosocial tendencies are quicker to cooperate than they are to engage in self-interested behaviour, and more self-interested individuals are quicker to engage in self-interested behaviour than cooperation (Hutcherson et al., 2015; Krajbich et al., 2015). Some recent work supports this idea in finding that prosocial participants were intuitive cooperators, while selfish participants were deliberative cooperators (Hackel et al., 2020). Therefore, it remains possible that cooperation in interdependent economic decision-making contexts may not be intuitive for most individuals, and thus priming intuition or reflection may have disparate effects based on individual dispositions. Experiment 1 provides a test of these theoretical viewpoints in the context of testosterone administration (see Experiment 1 methodology for details).

1.1.2. Onlookers in public goods games

The degree to which men make relatively prosocial or antisocial economic decisions can also be influenced by whether they are being observed, and particularly by individuals that they find attractive. Vugt and Iredale (2013), for example, found that in a public goods experiment, men made more prosocial economic decisions (i.e., contributed more) when they were observed by women but not men, whereas a parallel effect was not found among women. Further, public goods contributions were higher when men rated the observers as being more attractive. Researchers have suggested that the evolution of men's competition for women may underlie their public goods decisions in such a manner, where prosocial behaviour functions as a means to signal

replication found similarly that predictions were only supported for those who followed instructions (Bouwmeester et al., 2017a). Some have suggested that findings may thus be an artifact of selection biases (i.e., artificially selecting cooperative individuals in the first place). Nevertheless, findings remain equivocal, as rebuttals to selection bias concerns using the same data provide refutation, while two recent meta-analyses have come to different conclusions regarding the robustness of the predicted effects of the social heuristic hypothesis (Kvarven et al., 2019; Rand, 2019).

underlying quality, such as desirable personality qualities (e.g., trustworthiness) or genetic fitness (i.e., costly signalling; Gintis et al., 2001; Zahavi & Zahavi, 1999).

1.2. Testosterone and Economic Decision-Making

The novel idea that testosterone influences economic decision-making can be studied in both interdependent, social contexts—where economic decisions are typically framed as prosocial or antisocial in nature (i.e., cooperation, selfishness)—or in independent, non-social contexts, where decisions are framed in the form of risk preference (e.g., gambling). This dissertation incorporates both of these elements of economic choice.

1.2.1. Interdependent economic decision-making

Traditional wisdom suggests that testosterone is positively associated with aggressive, antisocial behaviours. However, correlational and experimental data examining such relationships with economic decision-making tasks paints a more complex picture. For example, some work has suggested that testosterone decreases generosity among men (Zak et al., 2009), whereas others have found that testosterone administration increases generosity among women, with opposite effects for participants who believed they received testosterone, regardless of whether they did or not (Eisenegger et al., 2010). Other work has found that when given testosterone, men will pay a proportionate cost to themselves to either act prosocially or antisocially toward a proposer in the ultimatum game, depending on how high the initial proposed offer was (Dreher et al., 2016). Others still find no effects at all on such economic decision-making (Zethraeus et al., 2009). A number of possibilities exist for the disparate findings, including different effects for men versus women—potentially resulting from the largely supraphysiological dosing used in women (Tuiten et al., 2000)—variation in the context under which economic choices are made, and hidden individual difference moderators.

As noted, the social heuristic hypothesis provides one contextual consideration in economic games for whether humans will act in intuitive, relatively prosocial ways, or reflective, relatively antisocial ways. Notably, recent work has found that testosterone can also promote intuitive (but incorrect) decision-making on a cognitive reflection task (Nave et al., 2017a)(but see Knight et al., 2020), raising the possibility that the effects of

the social heuristic hypothesis—that individuals making intuitive (i.e., fast) decisions act in more prosocial ways than those reflecting on decisions—could be enhanced by the administration of testosterone (tested in Experiment 1). Additionally, given the reviewed theoretical and experimental literature for observer effects in economic decision-making, it also seems possible that prosocial effects of testosterone under time pressure could be particularly prominent under conditions of being observed by a female (tested in Experiment 2).

1.2.2. Independent economic risk-taking

A small body of literature shows that testosterone may play an important role in economic risk taking (see Apicella et al., 2015, for review; see also Stanton, 2017). For example, researchers have found that circulating levels of testosterone, as well as increases in testosterone following a monetary win or loss, predict risk taking in a laboratory investment task and risk preferences task, respectively (Apicella et al., 2008, 2014). In other work, researchers found that testosterone was positively related to men's and women's risk-taking on the Iowa gambling task (Stanton, Liening, et al., 2011), similar to studies looking at the same task after testosterone administration, which found that women given testosterone (versus placebo) were more likely to select options with larger rewards but also larger punishments (van Honk et al., 2004). Outside of the laboratory, Coates and Herbert (2008) found that male financial traders made more money (implying that they took more risks) on days when their testosterone levels were the highest, which has been followed by lab-based testosterone administration trials showing that when given testosterone, male traders will bid higher amounts for financial assets (Nadler et al., 2018), and healthy young men will show increased preference for high volatility assets in a simulated trading environment (Cueva et al., 2015).

Nevertheless, some work has failed to support earlier findings (Boksem et al., 2013; Sapienza et al., 2009; Zethraeus et al., 2009), while other authors provide potential nuance to previously identified effects, finding that risk preferences were highest for those with both low and high testosterone (Stanton et al., 2011). Thus, questions remain as to (1) whether testosterone plays a causal role in risky economic decision-making, and (2) whether testosterone-induced risk-taking might be modulated by individual difference factors (see Importance of Individual Difference Moderators section for further discussion). Experiment 3 was designed to test these possibilities.

1.3. Executive Functioning

Executive functioning is an umbrella term referring to a complex set of higher-order cognitive processes that operate in a supervisory fashion for overall brain processing (Fossati et al., 2018; Miyake et al., 2000; Strauss et al., 2006). Although various definitions exist, scholars generally agree that the executive functions encompass skills that are critical for purposeful goal attainment and the regulation of one's thoughts and affect (Fossati et al., 2018; Miyake & Friedman, 2012). Such skills can be captured categorically by working memory, cognitive flexibility, and inhibitory control (Diamond, 2013), also referred to as "*updating* (constant monitoring and rapid addition/deletion of working memory contents), *shifting* (switching flexibly between tasks or mental sets), and *inhibition* (deliberate overriding of dominant or prepotent responses)" (Miyake & Friedman, 2012 p. 9), respectively.

Executive functions can jointly override drives, reflexes, impulses, and over-rehearsed behavioural patterns (Suchy, 2009). Further, they allow individuals to coordinate and maintain plans and goals, while simultaneously monitoring performance and inhibiting distractions from extraneous stimuli (Kane & Engle, 2002; Ybarra & Winkielman, 2012).

1.3.1. Testosterone and executive functioning

The possibility exists that testosterone is a biological variable that influences executive functioning, which in turn could affect various behavioural outcomes. Hints at such a regulatory role for testosterone can be found in non-human animal literature (see Tobiansky et al., 2018 for review). For example, an early foraging experiment found that male chicks treated with testosterone showed perseveration by continued pecking of familiar colour grains, whereas non-testosterone treated chicks showed behavioural flexibility by pecking familiar and novel colour grains without preference (Andrew, 1972). Subsequent findings in rats and chickens found that gonadectomy reduced a similar perseveration, while perseveration could be re-instated in chickens by replacement of testosterone (Archer, 1977; Rogers, 1974; Thompson & Wright, 1979). Other work has found that among spontaneously hypertensive male rats, implanting testosterone on postnatal day 10 predicted deficits consistent with the working memory difficulties found in humans with ADHD (King et al., 2000)—a mental health condition partly characterized

by deficits in executive functioning (see Willcutt et al., 2005 for meta-analysis). From this evidence, it seems possible that testosterone downregulates executive functioning.

Among humans, however, evidence is somewhat less clear. Indirect evidence for an effect of testosterone on executive functioning can be found by examining behavioural outcomes that depend, in part, on executive functions. For example, aggression—shown to be negatively related to executive functioning in childhood, adulthood, and in both healthy and pathological populations (Krämer et al., 2011; Micai et al., 2015; Ogilvie et al., 2011; Rohlf et al., 2018)—is more likely expressed among individuals who experience a rise in testosterone following some environmental challenge, such as a competition (Geniole et al., 2020). Further, among dominant and impulsive men, a rapid increase in testosterone from exogenous administration predicts subsequent aggression on a laboratory task (Carré et al., 2017; see also Geniole et al., 2019).

Studies that have more directly examined the influence of testosterone on executive functioning using classical neuropsychological tests have relied primarily on elderly samples (usually ≥ 60 years of age), given that both testosterone and executive functioning tend to decline with age (Fjell et al., 2017; Harman et al., 2001). However, the findings from these samples are generally mixed (for reviews, see Boss et al., 2014; Holland et al., 2011). On the one hand, some studies show inverse relationships between testosterone and executive functioning. Moffat et al. (2002), for example, found that those individuals with relatively higher testosterone had poorer attention and concentration scores at follow-up 10 years later. In a correlational study, Van Strien, Weber, Burdoff, and Bangma (2009) found that older men with higher testosterone concentrations demonstrated less inhibitory control (i.e., ability to inhibit inappropriate responses). Other work has found that testosterone levels were inversely related to an executive functioning composite comprised of the capacity to initiate and execute responses while monitoring performance, and sustained attention (Martin et al., 2008).

On the other hand, Yaffee, Lui, Zmuda, and Cauley (2002) found that older men with high (versus low) testosterone showed better performance on tasks of working memory and task switching, similar to a repeated administration study finding that testosterone supplementation over a one-month period improved working memory scores for older men relative to those who received placebo (Janowsky et al., 2000).

Other research still, however, has found no meaningful relationships between endogenous levels of, or exogenously administered, testosterone, and various indices of executive functioning, such as task switching (Haren et al., 2005; LeBlanc et al., 2010; Perry et al., 2001; Resnick et al., 2017; Zimmerman et al., 2011), cognitive flexibility (Huang et al., 2016), or working memory (Fonda et al., 2005). Androgen deprivation studies add further mixed findings. For instance, a review of studies using androgen deprivation for cancer patients found that between 46% to 69% of older men on androgen deprivation declined in at least one cognitive domain, one of the most common of which was executive functioning (e.g., working memory, task-switching, and visual scanning) (Nelson et al., 2008). Yet, more recent meta-analytic and longitudinal work has found no meaningful effect of androgen deprivation on older men's executive functioning (Alibhai et al., 2017; McGinty et al., 2014). Some authors have also found curvilinear effects on some measures (e.g., working memory) such that performance is best at moderate levels of testosterone relative to low or high testosterone (e.g., Matousek & Sherwin, 2010); such findings provide a parallel to other work showing that individuals with high and low (but not moderate) levels of testosterone show decreased aversion to economic risk (Stanton et al., 2011).

Studies examining the effects of testosterone on executive functioning (rather than global cognition or other cognitive domains not typically considered executive functioning[2]) in young adulthood are scarce. A small number of studies have examined executive functioning in children and adolescents, however, perhaps providing a closer approximation for expected effects in healthy young adults. In one study, Agoston, Gonzalez-Bolanos, Semrud-Clikeman, Vanderburg, and Sarafoglou (2017) examined parent-reported executive functioning difficulties for children (mean age of 8.41 years) with congenital adrenal hyperplasia (CAH)—a disorder characterized by excessive androgen production—as well as bone age advancement as a proxy for cumulative androgen exposure. Results indicated that boys (but not girls) with more cumulative androgen exposure showed the highest difficulties with inhibition, and among the whole sample, higher androgen exposure was associated with more difficulties in all other

2 There is literature focused on other cognitive domains in young adults, such as verbal memory, but scholars generally consider these as separate from the executive functions—which serve a more supervisory role over the more "basic" processes. Here, the focus is on executive functions rather than more basic cognitive domains.

executive function domains assessed (e.g., working memory, shifting, planning/organization). Other work in children with CAH (mean age 10.22) has found greater deficits in cognitive flexibility or “set shifting” on the Wisconsin Card Sorting Test relative to control children (although no association with serum testosterone level; Amr et al., 2019). In a recent longitudinal examination of healthy children, adolescents, and young adults aged 6 to 22, the authors found that among boys (but not girls), higher testosterone levels were associated with a positive prefrontal-hippocampal covariance, and such covariance was associated with lower performance on the monitoring and flexible shifting components of the BRIEF executive functioning measure (Nguyen et al., 2017). Thus, at least among younger populations, evidence seems more consistent with a deleterious, rather than facilitatory effect of testosterone on executive functioning.

There are at least two important gaps that can be identified from the literature on the link between testosterone and executive functioning. First, the primary focus on elderly populations neglects healthy younger men, to whom testosterone is highly relevant, playing an important role in various domains such as mate seeking (Roney & Gettler, 2015), competition (Carré & Olmstead, 2015), and dominance (Turan et al., 2014). Second, many previous studies used correlational designs, and those using experimental designs examined executive functioning in the context of chronic testosterone administration or deprivation over several weeks or months. Although understanding the influence of stable, trait-like testosterone levels on cognition and behaviour is important, chronic administration neglects testosterone’s dynamic nature, where it flexibly rises or falls in response to environmental inputs that signal adaptive challenges. Indeed, a host of findings in social neuroendocrinology show that changes in testosterone, rather than baseline levels, can predict future behaviour such as competitive decision-making, aggression, and risk-taking (for reviews, see Geniole & Carré, 2018; Zilioli & Bird, 2017). Thus, it remains possible that acute changes in testosterone, rather than trait-like levels, may share a stronger link with shifts in executive functioning. To date, no study has examined this possibility with experimental manipulation to mimic an acute rise in testosterone.

1.4. Importance of Individual Differences for Testosterone-Behaviour Relationships

An additional consideration of growing importance is the extent to which the effects of testosterone are modulated by individual differences. Personality traits, in particular, seem to be highly relevant in this regard. For example, both correlational and experimental work has found that testosterone is positively related to aggression, but only among individuals with dispositions marked by high trait dominance, high trait impulsivity (low self control), and relatively independent self-construals (i.e., seeing oneself as generally independent from, rather than interconnected with, other individuals) (Carré et al., 2017; Geniole et al., 2019; Welker et al., 2017). Similar patterns can be found in other domains, such as competition over opposite sex mates, where findings suggest that behaviours such as assertiveness, and the degree of "connection" between an individual and a prospective partner (i.e., perceived "clicking with" the person) are positively correlated with the man's testosterone level, but only among those who are high in trait dominance (Slatcher et al., 2011). Thus, the possibility exists that in the context of cooperative economic tasks, risk preference paradigms, or measures of executive functioning, that the effects of testosterone may be largely dependent on an individual's more stable dispositional qualities.

1.5. Goals of the Dissertation Experiments

It is evident that there remain gaps in our understanding of how testosterone influences economic decision-making and executive functioning. In the following chapters of this dissertation, I outline experiments that address these gaps by using double-blind, placebo-controlled administration paradigms that temporarily elevate men's testosterone levels to the high normal range, with the key goals as follows: determine the extent to which (1) testosterone plays a causal role in men's economic decision-making involving others (i.e., public goods dilemmas), (2) testosterone plays a causal role in men's risky economic decision-making when consequences pertain primarily to the decision-maker themselves (i.e., gambling decisions), (3) testosterone modulates executive functions of critical importance to various behavioural domains, and 4) contextual variables (e.g., priming an intuitive or a reflective response, presence or

absence of observers) and individual differences variables (e.g., trait dominance, trait self-control, self-construal) moderate the effects of testosterone in these domains.

Chapter 2. Experiment 1: Effect of Exogenous Testosterone on Cooperation Depends on Personality and Time Pressure

Note: This chapter represents the following published article:

Bird, B.M., Geniole, S.N., Procyshyn, T.L., Ortiz, T.L., Carré, J.M., and Watson, N.V. (2019). Effect of exogenous testosterone on cooperation depends on personality and time pressure. *Neuropsychopharmacology, 44*(3), 538–545.

2.1. Introduction

Cooperation is a defining feature of human social interaction (Bear & Rand, 2016), yet it remains a perplexing phenomenon: to cooperate with others confers benefits to the group as a whole, but because such an act necessarily involves a personal cost, it also creates the temptation to withhold cooperation in the hopes of benefitting from others' prosociality (Cone & Rand, 2014). Humans further possess the capability to switch from selfless to self-interested behaviours (and vice-versa) in relatively short-periods of time, raising the question as to what mechanisms act upon this behaviour. Such dynamics have inspired considerable research efforts to delineate the ultimate and proximate factors that influence human decision-making on whether or not to cooperate.

2.1.1. Social Heuristic Hypothesis and Decision-Making Frameworks

The *social heuristic hypothesis* posits that human intuitions determine if our default response is selfish or cooperative, with such intuitions shaped by daily experiences (Bear & Rand, 2016; Rand et al., 2014). Cooperation, it is argued, is advantageous in daily life: in our repeated interactions with others, reputational status is at stake, accompanied by the possibility of sanctions for good or bad behaviour, and thus we can successfully navigate these social interactions by cooperating. As a function of these daily experiences, humans can develop cooperative intuitions (Rand et al., 2012, 2014). Of course, some individuals cooperate for other reasons, such as to increase their own self-regard (typically referred to as "warm glow"; Andreoni, 1990; Crumpler & Grossman, 2008), but we review the literature on the social heuristic

hypothesis, which describes the functional utility of cooperating in daily life, as this literature specifically helped inform our hypotheses in the present experiment. The social heuristic hypothesis builds on a larger dual-process framework, arguing that our decisions arise as a function of either a) automatic, fast, rigid, relatively effortless, *intuitive* processes or b) deliberate, slow, flexible, effortful, *controlled* processes (Bear & Rand, 2016; Kahneman, 2003; Sloman, 1996; Stanovich & West, 1998; see Zaki & Mitchell, 2013 for review of dual process as relating to prosociality).

If intuitive processes are by definition automatic, and cooperation is an acquired intuition, then we should be more prone to cooperate under contexts of time constraint (i.e., forced intuitive decisions). In contrast, when given the chance to deliberate, the extra decision-making time may override cooperative intuitions and adjust behaviour toward the optimum for a given situation (Bear & Rand, 2016; Rand et al., 2014). In the context of one-shot economic encounters, in which there may be less concern about reputation or sanctions for good or bad behaviour, the optimum would be to act selfishly. [By optimum, we refer to the idea that in a given situation, there is a strategy that gives the highest expected utility. In a one-shot PGG, every dollar spent on the group project costs one dollar but yields only a private return of less than one dollar, and thus self-interested subjects should contribute nothing to the common project (Camerer & Fehr, 2004). Given that reputation can have a significant influence on repeated PGGs (e.g., McIntosh et al., 2013; Pfeiffer et al., 2012), and given that we are examining testosterone—a hormone strongly implicated in status and dominance-related behaviours—we also note here that acting in a self-interested manner does not have the same potential consequences for reputation. Some work supports this notion. For example, when participants are randomly assigned to a time-constraint condition (i.e., make a decision in less than 10 seconds) or a forced-delay condition (i.e., wait at least 10 seconds before making a decision), those in the time-constraint condition make significantly greater contributions to a shared pool of resources than do those in the forced-delay condition (Rand et al., 2012). [Some studies have failed to replicate this effect (e.g., Bouwmeester et al., 2017b; Tinghög et al., 2013; Verkoeijen & Bouwmeester, 2014) (but see Rand, 2016b, 2017; Rand et al., 2013), which has been attributed to participant compliance—when asked to respond rapidly, some participants nevertheless deliberate, or vice versa. When restricting analyses to those who comply with instructions, as was done in the original article, the effect of time-constraint on

cooperation appears robust (see Bouwmeester et al., 2017b for a recent multi-lab replication study), with further analyses suggesting that selection biases do not properly account for the finding of significant differences in compliant-only analyses but not intent-to-treat analyses (Rand, 2017).]

A separate, value-based decision-making framework suggests that cognitive processes involved in cooperative behaviour are not fixed, but instead hinge on individual differences (Levy & Glimcher, 2012; Wills et al., 2018). Specifically, it suggests that individuals with more prosocial tendencies are quicker to cooperate than they are to engage in self-interested behaviour, and more self-interested individuals are quicker to engage in self-interested behaviour than cooperation (Hutcherson et al., 2015; Krajbich et al., 2015). Indeed, some recent work supports this idea in finding that prosocial participants were intuitive cooperators, while selfish participants were deliberative cooperators (Wills et al., 2018). Therefore, cooperative behaviour may not be intuitive for every individual, and thus priming intuition or reflection may have disparate effects based on individual dispositions.

2.1.2. Effects of Testosterone on Behaviour and Decision-Making

Traditional wisdom suggests that testosterone is positively associated with aggressive, impulsive, and antisocial behaviours, and negatively associated with prosocial, cooperative behaviours. However, meta-analytic estimates indicate that the correlation between testosterone and human aggression is relatively weak (r = .08; see Archer et al., 2005). Critically, more recent work suggests that testosterone's relationship to human social behaviour—and decision-making more generally—may depend on social context and/or individual differences in specific personality domains. For instance, one study showed that testosterone increased the extent to which men either punished or rewarded their interaction partner, depending on whether the partner made unfair or fair offers in the ultimatum game, respectively (Dreher et al., 2016). Most relevant to intuitive decision-making, a single dose of testosterone (relative to placebo) reduced cognitive reflection among young men (Nave et al., 2017b) and, in another set of studies, increased reactive aggression, but only among men high in trait dominance, low in self-control (Carré et al., 2017), or with a relatively independent self-construal (Welker et al., 2017). Therefore, testosterone's effects on social behaviour and on intuitive

decision-making may depend not only on social context, but also on individual difference factors.

Combining this research on cognition and social neuroendocrinology, we aimed to address several key outstanding questions regarding cooperative behaviour, including if and how testosterone influences cooperation, if and how intuition or reflection might interact with testosterone to influence cooperation, and if these (potentially synergistic) effects depend on individual differences in personality (trait dominance, self-control, self-construal). To do so, we employed a relatively large, placebo-controlled, testosterone administration study, using a sample of 400 men (between-subjects design), and randomly assigned men to complete a one-shot public goods game (PGG) under time constraint (forced intuition) or time delay (forced reflection). Two, partially competing hypotheses guided our predictions. Based on the theoretical accounts and findings presented above, one hypothesis is that testosterone's promotion of intuitive decision-making (Nave et al., 2017) would exaggerate the prosocial effects of time-pressure (Rand et al., 2012) on cooperation (H1). On the other hand, because cooperation leaves individuals vulnerable to exploitation—a potential threat to the social status/dominance (Boksem et al., 2013) that testosterone is thought to promote (e.g., Eisenegger et al., 2011; Mazur & Booth, 1998)—testosterone may reduce cooperation (as in Boksem et al., 2013). Nevertheless, to the extent that weighing the benefits of cooperation against the status-related costs of exploitation requires cognitive effort and deliberation, we might expect these negative effects of testosterone to only exist when deliberation is possible (i.e., forced delay condition). In other words, time-constraint may buffer against the negative effects of testosterone on cooperation (H2).

Further, and regardless of whether time-constraint buffers against the negative effects of testosterone, or testosterone exaggerates the beneficial effects of time-constraint, we predicted that any interactions between intuition/deliberation and testosterone would be strongest among men high in a risk factor score comprised of previously-identified critical moderators of testosterone-behaviour relationships (H3), including high trait dominance, high impulsivity (low self-control), and independent self-construal (those feeling relatively disconnected from other individuals; Carré et al., 2017; Welker et al., 2017 see Methods section for calculation of this "Risk" score).

2.2. Methods

2.2.1. Participants

The participant sample consisted of 400 healthy young men between the ages of 18 and 40 years (M_{Age} = 22.8, *SD* = 4.7). Men were recruited in northern Ontario via online advertisements and from the online participant pool at Nipissing University, thus including students and members of the general public. Prospective participants were first screened via phone for eligibility, based on the following exclusion criteria: 1) age of less than 18 or more than 40 years, 2) participation in sports where testosterone is a banned substance, 3) taking medications known to interfere with steroid hormone concentrations, 4) drug or alcohol dependence, and/or 5) diagnosis of a mental illness. Eligible participants completed informed consent for all aspects of testing. All procedures were approved by the University's Research Ethics Board.

2.2.2. Procedure and materials

A procedural timeline is shown in Figure 2.1. Participants were tested individually at one of three starting times: 10:00AM, 12:30PM, or 2:30PM. After providing informed consent, participants answered online demographics questions and self-report personality measures (~25 mins). Next, a saliva sample was collected via passive drool and frozen at -20°C for future assay of baseline hormone concentrations, followed by a mouthwash sample for future DNA extraction. Using a randomized, double blind administration procedure, participants then received either 11 mg of testosterone nasal gel (Natesto™), or equivalent placebo. Following drug administration, participants completed the Point Subtraction Aggression Paradigm (reported in Geniole et al., 2019). Participants then completed the cooperation task for the current experiment, which was

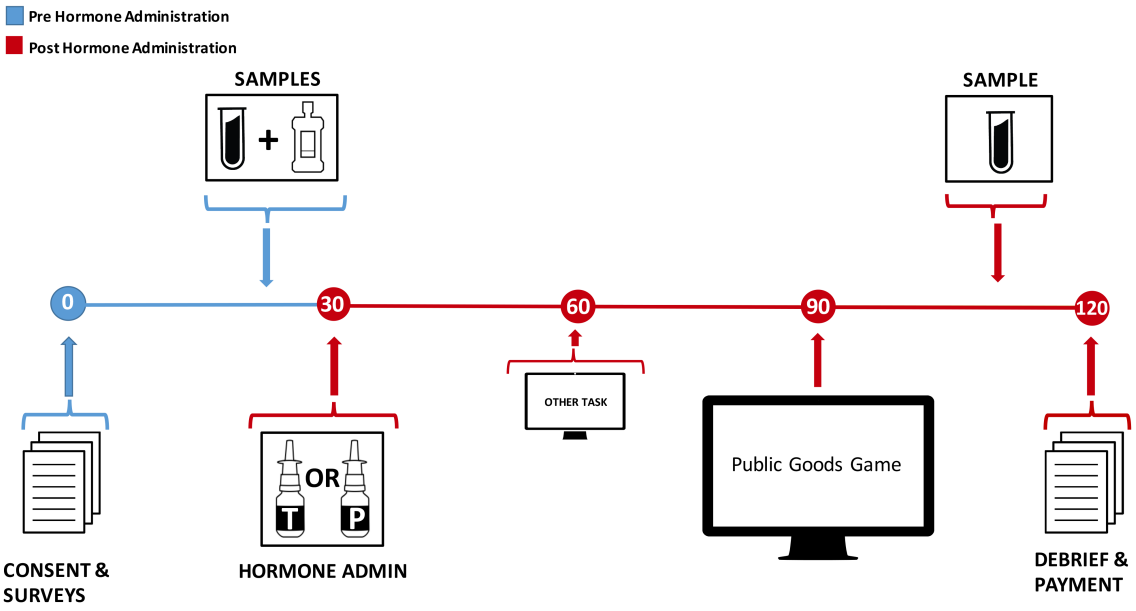

Figure 2.1. Procedural timeline. White numbers indicate time from the beginning of the study. Public goods game was played approximately 60 min following drug administration. Samples included saliva (for confirmation of drug manipulation) and mouthwash (for supplemental DNA extraction and androgen receptor analysis)

a one-shot public goods game (PGG), occurring approximately 60 minutes after drug administration.

2.2.3. Personality questionnaires and creation of the risk score

Recent work in the social neuroendocrinology literature has identified three key personality moderators of the effects of testosterone on social behaviour: self-control (Carré et al., 2017), self-construal (Welker et al., 2017, 2019), and dominance (Carré et al., 2009, 2017; Knight et al., 2017; Mehta et al., 2015; Slatcher et al., 2011). Results from these studies showed that the positive relationship between testosterone and behaviour (e.g., aggression, competitive decision-making, risk-taking) was strongest among individuals who were high in trait dominance, low in trait self-control (high impulsivity), or with relatively independent self-construal. Inherent in examining multiple individual moderators in a single model is a reduction in statistical power (see Kraemer, 2013; Wallace et al., 2013 for review). To address this issue, the present experiment combined individual moderators into a more powerful "risk" score index, in line with previous work (Evans et al., 2013; Kraemer, 2013; Wallace et al., 2013). To achieve this,

scores on each personality measure were first derived individually. Dominance scores were indexed by averaging participant responses (following standardization) on the International Personality Item Pool-Dominance (Goldberg et al., 2006) and the dominance subscale of the Dominance-Prestige Scale (Cheng et al., 2013) (see Carré et al., 2017 for this approach to combining these two measures). Self-control was indexed from the average of participant responses on the Barratt Impulsivity Scale (reverse-coded; Patton et al., 1995) and the Brief Self-Control Scale (Tangney et al., 2004). Self-construal was indexed from the 24-item Self-Construal Scale (Singelis, 1994) by subtracting the 12 "interdependent" sub-scale items from the 12 "independent" sub-scale items, where higher self-construal scores represent a more independent self-construal. The individual dominance, self-control (reverse-scored), and self-construal scores were then standardized and averaged to create the single risk factor score, such that higher risk score values indicated a greater risk for testosterone-induced anti-social behaviour (i.e., lower cooperation).

2.2.4. Hormone administration

Testosterone or placebo conditions were randomly assigned, and administration was conducted using a double-blind procedure. Men assigned to the testosterone condition received two syringes of Natesto™, each containing 5.5mg of gel, while men in the placebo condition received two syringes of an equivalent amount of non-active gel with similar physical properties (i.e., viscosity, color). Under the supervision of a research assistant, participants were instructed to apply the gel from one syringe to the lateral side of the left nostril, and the gel from the other syringe to the lateral side of the right nostril, and then to compress the nostrils toward the nasal septum to evenly spread the gel on nostril walls. Following administration, participants were instructed to immediately and thoroughly wash their hands in order to prevent unintentional contamination of any testing areas.

The present protocol was the first to employ the hormone methodology identified above in a sample of healthy, eugonadal men (see Rogol et al., 2016 for pharmacokinetics in hypogonadal men), and thus a pharmacokinetic pilot was first conducted in order to establish the time course in this population (see Geniole et al., 2019 for full methods). Briefly, using a separate sample of men, and a double-blind, cross-over design (with two-week wash out), male participants (n = 13) had a baseline

blood draw, then received 11mg of Natesto or equivalent placebo, followed by a blood draw at 15, 30, 60, and 180 mins post-administration. As expected, groups did not differ in serum testosterone concentrations at baseline, but significantly differed at all post-administration time points (all *ps* < .005; Cohen's *dz* range = 0.83 to 1.38). Notably, the greatest difference in testosterone concentrations occurred at 60 mins post administration—the time at which behavioural testing for the current experiment was conducted.

2.2.5. Time pressure vs. time delay public goods game

The public goods game (PGG) is a widely-used social dilemma paradigm for measuring cooperation among group members. Cooperation, as defined in the scientific literature and as used for the present experiment, is considered an act where one individual pays a cost for another to receive a benefit (Rand & Nowak, 2013). The PGG has been used for decades as a standard paradigm for measuring cooperation, as the nature of the game is an operationally-defined cooperation task: individuals in the PGG have the opportunity to pay a cost for the benefit of other group members. In a traditional PGG, participants are given a starting endowment and then tasked with deciding how much to give to a "common project", and how much to keep for themselves. Participants are told that all amounts given to the common project are multiplied by a factor (often tripled) and then split evenly among the members. Participant decisions are made in the context of contrasting optimal outcomes for themselves versus optimal outcomes for the group. In other words, the optimal strategy for an individual is not necessarily the optimal strategy for the group, and thus participants must decide whether to cooperate/act prosocially (i.e., give more money to the common project) or to not cooperate/act more selfishly (i.e., give less money to the common project) (Archetti & Scheuring, 2012).

For the present experiment, we employed a version of the PGG used in previous work to study the effects of time-pressure or time-delay on cooperation (Bouwmeester et al., 2017b; Rand et al., 2012), which was delivered using the online Qualtrics program (Qualtrics, Provo, UT), with all instructions presented on screen. Participants were first told that they would be playing a decision-making game with three other randomly assigned members of the study (in actuality, the computer program). It was then explained that the amount of money they earned from the game would depend on their

own decisions and the decisions of the other members of the group. Prior to playing, each participant was given a $4 (400 cent) endowment and was provided with examples of potential outcomes of the game.

Participants were then randomly assigned to the time-pressure condition or the forced-delay condition. Instructions were identical to those from (Bouwmeester et al., 2017b), with added bold capitalization to ensure saliency. In the time-pressure condition, participants' screens read "You must **MAKE YOUR DECISION IN LESS THAN 10 SECONDS!**" In the forced-delay condition, participants' screens read "Please carefully consider your decision. You must **WAIT AND THINK FOR AT LEAST 10 SECONDS BEFORE MAKING YOUR DECISION!"** Consistent with Bouwmeester et al. (2017b), a timer was shown on screen so that participants were aware of a) the time left to make a decision in the time-pressure condition (i.e., a timer counting down from 10), or b) the time left to wait before making a decision in the forced-delay condition (i.e., a timer counting up from 10). Participants selected their contribution amounts using an on screen slider ranging from 0 cents to 400 cents, with the slider starting in the middle position (no value was marked for the middle position). The program recorded each participant's contribution amount and the time at which they submitted their contribution. After participants made their decision, the results of their game were presented, including their own actual contribution amount, and the fictitious contributions of the ostensible other three group members.

2.2.6. Saliva collection and pharmacokinetic manipulation check

In addition to the pharmacokinetic study described above, we further verified that the administration procedure boosted participants' testosterone concentrations via collection of saliva samples at baseline (pre-hormone administration), and at the end of the study (80 mins post-administration). Saliva was collected via passive drool into a 5 ml polystyrene tube, and was subsequently frozen at -20 °C. Samples were later thawed and centrifuged, followed by extraction of the supernatant. Samples were assayed in duplicate using commercially available enzyme immunoassay kits from DRG International (Coefficients of variation: intra-assay = 8.45%; inter-assay = 12.46%).

2.2.7. Analytic approach

With censored data, as commonly found in PGG investigations, ordinary least squares regression approaches can be unduly influenced by a greater number of scores in the tail(s) of the distribution. To address this potential issue, and consistent with prior work examining the effects of time-pressure and delay in a one-shot PGG paradigm (Rand et al., 2012), main analyses of interest were conducted using a Tobit regression approach with robust standard errors, which allows for estimation of scores beyond the maximum response option available (i.e., 400 cents) while simultaneously accounting for potential heteroskedasticity in the residuals. Tobit regressions were conducted using the *survival* package for R (version 2.38; R Core Team, 2016; Therneau, 2015). We note, however, that using a simple linear regression approach yielded similar results.

The risk score variable was first standardized, allowing the unstandardized regression coefficients to represent the extent of change in cooperation (PGG contribution) for a one standard deviation increase in Risk Factor score. [For additional analyses presented with individual moderators (i.e., self-control, self-construal, and dominance), the same approach was used, where the unstandardized regression coefficient represented the change in PGG contributions for one standard deviation increase in the moderator. Individual moderator analyses are presented in Appendix A.] The Drug variable was similarly centered at zero, but with a one-unit distance between the testosterone and placebo conditions; thus, the unstandardized regression coefficients for Drug represent the difference in PGG contributions between those who received testosterone versus those who received placebo. Follow-up conditional effects or simple slope analyses, where indicated, were conducted at relatively low (-1 SD) and relatively high (+1 SD) levels of Risk Factor. In line with a recent multi-lab replication attempt (Bouwmeester et al., 2017b) of Rand et al.'s original work (2012), we present both intent-to-treat analyses, which involve all participants, regardless of whether they followed the time condition instructions, as well as compliant-only analyses, which involve only participants who correctly followed the instructions for their respective time condition (i.e., if in the time-pressure condition, made their contribution in less than 10 seconds; if in the forced-delay condition, waited at least 10 seconds before making their contribution).

2.3. Results

2.3.1. Testosterone manipulation check

Analysis of salivary testosterone confirmed that the manipulation was effective (t_{397} = 6.17, p < .001, Cohen's d = 0.62 for the difference in concentrations between placebo and testosterone groups following administration, measured at the end of the study), and as expected, the groups did not differ prior to administration (t_{395} = 0.25, p = .80, Cohen's d = 0.03). Further, participants were no better than chance (p = .32) at guessing the drug condition to which they were assigned (testosterone or placebo; guess correct = 47.4% of sample), suggesting they were not consciously aware of which substance they had received.

2.3.2. Effects of drug, time condition, and risk factor

Intent to treat

An intent-to-treat analysis examining the effects of Drug (testosterone or placebo), Time Condition (time-pressure or forced delay), Risk Factor (individual difference variable), and their interactions, revealed no main effects of Drug (b = -18.91, p = 0.48), or Risk Factor (b = -33.17, p = 0.22). The Time Condition effect was in the predicted direction of the social heuristic hypothesis (4), but not statistically significant (time-pressure contributions > forced-delay contributions, b = -33.17, p = 0.22). No significant two-way interactions were identified for Drug x Time Condition (b = -6.33, p = 0.91), Drug x Risk Factor (b = -18.18, p = 0.49), or Time Condition x Risk Factor (b = 24.57, p = 0.35). Notably, there was a significant Drug x Time Condition x Risk Factor interaction (b = -191.88, p < .001, see Figure 2.2). Follow-up analyses revealed that the Drug x Time Condition interaction was significant for men with relatively high risk factor scores (b = -198.20, p = .007), and for men with relatively low risk factor scores (b = 185.549, p = .017). Among men high in risk, testosterone decreased PGG contributions in the forced delay condition (b = -136.19, p = .007), but did not affect contributions in the time-pressure condition (b = 62.01, p = 0.24). Among men low in risk, however, there were no significant drug effects in either the forced delay (b = 92.04, p = .09) or the time-pressure condition (b = -93.51, p = .09). [Conducting the same analyses while controlling for participants' performance on the Point Subtraction Aggression Paradigm (Geniole et

al., 2019) performed earlier in the protocol left the findings unchanged, as did controlling for whether participants believed they had received testosterone or placebo, or for session testing time (See Supplementary Materials).] Additional post-hoc contrasts revealed that among men high in risk who received placebo, contributions were significantly lower in the time-pressure condition than the forced delay condition (b = 189.60, p = .016), whereas among men high in risk who received testosterone, contributions were significantly lower in the forced delay condition than in the time-pressure condition (b = -206.81, p = .015). Among low risk men receiving placebo, contributions were significantly higher in the time-pressure condition than the forced delay condition (b = -243.286, p = .007), but among low risk men receiving testosterone, this effect was abolished (b = 127.81, p = .13).

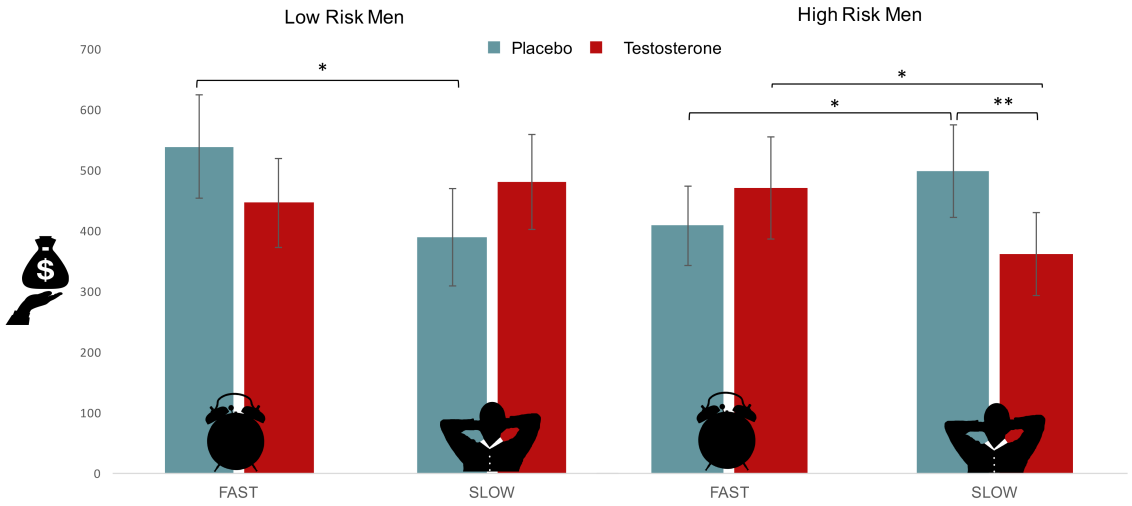

Figure 2.2. Effect of drug (testosterone versus placebo) on contributions in the public goods game (PGG) as a function of time condition (forced intuition = FAST; forced reflection = SLOW) and risk factor score (total N = 400; placebo = 201 [fast = 100, slow = 101], testosterone = 199 [fast = 99, slow = 100]). The Y-axis represents the Tobit model predicted PGG contribution values (note that Tobit estimates a latent variable beyond the maximum 400 cents, allowing a more reliable estimate). Error bars represent the 95% confidence intervals. For men high in risk (+1 SD), testosterone significantly decreased contributions in the forced reflection (SLOW) condition (p = 0.007) but not the time-pressure (FAST) condition (p = 0.24). For men low in risk (−1 SD), the effect of testosterone did not differ between the time-pressure condition and the forced reflection condition. Additional contrasts showed that high risk men receiving testosterone contributed significantly less in the forced reflection condition than the time-pressure condition (p = 0.015), whereas high risk men receiving placebo contributed significantly less in the time-pressure condition than the forced reflection condition (p = 0.016). For low risk men receiving placebo, contributions were significantly higher in the time-pressure condition than the forced reflection condition (b = −243.286, p = 0.007), but this difference was abolished by testosterone (b = 127.81, p = 0.13)

Compliant only

When we conducted the same analyses above but restricted our sample to men who followed the timing instructions (n = 282, 70.5% of the full sample) we found no main effect of Drug (b = -40.98, p = 0.21) or Risk Factor (b = -16.59, p = .29), but a significant main effect of Time Condition (time-pressure contributions > forced delay contributions; b = -172.41, p < .001). No significant two-way interaction effects were noted (|bs| = 7.01 – 50.51, ps = .19 – .82). Consistent with the intent-to-treat analysis, the Drug x Time Condition x Risk Factor interaction was significant (b = -213.08, p <

.001). Follow-up analyses again showed that among men with relatively high risk factor scores, the Drug x Time Condition interaction was significant (b = -263.59, p = .002), such that testosterone decreased contributions in the forced-delay condition (b = -165.76, p = .003) but did not differ from placebo in the time-pressure condition (b = 97.83, p = 0.14). Among men with relatively low risk factor scores, the Drug x Time Condition interaction did not reach statistical significance (b = 162.57, p = .09). [Given arguments that differences in the effect of cooperation between intent-to-treat analyses and compliant-only analyses may be due to selection biases (e.g., compliant individuals may have more of a particular trait; Bouwmeester et al., 2017b), we tested whether there were differences in individual dispositional qualities between those who followed instructions (compliant) and those who did not (non-compliant). No differences were found between the groups for self-construal (t (398) = -0.72, p = .47), dominance (t (398) = -0.35, p = .72), self-control (t (398) = 0.34, p = .73), or risk factor score (t (398) = -0.73, p = .47). See Appendix A for descriptive statistics and bivariate correlations.] Additional post-hoc contrasts revealed that among men high in risk who received placebo, there was no difference in contributions between the time-pressure condition and the forced delay condition (b = 119.17, p = .19), whereas among high risk men receiving testosterone, contributions were significantly lower in the forced delay condition than in the time-pressure condition (b = -385.99, p < .001). Among low risk men receiving placebo, contributions were significantly higher in the time-pressure condition than the forced delay condition (b = -371.72, p < .001), but—as with the intent-to-treat analysis—among low risk men receiving testosterone, this effect was abolished (b = -53.88, p = .59).

2.4. Discussion

Using placebo-controlled administration of exogenous testosterone in a relatively large sample of healthy young men, we have examined several novel aspects of the expression of cooperative behaviours, and specifically: if and how men's cooperation is influenced by exogenous testosterone in a time-pressure or time-delayed one-shot PGG, and if the effects of testosterone on men's cooperation in this context vary with individual differences in specific dispositional qualities (dominance, self-control, and self-construal). Findings revealed that 1) within the placebo group, time-pressure increased cooperation among low risk men, but decreased cooperation among high risk men; 2)

testosterone moderated this pattern by abolishing the time-pressure effect among low risk men, and—in high risk men—reversing the effect by selectively reducing offers under forced delay. The cooperation-reducing effects of testosterone after a forced-delay were robust to whether we analyzed all participants, or restricted analyses to only those who complied.

It has been argued that deliberation serves to override cooperative intuitions, thus facilitating the adjustment of behaviour toward the optimum for a given situation—which, in a one-shot encounter, would be to act selfishly (Bear & Rand, 2016; Rand et al., 2014). The results here do not support the idea that time-pressure alone can induce cooperative efforts, but are instead consistent with the idea that individual differences in disposition are important, and that testosterone can play a role in promoting behaviour that is more immediately advantageous to the individual, particularly for men with high dominance, low self-control, and independent self-construals. That the effects of testosterone on cooperation depended on these personality variables contributes to an emerging literature suggesting that the effects of testosterone in various social-behavioural domains (e.g., aggression, competitive decision-making, risk-taking; Carré et al., 2017; Geniole et al., 2019; Mehta et al., 2015; Welker et al., 2017, 2019) vary as a function of one's dispositional qualities.

Importantly, our results are consistent with a value-based decision-making framework suggesting that prosocial behaviour may not be intuitive for everyone. Wills et al. (2018) found that prosocial participants were intuitive cooperators, whereas more selfish participants were deliberative cooperators. Our findings reflect this idea: among men low in risk for antisocial behaviour, priming intuition was associated with more prosocial contributions than deliberation; among men high in risk for antisocial behaviour, however, priming deliberation was associated with higher contributions than intuition. Thus, our results suggest that individuals with low risk profiles may be intuitive cooperators, whereas individuals with high risk profiles may be deliberative cooperators, and that testosterone shifts these relationships such that intuitive cooperation among low risk men is abolished by testosterone, and deliberative cooperation among high risk men is reversed to deliberative defection.

Testosterone is argued to facilitate life history trade-offs, including survival versus reproduction, and mating versus parenting effort (Del Giudice et al., 2016; Hau &

Wingfield, 2011). In line with this idea, testosterone fluctuates rapidly in response to evolutionarily-salient stimuli, such as competitive wins or losses (Carré & Olmstead, 2015; Geniole et al., 2017), and interactions with potential mates (Roney et al., 2007); these fluctuations, in turn, map onto future behaviour in the same life history domains (see Zilioli & Bird, 2017 for review). Transcending these domains is testosterone's role in promoting the striving for, and maintenance of, status. It is possible that status concerns involve thoughts about the potential outcomes of the interaction, such as whether or not someone will exploit the contributor(s) (Boksem et al., 2013). Although speculative, testosterone may have reduced contributions in high-risk men as a means of protection against such exploitation and its potential negative consequences on status/dominance. Notably, this status-protection strategy may only be favored in the context of a one-shot, anonymous PGG, as was used here. In situations with repeated interactions with the same individual(s), or where the decisions are not anonymous (and reputational information can spread), there would be additional incentive to maintain a good reputation and contribute, despite concerns about exploitation. Indeed, individuals known by the group to contribute more (vs. less) are more respected and ascribed higher status within the group (e.g., Hardy & Van Vugt, 2006), and including a reputational component to repeated social dilemma games encourages cooperation (McIntosh et al., 2013; Pfeiffer et al., 2012). Therefore, when reputational information can spread, the beneficial effects of contributing may outweigh the negative effects of being exploited. This remains one hypothesis, which will require a direct test in future work. Other possibilities exist, and studies may want to compare them against the idea of reputational concerns. For example, it is possible that in the forced-delay condition, and without any prior information of the other players' contribution styles, high risk men on testosterone may have become less trustworthy of the other players, thus influencing contributions. [Trust may, however, be part of a more complex pathway to reduced contributions, where testosterone leads to reduced trust, leading to exploitation concerns, and thus reduced contributions.] Some work has found that changes in men's testosterone can reduce trust in emotionally neutral faces (Carré et al., 2014) (but see Bird et al., 2017) , and among women, can reduce trust in game partners (Boksem et al., 2013), suggesting this possibility here. The exact mechanisms by which testosterone, personality, and reflection interact to predict changes in cooperative behaviour in anonymous encounters will require future work, and may be strengthened by a contrast with a repeated trial PGG.

Testosterone's effects may also change depending on whether someone is directly watching the encounter, and particularly someone relevant to mating (e.g., an attractive member of the opposite sex). Evidence indicates that men's cooperation can indeed be modulated by observer status: contributions are higher in the presence of an attractive female, and also correspond to the degree to which men find the female observer attractive, arguably because of reputational status concerns that may influence mating opportunities (Van Vugt & Iredale, 2013). If testosterone promotes mating effort and status-seeking behaviours, the presence of a potential mate might dictate that a rise in testosterone from exogenous administration would exaggerate effects normally seen from observer status alone. Further, such effects might be particularly strong among men who have dispositions oriented towards status in the first place (e.g., highly dominant). Future research will be important for answering this question.

Given recent debates about the existence of intuitive cooperation effects (Bouwmeester et al., 2017b; Rand, 2016b, 2017; Rand et al., 2012, 2013, 2014; Tinghög et al., 2013; Verkoeijen & Bouwmeester, 2014), the present experiment allowed a further test of the social heuristic hypothesis. With an intent-to-treat approach, there was no main effect of time condition, although the effect was in the predicted direction (time-pressure contributions > forced-delay contributions). However, when restricting analyses to those who followed the instructions, contributions were significantly higher under time pressure than delay. Notably, the presence of a time-pressure effect for compliant-only individuals is consistent both with Rand et al.'s original work (2012) and a recent multi-lab replication (Bouwmeester et al., 2017b). Rand et al. (2012) found that when examining individuals who followed the instructions, time-pressure predicted increased cooperation relative to forced delay. Bouwmeester et al. (2017b) also found this same effect, but showed that the effect disappeared in the intent-to-treat analysis. Bouwmeester et al. had relatively low rates of compliance with the instructions for the time-pressure condition (34.1%), which Rand (2017) notes leaves the possibility that a causal effect of time-pressure on cooperation still exists. The present experiment had considerably higher rates of compliance in the time-pressure condition (80.9%), but still failed to find a time-pressure effect in the intent-to-treat analysis. It has been argued that intent-to-treat analyses may introduce biases by selecting for individuals who are cooperative in the first place (Bouwmeester et al., 2017b), but here we found no differences in personality between compliant and non-compliant individuals (see also

Rand, 2017). Further, our interactive effects of testosterone and dispositional risk in the forced delay condition were robust to whether participants were compliant with timing instructions, allowing greater confidence in the effect. Nevertheless, we also provide evidence to support a value-based framework, such that cooperative strategies differ based on individual differences in personality risk, and thus suggests that previous inconsistencies in support for the social heuristic hypothesis may be a function of failing to consider specific dispositional characteristics of participants.

Limitations and future directions

The present experiment focused exclusively on men. While this sex-specific focus may be considered a strength among a greater number of testosterone administration studies examining women, the question remains as to how the effects presented here might generalize to women. To date, the testosterone literature for women shows results that might be considered contradictory (e.g., increased cooperation following testosterone administration; Eisenegger et al., 2010b) (although see Boksem et al., 2013), but it is not clear whether differences for studies with women might be influenced by the supraphysiological levels of testosterone that are typically reached in the samples, differences in one shot paradigms versus those involving multiple encounters with the same individual, differences in participant beliefs about the effects of testosterone (e.g., Eisenegger et al., 2010b), or some other variable. Future research examining men and women in the same study, where allowed by regulatory jurisdictions, would be beneficial for disentangling any potential sex differences.

Mental health screening was conducted via phone in the initial phone interview process, and as per our exclusionary criteria, any individual who self-reported a developmental disability or psychological disorder was not eligible for the study. A limitation to this approach is that we could not independently verify diagnoses (e.g., via formal clinical diagnostic interview, review of medical records). Future studies could include more formal assessment of mental health disorders to increase the likelihood of accurate detection.

The majority of previous work has conducted behavioural testing approximately 4 hours post administration in women (Bos et al., 2012; Zilioli & Bird, 2017) following a study showing that the effects of sublingual testosterone administration on women's

vaginal pulse amplitude in response to sexual stimuli emerged at 4 hours post administration (Tuiten et al., 2000). However, previous work from our lab examining men has found that a single administration of testosterone can increase threat-related amygdala, hypothalamic, and periaqueductal gray reactivity to angry facial expressions within 90 mins post administration (Goetz et al., 2014), and effects of testosterone on aggressive behaviour are found within 60 mins post administration (Carré et al., 2017). We also find similar behavioural effects from exogenous testosterone administration on men's preferences for feminine faces when tested at 2 hours and 3 hours post administration (Bird et al., 2016), as well as effects on self-perceived dominance tested at 2 hours and 4 hours post administration (Welling et al., 2016). That effects in the present experiment are found within 60 mins suggests the possibility of a non-genomic mechanism, similar to findings in animal models with rapid effects of testosterone on brain function and behaviour (reviewed in Foradori et al., 2008). The possibility exists that the effects of testosterone and personality on cooperation would be found at even earlier time points (e.g., 15–30 mins post administration), as we found a significant increase in testosterone within 15 mins of administration. Future work may want to examine this possibility.

Our hypotheses were partially informed by the idea that testosterone can promote impulsive behaviour, such as reactive aggression. While testosterone did seem to increase cooperation in the time-pressure condition for high risk men, it did not reach statistical significance. It is possible that cooperation as an impulsive/intuitive behaviour is different than impulsive aggression following provocation. Given that testosterone is strongly implicated in social dominance behaviours, and reflexive dominance behaviours are often triggered by direct social threats (reviewed in Terburg & van Honk, 2013), testosterone may simply not function in the same manner in the context of having to make a cooperative decision under time-pressure as it does when an individual is directly provoked. A further distinction may be made between the one-shot PGG and paradigms typically used to examine aggressive responses. In the one-shot PGG, participants interact with "other participants" on one occasion only, and thus there is no risk for retaliation and/or social sanctions. In aggression paradigms like the PSAP, however, interactions with other participants are longer and dynamic, with many opportunities for retaliation throughout the task. Dreher et al. (2016) found that testosterone increased both prosocial and antisocial status-enhancing behaviours in

human men, but notably, their experiment involved repeated ultimatum games, where testosterone increased prosocial behaviour only following the receipt of large offers from their game partner. Therefore, in a one-shot PGG, testosterone may not predict impulsive prosociality, but may in a context of available information about game partners. It may be useful for future studies to employ exogenous testosterone administration in the context of a repeated PGG with time-pressure and forced-delay manipulations to allow a test of this hypothesis.

Chapter 3. Experiment 2: Effects of Exogenous Testosterone on Public Goods Contributions Depend on Personality and Observer Characteristics

3.1. Introduction

Social dilemmas are characterized by a tension between individual versus group benefit (Rand & Nowak, 2013). Humans show considerable variability in prosocial (i.e., cooperative, or group-benefitting) versus antisocial (i.e., selfish, or individual-benefitting) behaviour, suggesting the existence of important contributory factors to flexible decision-making. Research efforts have aimed to elucidate, for example, the relative contributions of cognition (e.g., intuitive versus deliberative choice; Rand, 2016a), personality (Thielmann et al., 2020), and the presence of observers (Bradley et al., 2018), to prosocial decisions. Much less is known, however, about whether certain biological factors, like hormones, can independently—or synergistically with important contextual and dispositional variables—contribute to prosocial versus antisocial behaviour. Recent insights from behavioural endocrinology have opened this possibility, finding that following deliberation, testosterone (versus placebo) reduces prosocial behaviour, with strongest effects among men who are at relatively high dispositional risk for testosterone-induced antisocial behaviour (Bird et al., 2019).

3.1.1. Testosterone, antisociality, and prosociality

Inspired by early non-human animal work, testosterone has often been studied in the context of competitive and antisocial behaviours, such as aggression. Yet, meta-analytic evidence for a link between basal testosterone and human aggression suggests a weak relationship that is specific to men (Geniole et al., 2020), showing somewhat stronger—but variable—effects for contextually-influenced rapid changes in testosterone. Moving beyond the earlier simple view that testosterone drives predominantly aggressive, anti-social human behaviour, more recent theoretical perspectives instead propose that testosterone fluctuates rapidly in evolutionarily-relevant contexts (e.g., competition, presence of mates), ultimately promoting behaviours that can directly or indirectly enhance reproductive fitness (Geniole & Carré, 2018; Zilioli & Bird, 2017). From this perspective, rapid changes in testosterone may

promote either prosocial or antisocial behaviours, depending on the possible fitness-related consequences, such as the relative risk or benefit to one's social status or mating opportunities. Consistent with this view, past research has found that testosterone can differentially promote antisocial or prosocial status-enhancing behaviours, depending on whether participants are provoked or rewarded, respectively (Dreher et al., 2016). Other work has found that the presence of an attractive female (but not male) can lead to increased testosterone concentrations and subsequent physical risk-taking, possibly because such behaviour may advertise desirable qualities (e.g., health, vigor) to prospective mates (Ronay & Hippel, 2010).

3.1.2. Onlookers, mating, and cooperation

In certain contexts, prosocial behaviour may also serve as a sexual display strategy. For instance, in a public goods experiment, Van Hugt and Iredale (2013) found that men made more prosocial economic decisions when observed by an audience of women versus men. Further, prosocial contributions were positively related to men's ratings of female observer attractiveness, similar to Raihani and Smith (2015), who found that males donated more to a fundraiser when the individual collecting funds was an attractive female. Other work showed that among single men, awareness that a woman was part of the game similarly led men to make more prosocial economic contributions (Tognetti et al., 2016). Such findings are complemented by other work confirming that women find prosocial qualities to be attractive in a partner (Barclay, 2010; Farrelly, 2011; Margana et al., 2019), and that altruistic men enjoy more mating success (Arnocky et al., 2017). Considered together, researchers have argued that sexual selection pressures in the ancestral environment—wherein prosocial behaviour may have functioned as a courtship display by signalling desirable mate qualities (Barclay, 2016; Gintis et al., 2001; Maestripieri et al., 2017)—predisposed men to compete for mates via prosocial public goods decisions (also referred to as 'competitive helping').

To the extent that prosociality serves as a mating signal, and that a rapid increase in testosterone functions to flexibly promote behaviours that can increase reproductive fitness, it stands to reason that a rapid increase in testosterone may further enhance men's prosociality when mating cues are more salient (e.g., a woman is watching). Recent work has found that testosterone can enhance prosocial decisions in

the presence of a male observer (Wu et al., 2020) and, among men high in personality risk for testosterone-induced antisocial behaviour (i.e., individuals high in trait dominance, low in self-control, and with independent self-construals) can reduce prosocial decisions when there is no observer (Bird et al., 2019). It remains unknown, however, if and how a rapid increase in testosterone differentially affects men's prosocial decisions in the presence of a female, relative to a male or no observer at all, and whether the characteristics of the observer—particularly attractiveness (cf. Margana et al., 2019, for relevance in female mate choice)—modulate these effects (see Carré & Robinson, 2020 for a review of testosterone administration studies).

3.1.3. The present experiment

The present experiment was designed to replicate and extend previous findings (Bird et al., 2019) by examining the effects of exogenous testosterone on men's prosocial decisions under varied observational conditions[3]. Consistent with Bird et al. (2019), it was predicted that a rapid increase in testosterone via single-dose administration would reduce public goods contributions in the no observer condition, but only to the extent that individuals were relatively high in a personality risk factor for testosterone-induced antisocial behaviour (see also Carré et al., 2017; Geniole et al., 2019; Welker et al., 2017 for relevant personality moderation of testosterone effects). Given that most of the behavioural actions of T are directly or indirectly involved in reproduction, it was predicted that the effects of testosterone in the observer conditions would depend on the sex of the observer, such that augmented testosterone would increase prosocial contributions when a female was watching relative to when a male was watching. To the extent that a mating mechanism drives such an effect, it was predicted that testosterone's effect on increased prosocial contributions under female observation would be particularly strong among single men, and men with unrestricted sociosexual orientations, given that both of these groups are have shown greater attention to mating cues over their pair-bonded or restricted counterparts (Ma et al., 2019; Maner et al., 2009; Mitrovic et al., 2018). As indicated later, additional analyses

3 Pre-registration information available at: https://osf.io/wcg6b/?view_only=f83a6901a6254277af56996299a6c277

examined whether perceived observer characteristics (e.g., attractiveness) interacted with primary study variables to predict prosocial contributions.

3.2. Methods

3.2.1. Participants

The participant sample consisted of 120 men between the ages of 18 and 38 years (M_{Age} = 22.03, SD = 3.94). Men were recruited in northern Ontario via online advertisements and from the online participant pool at Nipissing University, thus including students and members of the general public. Prospective participants were first screened via phone for eligibility; exclusionary criteria, which were determined via telephone interview, included age less than 18 or more than 40 years, belonging to a sports team where testosterone is a prohibited substance, currently prescribed or taking medications that are known to interfere with concentrations of steroid hormones, substance dependence, or diagnosis of a mental illness. The experiment procedures were approved by the University's Research Ethics Board, and the eligible participants provided informed written consent for all aspects of testing.

During the study, one participant did not complete the task on either day, three did not complete both testing sessions, three experienced computer errors on one of the days, and one participant erroneously received the same hormone treatment on both days. All available data were used, with the exception of the individual who received the same drug treatment, in which case we used the data from day one only. Thus, the final sample consisted 119 men, 7 of whom were missing data for one of the days. Given that observer-related hypotheses rested on a testosterone-induced mating mechanism, analyses involving female and male observers were conducted among self-reported heterosexual participants (n = 112) and, in the case of examining relationship status and sociosexual orientation, those who were heterosexual and did not change their relationship status between days of testing (n = 105).

3.2.2. Procedure and materials

The experiment employed a double blind, placebo-controlled, within-subject crossover design whereby participants received 11 mg of intranasal testosterone

(Natesto^{TM}) or placebo on alternating days, with a two-week washout period between testing sessions (see Geniole et al., 2019; Luberti et al., 2021 for pharmacokinetics). Participants were tested in individual testing rooms between 9:30AM and 5:30PM. On the first testing day, participants provided informed consent, and then completed demographic and self-report questionnaires. Next, they provided a saliva sample to establish variability in baseline testosterone concentrations, and then provided a mouthwash sample to be used for a future DNA study. Next, under the supervision of a research assistant, participants self-administered the testosterone (or placebo), followed by a 30 minute wait to allow for drug uptake, and the completion of psychometric tasks unrelated to the present study. At 60 minutes post-administration, participants then completed the cooperation task for the current experiment, consisting of a one-shot public goods game; this experimental timeline is thus consistent with the post-administration timing of Bird et al. (2019). After completion of all behavioural testing, participants provided a final saliva sample. After testing on their second day, participants were asked to guess on which day they believed they had received testosterone. Participant guesses were no better than chance accuracy (49.5% correct; t_{112} = .094, p = .926), indicating that there were no consciously detectable effects of testosterone.

3.2.3. Personality questionnaires and creation of the risk score

The personality risk score represents a composite of dominance, self-control, and self-construal—traits that have been shown to critically moderate testosterone-behaviour relationships (Carré et al., 2009, 2017; Knight et al., 2017; Slatcher et al., 2011; Welker et al., 2017, 2019). The risk score was derived using a previously-established method (Bird et al., 2019; Geniole et al., 2019) by first deriving scores on each measure individually. Dominance scores were indexed as an average of the standardized responses to the International Personality Item Pool-Dominance (Goldberg et al., 2006) and the dominance subscale of the Dominance-Prestige Scale (Cheng et al., 2013). Self-control scores were indexed as an average of the standardized responses to the Barratt Impulsivity Scale (reverse scored; Patton et al., 1995) and the Brief Self-Control Scale (Tangney et al., 2004), which is subsequently reverse scored to allow for appropriate averaging with the other measures. Self-construal was derived from the 24-item Self-Construal Scale (Singelis, 1994) by subtracting the twelve items on the interdependent subscale from twelve items on the independent subscale. The

individually-derived scores were then standardized (i.e., z-scored) and averaged to create the personality risk score, with higher scores indicating greater risk for testosterone-induced antisocial behaviour.

3.2.4. Hormone administration, saliva collection, and pharmacokinetic manipulation check

On the day in which men were randomized to receive testosterone, they were given two syringes of Natesto, each containing 5.5mg of gel (11mg total). For placebo day, men were given two syringes of an equivalent amount of the gel vehicle with similar physical properties (i.e., viscosity, color). Under the supervision of a research assistant, participants applied the testosterone or placebo gel from one syringe to the lateral inner surface of each nostril, and then compressed the nostrils toward the septum to achieve even gel spread. Before testing commenced, computer components that the participant would touch were covered with a protective sheet in order to avoid contamination between participants. Additionally, after participants had applied the testosterone or placebo, they were instructed to immediately and thoroughly wash their hands prior to touching the computer. At the conclusion of each testing session, potentially contaminated surfaces were wiped with a 70% alcohol cleaning solution.

In order to confirm the hormonal manipulation, salivary hormone samples were collected at baseline (prior to hormone administration) and after behavioural testing was complete. For each sample, participants chewed on salivette swabs (DRG International) for approximately 30 seconds until saturated, and the samples were subsequently stored at -20 °C. For hormonal assay, samples were thawed and centrifuged, followed by extraction of the supernatant. Assays were run in duplicate using commercially available enzyme immunoassay kits from DRG International (Coefficients of variation: intra-assay = 9.34%; inter-assay = 6.87%). A mixed ANOVA (within-subject factors: time [pre vs. post]; drug [placebo vs. testosterone]; between-subject factor: drug order [testosterone day 1 vs. placebo day 1]) revealed a significant time by drug interaction ($F_{1, 113} = 10.793$, $p = .001$, $n^2_p = .087$). As expected, testosterone concentrations significantly differed at post-administration ($t_{114} = 3.340$, $p = .001$, $dz = .311$) but not pre-administration ($t_{114} = 1.173$, $p = .243$, $dz = .109$), confirming that the drug manipulation was successful.

3.2.5. Public goods game

The public goods game (PGG) is a widely-used behavioural economic paradigm for measuring prosocial (cooperative and group-oriented) versus antisocial ("selfish" and individual-oriented) decision-making. Participants are given a starting endowment of $4 (400 cents) and tasked with determining how much to give to a common project with three other ostensible players, and how much to keep for themselves. Participants are told that the amount contributed to the common project is tripled, and then split evenly among the other group members. Consequently, every $1 that a participant contributes to the common project will benefit other members, but results in a personal return that is less than $1. Thus, there exists tension between the strategy that maximizes individual benefit (contributing 0 cents) and the strategy that maximizes group benefit (contributing the full 400 cents).

All participants in the present experiment completed a forced reflection one-shot public goods game (Bird et al., 2019). Prior to making their decision about how much to contribute to the common project, participants were told to wait at least 10 seconds and to carefully consider their decision (i.e., forced delay condition)[4]. Participants played three iterations of the one-shot public goods game, corresponding to no observer (i.e., neutral condition), female observer, and male observer. In order to replicate Bird et al. (2019), which did not employ observer conditions, the neutral (no observer) condition was always presented to participants first. The order of female observer and male observer conditions was then randomized across participants.

Observer conditions

For the observer conditions, two male and two female actors recorded short video clips (~5 seconds) and provided photographs of themselves. In the short video clips, shown to participants before they made their contribution in the observer conditions, the actors behaved as if the video was a live feed where they could see the participant; a few seconds into the video, they also performed a hand wave (as if they were waving at participants) to enhance believability. Note that two male and two female

4 Findings from Bird et al. (2019) indicated that the interactive effects of testosterone and personality were most robust in the forced reflection condition (versus a time-pressure condition). To maximize power and allow for a test of replication in the neutral (no observer condition), we exclusively employed the forced reflection condition for the present experiment.

actors were used so that there were different observers for a participant's first and second testing day (randomized across participants). After watching the first video, participants completed their first observer PGG round (female watching or male watching), during which they saw the exact same screen as the neutral (no spectator) condition, except with the photograph of the spectator in the top corner of the screen to further reinforce the idea, and remind participants, that they were being watched. After the first observer PGG round was complete, participants were then shown the second actor video (which was of the opposite sex to the first observer condition). After completing the neutral round and the two observer rounds of the PGG, participants were asked to rate the extent to which they found the female and male observers to be attractive, dominant, and kind (Likert scale; 1 = not at all; to 7 = very much so)[5], and if the participant knew the female/male watching them (1 = no, 2 = s/he looks familiar, 3 = s/he is definitely familiar, 4 = I have seen her/him many times before and we have spoken, 5 = I know this person well).

3.2.6. Analytic approach

Given the nature of the models, which include a continuous moderator of repeated measures effects, and the limitations of modelling such interactions using ANOVAs/robust ANOVAs in common statistical software, we deviated from the pre-registered ANOVA-based plan, instead conducting analyses using robustly-fit mixed level models (Koller, 2016) in R/R-Studio software (R Core Team, 2021; RStudio Team, 2021). In addition to greater software and model compatibility, this recommended approach also allowed for more powerful hypothesis tests and less biased estimates (Brown, 2021; Kristensen & Hansen, 2004). The maximal random-effects structures were specified and trimmed until convergence (Barr et al., 2013), and significance was determined using Satterthwaite approximations for degrees of freedom (Luke, 2017). Given the computational load for some mixed effects models, and the limited number of repeated measurements for a given variable, random intercept only models were conducted when necessary to avoid singular fit issues or non-convergence. Categorical predictors (drug, observer condition, relationship status) were centred using a between group distance of one unit, with the respective regression coefficients thus representing

5 See Appendix B for examination of dominance and kindness, which are not central to the hypotheses from the present experiment.

group differences in PGG contributions. Consistent with the participants' personality risk factor scores, the sociosexuality scores and ratings of observer attractiveness were standardized (i.e., z-scored), with the respective regression coefficients representing the extent of change in PGG contributions for a one standard deviation increase in the corresponding variable. Where indicated, conditional effects analyses were conducted at relatively low (-1 SD) or high (+1 SD) levels for continuous moderators.

3.3. Results

An initial check for order effects (placebo then testosterone vs. testosterone then placebo) was conducted in a model with drug, drug order, risk factor, observer condition, and their interactions. Results did not reveal any higher order interactions involving drug order (*p*s 0.457 – 0.984), suggesting that PGG contributions were not dependent on the order in which individuals received testosterone or placebo. Drug order was thus dropped from subsequent analyses.

3.3.1. Attempted replication: effects of drug and risk factor in the neutral condition

Examining the effects of drug and risk factor for the neutral condition revealed a non-significant main effect of drug (b = -2.90, SE = 1.65, p = .082). A significant main effect for the risk factor was found (b = -15.92, SE = 5.78, p = .007), but was qualified with a drug x risk interaction (b = -3.16, SE = 1.63, p = .056). Conditional analysis revealed a pattern consistent with the hypothesized effect, such that testosterone reduced PGG contributions among men high (+1 SD) in the risk factor score (b = -6.05, SE = 2.34, p = .010), but not men low (-1 SD) in the risk factor score (b = 0.26, SE = 2.31, p = .910). (see Figure 3.1).

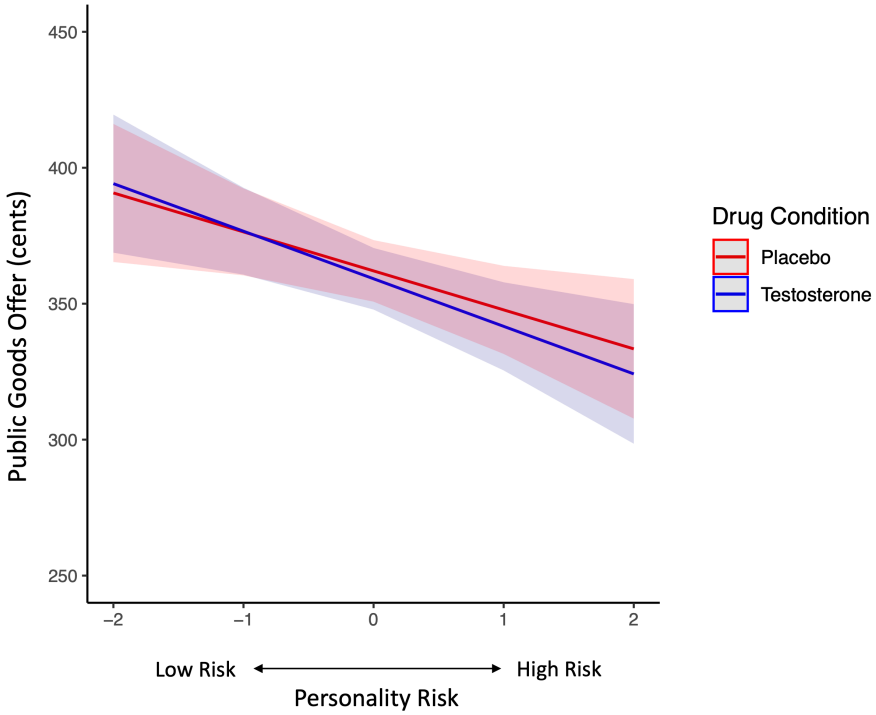

Figure 3.1. Effects of drug and risk factor for the neutral (no observer) condition.

3.3.2. Effects of drug, risk factor, and observer conditions (female observer, male observer)

When examining the effects of drug, risk factor, and observer condition (female observer, male observer), there was no three-way interaction. Rather, and consistent with the neutral condition, a significant two-way interaction between drug and risk factor was observed (b = -2.62, SE = 0.98, p = .008). Conditional analysis again revealed that testosterone reduced public good contributions among men high (+1 SD) in the risk factor score (b = -6.05, SE = 1.45, p < .001), but not men low (-1 SD) in the risk factor score (b = -0.81, SE = 1.35, p = .55), regardless of whether a male observer or female observer was watching them (see Figure 3.2). Controlling for participants' perception of observer familiarity did not meaningfully change the results.

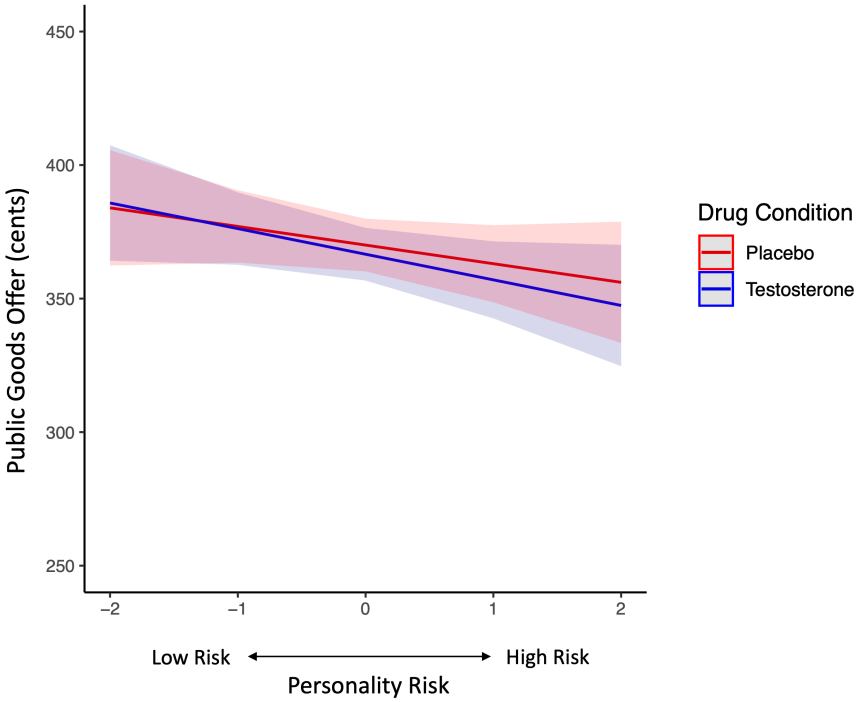

Figure 3.2. Effects of drug and risk factor for the male and female observer conditions.

When including all observer conditions in the model (no observer, female observer, male observer), PGG contributions were predicted by a drug x risk factor interaction (b = -3.30, SE = 0.98, p < .001). Conditional effects revealed that testosterone reduced public good contributions among men high (+1 SD) in the risk factor score (b = -6.77, SE = 1.44, p < .001), but not men low (-1 SD) in the risk factor score (b = -0.17, SE = 1.35, p = .90). See Table 3.1 for results of the full model.

Table 3.1. Effects of drug, risk, and condition (no observer, female observer, male observer) on PGG contributions.

Predictors (fixed effects)	*estimates*	*se*	*LLCI – ULCI*	*p*
(Intercept)	364.39	5.55	353.51 – 375.26	< .001
Drug	-3.47	1.00	-5.42 – -1.52	< .001
Risk	-9.80	5.59	-20.76 – 1.16	.083
Condition	0.47	0.60	-0.71 – 1.65	.432
Drug x Risk	-3.30	0.98	-5.22 – -1.38	< .001
Drug x Condition	-0.13	1.20	-2.49 – 2.23	.913
Risk x Condition	0.25	0.60	-0.92 – 1.43	.671
Drug x Risk x Condition	0.21	1.20	-2.14 – 2.56	.860

Conditional Effects of Drug:				
Low Risk men	-0.17	1.35	-2.82 – 2.48	.900
High Risk men	-6.77	1.44	-9.60 – -3.94	< .001

3.3.3. Secondary and Exploratory Analyses

Effects of drug, observer condition, and relationship status

Examining the effects of drug, observer condition (male observer, female observer), and relationship status (single, paired) did not reveal any significant main effects or interactions (*ps* .697 – .984). Adding risk to the model revealed significant effects for drug (b = -1.84, SE = 0.46, p <.001), drug x risk (b = -1.29, SE = 0.44, p = .004), and drug x relationship status (b = 1.97, SE = 0.92, p = .034). Decomposing the drug x relationship status interaction revealed that testosterone reduced contributions among single men (b = -2.84, SE = 0.67, p <.001) but not among paired men (b = -0.87, SE = 0.64, p = .177). See Figure 3.3.

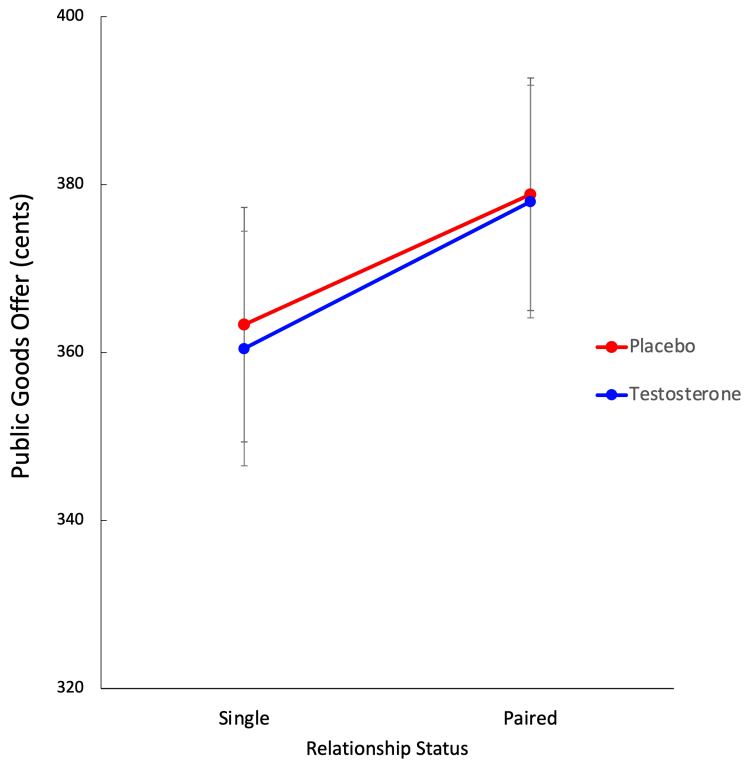

Figure 3.3. Effects of drug and relationship status for the male and female observer conditions

Effects of drug, observer condition, and participant-rated observer attractiveness

Examining the effects of drug, observer condition (male observer, female observer), and observer attractiveness revealed a significant main effect of drug (b = -0.08, SE = 0.04, p = .048). Adding risk to the model revealed a drug x observer x risk x attractiveness interaction (b = -4.01, SE = 1.96, p = .043). For the female observer condition, the effects of drug, risk, and observer attractiveness interacted such that testosterone reduced PGG contributions for high risk men, but only when the female observer was rated as relatively low—not high—in attractiveness. The PGG contributions of low risk men were not meaningfully affected by testosterone or female observer attractiveness (see Figure 3.4). For the male observer condition, there was no interaction between drug, risk, and attractiveness. See Table 3.2 for full results of both observer conditions.

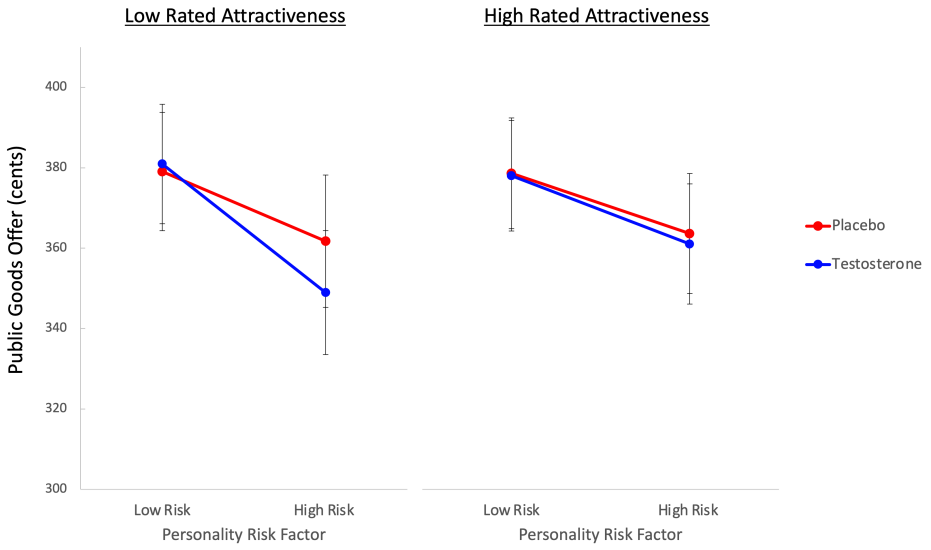

Figure 3.4. Effects of drug, risk, and participant-rated observer attractiveness for the female observer condition

Table 3.2. Effects of drug, risk, and participant-rated observer attractiveness (Att.) for the female observer and male observer conditions

Predictors (fixed effects)	*estimates*	*se*	*LLCI – ULCI*	*p*
Female Observer				

(Intercept)	368.88	5.19	358.70 – 379.06	< .001
Drug	-3.52	1.46	-6.38 – -0.65	.017
Risk	-10.15	5.15	-20.24 – -0.05	.051
Att.	1.20	0.90	-0.55 – 2.96	.180
Drug x Risk	-4.16	1.53	-7.17 – -1.16	.007
Drug x Att.	1.93	1.72	-1.44 – 5.30	.262
Risk x Att.	2.18	0.83	0.56 – 3.80	.009
Drug x Risk x Att.	3.17	1.59	0.06 – 6.27	.047
Drug x Risk at:				
Low Att.	-7.33	2.97	-13.16 – -1.50	.014
High Att.	-1.00	0.94	-2.85 – 0.85	.291
Conditional Effects of Drug:				
High Risk men, Low Att. female	-12.78	4.36	-21.33 – -4.23	.004
Low Risk men, Low Att. female	1.88	4.09	-6.14 – 9.89	.646
Male Observer				
(Intercept)	369.88	5.18	359.73 – 380.03	< .001
Drug	-1.72	1.18	-4.04 – 0.59	.146
Risk	-8.28	5.13	-18.34 – 1.78	.109
Att.	0.44	0.64	-0.82 – 1.70	.492
Drug x Risk	-1.96	1.24	-4.40 – 0.47	.115
Drug x Att.	1.01	1.12	-1.18 – 3.21	.365
Risk x Att.	0.61	0.60	-0.56 – 1.78	.306
Drug x Risk x Att.	-0.85	1.06	-2.92 – 1.23	.424

Effects of drug, observer condition, and sociosexual orientation

Examining the effects of drug, observer condition (male observer, female observer), and sociosexual orientation revealed a significant main effect of drug (b = -2.17, SE = 0.61, p < .001), which was qualified by a drug x sociosexual orientation interaction (b = -3.16, SE = 0.63, p < .001). Decomposing the interaction revealed that testosterone significantly reduced contributions among men with relatively unrestricted sociosexual orientations (b = -5.34, SE = 0.89, p < .001) but not men with relatively restricted sociosexual orientations (b = 0.99, SE = 0.83, p = .236). Results showed a similar drug x sociosexual orientation interaction when separately examining the female observer (b = -6.32, SE = 1.89, p = .001) and the male observer condition (b = -6.42, SE = 1.87, p < .001). This effect was not further moderated by the addition of the risk factor (see Appendix B).

Effects of drug, sociosexual orientation, and participant-rated observer attractiveness

Given that earlier analyses indicated a) observer-specific interactions between drug, disposition (risk) and observer attractiveness, and b) drug x sociosexual orientation interactions, we examined in exploratory analysis the potential for testosterone to differentially affect PGG contributions as a function of participant sociosexual orientation and participant ratings of observer-specific attractiveness. This analysis allowed us to explore two, partially-overlapping hypotheses. First, as noted prior, female attractiveness may serve to buffer against a testosterone-induced reduction in PGG contributions, particularly among those with certain dispositions. To the extent that such an effect extends to individual differences in sociosexuality, it was anticipated that in the female observer condition, testosterone would reduce PGG contributions among those with relatively unrestricted sociosexuality, but only to the extent that the female observer was relatively low in rated attractiveness (i.e., high attractiveness buffering effect). Alternatively, in keeping with the idea that testosterone may promote mating-relevant signalling—particularly among men who are oriented toward short-term mating (i.e., unrestricted sociosexual orientation)—it seemed possible that testosterone would instead increase PGG contributions for men with relatively unrestricted sociosexual orientations, but only to the extent that the female observer was rated relatively high in rated attractiveness (i.e., high attractiveness faciliatory effect).

To test these possibilities, an analysis for the female observer condition examined the effects of drug, sociosexual orientation, and observer attractiveness. As reported in Table 3.3, drug, sociosexual orientation, and rated attractiveness interacted such that testosterone reduced PGG contributions in the presence of a female low in rated attractiveness, but only for men with relatively unrestricted sociosexual orientations. Testosterone also reduced PGG contributions for unrestricted men in the presence of a female high in rated attractiveness, but to a substantially smaller degree (See Figure 3.5).

Table 3.3. Effects of drug, sociosexual orientation (SOI), and participant-rated observer attractiveness (Att.) for the female observer and male observer conditions.

Predictors (fixed effects)	*estimates*	*se*	*LLCI – ULCI*	*p*
Female Observer				

(Intercept)	367.87	5.35	357.38 – 378.35	< .001
Drug	-7.83	2.23	-12.21 – -3.45	< .001
SOI	-12.11	5.40	-22.68 – -1.53	.027
Att.	1.00	1.39	-1.73 – 3.73	.472
Drug x SOI	-14.30	2.10	-18.40 – -10.19	< .001
Drug x Att.	5.46	2.65	0.28 – 10.65	.040
SOI x Att.	4.47	1.35	1.82 – 7.12	.001
Drug x SOI x Att.	10.55	2.50	5.64 – 15.46	< .001
Drug x SOI at:				
Low Att.	24.85	4.26	-33.20 – -16.50	< .001
High Att.	-3.75	1.78	-7.23 – -0.27	.036
Conditional Effects of Drug:				
Unrestrict. SOI, Low Att. female	-38.14	6.38	-50.64 – -25.64	< .001
Restrict. SOI, Low Att. female	11.56	6.16	-0.52 – 23.63	.062
Unrestrict. SOI, High Att. female	-6.11	2.34	-10.69 – -1.53	.009
Restrict. SOI, High Att. female	1.38	2.56	-3.63 – 6.39	.589
Male Observer				
(Intercept)	368.68	5.32	358.25 – 379.10	< .001
Drug	-3.32	1.82	-6.90 – 0.26	.070
SOI	-9.45	5.37	-19.98 – 1.08	.081
Att.	0.27	0.99	-1.68 – 2.22	.788
Drug x SOI	-7.52	1.86	-11.17 – -3.88	< .001
Drug x Att.	1.24	1.73	-2.16 – 4.63	.476
SOI x Att.	-2.54	1.01	-4.52 – -0.57	.012
Drug x SOI x Att.	-4.24	1.83	-7.83 – -0.65	.021
Drug x SOI at:				
Low Att.	-3.28	1.58	-6.37 – -0.20	.038
High Att.	-11.76	3.33	-18.30 – -5.23	< .001
Conditional Effects of Drug:				
Unrestrict. SOI, Low Att. male	-7.84	2.21	-12.18 – -3.50	.005
Restrict. SOI, Low Att. male	-1.27	2.19	-5.57 – 3.02	.562
Unrestrict. SOI, High Att. male	-13.85	4.87	-23.39 – -4.30	.005
Restrict. SOI, High Att. male	9.68	4.37	1.12 – 18.25	.028

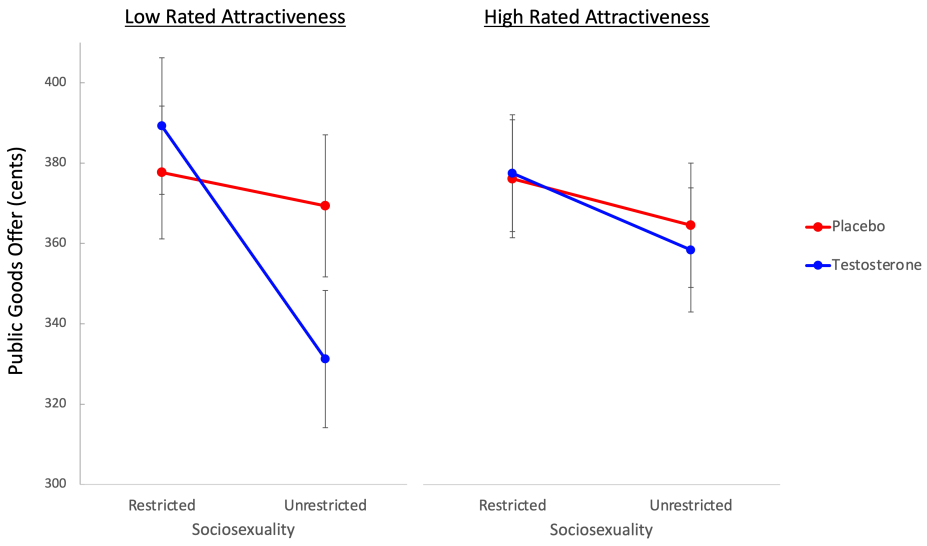

Figure 3.5. Effects of drug, sociosexual orientation, and participant-rated observer attractiveness for the female observer condition

In the male observer condition, drug, sociosexual orientation, and attractiveness interacted in a pattern different from the female observer condition. With male observers, testosterone reduced PGG contributions among unrestricted men for the observers both relatively low and high in rated attractiveness; for restricted men, testosterone did not affect contributions for the observers relatively low in rated attractiveness, but increased contributions for the observers relatively high in rated attractiveness (See Figure 3.6).

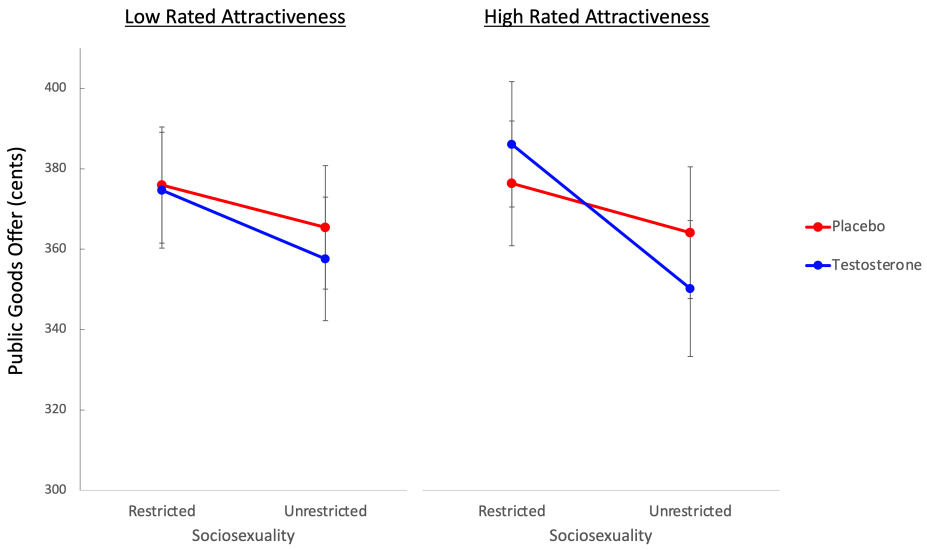

Figure 3.6. Effects of drug, sociosexual orientation, and participant-rated observer attractiveness for the male observer condition.

Given the relevance of participant relationship status to mating, the above analyses were also modelled with participant relationship status (single, paired) in place of sociosexual orientation. For the female observer condition, drug, relationship status, and observer attractiveness interacted (b = -3.44, SE = 1.51, p = .024), reflecting a significant drug x attractiveness interaction for participants who were single (b = 3.15, SE = 1.09, p = .004) but not paired (b = -0.29, SE = 1.04, p = .780). Testosterone significantly reduced contributions for single men when the female observer was rated low in attractiveness (b = -6.92, SE = 2.00, p < .001), but not rated high in attractiveness (b = -0.63, SE = 0.64, p = .327). For the male observer condition, there was no observed interaction between drug, relationship status, and observer attractiveness (b = -0.59, SE = 1.00, p = .557).

3.4. Discussion

The present experiment examined the extent to which testosterone independently, or synergistically with participant disposition and observer characteristics, influences men's prosocial economic decisions. Results first provide a conceptual replication of Bird et al. (2019) by demonstrating that in the absence of an observer, testosterone reduced prosocial contributions, specific to men who were relatively high in

a personality risk factor for testosterone-induced anti-sociality. This collective evidence suggests that testosterone can enhance self-interested behaviour, depending on whether individuals are already predisposed to act in such a way. Such a disposition-moderated testosterone effect is also consistent with other recent single-dose administration investigations, which have shown that an acute rise in testosterone potentiates aggressive behaviour, but only to the extent that individuals are high in trait dominance, low in self-control, and have relatively independent self-construals (Carré et al., 2017; Geniole et al., 2019).

In contrast, the hypothesis that testosterone would enhance a prosocial effect under female observation was not supported. Rather, primary analyses indicated that among men high (but not low) in personality risk, testosterone reduced prosocial decisions, regardless of the presence or sex of the observer. Given the idea that testosterone may facilitate mating-related behaviours, the present experiment also examined the extent to which the effects of testosterone may be moderated by characteristics that are highly relevant to mating, including one's relationship status, sociosexuality, and participant ratings of observer attractiveness. Results indicated that under observation by a female, testosterone reduced prosocial decisions among unrestricted men, but most strongly when the participant considered the female observer to be relatively low in attractiveness. A similar effect was found with relationship status, such that testosterone reduced prosocial decisions among single (but not paired) men when the female observer was rated relatively low in attractiveness. Contrasting patterns were noted under observation by a male, however, such that testosterone tended to increase prosocial decisions among restricted men when the male observer was rated relatively high in attractiveness, whereas testosterone clearly reduced prosocial decisions among unrestricted men, regardless of the rated attractiveness of the male observer.

The findings here raise the possibility that in some contexts, rather than playing a faciliatory role in enhancing prosocial displays, female attractiveness may—at least in the presence of men with unrestricted sociosexual orientations—serve to partially buffer against a deleterious effect of testosterone on prosocial decisions. The pattern of results for male observers is interpreted with caution, but suggests interesting considerations for theory and future research. Why might testosterone differentially influence prosocial choice based on the decision-maker's sociosexuality and the perceived attractiveness of

a male observer? One possibility is that testosterone enhances behavioural signals of dominance (e.g., reduced prosociality) when men are more inclined toward short-term—and thus competitive—mating, given that dominant displays can facilitate the obtainment or maintenance of social status (Bochon et al., 2020) as part of a larger constellation of intrasexual competition strategies. Given that attractive men hold an advantage in the mating arena, it seems possible that testosterone would enhance dominant displays most prominently in this context, given the threat that an attractive man could pose to other men who are mating motivated. Attractive men, however, are also rated as higher in social status (Bjornsdottir & Rule, 2017), offering potential coalitional benefits. For men who are less short-term mating motivated (i.e., restricted sociosexual orientations), testosterone may instead facilitate a prosocial signal, serving to enhance the likelihood of reciprocity and/or group cohesion with a desirable individual. Such a speculation would require a direct test in future work, but would be conceptually consistent with the idea that testosterone can promote both prosocial and antisocial behaviours, depending on threats or benefits to fitness (e.g., status), and relevant individual differences (Dreher et al., 2016; Geniole & Carré, 2018; Zilioli & Bird, 2017)

Limitations and future directions

The present experiment focused exclusively on a sample of young men. Although the link between testosterone dynamics and behavioural sequelae appear specific to men for some widely-studied contexts (e.g., aggression; Geniole et al., 2020), the examination of how an appropriately-dosed single administration of testosterone affects women under varied observational conditions would provide a useful extension and comparison to samples of men, particularly if conducted within a single mixed-sex investigation.

There exist other methodological considerations that are worth exploring in future work. In the present experiment, participants completed a one-shot paradigm under different observational conditions, which allowed a more direct comparison to other recent work. Some researchers have argued that even in one-shot encounters, where reputational consequences may be unclear, individuals are likely to nevertheless act on the heuristic that reputation is *typically* at stake (Jordan & Rand, 2020). Although the salience of reputation and mating-relevance in the present experiment may have been enhanced by the inclusion of male and female observers, it would nevertheless be useful

for future work to examine the interactive roles of testosterone, individual differences in mating-related variables, and observer characteristics using a repeated interaction paradigm, where reputational information can spread. Further, additional benefit may come from examining whether the inclusion of a clear future interaction with the observer (e.g., a post-game conversation or coalitional task), or whether the direct presence of the observer in the room during game play, has a modulatory effect on the effects of testosterone.

3.5. Conclusion

The findings from the present experiment add to a growing body of work suggesting that the effects of exogenous testosterone on men's behaviour depend on individual dispositions and contextual information. In the context of a neutral (no observer) public goods game, testosterone reduces prosocial contributions among men higher in dispositional risk for testosterone-induced anti-social behaviour, shown here and in past work (Bird et al., 2019). In the context of a public goods game that includes an observer, the possibility of a more complex relationship is evident, with testosterone effects that differ by mating psychology (e.g., sociosexual orientation), plus the sex and perceived characteristics (e.g., attractiveness) of the observer. Future work will be useful for delineating the boundaries and mechanisms of such effects.

Chapter 4. Experiment 3: Single-dose Testosterone Downregulates Select Executive Functions but not Iowa Gambling Task Performance

4.1. Introduction

A growing body of work indicates that acute increases in testosterone, from both environmentally-influenced endogenous release and exogenous administration, can modulate competitive (Carré & McCormick, 2008; Mehta et al., 2015) and aggressive behaviours (Carré et al., 2017; Carré & Olmstead, 2015; Geniole et al., 2019). The cognitive mechanisms by which testosterone might promote such behaviour over alternatives, however, remain poorly understood. One untested possibility is that a rapid increase in testosterone—rather than stable, trait-like levels, which show relatively weak relationships with key behaviours like aggression (see Geniole et al., 2020)—could downregulate key executive functions, thus disrupting the cognitive processes involved in governing behaviour. There also exists the possibility that testosterone's effects may extend beyond social, interdependent contexts (e.g., competition, mating) to modulate tradeoffs in non-social contexts, such as with economic decision-making tasks examining individual sensitivity to reward or punishment.

4.2. Testosterone and Executive Functioning

The executive functions—also referred to as cognitive control or executive control—refer to a set of complex higher order cognitive processes that monitor and regulate goal-directed behaviour (Baggetta & Alexander, 2016). Although the literature on human executive functioning is vast, there is general agreement that executive functions can be largely captured categorically by inhibition (e.g., self-control over impulses), working memory (information temporarily maintained in an accessible state for ongoing processing), and cognitive flexibility (adaptive modification of attention or mental representations in response to new task demands), working together to execute higher order functions like task planning (Diamond, 2013).

The executive functions jointly override impulses, drives, and over-rehearsed behavioural patterns (Doebel, 2020; Suchy, 2009). As a result, they play an important

role in the top-down control of many of the behaviours that have been studied in social neuroendocrinological investigations of testosterone, such as risk-taking (Apicella et al., 2014; Ronay & Hippel, 2010), intuitive versus deliberative choice (Bird et al., 2019), and aggressive behaviour (Carré et al., 2017; Geniole et al., 2019). Indeed, indices of executive functioning have shown inverse relationships with risk-taking (Pharo et al., 2011; Reynolds et al., 2019) and aggression across a variety of demographics (Micai et al., 2015; Ogilvie et al., 2011; Rohlf et al., 2018). Consequently, it is plausible that one mechanism by which testosterone acts on behaviours such as aggression is by moderating executive functioning. No direct investigations of the effects of acute increases in testosterone on executive functioning have been published to date. Two indirectly-related studies have shown mixed results. In one of these studies (Nave et al., 2017), the authors administered a single-dose of testosterone (versus placebo) to healthy young men, and found that testosterone reduced cognitive reflection, arguably a reflection of inhibitory executive processing (Missier et al., 2012). However, additional tests of the strength and replicability of this finding suggested weak and highly variable effects (Knight et al., 2020).

Given the tendency for both testosterone and executive functioning to decline with age (Fjell et al., 2017; Harman et al., 2001), more direct examinations of testosterone and executive functioning have been conducted primarily with clinical samples of elderly men. Nevertheless, to the best of our knowledge, none of these studies have examined the effects of single-dose testosterone on executive functioning. Rather, findings using other methodology—namely correlative—are mixed, with some studies showing inverse relationships between basal testosterone and executive functioning measured concurrently (e.g., Moffat et al., 2002) or at follow-up ten years later (Van Strien et al., 2009), and others showing positive relationships between basal testosterone (Yaffe et al., 2002), or repeatedly administered testosterone supplementation, and executive function task performance, albeit with relatively small effect sizes (e.g., Hedge's g = .16; Tan et al., 2019).

In younger adult samples, studies of the relationship between testosterone and executive functioning (rather than other cognitive domains that are not generally considered executive functioning, such as verbal memory or mental rotation) are surprisingly scarce, and among those that have, generalization is difficult due to unique sample characteristics, different administration methodology, or the manipulation of

additional physiological variables. For example, in one study, healthy men aged 18 to 39 years completed executive function tasks of selective attention, goal maintenance, and working memory, and then underwent 28 days of exercise- and diet-induced energy deficiency, followed by four doses of intramuscular injections of testosterone or placebo that were spaced over approximately three weeks. Tasks were repeated at the end of the hormone administration period, and results indicated no pre- to post- differences between the testosterone and placebo groups on any of the executive functioning measures (Carmichael et al., 2021). In another study, a sample of middle-aged men (mean age of 48 years) with sleep apnea were randomized to receive three intramuscular injections of testosterone over a 12-week period, with executive function tasks (task-planning and cognitive flexibility) performed at multiple time-points over the study. Results similarly indicated no differences in executive task performance between the testosterone and placebo groups (Melehan et al., 2016).

There exist several clear gaps in the current literature on testosterone and executive functioning. First, the overwhelming majority of studies focusing on elderly populations, neglects healthy adult men—to whom testosterone is highly relevant for a constellation of reproductively-relevant behaviours, such as mate seeking (Roney & Gettler, 2015), competition (Carré & Olmstead, 2015), and dominance (Turan et al., 2014). Second, studies have relied on measuring endogenous testosterone levels at baseline, or made outcome comparisons based on chronic testosterone supplementation (or deprivation; Nelson et al., 2008) over several weeks or months, which neglects the dynamic flexibility of acute testosterone changes—and their stronger associations (over baseline levels) with a host of adaptive behaviours in adults (Geniole et al., 2020; Geniole & Carré, 2018; Zilioli & Bird, 2017). Therefore, it remains possible that in adult men, an acute increase in testosterone—more so than trait-like circulating levels—may negatively predict performance on executive functioning indices, which could provide an important first step to identifying a possible cognitive mechanism through which testosterone release influences behavioural action.

4.3. Testosterone and Economic Decision-Making

Testosterone in humans is often studied in the context of status-seeking, dominance, and/or aggressive behaviours, arguably because these behaviours are highly relevant to the tradeoff between mating (e.g., mate-seeking, copulation) over

parenting—of which testosterone is thought to mediate (Hau & Wingfield, 2011). But, there is a growing interest in how testosterone may influence risk-benefit tradeoffs for more independent (i.e., non-social) behaviours such as economic risk-taking (for reviews, see Apicella et al., 2015; Stanton, 2017). The evidence to date in this area has been mixed. Correlational studies, for example, have found that circulating levels of testosterone, and increases in testosterone following a monetary win or loss, predict laboratory investment risk-taking and risk preferences, respectively (Apicella et al., 2008, 2014). Supporting field work found that male stock traders made more money—possibly due to risk-taking—on the days in which their testosterone levels were high (Coates & Herbert, 2008), which was further supported by testosterone administration studies, which showed that when given testosterone, male traders bid higher amounts of financial assets (Nadler et al., 2018) and healthy young men demonstrated preference for highly volatile assets (Cueva et al., 2015). In contrast, other recent correlational and experimental work in healthy young men has failed to find any consistent effects of testosterone on loss aversion and economic risk-taking with the Balloon Analogue Risk Task—a non-social task where each button click earns a participant money, but simultaneously inflates an on-screen balloon that can "pop" if over inflated, in which case earnings are negated (Stanton et al., 2021).

The Iowa gambling task (IGT; Bechara et al., 1994) represents a unique and well-studied non-social economic paradigm where participants navigate options of short-term advantage but long-term disadvantage (high immediate reward, long-term losses) versus a less attractive short-term option but longer-term advantage (low immediate reward, long-term gains). Past work suggests that testosterone may modulate decision-making on this particular task. For example, two correlational studies found that men's and women's circulating levels of testosterone were either positively or curvilinearly related to disadvantageous choices (i.e., larger short-term reward but higher long-term loss) on the IGT (Stanton, Liening, et al., 2011; Stanton, Mullette-Gillman, et al., 2011b). In the only related single-dose experimental study to date, van Honk and colleagues (2004) similarly found that women who were given testosterone (versus placebo) were more likely to select disadvantageous options in the IGT. In a separate study, healthy men who were repeateadly administered an aromatase inhibitior (thus increasing testosterone levels) did not show any difference in IGT performance over men who were administered an aromatase inhibitor plus estradiol (Goudriaan et al., 2010). It remains

unknown, however, to what degree testosterone, and particularly elevated testosterone from a single administration, may play a causal role in modulating men's performance on the IGT.

4.4. The Present Experiment

This pre-registered experiment[6] was designed to address the outstanding questions of whether an acute increase in testosterone can play a causal role in (a) men's executive functioning and (b) men's decision-making on the IGT. We additionally sought to examine whether these key outcomes are moderated by dispositional characteristics (namely self-control) relevant to testosterone-behaviour relationships and executive functioning. Based on the premise that T may inhibit behavioural flexibility (Tobiansky et al., 2018), and that testosterone can promote behaviours that are inversely correlated with executive functioning (e.g., aggression), it was predicted that testosterone (versus placebo) would largely down regulate executive functioning indices of cognitive flexibility, response inhibition, and task-planning ability. Further, given evidence that the behavioural effects of testosterone can depend on individual differences in disposition—particularly self-control (Carré et al., 2017; Geniole et al., 2019)—it was predicted that any deleterious effects of T on executive functioning would be exaggerated among those with relatively low self-control. Given a general lack of research on testosterone and working memory in young adults, the prediction for working memory in the present experiment was based on evidence in older men that androgen deprivation can impair (Nelson et al., 2008), and testosterone replacement improve, performance on working memory tests (Warren et al., 2008)(but see Resnick et al., 2017). We remained agnostic as to whether self-control would moderate such an effect of testosterone on working memory. Based on previous findings showing that testosterone may reduce advantageous choices on the IGT (Stanton, Liening, et al., 2011; van Honk et al., 2004), it was predicted that testosterone (versus placebo) would similarly reduce advantageous choices on the IGT, and particularly among men with relatively low dispositional self-control.

6 Study details, including predictions stratified by individual task outcomes, are available at: https://osf.io/vths7/?view_only=ad776bd97ed041968475c3236c238c30

4.5. Methods

4.5.1. Participants

The participant sample consisted of 120 healthy men[7] between the ages of 18 and 44 years (M_{Age} = 23.45, *SD* = 5.08). One participant was excluded from all analyses due to difficulty administering the drug, whereas other exclusions were dependent on the task, as follows: Victoria Stroop (*n* = 3 recording error), digit span (*n* = 7 computer error; *n* = 1 improper task completion; *n* = 1 stimuli error), tower of London (*n* = 5 recording error; *n* = 5 stimuli error); Go/NoGo (*n* = 6 computer error; *n* = 2 improper task completion), and Iowa gambling (*n* = 1 stimuli error; *n* = 1 task non-completion).

Study recruitment was conducted in northern Ontario via community posters in the general community (e.g., malls, grocery stores, bus stations); recruitment booths at the local university and college; online advertisements; university research participant pool; and via phone contact with previous study participants who had consented to being contacted for future studies. Thus, participants included students and members of the general public. Prospective participants were first screened via telephone for exclusion criteria, which included (1) being outside the ages of 18 to 45; (2) currently taking prescription medication for medical conditions affecting hormone concentrations (e.g., hypogonadism, Cushing's disease); (3) current diagnosis of a psychiatric disorder (e.g., major depressive disorder; attention-deficit/hyperactivity disorder); (4) current diagnosis of a heart condition or prostate cancer; (5) alcohol and/or drug dependency; and (6) membership in a team or organization for whom testosterone is a banned substance (e.g., student-athletes). The experiment procedures were approved by the University's Research Ethics Board, and the eligible participants provided informed written consent for all aspects of testing.

7 Note that the sample size deviates from the pre-registered intended sample of 300 men. Data collection for the current experiment was interrupted with the onset of the COVID-19 pandemic, which prohibited in-person testing. Therefore, the sample size here reflects data collected prior to the pandemic restrictions. We note that the final sample of 119 men is approximately 30% larger than the average sample size of all past testosterone administration studies (Carré & Robinson, 2020).

4.5.2. Procedure and materials

The experiment employed a double blind, placebo-controlled, between-subjects design, whereby participants were randomized to either (1) receive 11 mg (two syringes, 5.5mg each) of intranasal testosterone (Natesto), or (2) receive an equivalent amount of the gel vehicle functioning as a placebo. Testing was conducted in individual testing rooms between 9:30AM and 4:30PM. After providing informed consent, participants completed demographic and self-report questionnaires, followed by a saliva sample via passive drool to assay variability in baseline testosterone concentrations. Under the supervision of a research assistant who was blind to experimental condition, participants then self-administered the drug (testosterone or placebo) by applying the gel to the lateral inner surface of each nostril (one syringe each), and then compressed the nostrils toward the septum to achieve even gel spread. To avoid accidental contamination of the testing components that participants would touch, computer components were wiped with a 70% alcohol cleaning solution, and then covered with a protective sheet between sessions. Following gel administration, participants were instructed to immediately and thoroughly wash their hands.

While waiting for drug uptake, anthropometric measures for an unrelated study were recorded from participants, then a second saliva sample was collected immediately prior to behavioural testing. Consistent with past work using this dosage and route of administration, behavioural testing began approximately 30 minutes after drug intake, a time at which serum testosterone levels are significantly elevated (remaining so for approximately 3 hours post-administration) and behavioural effects are observed in domains such as aggression (Geniole et al., 2019; see also Luberti et al., 2021 for further pharmacokinetic work). Behavioural testing was completed over approximately 60 minutes, which included all tasks reported below, followed by two tasks unrelated to the hypotheses in the present experiment. At the end of testing, participants were asked to guess the condition to which they were assigned. A binomial test found that participants were no better than chance accuracy at guessing their condition (53% correct; p = .566), indicating no consciously detectable effects of testosterone.

4.5.3. Questionnaires

Self-Control

Participants completed a battery of demographic and self-report measures. As in previous testosterone administration work (Bird et al., 2019; Carré et al., 2017; Geniole et al., 2019), we employed a self-control index comprised of the Barratt Impulsivity Scale (BIS; Patton et al., 1995) and the Brief Self-Control Scale (BSC; Tangney et al., 2004). The BIS consists of 30 items that ask participants to rate the extent to which each statement is true of them on a 4-point Likert-type scale, with response options ranging from 1 (rarely/never) to 4 (almost always/always). Example items include “I plan tasks carefully” and “I act on impulse.” The BSC consists of 13 items that ask participants to rate the extent to which each statement is reflective of how they typically are, using a 5-point Likert-type scale with response options ranging from 1 (not at all) to 5 (very much). Example items include “I am good at resisting temptation” and “I wish I had more self-discipline.” A self-control composite was created using the method from past work (Bird et al., 2019; Carré et al., 2017; Geniole et al., 2019), by first reverse scoring the BIS, and then taking the average of the standardized (z-scored) individual BIS and BSC measures.

Exploratory measures of individual differences

For exploratory purposes in the IGT analyses, participants completed measures of emotion regulation and problematic gambling history. Emotion regulation was measured with the 16-item version of the Difficulties in Emotion Regulation Scale (DERS-16; Bjureberg et al., 2016), which asks participants to indicate how often statements apply to them, with response options that range from 1 (almost never / 0-10% of the time) to 5 (almost always / 91-100% of the time). Sample items include “When I’m upset, I have difficulty getting work done” and “When I’m upset, my emotions feel overwhelming.” Higher DERS-16 scores reflect greater difficulties regulating emotion. Problematic gambling history was measured with the Problem Gambling Severity Index (PGSI; Ferris & Wynne, 2001). The PGSI is a 9-item questionnaire that asks participants to indicate how often they have experienced various gambling difficulties within the past 12-months, with response options that range from 0 (never) to 3 (almost always). Sample items include “Have you borrowed money or sold anything to get money to gamble?” and “Have people criticized your betting or told you that you had a gambling problem, regardless of whether or not you thought it was true?” Higher PGSI scores reflect greater risk for problematic gambling.

4.5.4. Executive Functioning Tasks

All tasks were administered with the Psychology Experiment Building Language 2.0 software (Mueller & Piper, 2014).

Victoria Stroop Task

This shortened version of the classic Stoop task measures cognitive flexibility (Spreen & Strauss, 1998). Stimuli in the task include three screens, each containing six rows of four items. On the first screen (the dot task), participants quickly select a key that corresponds to colours of dots (red, green, blue, yellow). On the second screen (the word task), participants quickly select the colour that corresponds to neutral words that are written in red, green, blue, or yellow colour. On the third and final screen (the "interference" task), participants again have to select the colour that corresponds to words written in red, green, blue, or yellow, but the words themselves are colours (e.g., the word "yellow" might appear in blue text). Thus, the task requires participants to inhibit the tendency to read an incorrect word or colour based on interfering stimuli. Reaction time (RT) is recorded for each trial, allowing the calculation and comparison of efficiency, as calculated with a colour task RT/dot task RT ratio (i.e., high interference/no interference), as well as a colour task RT/word task RT ratio (i.e., high interference/low interference). To the degree that reaction time is progressively longer from the dot to word to colour task, the colour/dot ratio would be expected to be higher than the colour/word ratio. Additional outcomes include the number of errors per task (any incorrect colour selection for a given stimuli), and the number of intrusions on the colour task (e.g., an intrusion would be recorded if the participant reads the word "blue" written in yellow font, and indicates that the font colour is blue rather than yellow).

Digit Span Task

The digit span task is a measure of working memory that dates back to as early as the 1800s (reviwed in Richardson, 2007). For each trial, the participant is presented with a series of single digit numbers, and subsequently must recall the entire series, in the same order as presented, for the trial to be scored as correct. The length of the series systematically increases across trials, thereby increasing the difficulty level. The primary measure recorded was forward digit span (or "memory span"), which is defined

as the longest series of digits correctly recalled before two consecutive incorrect trials of the same digit length.

Tower of London Task

The Tower of London task is a measure of task planning ability originally designed by Shallice et al. (1982), with a commonly-employed revised version by Phillips et al. (1999). Participants are required to move virtual rings across various place holders in order to match a pre-specified arrangement model, all while minimizing the total number of moves to accomplish their goal. Participants completed the task three times using the same fixed order of three blocks (eight trials each) as Phillips et al. (1999). The primary outcome measure was the number of participant moves beyond the minimum required to solve the puzzles for each of the three blocks, therefore allowing for examination of between-subject (i.e., testosterone versus placebo) and within-subject (i.e., block 1 vs. block 2 vs. block 3) effects.

Go/No Go Task

The Go/NoGo task is a well validated measure of response inhibition (Donders, 1969). In the current version (Bezdjian et al., 2009), target stimuli and distractor stimuli are presented in a continuous stream, and participants perform a binary decision on each stimulus. For valid target stimuli, participants initiate a motor response (i.e., a button press signaling "Go"), while participants must inhibit a motor response for distractors (i.e., "No Go"). In the current version there are two conditions, one using the letter “P” as the Go target and “R” as the No Go distractor, and a second condition using the reverse (“R” as Go target and “P” as No Go non-target). The primary outcome measure was commission errors as an index of behavioural disinhibition (i.e., failing to inhibit a response on the “No Go” letter), with additional examination of omission errors (i.e., failing to respond on a “Go” letter).

4.5.5. Economic Decision Making Task

Iowa Gambling Task

The IGT (Bechara et al., 1994) measures economic decision-making by using probabilistic learning with monetary rewards and punishments. Participants are given a

virtual $2000 starting endowment and instructed that the goal of the task is to maximize earnings above and beyond that initial amount. During the task, participants are presented with 4 virtual decks of cards. Decks differ from each other in the balance of reward versus punishment cards, such that two decks are more disadvantageous (offering high immediate financial gains but also substantially reduced long-term gains), and two decks are more advantageous (offering lower immediate rewards but also considerably lower penalties, allowing greater long-term gains). For each of the 100 trials of the task, participants can select a card from any deck they would like, subsequently learning the amount that they were rewarded (i.e., monetary gain) or punished (i.e., monetary loss) for their choice. The primary outcome is the percentage of advantageous choices made on each of the five blocks of twenty trials each.

4.5.6. Analytic Approach

For tasks involving repeated measurement blocks (Victoria Stroop, Tower of London, Go/NoGo, IGT), analyses deviate from the pre-registered ANOVA-based plan, instead employing robustly-fit multi-level models, which are recommended because they provide less biased estimates and more powerful hypothesis tests, while accounting for influential cases and heteroscedasticity in the residuals (Brown, 2021; Koller, 2016; Kristensen & Hansen, 2004). The maximal random-effects structures were specified and trimmed until convergence (Barr et al., 2013), and significance was determined using Satterthwaite approximations for degrees of freedom (Luke, 2017). Analyses were conducted using R/R-Studio software (R Core Team, 2021; RStudio Team, 2021) with the robustlmm package (Koller, 2016) for tasks with repeated measurement blocks, and the robustbase package (Maechler et al., 2021) for the digit span task. To remain consistent with past work examining the effects of testosterone on IGT performance (Stanton, Liening, et al., 2011; van Honk et al., 2004) the outcome was modelled with linear and quadratic (i.e., block^2) effects for block. Categorical predictors (e.g., drug) were centred prior to analysis with a one-unit distance, with the respective regression coefficients thus representing category differences in the outcome variable. Consistent with the standardized self-control index, other individual difference variables (problematic gambling, emotion dysregulation) were standardized (i.e., z-scored), with the respective regression coefficients representing the extent of change in the outcome variable for a one standard deviation increase in the corresponding variable. Where

indicated, conditional effects analyses were conducted at relatively low (-1 SD) or high (+1 SD) levels for continuous moderators.

4.6. Results

4.6.1. Victoria Stroop Task

Efficiency

Examining the effects of drug (placebo, testosterone) and reaction time ratio (colour/dot, colour/word) on efficiency scores revealed a main effect of ratio. The pattern was unexpected, such that efficiency was less prominent for the colour/dot ratio than the colour/word ratio (b = 0.26, SE = 0.02, p < .001). To clarify the pattern of this main effect, a model with drug (placebo, testosterone) and task (dot task, word task, colour task) on participant reaction times revealed a main effect of task (b = -1.97, SE = 0.53, p < .001), such that participants showed a reduction in reaction time from the dot task (no interference) to the word task (low interference), and from the word task (low interference) to the colour task (high interference) (ps < .001). This decrease (rather than increase) in reaction times over tasks accounts for the unexpected main effect of ratio. No main effect was observed for drug (b = -0.02, SE = 0.06, p = .777), nor was there a drug by ratio interaction (b = -0.06, SE = 0.05, p = .197). Examining the effect of drug on reaction times for each task alone did not reveal any significant differences between testosterone and placebo for the dot task (b = -0.91, SE = 2.12, p = .67), word task (b = 0.60, SE = 1.84, p = .74), or colour task (b = -0.29, SE = 2.12, p = .89).

Examining the moderating role of self-control for efficiency scores did not reveal any drug x self-control (b = -0.05, SE = 0.06, p = .396) or ratio x self-control (b = -0.02, SE = 0.03, p = .334) interactions, nor a three-way drug x ratio x self-control interaction (b = 0.05, SE = 0.05, p = .355). Examining the moderating role of self-control for reaction times similarly did not reveal any drug x self-control (b = -2.06, SE = 1.95, p = .293), task x self-control (b = 0.39, SE = 0.58, p = .506) interactions, nor a three-way drug x task x self-control interaction (b = -1.53, SE = 1.16, p = .187). A main effect of self-control was observed, such that reaction times were longer for individuals with higher self-control (b = 2.01, SE = 0.98, p = .044).

Errors

Examining the effects of drug and task on the number of errors revealed a main effect of task (b = 0.28, SE = 0.08, p < .001) in the expected direction, such that significantly more errors were made as the level of task difficulty increased (ps < .001), suggesting that the previously noted increase in reaction times over tasks was not an indication of better performance. No main effect of drug (b = 0.01, SE = 0.26, p = .96) or a drug x task interaction (b = 0.17, SE = 0.16, p = .277) were observed. Examining the moderating role of self-control produced a significant drug x self-control interaction (b = 0.66, SE = 0.28, p = .020), but conditional effects showed that testosterone was associated with only marginally more errors among individuals with higher (+1 SD) self-control (b = 0.68, SE = 0.37, p = .072), and marginally less errors among those with lower (-1 SD) self-control (b = -0.64, SE = 0.38, p = .098). No task x self-control (b = -0.04, SE = 0.08, p = .636) or drug x task x self-control interaction was found (b = 0.07, SE = 0.17, p = .679).

Intrusions

Testosterone did not meaningfully affect the number of intrusions that participants experienced (b = -0.11, SE = .22, p = .613). Examining the potential moderating role of self-control produced a marginally significant drug x self-control interaction (b = 0.44, SE = 0.23, p = .058), although conditional effects did not indicate a meaningful differential effect between testosterone and placebo for individuals with low self-control (b = -0.50, SE = 0.32, p = .114) or high self-control (b = 0.37, SE = .31, p = .234).

4.6.2. Digit Span

Testosterone (vs. placebo) did not show a significant difference for digit span (b = -0.20, SE = 0.52, p = .701). Examining the potential moderating role of self-control revealed a drug x self-control interaction (b = -0.70, SE = 0.30, p = .021). Conditional effects showed that among individuals with low self-control, testosterone (vs. placebo) did not significantly affect digit span (b = 0.55, SE = 0.41, p = .188). Among individuals with high self-control, however, testosterone (vs. placebo) was associated with reduced digit span (b = -0.86, SE = 0.41, p = .04).

4.6.3. Tower of London

Examining the effects of drug and block (1, 2, 3) on the number of extra moves required to solve the puzzle revealed a significant main effect of drug (*b* = 1.97, *SE* = 0.90, *p* = .030), such that testosterone (vs. placebo) caused an increase in the number of moves required to solve the puzzles. A marginally significant drug x block interaction was also observed (*b* = -1.53, *SE* = 1.01, *p* = .072). Decomposing the interaction revealed that testosterone (vs. placebo) increased the number of moves beyond the minimum on block 1 (*b* = 3.96, *SE* = 1.42, *p* = .005) and block 2 (*b* = 1.97, *SE* = 0.90, *p* = .028), but not block 3 (*b* = 0.02, *SE* = 1.42, *p* = .989) (see Figure 4.1). Examining the moderating role of self-control did not produce any block x self-control (*b* = 0.41, *SE* = 0.60, *p* = .498), drug x self-control (*b* = -0.66, *SE* = 0.97, *p* = .497), or drug x block x self-control interactions (*b* = -0.68, *SE* = 1.18, *p* = .567).

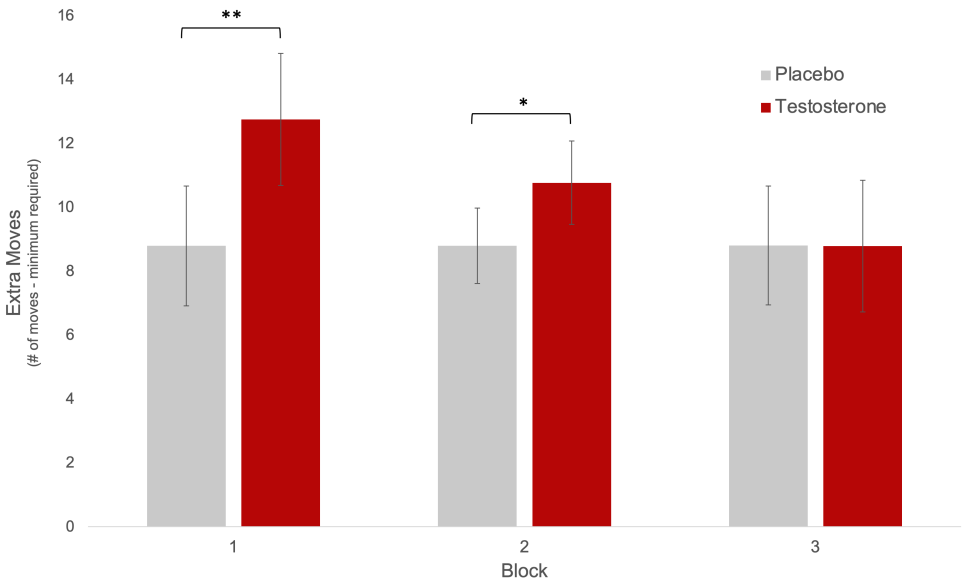

Figure 4.1. Effects of drug and block on the number of extra moves required to solve the puzzles on the Tower of London task. **p* < .05, ***p* < .01. Error bars represent the 95% CIs.

4.6.4. Go/No Go

Commission Errors

Examining the effects of drug and block (1, 2) on the number of commission errors revealed main effects for block (b = -8.95, SE = 0.47, p < .001) and drug (b = 1.59, SE = 0.66, p = .018) that were qualified by a drug x block interaction (b = -1.86, SE = 0.94, p = .05). Decomposing the interaction revealed that testosterone (vs. placebo) produced more commission errors in block 1 (b = 2.52, SE = 0.81, p = .002) but not block 2 (b = 0.65, SE = 0.81, p = .420) (see Figure 4.2). Examining the moderating role of self-control did not produce drug x self-control (b = 0.30, SE = 0.72, p = .681), block x self-control (b = 0.29, SE = 0.54, p = .596), or drug x block x self-control interactions (b = -0.22, SE = 1.07, p = .836).

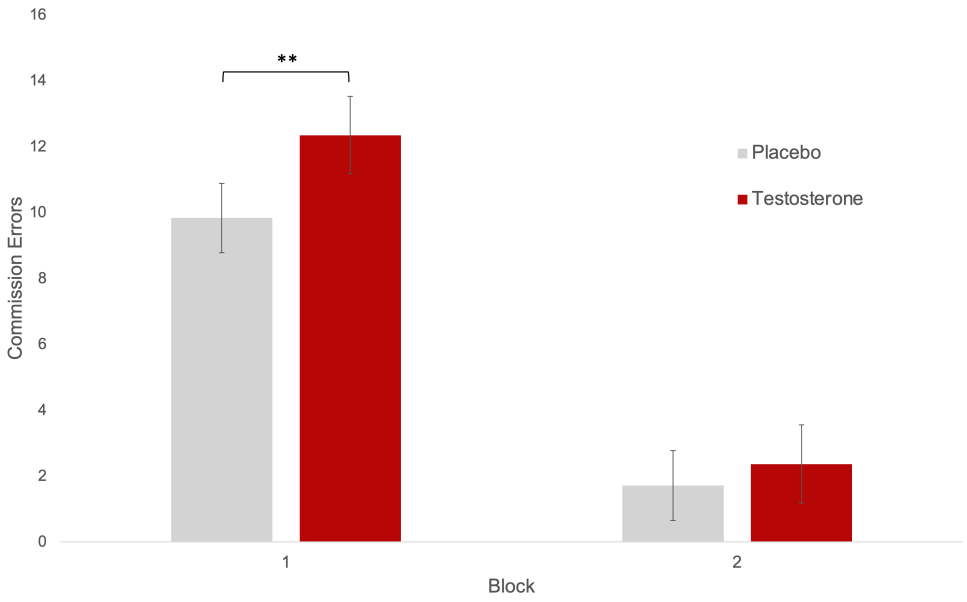

Figure 4.2. Effects of drug and block on commission errors for the Go/NoGo task. **p < .01. Error bars represent the 95% CIs.

Omission Errors

Examining the effects of drug and block on number of omission errors revealed a main effect for block (b = -0.25, SE = 0.08, p = .003), such that omission errors decreased from block 1 to block 2. The effect of drug showed a non-significant trend toward testosterone (vs. placebo) producing more omission errors (b = 0.153, SE = 0.08,

p = .065), and there was no drug x block interaction (*b* = -0.17, *SE* = 0.16, *p* = .304). When added to the model, self-control did not significantly interact in two-way or a three-way interaction (*ps* .107 – .792)[8].

4.6.5. Iowa Gambling Task

Examining the effects of drug and block on percentage of advantageous choices revealed a non-significant effect of drug (*b* = 1.93, *SE* = 6.55, *p* = .769). As would be expected from past work (Stanton, Liening, et al., 2011; van Honk et al., 2004), significant linear (*b* = 21.64, *SE* = 3.36, *p* < .001) and quadratic (*b* = -2.43, *SE* = 0.54, *p* < .001) main effects were observed for block, suggesting a learning effect for all participants whereby the percentage of advantageous choices significantly increased over trials. Contrary to the central hypothesis, the block effect was not qualified by linear (*b* = -0.42, *SE* = 5.02, *p* = .933) or quadratic (*b* = 0.14, *SE* = 0.81, *p* = .863) drug x block interactions (see Figure 4.3).

8 Due to singular fit (i.e., over-fitting) of the model examining possible moderation by self-control, the reliability of estimates is significantly reduced, and thus they are not reported here. Nevertheless, a traditional (non multi-level) linear model similarly showed no moderation effects by self-control.

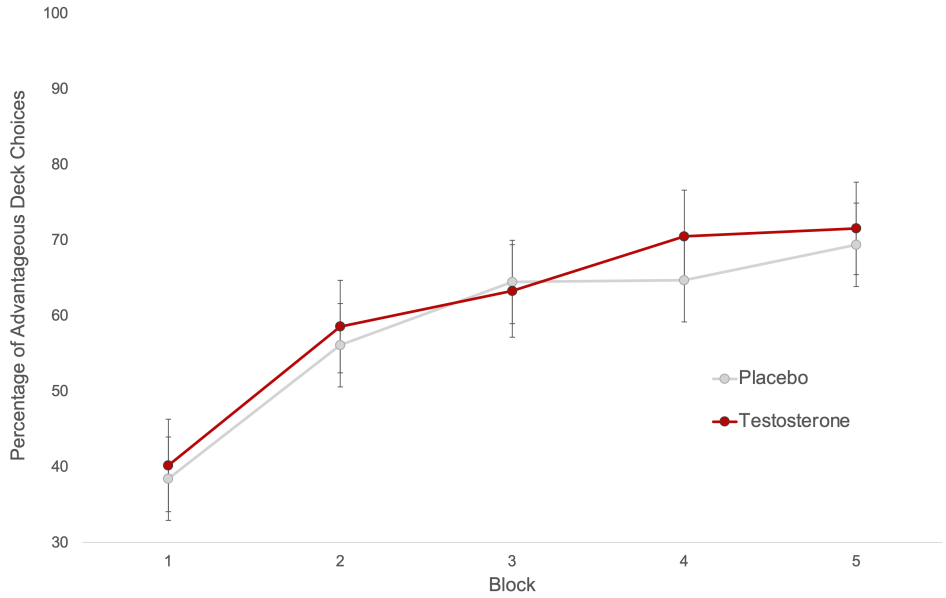

Figure 4.3. Effects of drug and block on the percentage of advantageous choices in the Iowa Gambling Task. Error bars represent the 95% CIs

Examining the moderating role of self-control did not reveal a significant drug x block x self-control interaction, nor any two-way interactions (see Table 4.1).

Table 4.1. Effects of drug, block, and self-control on percentage of advantageous choices in the Iowa Gambling Task

Predictors (fixed effects)	*estimates*	*se*	*LLCI – ULCI*	*p*
(Intercept)	18.76	5.16	8.63 – 28.89	< 0.001
Drug	5.45	7.68	-9.64 – 20.53	0.479
Block	22.95	3.71	15.67 – 30.23	<0.001
Block (Quadratic)	-2.64	0.61	-3.83 – -1.45	<0.001
Self-control	-9.21	6.10	-21.18 – 2.77	0.132
Drug x Block	-3.59	5.52	-14.43 – 7.25	0.516
Drug x Block (Quadratic)	0.65	0.90	-1.13 – 2.42	0.474
Drug x Self-control	-3.53	8.34	-19.92 – 12.86	0.672
Block x Self-control	6.54	4.38	-2.07 – 15.15	0.136
Block (Quadratic) x Self-control	-1.10	0.72	-2.50 – 0.31	0.127
Drug x Block x Self-control	6.35	5.99	-5.42 – 18.13	0.290
Drug x Block (Quadratic) x Self-control	-0.97	1.00	-2.89 – 0.96	0.323

In planned exploratory analyses, individual differences in problematic gambling history similarly did not interact with drug and/or block (*ps* .075 – .420). An unpredicted

block x problem gambling interaction emerged (*b* = -3.18, *se* = 1.62, *p* = .050), which reflected a higher percentage of advantageous choices in block 1 for individuals high (vs. low) in problem gambling (*p* = .044), but a largely opposite pattern for the remaining blocks, such that individuals high (vs. low) in problem gambling showed a lower percentage of advantageous choices for blocks 2 to 5 (*ps* .004 – .119). Exploring the potential moderating effect of emotion dysregulation similarly did not reveal any two-way or three-way interactions with drug and/or block (*ps* .216 – .903).

4.7. Discussion

The present experiment examined the extent to which an acute increase in testosterone affects men's (a) executive functioning and (b) economic decisions on the IGT. The effect of testosterone on executive function varied by task and domain. Predictions were supported for two of the executive function tasks. On the Tower of London task, participants in the testosterone group required significantly more moves (beyond the minimum) to complete the puzzles than individuals in the placebo group, thus supporting the prediction that testosterone would downregulate task planning ability. Examination of the drug effect at each of the three blocks revealed that testosterone (vs. placebo) significantly increased extra moves on block 1 and block 2, but not on block 3. As illustrated in Figure 4.1, these results show that the effect was ameliorated by the third block, suggesting that the deleterious effects of testosterone on task planning ability may be eventually overcome with repetition. Predictions were also supported in the Go/NoGo task, such that testosterone promoted disinhibtion, as indexed by increased commission errors (failing to withhold a motor response). Similar to the Tower of London task, the effect of testosterone treatment appeared specific to the initial block of trials, whereas the effect was no longer present in the second block—suggesting an eventual amelioration of testosterone-induced disinhibition. Effects on the Go/NoGo task were not further moderated by self-control.

Null effects of testosterone were observed for outcomes on the Victoria Stroop task and the digit span task, thus not supporting the prediction that testosterone alone would negatively affect cognitive flexibility and positively affect working memory, respectively. Interestingly, interaction effects between drug and self-control were observed for the number of errors and the number of intrusions on the Victoria Stroop task, such that testosterone (versus placebo) trended toward increasing errors and

interference among individuals high in self-control, with an opposite but weaker pattern for individuals low in self-control. A drug x self-control interaction was similarly observed for the digit span task, such that testosterone decreased digit span among those high in self-control but did not affect those with low self-control. We interpret these self-control moderation effects with caution, given that conditional effects for the Stroop outcomes failed to surpass traditional levels of statistical significance, and the absence of predictions for the direction of such effects. It is worth noting, however, that recent work found that testosterone may reduce cognitive reflection among individuals high in self-control (Knight et al., 2020). To the degree that trait self-control or self-regulation serves as an index of one's executive functioning (Hofmann et al., 2012), and that the cognitive reflection task is at least an indirect measure of executive function, it is possible that testosterone therefore exerts domain-specific negative effects on executive functioning most prominently among those who are already higher in functioning (e.g., high self-control, high executive function). Future work will certainly be needed to examine this possibility more directly.

The extent to which testosterone influences economic decision-making, such as gambling, remains poorly understood. Although early correlational evidence in men and women (Stanton, Liening, et al., 2011) and experimental evidence in women (van Honk et al., 2004) suggested the possibility that testosterone may reduce advantageous choice on the IGT, recent experimental work using other independent (non-social) economic tasks failed to find effects of testosterone on loss aversion and economic risk-taking (Stanton et al., 2021). The present investigation supports the notion that a rapid increase in testosterone, at least in the context of men's decisions on the IGT, does not meaningfully shift individual decision-making strategies to be more or less risky. As noted prior, recent theoretical accounts suggest that rapid fluctuations in testosterone serve to promote behaviour that can protect or enhance reproductive fitness (Geniole & Carré, 2018; Zilioli & Bird, 2017). In considering the null IGT findings from this perspective, it seems possible that testosterone did not meaningfully affect economic decisions because such an independent context is largely devoid of salient benefits to status or reproduction. We extend this line of reasoning to hypothesize that testosterone will affect economic decision-making most strongly when the task is social or inter-dependent in nature—but less so, or unpredictably, in non-social or independent contexts. If supported in future investigations, this hypothesis may partially explain why

the effects of acute testosterone administration on economic decision-making have been found in socially-oriented tasks like the ultimatum game (Dreher et al., 2016), but not the Balloon Analogue Risk Task (Stanton et al., 2021) or the IGT (as in the present experiment).

Limitations and future directions

The tasks in the present experiment tested selected components of executive functioning, theoretically playing an important role in behaviours that are studied in the context of social neuroendocrinology. Although tasks were chosen to represent a spread of executive function domains, there nevertheless exist a host of other classic neuropsychological tasks that could provide additional useful information. For example, the Wisconsin Card Sorting Test (WCST) requires participants to classify cards based on four rules that are unknown to the participant; following each decision, participants are only provided feedback about whether they have categorized the card correctly or not. Notably, and again unbeknownst to participants, the classification rule in the WCST changes every 10 cards, and therefore requires participants to learn a new rule shortly after they have learned the previous. Examining the influence of testosterone on WCST performance would provide a useful complement to the present research by determining whether a deleterious effect of testosterone on executive functioning, which was eventually ameliorated in the present experiment following repetition, would instead be preserved under changing schedules of reinforcement.

The present experiment also relied on a sample of healthy adult men, the reasons for which are several. First, the majority of past testosterone administration studies have been conducted in women, several of which have used dosing regimens that push testosterone well into the supraphysiological range, thus making interpretations and generalizations difficult. Second, at the time of experiment conceptualization, Canadian regulatory restrictions on using testosterone for women created a barrier to studying a mixed-sex sample. Third, key behavioural phenomena of interest within social endocrinology have shown effects that are specific to, or strongest among, men (e.g., aggression; Geniole et al., 2020). Nevertheless, the current focus on a sample of men leaves open the question as to whether the effects (or, for some tasks, the lack thereof) in the present experiment would extend to women. Recent work has established a suitable dosing regimen for examining the effects of single-dose intranasal

testosterone in both men and women (Luberti et al., 2021), and thus where regulatory barriers do not prevent using testosterone in this population, it would be useful for future studies to simultaneously test executive functioning outcomes and economic-decision making in both sexes.

Given the indication that trait self-control may play a modulatory role between testosterone and at least some executive functions, future investigations would benefit from examining executive functioning across a range of domains. As noted, the present findings, combined with some past work (Knight et al., 2020), indicate the possibility that testosterone may downregulate executive functioning most prominently among those who are higher in trait self-control.

4.7.1. Conclusion

The present experiment indicates that acute increases in testosterone may downregulate certain executive functions, and contributes to our understanding of the cognitive mechanisms by which testosterone—and particularly acute increases in testosterone—may potentiate human behavioural action. Further, results from the current experiment cast doubt on the possibility that an acute increase in testosterone causally modulates men's advantageous choices on the IGT. Future work will be useful for determining the extent to which testosterone downregulates executive functioning as measured by other tasks, whether effects are equivalent between the sexes when using sex-appropriate dosing (i.e., that push testosterone levels to the high normal, rather than supraphysiological, range), and directly testing whether such an effect may in turn account for testosterone's effects on aggressive and competitive behaviour.

Chapter 5. General Discussion

5.1. Summary of Experiments and Key Findings

The goal of this dissertation was to examine the effects of testosterone on economic decision-making and executive functioning. Experiment 1 was designed to examine the potential causal effects of testosterone on economic decision making in the one-shot public goods game, and determine whether such effects varied as a function of time pressure or individual differences in personality "risk" for testosterone-induced antisociality—comprised of trait dominance, self-control, and self-construal. Using a between-subject design, men received testosterone or placebo, and subsequently played a one-shot public goods game in which they were randomized to make their decision either under time-pressure (i.e., forced intuition), or under time-delay (forced reflection). Results indicated that drug interacted with time-pressure condition and personality risk to predict outcomes. Specifically, for individuals in the placebo group, time-pressure increased cooperation (i.e., higher economic contributions) among men low in personality risk (low dominance, high self-control, and with interdependent self-construals), but decreased cooperation among men high in personality risk (high dominance, low self-control, and with independent self-construals). Testosterone further moderated this pattern, however, such that it (1) abolished the time-pressure effect in low-risk men (i.e., economic contributions became effectively equalized between low and high risk men receiving testosterone in the time-pressure condition), and (2) reversed the time-delay effect in high risk men by selectively reducing contributions.

Experiment 2 was designed to replicate and extend Experiment 1 by examining the extent to which testosterone's effects on economic decision making in a time-delay one-shot public goods game would differ based on the presence and individual characteristics of an observer, and the participant's individual disposition (e.g., personality risk; sociosexuality). Using a within-subject design, men were randomized to receive testosterone or placebo, and subsequently played three iterations of the one-shot public goods game: no observer; female observer; and male observer. Following a two-week washout period, participants received the opposite condition to that received on day 1 (testosterone or placebo), and again played the same iterations of the one-shot public goods game, with a different male and female observer (randomized for day 1 or

day 2). Conceptually replicating Experiment 1, results indicated that testosterone reduced cooperation (i.e., lower economic contributions) among men high in personality risk when there was no observer to the game. However, the testosterone-induced reduction in cooperation for high-risk men was similarly observed in the female and male observer conditions. Notably, in the observer conditions, testosterone interacted with participant sociosexuality and the attractiveness ratings of observers, as follows: (1) male observer condition: when the male observer was rated as relatively high (not low) in attractiveness, testosterone increased contributions for men with restricted sociosexuality (i.e., long-term, committed mating orientations), but decreased contributions for men with unrestricted sociosexuality (i.e., short-term, uncommitted mating orientations); (2) female observer condition: when the female observer was rated as relatively low (not high) in attractiveness, testosterone most prominently decreased contributions for men with unrestricted sociosexuality.

Experiment 3 was designed to expand beyond Experiment 1 and 2 by examining the effects of testosterone on executive functioning, and economic decision-making on a task that is relatively independent (i.e., non-social) in nature. Using a between-subject design, men were randomized to receive testosterone or placebo, and subsequently completed a series of executive functioning tasks, as well as the IGT. Main findings indicated that testosterone most clearly down-regulated task planning and inhibition on the Tower of London task and Go/NoGo tasks, respectively. The effects of testosterone on economic decision making in the IGT were null and did not vary as a function of individual differences in self-control or problematic gambling.

5.2. Discussion and Avenues for Future Work

The experiments presented herein provide a number of important contributions to our current knowledge. From a methodological perspective, the experiments employed randomized, placebo-controlled, single-dose exogenous testosterone administration paradigms, allowing for critical tests of hypothesized causal relationships between a rapid increase in testosterone and the behavioural outcomes of interest. Such designs have the advantage of controlling and disaggregating the possible bidirectional relationships (i.e., behaviour → testosterone increase; testosterone increase → behaviour) that are ambiguous in the correlational designs that currently form a substantially larger part of the literature. In addition to using a testosterone

administration paradigm more generally, the studies here were also among the first to employ the Natesto intranasal testosterone formulation in a behavioural context, which offered the additional advantage of experimentally mimicking the natural rapid increase in testosterone (i.e., within 15-minutes) that can be observed in a host of environmental contexts, such as following competition (Geniole et al., 2017; Geniole & Carré, 2018) or exposure to mating-relevant stimuli (Roney & Gettler, 2015; Zilioli & Bird, 2017). Such an approach contrasts with other administration methods, such as single-dose or chronically administered topical gel or injections, each of which are useful in their own rights, but are less reflective of the speed with which testosterone can change in natural contexts. Thus, the dissertation experiments provide good ecological approximations of men's natural testosterone increase, and therefore may be useful templates from which future studies can design administration protocols that aim to understand the rapid effects of testosterone on human behaviour.

Experiments 1 and 2 collectively show that the effects of testosterone on interdependent economic decision-making can vary as a function of the individual's dispositional qualities (e.g., personality), adding to a small but growing literature that demonstrates personality moderation of testosterone effects. Studies one and two also suggest that the effects of testosterone can be more complex, with effects that depend on the context in which decisions are made, such as under environmental pressure to act quickly (or to wait and think carefully). Moreover, evidence from experiment 2, in particular, indicates that such contextual effects can themselves be dependent on the participant's disposition, such as interactions between participant sociosexuality and the sex and perceived attractiveness of observers.

Beyond the moderation effects of personality and context, Experiment 3 provides a test of a more general cognitive mechanism by which testosterone might exert behavioural effects. As reviewed in that chapter, most studies examining the effects of testosterone and executive functioning have focused on older adult men in the context of repeated and often longer-term testosterone administration for medical reasons (e.g., hypogonadism). Yet, testosterone—and particularly acute fluctuations in testosterone—plays a key role in behaviours for younger adults as well, with relevance to sex and mating, competition, and aggression, among other behaviours. Experiment 3 provides the first evidence that a rapid increase in testosterone can modulate at least some executive functions, thus providing a critical step in establishing a potential causal

cognitive mechanism. Future work would benefit not only from examining additional domains and tasks of executive functioning, but also more directly testing whether testosterone's downregulation of executive functions can account for variability in key behavioural domains of interest. In other words, a logical future experiment could administer testosterone or placebo, measure executive functioning via domain-specific tasks, and then measure the behavioural outcome (e.g., aggression); such a design would allow for a test of whether downregulated executive function mediates the link between testosterone and aggression or other behaviours.

The current literature on testosterone and economic decision-making shows generally mixed results, the reasons for which may include, for example, the sex of the participants, testosterone methodology (endogenous measurement vs. exogenous administration; single vs. repeated administration; dosage), the "file drawer" problem (Franco et al., 2014), or hidden moderators. Here, I add to these possibilities with a theoretical reason for why the results have been mixed. Evidence indicates that men's testosterone rapidly increases both in anticipation of, and in response to, environmental stimuli that hold relevance for human mating, such as exposure to opposite sex individuals and/or to competition (Geniole & Carré, 2018; Zilioli & Bird, 2017). Theoretical accounts based on this literature suggest that such rapid increases in testosterone serve to promote behaviour that ultimately favours reproductive fitness (Geniole & Carré, 2018; Zilioli & Bird, 2017). From this perspective, it raises the possibility that an effect of testosterone on economic decision making would be most specific to situations that more directly involve adaptive signals, and thus would include more social or interdependent contexts because of the potential consequences to status or mating. This could potentially help explain why testosterone has shown a more clear effect on economic tasks like the public goods game (as per experiments reported herein) or the ultimatum game (e.g., Dreher et al., 2016), where differential effects of prosocial and antisocial economic choice have possible ramifications for enhancing status. In contrast, decisions made in independent, non-social economic contexts, such as with the IGT, hold much less obvious consequences for status and/or reproduction, thus possibly accounting for the null effects found in Experiment 3 and with similar non-social tasks like the Balloon Analogue Risk Task (e.g., Stanton et al., 2021). Such a differential effect on social over non-social economic decision making would also be analogous to findings in other behavioural domains, such as evidence that exogenous

testosterone potentiates aggression when individuals are provoked in a social context (e.g., game play with another human) but not in non-social context (e.g., malfunctioning joystick in an independent game; Panagiotidis et al., 2017). Future work would benefit from directly comparing social to non-social economic decision-making tasks within the same testosterone administration study, and from modifying the status-relevant components in a given task (e.g., known identities vs. anonymous game participants; possibility to interact with other game members on a leadership task after the economic task) to explore the hypotheses that testosterone effects would be strongest in social over non-social economic decision-making, with particularly prominent effects observed when the reputational and/or mating-related consequences are most obvious.

5.3. Conclusion

In conclusion, the findings presented within this dissertation suggest that a rapid increase in testosterone can play a causal role in modulating men's economic decision-making and executive functioning, with effects that vary by individual disposition and the context of the decision. Future work that builds on these administration paradigms will help clearly elucidate the mechanistic pathways and boundaries of effects, helping to inform and refine behavioural accounts of decision-making that span social neuroendocrinology, evolutionary psychology, behavioural economics, and clinical psychology.

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Appendix A. Supplemental Materials for Experiment 1.

Individual difference moderators comprising the Risk Factor score

Moderator analyses using the individual difference variables comprising the risk factor score are presented below. The regression models included Drug Condition, Time Condition, an individual difference variable (models run three times—once for each moderator: dominance, self-control, and self-construal), and all two-way and three-way interactions. We further ran a single model with simultaneous inclusion of all individual difference variables. As with analyses involving the Risk Factor score, these analyses were conducted first with the whole sample (i.e., intent-to-treat) and then with the compliant-only sample, and are presented in this order for each individual difference variable. Descriptive statistics for scores on these variables are presented in Table A1, with bivariate correlations presented in Table A2.

Table A1. Descriptive statistics stratified by drug group.

Variable		Testosterone		Placebo	
		M	*SD*	*M*	*SD*
Age		23.06	4.88	22.55	4.49
Risk Score		-0.04	0.65	0.04	0.66
	Dominance	-0.05	0.91	0.05	0.93
	Self-Control	0.03	0.91	-0.03	0.93
	Self-Construal	0.33	0.86	0.39	0.90
PGG Contributions		320.06	121.09	326.48	116.67

Note. PGG = Public Goods Game. No significant differences between testosterone and placebo groups on traits, *t*s 0.59 – 1.0, *p*s .31 – .55.

Table A2. Bivariate correlations among the individual difference moderators, risk factor, and contributions in the Public Goods Game.

	1	2	3	4	5
1. Self-Construal	-	.144**	.284**	.582**	-.031
2. Self-Control		-	-.276**	-.578**	.031

3. Dominance	-	.797**	-.092
4. Risk Factor		-	-.079
5. PGG Contributions			-

Note. N = 400 men. Risk Factor is comprised of the average of the standardized scores for self-construal, self-control (reverse), and dominance. Higher scores on Self-Construal are associated with a more independent self-construal. PGG = Public Goods Game.

Self-control

Using the full sample, there were no main effects of Drug, Time Condition, or Self-control (|*bs*| = 8.96 – 34.93, *ps* = .21 – .59), nor any significant two-way interactions (|*bs*| = 10.19 – 23.69, *ps* = .40 – .84). The Drug x Time Condition x Self-Control interaction was significant (*b* = -157.21, *p* = .005). Follow-up analyses revealed a significant Drug x Time Condition interaction for men relatively low in Self-control (*b* = -168.48, *p* = .02), with somewhat reduced contributions following testosterone in the forced-delay condition (*b* = -88.81, *p* = .08), but not the time-pressure condition (*b* = 79.67, *p* = .14). For men relatively high in Self-control, the Drug x Time Condition interaction was marginally significant (*b* = 145.94, *p* = .08), but effects did not differ based on forced-delay (*b* = 48.03, *p* = .39) or time-pressure (*b* = -97.91, *p* = .12).

When restricting analyses to only men who complied with Time Condition instructions, a significant main effect of Time Condition was found (time-pressure contributions > forced-delay contributions, *b* = -169.00, *p* < .001). No other main effects or two-way interactions were significant (|*bs*| = 4.1 – 70.9, *ps* = .29 – .91). The three-way interaction between Drug, Time Condition, and Self-control was significant (*b* = -166.26, *p* = .019). Follow-up analyses indicated that the Drug x Time Condition interaction was significant among men with low self-control (*b* = -237.16, *p* = .009), such that testosterone reduced contributions in the forced-delay condition (*b* = -126.95, *p* = .025), but not the time-pressure condition (*b* = 110.21, *p* = .12). The Drug x Time Condition interaction was not significant for men low in Self-control (*b* = 95.37, *p* = .37).

Self-construal

For the full sample, no main effects or two-way interactions were significant (|*bs*| = 4.10 – 29.14, *ps* = .28 – .76). However, there was a significant Drug x Time Condition

x Self-Construal interaction (*b* = -135.96, *p* = .013). Follow-up analyses revealed that the Drug x Time Condition was significant among men with relatively independent self-construals (*b* = -156.45, *p* = .04), such that testosterone reduced contributions for independent men in the forced-delay condition (*b* = -106.59, *p* = .053), but had no significant effect in the time-pressure condition (*b* = 49.87, *p* = .342). Among men with relatively interdependent self-construals, the Drug x Time Condition interaction was not significant (*b* = 115.46, *p* = .135).

When restricting analyses to only men who complied with the Time Condition instructions, there was a main effect of Time Condition (time-pressure contributions > forced-delay contributions, *b* = -169.52, *p* < .001), but no other main effects or two-way interactions (|*bs*| = 6.29 – 67.88, *ps* = .18 – .70). As with the whole sample, there was a significant Drug x Time Condition x Self-Construal interaction (*b* = -166.43, *p* = .012), with follow up analyses indicating a significant Drug x Time Condition interaction for men with relatively independent self-construals (*b* = -234.32, *p* = .009) but not men with relatively interdependent self-construals (*b* = 98.55, *p* = .30). For men with independent self-construals, testosterone decreased contributions in the forced-delay condition (*b* = -140.20, *p* = .027), but had no significant effect in the time-pressure condition (*b* = 94.12, *p* = .14).

Dominance

Among the whole sample, there were no main effects of Drug (*b* = -13.21, *p* = 0.63), or Time Condition (*b* = -28.86, *p* = 0.29). A marginal main effect of Dominance (*b* = -23.08, *p* = .095) was suggestive of dominant men tending to give somewhat lower contributions than low dominant men. The two-way interactions (Drug x Time Condition, Drug x Dominance, Time Condition x Dominance) were non-significant (|*bs*| = 10.63 – 26.63, *ps* = .33 – .84), and the three-way interaction approached significance (Drug x Time Condition x Dominance: *b* = -87.73, *p* = .11). Probing the three-way interaction did not reveal any significant Drug x Time Condition interactions for men relatively high (*b* = -98.36, *p* = .20) or low (*b* = 77.10, *p* = .33) in dominance, although for high dominant men, testosterone slightly reduced contributions in the forced-delay condition (*b* = -80.14, *p* = .09) but not in the time-pressure condition (*b* = 9.22, *p* = .87).

When restricting analyses to only men who complied with the Time Condition instructions, there was a main effect of Time Condition such that time-pressure increased contributions compared to forced-delay (b = -167.28, p < .001). There was no main effect of Drug (b = -33.11, p = .32), and the same marginal main effect of Dominance was found as for the whole sample (b = -25.67, p = .13). Also consistent with the analyses with the whole sample, no significant two-way interactions were found (|bs| = 11.46–57.96, ps = .28 – .74), with a three-way interaction approaching significance (Drug x Time Condition x Dominance: b = -106.25, p = .12). Follow-up analyses indicated a marginal Drug x Time Condition interaction for men relatively high in dominance (b = -164.21, p = .07) such that for high in dominance, testosterone was associated with reduced PGG contributions in the forced-delay condition (b = -126.68, p = .03) but not the time-pressure condition (b = 37.53, p = .59). For men low in dominance, testosterone did not interact with Time Condition to predict PGG contributions (b = 48.29, p = .63).

Single model with inclusion of all moderators

Among the whole sample, there were no main effects of Drug (b = -22.36, p = .40) or Time condition (b = -35.06, p = .19). There were no main effects of any individual difference variables, no two-way interactions, and no Drug x Time condition x Dominance interaction (|bs| = 0.03 – 38.17, ps = .20 – .99). Consistent with the models run with the moderators individually, significant three-way interactions were found for Drug x Time condition x Self-construal (b = -152.88, p = .009), and Drug x Time Condition x Self-Control (b = -175.31, p = .002).

When restricting the analysis to only those who complied with timing instructions, the testosterone group were less cooperative, though this effect did not reach statistical significance (b = -46.60, p = .14). Moreover, there was a significant main effect for Time condition (forced-delay contributions < time-pressure contributions; b = -172.46, p < .001). There were no main effects of any individual difference variables, no two-interactions, and no Drug x Time condition x Dominance interaction (|bs| = 0.35 – 52.40, ps = .19 – .98). Again, consistent with the models for the individual moderators and the inclusive model with all participants, significant three-way interactions were observed for Drug x Time condition x Self-Construal (b = -179.42, p = .01), and Drug x Time condition x Self-Control (b = -175.00, p = .01).

Genotyping for androgen receptor CAG repeat polymorphism

DNA was collected and extracted from mouthwash (Heath et al., 2001) via the standard phenol-chloroform method. DNA concentrations were determined using a Nanodrop ND-1000 Spectrophotometer and standardized to 10ng/ µL for the polymerase chain reaction protocol. A forward primer (TCCAGAATCTGTTCCAGAGCGTGC) and reverse primer (GCTGTGAAGGTTGCTGTTCCTCAT) were used to amplify the CAG repeat polymorphism in exon 1 of the androgen receptor (AR) gene. Products were analyzed using LI-COR DNA Analyzer 4300 with a custom ladder and CAG repeat length was ascertained using Gene ImagIR software (Scanalytics). Consistent with prior studies using healthy populations (Maney, 2017), CAG repeat numbers for the present experiment ranged between 10 and 30.

Because CAG repeat length is known to vary across ethnicity (Sartor et al., 1999), as was true in the present sample (see Table A3), analyses testing the moderating role of CAG repeat number were restricted to Caucasian men (n = 322) to avoid ethnic confounds. The number of CAG repeats was undeterminable for 8 men, resulting in a sample size of n = 314 for analyses involving this genetic variable.

Table A3. CAG repeat length stratified by ethnic group.

	White	Black	Native/Aboriginal	Other	Non-White*
n	314	23	27	28	78
M	18.69	15.74	19.04	17.39	17.47
SD	2.89	2.40	3.46	2.84	3.21
Min	10	11	12	10	10
Max	30	21	29	22	29

* The Non-White category comprises the Black, Native/Aboriginal, and “Other” categories. CAG repeats varied by ethnicity, $F(3,391) = 8.99$, $p < .001$, with significantly longer CAG repeats for White vs. Black ($p < .001$) and Other ($p = .024$), Native/Aboriginal vs. Black ($p < .001$) and Other ($p = .037$), and Other vs. Black ($p = .044$); White vs. Non-White groups also differed significantly ($p = .001$).

Testing a moderating role of CAG repeat number

A lower number of repeats of the CAG motif in exon 1 of the human androgen receptor gene is associated with greater sensitivity to androgens (Chamberlain et al., 1994; Maney, 2017). To test the degree to which the effects of Drug Condition, Time Condition, Risk Factor, or their interactions differed depending on participants' androgen receptor sensitivity (CAG repeat length), a model was run examining the potential main and interactive effects of these four variables. Results revealed a main effect of Risk Factor, such that individuals with relatively high risk scores contributed less in the PGG than individuals with relatively low risk scores (b = -31.59, p = .04). The same three-way interaction identified in both the intent-to-treat and compliant-only analyses reported in the manuscript was again significant (Drug x Time Condition x Risk Factor, b = -149.04.02, p = .01). No other main effects, two-way interactions, or the four-way interaction were significant (|bs| = 0.41–42.44, ps = .17 – .98). Notably, a marginal Drug x Time Condition x CAG repeat interaction was found (b = 108.587, p = .078), with slightly stronger effects when excluding Risk from the model (Drug x Time Condition x CAG repeats: b = 123.31, p = .05). Probing this effect revealed a marginal Drug x Time Condition interaction for men with relatively low CAG repeats (b = -150.63, p = .08), but not men with relatively high CAG repeats (b = 95.99, p = .30). For men with relatively low CAG repeat lengths, testosterone reduced contributions in the forced delay condition (b = -115.18, p = .054), but did not significantly affect contributions in the time-pressure condition (b = 35.45, p = .57).

Controlling for PSAP performance, "belief effects", and session time

Our main analysis was repeated while controlling for participants' performance on a task completed earlier in the protocol (Point Subtraction Aggression Paradigm; PSAP). Results were unchanged, such that the same highly significant Drug x Time Condition x Risk Factor interaction emerged (b = -190.085, p < .001), with no main effects of Drug, Time Condition, Risk Factor, or their two-way interactions (|bs| = 9.93 – 33.25, ps = .22 – .84). We ran the same analysis while controlling for whether participants believed they received testosterone or placebo (i.e., the "belief effect"; (Eisenegger et al., 2010a), and again, results were unchanged, with a significant Drug x Time Condition x Risk Factor interaction (b = -194.80, p < .001) and no main effects of Drug, Time Condition, or Risk, nor any two-way interactions (|bs| = 0.72 – 32.82, ps = .22 – .99). Finally, we ran the analysis while controlling for session time, and results were once again the same, with a significant Drug x Time Condition x Risk Factor

interaction (b = -191.63, p < .001), and there were no main effects of Drug, Time Condition, Risk Factor, or their interactions (|bs| = 2.14 – 33.25, ps = .23 – .97).

Appendix A. Supplemental References

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Appendix B. Supplementary Materials for Experiment 2.

Table B1. Effects of Drug, Observer Condition (female, male), Observer Kindness (Kind), and Risk.

Predictors (fixed effects)	*estimates*	*se*	*LLCI – ULCI*	*p*
(Intercept)	368.92	5.26	358.62 – 379.22	< .001
Drug	-3.65	0.92	-5.45 – -1.84	< .001
Observer	-0.30	0.91	-2.08 – 1.48	.739
Kind	1.02	0.58	-0.11 – 2.16	.078
Risk	-7.86	5.20	-18.06 – 2.34	.134
Drug x Observer	0.17	1.82	-3.38 – 3.73	.924
Drug x Kind	1.87	1.09	-0.26 – 4.00	.087
Observer x Kind	0.43	1.06	-1.65 – 2.51	.685
Drug x Risk	-4.40	0.91	-6.20 – -2.61	< .001
Observer x Risk	-0.79	0.91	-2.58 – 1.00	.387
Kind x Risk	-1.84	0.57	-2.96 – -0.73	.001
Drug x Observer x Kind	-2.75	1.97	-6.62 – 1.12	.171
Drug x Observer x Risk	1.20	1.82	-2.38 – 4.78	.512
Drug x Kind x Risk	4.21	1.05	2.14 – 6.27	< .001
Observer x Kind x Risk	1.29	0.99	-0.66 – 3.23	.195
Drug x Observer x Kind x Risk	-2.76	1.93	-6.54 – 1.03	.160
Drug x Kind at:				
Low Risk	-2.34	1.50	-5.29 – 0.61	.121
High Risk	6.08	1.52	3.09 – 9.06	< .001
Conditional Effects of Drug:				
High Risk, Low Kind	-14.13	2.04	-18.12 – -10.13	< .001
High Risk, High Kind	-1.98	2.03	-5.96 – 2.01	.332

Table B2. Effects of Drug, Observer Condition (female, male), Observer Dominance (Dom), and Risk.

Predictors (fixed effects)	*estimates*	*se*	*LLCI – ULCI*	*p*
(Intercept)	369.82	5.11	359.80 – 379.84	< .001
Drug	-1.72	0.51	-2.72 – -0.71	< .001
Observer	-0.40	0.51	-1.40 – 0.60	.430
Dom	0.39	0.32	-0.23 – 1.01	.217

Risk	-8.67	5.06	-18.59 – 1.25	.090
Drug x Observer	-0.35	1.02	-2.35 – 1.65	.734
Drug x Dom	0.98	0.61	-0.22 – 2.18	.111
Observer x Dom	0.72	0.59	-0.43 – 1.87	.218
Drug x Risk	-1.39	0.52	-2.41 – -0.36	.008
Observer x Risk	-0.47	0.53	-1.51 – 0.58	.382
Dom x Risk	-0.07	0.30	-0.65 – 0.51	.823
Drug x Observer x Dom	-0.56	1.14	-2.80 – 1.68	.625
Drug x Observer x Risk	0.38	1.06	-1.69 – 2.46	.717
Drug x Dom x Risk	-0.28	0.53	-1.30 – 0.75	.600
Observer x Dom x Risk	0.48	0.49	-0.48 – 1.45	.324
Drug x Observer x Dom x Risk	-0.58	0.94	-2.42 – 1.25	.537
Conditional Effects of Drug:				
Low Risk	-0.33	0.68	-1.66 – 1.00	.628
High Risk	-3.10	0.78	-4.64 – -1.57	< .001

Table B3. Effects of Drug, Risk, and Sociosexual Orientation (SOI) for the male and female observer conditions.

Predictors (fixed effects)	*estimates*	*se*	*LLCI – ULCI*	*p*
Female Observer				
(Intercept)	368.21	5.60	357.22 – 379.19	< .001
Drug	-2.44	2.10	-6.56 – 1.68	.249
Risk	-11.02	6.05	-22.87 – 0.83	.072
SOI	-7.11	5.75	-18.39 – 4.17	.220
Drug x Risk	-2.14	2.22	-6.48 – 2.21	.337
Drug x SOI	-6.54	2.18	-10.82 – -2.26	.004
Risk x SOI	-7.67	5.61	-18.66 – 3.32	.175
Drug x Risk x SOI	-1.75	2.05	-5.77 – 2.28	.397
Conditional Effects of Drug:				
Restricted SOI	4.10	2.86	-1.52 – 9.71	.604
Unrestricted SOI	-8.98	3.19	-15.23 – -2.73	.006
Male Observer				
(Intercept)	368.19	5.66	357.09 – 379.29	< .001
Drug	-5.75	2.10	-9.86 – -1.64	.007
Risk	-8.14	6.11	-20.11 – 3.84	.186
SOI	-6.40	5.82	-17.80 – 5.00	.274
Drug x Risk	-4.51	2.21	-8.84 – -0.18	.044

Drug x SOI	-6.18	2.18	-10.44 – -1.91	.006
Risk x SOI	-3.41	5.67	-14.52 – 7.70	.549
Drug x Risk x SOI	-3.15	2.05	-7.16 – 0.86	.127
Conditional Effects of Drug:				
Restricted SOI	0.43	2.85	-5.16 – 6.03	.880
Unrestricted SOI	-11.93	3.18	-18.16 – -5.70	< .001