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Testosterone administration increases social discounting in healthy males

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ABSTRACT

Although testosterone is thought to induce antisocial and aggressive behavior, research on social economic interactions has associated it with prosocial and affiliative behavior. Here, we investigated the effects of testosterone on social distance-dependent generosity in an economic discounting task where participants chose between selfish and generous alternatives. We administered testosterone gel or placebo to men in a double-blind, randomized design and measured how willing they were to share rewards with close and distant others. Across two studies (total n = 174), testosterone administration consistently increased social discounting, that is participants became more selfish, particularly with regard to distant others (vs. close others). This effect was not explained by testosterone-induced increases in social distance perception. Our findings provide causal evidence that-testosterone reduces generosity in human economic decision-making. Moreover, they suggest that the valuation and the perception of social distance are independently affected by testosterone.

1. Introduction

Testosterone is a steroid hormone that plays a central role in physical masculinization and sexual function (Mooradian et al., 1987). It is associated with antisocial and aggressive behavior in both non-humans and humans (e.g. Gleason et al., 2009; Mazur and Booth, 1998). For example, field studies found that more-violent male and female prison inmates had higher testosterone levels than less-violent inmates (Dabbs and Hargrove, 1997; Dabbs et al., 1995). However, these findings are far from conclusive, particularly in the human literature. First, meta-analytic evidence suggests that the relationship between testosterone and aggression is small in magnitude (r = 0.08, Archer et al., 2005; see also Book et al., 2001); second, experimental evidence, including recent-testosterone administration studies, indicates that individual differences in personality (Carré et al., 2016; Mehta et al., 2015; Norman et al., 2016) and genetic factors (Geniole et al., 2019) moderate the link between testosterone and aggression (for a review, see Carré and Archer, 2018).

Economic games can serve to study the link between testosterone and non-physical forms of aggression. For example, in the classic Ultimatum Game, two players are asked to divide an amount of money between them. The responder usually rejects unfair offers from the proposer, and rejection of unfair offers can be interpreted as proxy of reactive (non-physical) aggression (Güth et al., 1982). Studies using the Ultimatum Game as a model for understanding the hormonal underpinnings of aggressive behavior found that higher endogenous testosterone levels were associated with a higher propensity to reject unfair offers (Burnham, 2007; Mehta and Beer, 2010). This relationship has been conceptually supported by some testosterone administration studies (i.e., increased punishment of proposers who made unfair offers rather than increased rejection rate per se; Dreher et al., 2016; see also Zak et al., 2009 reporting reduced offer size in proposers). However, other studies have reported null results (e.g. Cueva et al., 2017; Eisenegger et al., 2010; Zethraeus et al., 2009) and one study has even reported a trend-level increase in the propensity to accept unfair offers after testosterone administration (Kopsida et al., 2016). As in the case of the broader testosterone/aggression literature, these heterogeneous findings seem to suggest that important moderators at the sample (e.g., sex differences) and research design level (e.g., method used to deliver testosterone) might modulate the link between testosterone and behavior in the Ultimatum Game.

A complementary line of research has associated testosterone with

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prosocial behavior. For instance, testosterone administration increased reciprocity when repaying trust (Boksem et al., 2013) as well as the propensity to reward proposers who made fair offers in the Ultimatum Game (Dreher et al., 2016). Notably, most of the findings are based on social economic games in which the distinction between prosocial motives and other social motives, such as reputation building, strategic responding, and status management, is convoluted (Eisenegger et al., 2011). Testing the effects of testosterone using paradigms that less ambiguously target prosocial motives is necessary to more accurately understand the effect of testosterone on prosocial behavior.

In the present study, we aimed at investigating the role of testosterone in human generosity by combining testosterone administration with a social discounting task, where prosociality in the form of generosity was less confounded with other social motives. In each trial, healthy male participants were asked to choose between a selfish and a generous alternative. The generous alternative involved sharing money with either a close or a distant other, whereas the selfish alternative yielded a payoff only for the participant (Jones and Rachlin, 2006; Strombach et al., 2015). We combined this task with testosterone administration in a double-blind, placebo-controlled, between-subjects design to test whether and how testosterone modulates generosity.

Generosity tends to decrease with social distance, that is people typically are more selfish with distant others than with close others (Jones and Rachlin, 2006; Margittai et al., 2015; Soutschek et al., 2016, 2017; Strombach et al., 2015). Testosterone has been linked to parochial altruism such that individuals with endogenously high levels of testosterone behave in a more prosocial fashion towards ingroup (i.e., closer) individuals and more selfishly towards outgroup (i.e., more distant) individuals (Diekhof et al., 2014). Accordingly, one possibility would be that-testosterone decreases generosity towards distant others, but increases generosity towards close others.

We also aimed at investigating the perception of social distance as a potential channel through which testosterone may affect social distance-dependent generosity. Changes in perception of social distance are sufficient for affecting social decisions (c.f., Bohnet and Frey, 1999). To operationalize this mechanism, participants were asked to use computer avatars to represent the psychological distance between themselves and individuals of varying social distances (modified from Vekaria et al., 2017). Based on the testosterone/parochialism link described above (Diekhof et al., 2014), we tested the hypothesis that-testosterone-induced changes in generosity are mediated by testosterone-induced changes in social distance perception. Specifically, we hypothesized that increases in generosity would be mediated by reduced distance perception, while reductions in generosity would be mediated by increased distance perception.

2. Study 1

2.1. Methods

2.1.1. Participants

We recruited 63 male participants (discovery sample; mean age = 21.3 years, *SD* = 1.5, age range = 19–26) through advertisements on the university campus. The sample size of Study 1 was determined based on our past work using a similar protocol (Wu et al., 2018). Data of five participants were excluded from analysis. Three of them did not follow the task instructions, one participant did not finish the experiment, and one participant's data could not be fit by a hyperbolic social discounting function (see below). This left 58 participants (mean age = 21.2 years, *SD* = 1.4, range = 19–25), 29 who received testosterone and 29 who received placebo.

Participants were screened with a telephone interview to exclude individuals taking psychotropic medications and those with a history of psychiatric or neurological disorders. We studied males as the dosing and pharmacokinetics of a single dose of Androgel has been established for men only (Eisenegger et al., 2013). Participants were instructed to abstain from alcohol, caffeine, and smoking for 24 h before the testing session. The study was conducted in accordance with the Declaration of Helsinki and approved by the Medical Research Ethics Committee of Shenzhen University. All participants provided written informed consent and were paid RMB 200 (~$30) as a flat fee plus a variable amount depending on their decisions during the social discounting task (see below).

2.1.2. Testosterone administration

Participants engaged in a double-blind, placebo-controlled, between-participant design. All sessions started at 13:00 and lasted approximately 4.5 h. Participants in the testosterone condition received a single dose of 150 mg testosterone gel [Androgel®]. Participants in the placebo condition received a colorless hydroalcoholic gel. In both conditions, a male research assistant, who was blind to both the experimental conditions and the purpose of the study, applied the gel to participants' shoulders and upper arms. The decision-making task commenced 3 h post-dosing following similar testing protocols (Eisenegger et al., 2013; Wu et al., 2018; see also Supplementary Material for additional data establishing the time course for Androgel in Study 1). Participants also completed two additional tasks of social cognition following the social discounting study, one on risky decision-making and the other on social interactions. These tasks are not reported here. During the waiting period, participants rested in the testing rooms and were provided with newspapers and magazines that were not related to the study.

2.1.3. Social discounting task

The social discounting task was a modified version of the task used by Strombach et al. (2015). The task was presented using E-Prime (version 2.0; Psychology Software Tools, Inc., PA, USA). At the start of the experiment, we instructed participants to familiarize themselves with the concept of social distance. Using a 20-point scale (1 = very close; 20 = not close), participants were asked to rate their closeness to the following individuals: mother, father, sibling, partner, child, grandparent, family member, kin, best friend, member of circle of friends, colleague, neighbor, acquaintance, and stranger. In case some of these people did not exist in the participant's social environment, the corresponding trial was skipped. We used this protocol to familiarize participants with the concept of social distance and to make them think about their social network.

In preparation of the main task, we asked participants to parse their social environment and identify people who were at the following social distances: 1, 2, 3, 5, 10, 20, 50, and 100. Except for social distances 50 and 100 (mere acquaintances and complete strangers), participants reported on a paper the names of the person at each social distance, their relationship with the other person, and the contact information for payment purposes. We explicitly instructed participants to only consider individuals towards whom they held positive or neutral attitudes. To ensure participants remembered which person they had assigned to different distances during the main task, the paper containing this information was put on the desk in front of them. Participants were encouraged to look at the paper if they were to forget the person relevant for a particular trial.

In each trial of the main task, participants chose between (a) a selfish alternative (receiving a variable, larger amount of money) and (b) a generous alternative (receiving a constant, smaller amount of money and bestowing the same amount of money to the specified person at one of the eight social distance levels). The selfish alternative varied from RMB 130 to RMB 290, in nine increments of RMB 20. In the generous alternative, both the participant and the person shown in the trial received RMB 130. We used the same amounts as Ma et al., 2015 and Pornpattananangkul et al., 2017, who used the social discounting task in Chinese participants. Each combination of social distance and selfish amount was presented once during the experiment, resulting in a total of 72 unique trials (8 distances X 9 selfish amounts). The task comprised eight blocks, with each block representing one person at a specific social distance. Within each block, the order of the selfish amounts was randomized. Moreover, the order of the blocks was randomized across participants. We used a block design to minimize the cognitive load of switching between people at different social distance levels.

The task was incentive-compatible such that one trial was randomly selected, and 5% of the chosen amount(s) was paid out at the end of the experiment. With generous choices for partners at social distance 50 or 100, a random person in the same building or on campus received the money. All payments were implemented via “Alipay”, a popular smartphone payment platform in China. Participants were asked to provide the Alipay account, which often coincides with the phone number, of the person associated with a specific social distance at the beginning of the study. With payments to others, the specified person only received one message on Alipay stating that the transferred amount was part of a compensation in a psychological experiment one of their friends or relatives participated in. No further explanation was given.

In each trial, social distance information was presented by using both numbers and icons (see Fig. 1A). The numbers (1, 2, 3, 5, 10, 20, 50, or 100) indicated the social-distance levels of partners. Two icons were used. The leftmost icon was purple and represented the participant. The yellow icon represented the partner. In each trial, the distance between the purple and yellow icons corresponded to the social distance. The two alternatives were presented alphanumerically. Participants had unlimited time to make a decision. This was followed by a 1 s inter-trial interval (ITI), during which participants viewed a fixation cross.

2.1.4. Social distance construal task

The social distance construal task was adapted from Vekaria et al. (2017). Similar to the social discounting task, this task required participants to consider several different social relationships that varied in social distance. Using computer avatars, participants selected a physical distance that best represented the social distance between them and the other person. In each trial, participants were presented with a virtual stage depicted as a grid on which an avatar labeled “You” was positioned in a random corner of the grid (see Fig. 1B). Next, a second avatar, which was labeled as one of the possible other individuals, appeared in the grid. For example, “Chinese citizen” referred to a non-specified person with Chinese nationality. Participants were asked to position the second avatar anywhere on the stage by moving it with the computer mouse. Each trial ended after a location was selected. The task was presented in Microsoft PowerPoint, and the order of other individuals was randomized across participants. All participants performed the social distance construal task after the social discounting task. The seven specific social relationships included: (1) relative by blood; (2) relative by marriage; (3) close friend; (4) next-door neighbor; (5) co-worker; (6) Chinese citizen; (7) citizen of another country.

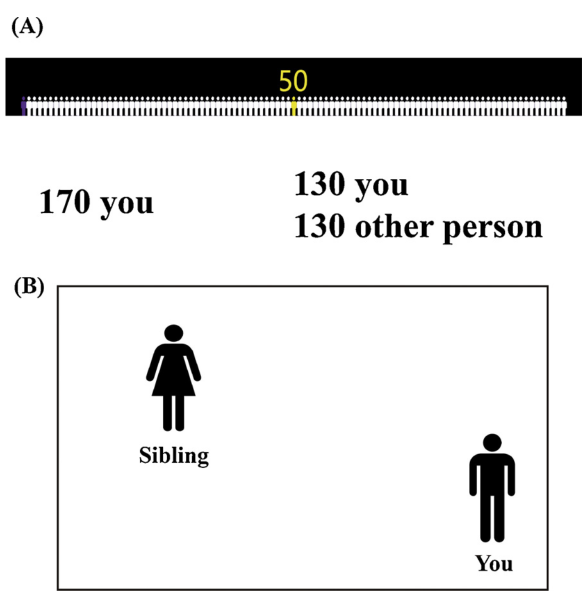

Fig. 1. Experimental tasks. (A) Social discounting task measuring generosity as a function of social distance. In each trial, participants were asked to decide between a selfish and a generous alternative, with the amount of the selfish alternative varying across trials and social distance of the other person varying across blocks. (B) Social distance construal task measuring perception of social distance. Participants were asked to use computer avatars to indicate the psychological distance between themselves and individuals at varying social distances.

2.1.5. Selfishness/generosity measure

To determine how testosterone affected selfishness/generosity, we followed previously published approaches (Jones and Rachlin, 2006; Soutschek et al., 2017; Strombach et al., 2015). Specifically, we first determined subjective indifference points for each social distance level using logistic regression. These indifference points correspond to the selfish reward amount at which a participant chooses the selfish and the generous alternative equally often (50%). Each indifference point thereby identifies the amount of money a participant is willing to forgo for a person at a specific social distance (Jones and Rachlin, 2006).

When participants exclusively chose the selfish or the generous alternative throughout a particular social distance level, the amount forgone would be set at half of an increment below and above the range of selfish alternatives (i.e., at RMB 120 and 300, respectively). We then subtracted RMB 130 (the amount participants would have earned if they had chosen the generous alternative) from the calculated amount, resulting in the amount forgone as the actual cost of choosing generously. Thus, the amount forgone served as a measure of generosity. We used this measure to formalize how generosity decreases as social distance increases, in keeping with the literature (Jones and Rachlin, 2006; Soutschek et al., 2017; Strombach et al., 2015). In our paradigm, selfishness was the opposite of generosity.

In our first analysis, we imposed no model on the relationship between generosity and social distance, thereby making no assumptions about the shape of the discounting curve. Specifically, we determined the area under the curve (AUC) of the amounts forgone at each social distance for each group. We calculated AUC for each participant by normalizing amount forgone v as a percentage of maximum v, normalizing social distance D as a percentage of maximum D, connecting the amount forgone points by straight lines, and then summing the trapezoids formed (Fig. S3; Vekaria et al., 2017). Following standardization, AUC can vary from 1 (no discounting) to 0 (maximal discounting). AUC can be interpreted as model-free measure of generosity (Myerson et al., 2001). Using two-sample t-tests, we assessed group differences in AUC.

In a second set of analyses, we investigated generosity as a function of social distance with a social discounting model (Jones and Rachlin, 2006). We fitted the amount forgone at each social distance to the standard hyperbolic model, $v = V/(1 + kD)$ (Jones and Rachlin, 2006), where v was the amount forgone at each social distance, D was the social distance level, and V and k were free parameters representing the intercept (willingness to be generous at $D = 0$) and slope of the function (steepness by which willingness to be generous decreased as a function of social distance). Thus, V indexed generosity at close social distances, with high values reflecting increased generosity towards close others, while k represented the degree of decline in generosity with increasing social distance, with larger values reflecting steeper declines.

To some extent, V and k were linked such that increases in the slope of the function (k) tended to be compensated by concomitant increases in V. We therefore considered independent model-free confirmation of commonly increasing effects of testosterone on both V and k by assessing amounts forgone for others at each social distance level. We used two-sample t-tests to investigate testosterone effects on V and k and on amounts forgone for others.

2.1.6. Social distance construal measure

We determined perceived social distance for each of the social relationships by calculating the length in pixels of the hypotenuse of the triangle formed by the self-avatar position and the second avatar using the Pythagorean equation ($a^2 + b^2 = c^2$) (Vekaria et al., 2017). We then analyzed these values with a mixed-measure ANOVA including Treatment (testosterone vs. placebo) as the between-subjects factor and social distance as the within-subject factor. Bonferroni correction was applied to account for multiple comparisons.

We used the calculated hypotenuses to derive an index that captured individual differences in social distance perception. Specifically, we regressed the hypotenuses against the presented social distance level within each participant. Steeper slopes indicated that participants increased their perceived distance more strongly in response to a given increase in presented distance. Thus, these slopes captured individual sensitivity in social distance perception. Finally, we tested whether social distance perception as captured by this slope index statistically mediated the hypothesized effect of testosterone on generosity, as indexed by AUC. We bootstrapped (20,000 iterations) the bias-corrected 95% confidence interval for the indirect effect using the SPSS version of INDIRECT macro (Preacher and Hayes, 2008).

2.1.7. Open practices

All the data and analysis scripts are available on the project's Open Science Framework (OSF) page: https://osf.io/f57er/

2.2. Results

2.2.1. Social distance reduces generosity

As expected, amounts forgone decreased significantly as social distance increased, b = -1.13, SE = 0.06, t = -19.74, $p < .001$, 95% CI= [-1.24, -1.01], $R^2 = 0.57$. Both the testosterone group (b = -1.23, SE = 0.08, t = -15.19, $p < .001$, 95% CI= [-1.39, -1.07], $R^2 = 0.58$) and the placebo group (b = -1.02, SE = 0.08, t = -12.8, $p < .001$, 95% CI= [-1.17, -0.86], $R^2 = 0.56$) showed this effect (see Fig. 3A), indicating that, regardless of the treatment condition, generosity decreased as social distance increased (Jones and Rachlin, 2006; Soutschek et al., 2017; Strombach et al., 2015).

2.2.2. Testosterone reduces generosity

Compared to placebo, testosterone appeared to reduce the amount participants were willing to forgo (Fig. 2A). To confirm this impression statistically, we first-tested whether testosterone administration had an effect on AUC, our model-free measure of generosity (see Methods). The testosterone group (M = 0.24, SD = 0.16) showed significantly smaller AUC measures (Fig. 3A) than the placebo group (M = 0.36, SD = 0.19), t_{56} = -2.67, p = 0.01, 95% CI= [-0.22, -0.03], Cohen's d = 0.70. Thus, compared to placebo, testosterone reduced generosity overall, as indexed by the model-free measure of generosity.

Next, we examined whether testosterone influenced the shape of the social discounting function, separately assessing changes in generosity towards close and distant others. For this purpose, we fitted a standard hyperbolic discounting model to the amount forgone for each participant individually (see Methods). This model qualitatively captured individual discounting behavior (see Fig. 2A). A between-group comparison of model parameters indicated two effects. First, the testosterone group (M = 0.19, SD = 0.15) showed steeper discounting (k) than the placebo group (M = 0.03, SD = 0.21), t_{56} = 3.21, p = .002, CI= [0.06, 0.25], Cohen's d = 0.84. Second, participants in the testosterone group (M = 177.81, SD = 36.12) showed higher V than those in the placebo group (M = 131.77, SD = 73.54), t_{56} = 3.03, p = .004, CI= [15.56, 76.52], Cohen's d = 0.79. At a first glance, these findings seemed to suggest that-testosterone increased generosity for closer others but decreased it for more distant others. However, because V and k tended to be intrinsically linked (increases in k were associated with increases V), these results need to be interpreted with caution and corroborated by model-free analyses of behavior, which we report next.

We assessed the effects of testosterone on amounts forgone for others in an 8 × 2 mixed ANOVA with average amounts forgone as the dependent variable. Model-free analysis revealed a significant interaction between group and social distance, $F(7, 392) = 2.65$, p = .028, η_p^2 = .045. In simple effect analyses (where we used Bonferroni correction to control for multiple comparisons), the testosterone group showed significantly smaller amounts forgone for distant others compared to the placebo group (social distances 20, 50, and 100), t (56) = -2.87, p = 0.006, CI= [-53.74, -9.54], Cohen's d = 0.75, t (56) = -2.22, p = 0.03, CI= [-42.33, -2.17], Cohen's d = 0.58, t (56) = -2.28, p = .026, CI= [-44.47, -2.89], Cohen's d = 0.60. In contrast, we found no group differences at closer levels of social distance (social distances 1, 2, 3, 5, and 10), t (56) = 0.13, p = .90, CI= [-9.70, 11.08], Cohen's d = 0.03, t (56) = 0.59, p = .56, CI= [-12.57, 23.11], Cohen's d = 0.16, t (56) = -1.26, p = .21, CI= [-31.20, 7.13], Cohen's d = 0.33, t (56) = -0.41, p = .68 CI= [-23.55, 15.53], Cohen's d = 0.11, and t (56) = -1.34, p = .19, CI= [-42.74, 8.55], Cohen's d = 0.35. Thus, compared to placebo, testosterone reduced generosity at higher – but not lower – levels of social distance (reflected by both the model-based effect on k and the model-free interaction and post-hoc tests). Notably, the apparent model-based increases in generosity at close social distances (V) were not borne out by concomitant model-free differences at short social distances, illustrating the importance of corroborating model-based

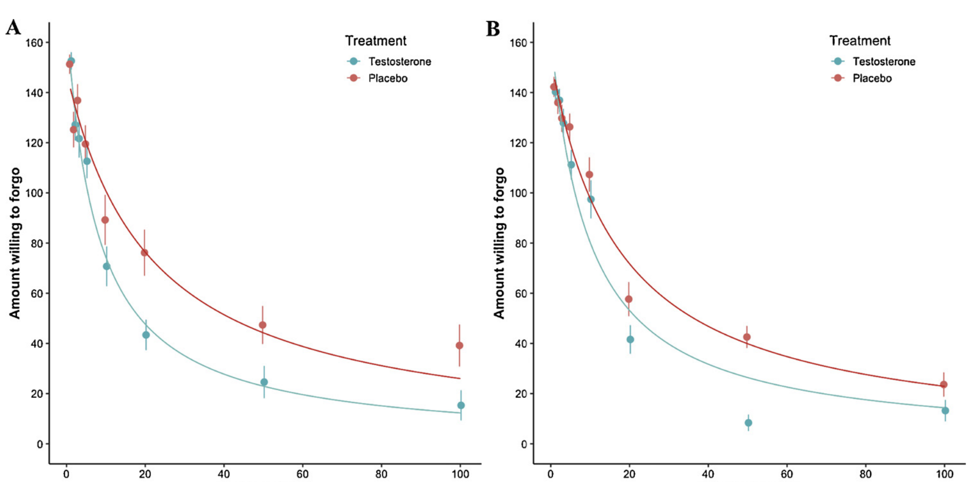

Fig. 2. Effects of testosterone administration on generosity as a function of social distance. To quantify generosity, we used the mean amount of money participants decided to forgo for other persons at increasing social distance. The lines represent the fit of hyperbolic models to amounts forgone. Generosity decreased with increasing social distance, in both testosterone and placebo groups. Importantly, compared to placebo, testosterone more strongly reduced generosity towards distant others than towards close others (i.e. steeper social discounting), in both Study 1 (A) and Study 2 (B). Error bars represent standard errors of the mean.

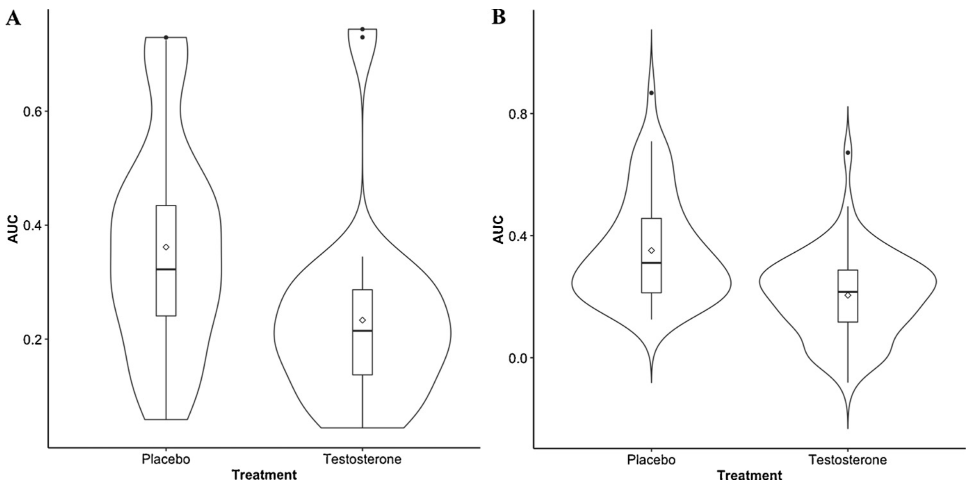

Fig. 3. Effects of testosterone administration on model-free measure of generosity as indexed by AUC. The testosterone group showed reduced generosity (smaller AUC) than the placebo group, in both Study 1 (A) and Study 2 (B). In the box-whisker contours, the hallow points represent mean values for each group. The boxes represent the first (bottom) and third (top) quartiles. The band represents the median. The shaded areas represent the relative percentage (frequency) of participants with corresponding AUC values.

with model-free analyses. In sum, our findings support the conclusion that-testosterone reduced generosity primarily towards distant rather than close others.

2.2.3. (Lack of) testosterone effects on social distance perception

Next, we asked whether testosterone affected perceptions of social distance differently than placebo. In a 2 (between-participant factor: testosterone vs. placebo) X 7 (within-participant factor: seven social relationships) mixed ANOVA, we found a significant main effect of social relationship, $F(6, 336) = 222.55$, $p < .001$, $\eta_p^2 = .80$. As expected, tests of within-subject contrasts revealed a linear relationship between presented and perceived social distance (see Fig. 4), $F(1, 56) = 600.73$, $p < .001$, $\eta_p^2 = .92$, demonstrating that increases in presented social distance were associated with increases in perceived social distance. More importantly, the two groups differed marginally in their social distance perception, $F(1, 56) = 3.30$, $p = .075$, $\eta_p^2 = .06$. Specifically, testosterone tended to increase perceived social distances compared to placebo, regardless of social distance. The interaction between groups and relationship distance was not significant, $F(6, 336) = 1.69$, $p = .16$, $\eta_p^2 = .03$.

2.2.4. Testosterone effects on generosity are independent of effects on perception

Given that-testosterone administration increased social discounting significantly and social distance perception at trend level, we tested whether social distance perception explained generosity decisions. First, the results in the social discounting task on AUC remained qualitatively the same when we included social distance perception as a covariate (see Methods) (main effect of treatment, $b = -0.12$, $SE = 0.05$, $t = -2.59$, $p = .01$, 95% CI = [-0.21, -0.03], $R^2 = 0.11$). Second, we conducted a mediation analysis to examine whether testosterone influenced social discounting via social distance perception. The slope of social distance perception was used as a mediator (see Methods). The 95% bias-corrected confidence interval for the indirect effect was [-0.0054, 0.0434] (estimated indirect effect = 0.0023, SE = 0.0082). Because the confidence interval included zero, we cannot conclude that social distance perception mediated the relationship between testosterone administration and social discounting (i.e., AUC of the amount forgone).

3. Study 2

Given that there is growing concern with the reproducibility of published hormonal research (Lane et al., 2016; Nave et al., 2015) and psychological science in general (Open Science Collaboration, 2015), we conducted Study 2, which provides a direct replication test of Study 1.

3.1. Methods

3.1.1. Participants

We recruited 121 male participants for Study 2 (replication sample; mean age = 21.7 years, $SD = 2.0$; age range = 18–27). The sample size of Study 2 was determined based on the effect size (AUC, Cohen's d = 0.70) of Study 1. Using G*Power 3.1 (Faul et al., 2007), we set α at 0.05 and $1 - \beta$ at .95, resulting in a sample size of 110 participants (55

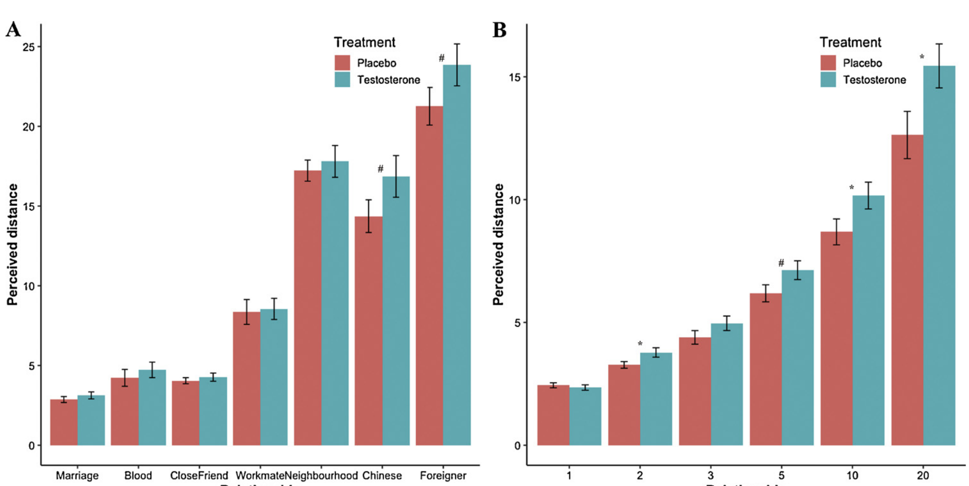

Fig. 4. Effects of testosterone administration on social distance perception in the social distance construal task. Testosterone increased mean perceived distance across social relationships at trend level in Study 1 (A) and increased perceived distance particularly for distant others in Study 2 (B). Error bars represent standard errors of the mean. Symbols indicate significance in the two-sample t test (# $p < .1$ * $p < .05$).

per group). We recruited 121 participants to allow for possible non-compliance or impossibility of model fit.

In Study 2, two participants always chose the same option, and three participants' data could not be fit by the hyperbolic function. These five participants were excluded, leaving 116 participants for the final analysis (mean age = 21.7 years, *SD* = 2.0, range = 18–27), with 61 in the testosterone condition and 55 in the placebo condition.

3.1.2. Testosterone administration

We followed the same testosterone administration protocol as in Study 1.

3.1.3. Social discounting task

Participants performed the same social discounting task as in Study 1.

3.1.4. Social distance construal task

To increase comparability with the social discounting task, we slightly modified the social distance construal task for Study 2. In particular, each participant was asked to consider the distance between himself and the individuals specified for various distances (1, 2, 3, 5, 10, 20) of the social discounting task. We excluded social distances 50 and 100, because pilot studies showed that it was difficult for participants to construct distances for mere acquaintances and complete strangers.

3.1.5. Data analysis

We followed the same data analysis protocol as in Study 1.

3.2. Results

3.2.1. Testosterone reduces generosity: replication

Study 1 suggested that-testosterone reduced generosity and there was a trend effect of testosterone increasing social distance perception. Study 2 represents an adequately-powered replication of Study 1. As in Study 1, amount forgone decreased with increasing social distance, b = -1.28, SE = 0.04, t = -29.46, $p <$ .001, 95% CI = [-1.37, -1.20], R^2 = 0.58 in both the testosterone group (b = -1.33, SE = 0.06, t = -20.91, $p <$ .001, 95% CI = [-1.45, -1.20], R^2 = 0.56) and the placebo group (b = -1.23, SE = 0.06, t = -20.94, $p <$ .001, 95% CI = [-1.34, -1.11], R^2 = 0.59). Corroborating findings from Study 1, testosterone administration significantly reduced the model-free measure of generosity, as indicated by a smaller AUC of amounts forgone in the testosterone (M = 0.21, SD = 0.14) compared to the placebo group (M = 0.34, SD = 0.17), t_{114} = -4.76, $p <$ .001, 95% CI = [-0.19, -0.08], Cohen's d = 0.88.

The standard hyperbolic model fit to average amounts forgone qualitatively captured behavior for both the testosterone and the placebo group (see Fig. 2B). In line with Study 1, the testosterone group (M = 0.20, SD = 0.25) showed steeper discounting (k) than the placebo group (M = 0.03, SD = 0.14), t_{114} = 4.37, $p <$ .001, 95% CI = [0.09, 0.25], Cohen's d = 0.82. We again found higher V in the testosterone group (M = 183.35, SD = 63.41) compared to the placebo group (M = 144.61, SD = 66.33), t_{114} = 3.22, p = .002, 95% CI = [14.87, 62.62], Cohen's d = 0.60. Thus, also the model-based analysis of Study 2 replicated Study 1 and showed reduced generosity after testosterone administration.

In a 8 (social distance) X 2 (treatment) mixed ANOVA with averaged amounts forgone as dependent variable, social distance significantly interacted with treatment, F(7, 798) = 2.994, p = .010, η_p^2 = .026. Simple effect analyses revealed that-testosterone significantly reduced amount forgone at D (social distance) = 5 (t_{114} = -2.15, p = .034, 95% CI = [-32.90, -1.31], Cohen's d = .40) and D = 50 (t_{114} = -5.97, p = .017, 95% CI = [-43.29, -21.72], Cohen's d = 1.10), but not at other social distances, D = 1 (t_{114} = -0.28, p = .78, 95% CI = [-14.90, 11.20], Cohen's d = 0.05), D = 2 (t_{114} = -0.03, p = .97, 95% CI = [-13.11, 12.66], Cohen's d = 0.01), D = 3 (t_{114} = -0.05, p = .96, 95% CI = [-15.52, 14.70], Cohen's d = 0.01), D = 10 (t_{114} = -0.67, p = .51, 95% CI = [-27.29, 13.57], Cohen's d = 0.12), D = 20 (t_{114} = -1.48, p = .14, 95% CI = [-30.27, 4.34], Cohen's d = 0.28), D = 100 (t_{114} = -1.14, p = .26, 95% CI = [-19.10, 5.11], Cohen's d = 0.21). These results overlapped partially with those of Study 1, which also found group differences at D = 50, but not at D = 5. Overall, the two studies converge with regard to the model-based effect of testosterone on k (i.e., testosterone induced reduction in generosity as social distance increased). Similar to Study 1, the apparent model-based increases in generosity at close social distances (V) were not supported by model-free analysis at close social distances. If anything, generosity decreased also at close social distances.

3.2.2. Testosterone increases social distance perception

Similar to Study 1, testosterone increased perceived social distance, F(1, 114) = 5.56, p = .02, η_p^2 = .046, an effect further qualified by a significant interaction between treatment condition and social distance level, F(5, 570) = 3.82, $p <$ .05, η_p^2 = .032. Simple effect analyses showed that-testosterone treatment increased social distance perceptions at D = 2 (t_{114} = 2.13, p = .035, 95% CI = [0.04, 1.02], Cohen's d = 0.40), D = 10 (t_{114} = 2.04, p = .044, 95% CI = [0.04, 3.17], Cohen's d = 0.38), and D = 20 (t_{114} = 2.29, p = .024, 95% CI = [0.41, 5.74], Cohen's d = 0.42), but not at other levels, D = 1 (t_{114} = -0.65, p = .52, 95% CI = [-0.41, 0.21], Cohen's d = 0.12), D = 3 (t_{114} = 1.45, p = .15, 95% CI = [-0.22, 1.44], Cohen's d = 0.27). There was a trend effect at D = 5 (t = 1.93, p = .056, 95% CI = [-0.02, 2.10], Cohen's d = 0.36). Together, testosterone increased social distance perception at both short and intermediate distances.

3.2.3. Testosterone effects on generosity are independent of effects on perception

The finding that-testosterone reduced AUC in the social discounting task remained qualitatively the same when we used the social distance perception index (Methods) as a covariate (main effect of treatment, b = 0.14, SE = 0.04, t = 3.73, $p <$ .001, 95% CI = [0.07, 0.22], R^2 = 0.22. Similar to Study 1, we tested whether the effect of testosterone on social discounting was mediated by social distance perception. The 95% bias-corrected confidence interval for the indirect effect was [-0.0061, 0.0263] (estimated indirect effect = 0.0064, SE = 0.0085), again suggesting that social distance perception did not mediate the relationship between testosterone administration and social discounting (as measured with the AUC of the amount forgone).

4. General discussion

In two studies among young, healthy men, we showed that a single dose of testosterone compared to placebo reduced both model-free and model-based measures of generosity. Reduced generosity was particularly evident for interactions with distant others. We also found that-testosterone increased perception of social distance (at trend level in Study 1, and significantly in Study 2); however, perception of social distance did not mediate the effect of testosterone on generosity. These results extend recent research showing that exogenous hormones influence value-based decision-making in human social interactions (Margittai et al., 2018).

Our data provide causal evidence that-testosterone reduces generosity and is in line with previous studies linking testosterone and antisocial behavior (Archer, 2005). Our data also suggest that-testosterone increases selfishness particularly towards distant others. This finding complements the report that circulating levels of testosterone positively correlate with increased outgroup antagonism (Diekhof et al., 2014). However, Diekhof and colleagues also found a correlation between higher endogenous testosterone levels and increased ingroup favoritism (i.e., parochial altruism), which was not borne out by our data. One possible explanation for this discrepancy may be that dominance concerns and strategic considerations regarding the ingroup played a smaller role in our task compared to the parochial altruism task of Diekhof et al. (2014). A similar explanation might account for the discrepancy between the current findings and previous studies reporting that-testosterone increases pro-social behaviors (e.g. reduced lying, Henderson et al., 2018; Wibral et al., 2012; Ultimatum Game generosity, Eisenegger et al., 2010). The social status hypothesis – that is the notion that status-enhancement motives could generate both pro- and anti-social behaviors (Dreher et al., 2016; Eisenegger et al., 2011; Nave et al., 2018) – appears to be a promising theoretical framework to explain these inconsistencies in the literature; however, only a few studies to date have tested this hypothesis directly (Nave et al., 2018; Wu et al., 2017) and more corroborating evidence is needed.

We found evidence in support of a causal link between testosterone and one form of non-physical aggression, i.e. selfishness at the expense of distant others. However, it is worth keeping in mind that the meta-analytic link between testosterone and aggression is weak (Archer et al., 2005) and that it appears to be moderated by individual and situational factors (Carré and Archer, 2018). Moreover, it is also conceivable that-testosterone plays a more prominent role in some forms of aggression than in others. Note that in our task neither others nor participants reacted to particular decisions. Thus, our task may have measured a more generic form of aggression than the ultimatum game where proposer behavior could be viewed as proxy for proactive aggression (Carré et al., 2016) and responder behavior as proxy for reactive aggression.

Lastly, we found that-testosterone-induced changes in generosity were not mediated by testosterone-induced increases in the perception of social distance as measured by the distance construal task. This pattern is similar to a recent dissociation between the valuation of others' welfare and the social distance representation in a sample of extreme altruists (Vekaria et al., 2017). Specifically, in their study, Vekaria and colleagues found that increased generosity among kidney donors was not accounted for by variations in social distance construal. Our findings complement those of Vekaria and colleagues by showing that perception and valuation of social distance can be dissociated not only at the extreme end of the prosociality spectrum, but also in a sample of healthy young male students. Moreover, our study is among the first to directly compare (and report separate) effects of testosterone on value-based decision-making (Dreher et al., 2016) and distance perception (Wagels et al., 2017).

While testosterone reduced the model-free measure of generosity in our two samples of men, a recent study using the same social discounting task found that a dopamine D2/D3 antagonist increased generosity in men compared to women (Soutschek et al., 2017). Moreover, compared to generous decisions, selfish decisions elicited stronger ventral striatum activity in men, but not in women, who showed the opposite pattern of activation (Soutschek et al., 2017). Importantly, testosterone receptors are located on dopamine neurons projecting to the ventral striatum (Creutz and Kritzer, 2004; see also Wood, 2008), and administration of a single dose of testosterone increases ventral striatum reactivity during reward anticipation (Hermans et al., 2010). Thus, it is possible that dopamine-mediated activity in these areas may implement the behavioral effects found in our study. Future studies combining testosterone administration and functional brain imaging are needed to identify the neural mechanisms through which testosterone influences social discounting.

Higher testosterone levels and lower cytosine-adenine-guanine (CAG) repeats in the androgen receptor (AR) gene (Comings et al., 1999) are associated with elevated levels of externalizing (Maras et al., 2003), such as antisocial behavior, aggression, and violation of social norms (Hinshaw, 1992). Concomitantly, adolescents with externalizing symptoms are more likely to choose the selfish alternative in the social discounting task (Sharp et al., 2012). A recent study showed that the effects of testosterone administration on human aggression critically depend on the number of CAG repeats in the AR gene (Geniole et al., 2019). Our research helps synthesizing these different lines of research by pointing at-testosterone as the potential underlying hormonal mechanism for some of the reported findings.

Some limitations should be noted. First, we investigated only male participants. Given that-testosterone contributes to the development of sex-related variations in human behavior (Goetz et al., 2019; Hines, 2010) and females are overall more generous than males in the present task (Soutschek et al., 2017), it is worth testing whether the results found here are generalizable to women. Second, the social discounting and distance construal tasks were related, but used partially different social relationships in Study 1. We chose this approach to keep the distance construal task consistent with previous published work (Vekaria et al., 2017). In Study 2, the social relationships in the distance construal task were the same as in the social discounting task. However, the distance levels 50 and 100 were omitted in the distance construal task. Future studies may want to fully match social distance levels in both tasks. Third, a recent study showed that-testosterone changes in men are positively associated with aggression among individuals with more independent self-construal (Welker et al., 2017). Given that the present study was conducted among Chinese participants, who tend to be more collectivistic (Markus and Kitayama, 1991), future research should test whether the effects reported in this study generalizes to participants from Western societies. Fourth, in accordance with the social heuristic hypothesis – that is the prediction that being pressured to make a decision promotes cooperation, recent research showed that-testosterone administration and personality traits interact with time-pressure in predicting human cooperative behavior (Bird et al., 2019). We encourage future research to combine testosterone administration with a time-pressure manipulation in a social discounting task to directly investigate the social heuristic hypothesis in our task. Fifth, our participants could have been motivated to be generous in the social discounting task if they assumed that recipients would know who the payment came from. One could expect such reputation motives to matter more when recipients are known to participants. In contrast, our findings apply primarily to unknown recipients. Still, future studies may want to specifically investigate the role of testosterone for reputation motives in prosocial behavior.

In conclusion, our findings establish a novel causal link between increased testosterone and decreased human generosity in an economic decision task. Moreover, they indicate that-testosterone increases social distance perception. Our study also showed that these two effects are independent of each other. Together, these findings highlight the importance of considering distance of interaction partners when studying pharmacological effects on social decision-making.

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Author contributions

YW, SZ, HL and PNT designed the study. YW and JL collected the data. YW, JL, YW and HD analyzed the data. YW wrote the first version of the paper, SZ and PNT provided critical revisions. All authors approved the final version for submission.

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Appendix A. Supplementary data

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