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Running title: Testosterone and prosocial learning

Can testosterone modulate prosocial learning in healthy males?

A double-blind, placebo-controlled, testosterone administration study

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Abstract

Testosterone is associated with both aggressive and prosocial behavior, which depend on the social context and the trade-off between self- and other-interest. However, little is known about the effects of testosterone on prosocial behavior in a context without such trade-offs. The present study aimed to investigate the effects of exogenous testosterone on prosocial behavior by using a prosocial learning task. Healthy male participants (n =120) received a single dose of testosterone gel in a double-blind, placebo-controlled, between-participants experiment. Participants performed a prosocial learning task in which they were asked to learn to gain rewards for three different recipients, i.e., self, other and computer, by choosing symbols associated with potential rewards. The results showed that testosterone administration increased the learning rates across all the recipient conditions (d_{other} = 1.57; d_{self} = 0.50; $d_{computer}$ = 0.99). More importantly, participants in the testosterone group had a higher prosocial learning rate than those in the placebo group (d = 1.57). These findings suggest that testosterone generally enhances reward sensitivity and prosocial learning. The present study corroborates the social status hypothesis, according to which testosterone promotes status-seeking prosocial behavior when it is appropriate to the social context.

Keywords: testosterone; prosocial; social status; reinforcement learning

1. Introduction

It is well established that testosterone is associated with aggression such that animals with higher testosterone levels tend to be more aggressive (Barkley & Goldman, 1977; Evans & Brain, 1978). A meta-analysis of human studies revealed a significant positive correlation between baseline testosterone and aggression (r = 0.054) (Geniole et al., 2020). In a competitive context, testosterone fluctuation has been found to facilitate aggressive behavior (i.e., antisocial behavior, Batrinos, 2012). For example, testosterone has been found to elicit reactive (non-physical) aggression in social interaction. Individuals with higher endogenous testosterone levels have shown a higher propensity to reject unfair offers, which was considered as reactive aggression in the ultimatum game (UG) (Mehta & Beer, 2010). Dreher et al. (2016) found that individuals with testosterone administration exhibited more aggressive behavior by strongly punishing proposers who proposed unfair offers. These studies support the link between testosterone and aggression.

Note that there is increasing recognition that testosterone could also induce prosocial behavior (Boksem et al., 2013; Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010; van Honk et al., 2016; Wu, Zhang, Ou, Hu, & Zilioli, 2020). For instance, testosterone administration increases fair bargaining offers in the UG (Eisenegger et al., 2010). Higher testosterone levels are associated with increased ingroup cooperation during competition (Reimers & Diekhof, 2015). In the study of Dreher et al. (2016), when receiving fair or advantageous offers, participants with testosterone administration exhibited more prosocial behavior by increasing the reward for the

proposers. Thus, the relationship between testosterone and social behavior (i.e., aggressive or prosocial behavior) could be context-dependent. The social status hypothesis provides further explanation of the effects of testosterone on social behavior. Specifically, testosterone can facilitate either aggressive or prosocial behaviors depending on whether individuals need to gain or maintain status during social interaction (Eisenegger, Haushofer, & Fehr, 2011).

The social status hypothesis suggests that the relationship between testosterone and social behavior is context-dependent, however, most previous studies did not separate the interest of self and others when manipulating the social context. For instance, individuals need to make a trade-off between self-interest and other-interest before engaging in aggression or prosocial social behavior (Boksem et al., 2013; van Honk et al., 2016; Wu et al., 2020). It remains unclear whether testosterone could facilitate either aggressive or prosocial behaviors in contexts without such trade-offs.

To address this issue, we used a reinforcement-learning-based prosocial learning paradigm adapted from Lockwood et al. (Cutler et al., 2021; Lockwood, Apps, Valton, Viding, & Roiser, 2016). In this paradigm, participants need to learn to gain rewards for different recipients, including themselves, others, and the computer, by choosing symbols associated with a potential reward. Importantly, the rewards for self and others, in this study, were independent from each other, which avoided a conflict of interests between self and others. The reinforcement learning theory (Sutton & Barto, 2018), which states that learning is driven by the difference between the individual's

predicted outcome and the actual outcome (i.e., prediction errors), was applied in the present study. The reinforcement learning theory provides a robust framework for describing how humans learn, to characterize prosocial learning (Báez-Mendoza, Harris, & Schultz, 2013). According to the social status hypothesis, we hypothesized that testosterone administration would enhance prosocial behavior such that the learning rate for others would be increased, as the participants did not need to gain resource or status when learning for others (prosocial learning) in the task.

2. Methods

2.1. Participants

One hundred and twenty healthy males (mean age = 21.0 years, *SD* = 1.9; age range =18~26) were recruited for this study. Participants were instructed to abstain from alcohol, caffeine, and smoking for 24 h before the testing session. Each participant received a single dose of Androgel® or a placebo gel in a double-blind, placebo-controlled, between-participants design. This study was conducted in accordance with the Declaration of Helsinki and was approved by the local research ethics committee. All participants provided written informed consent. Participants were paid a flat fee of 120 Chinese Yuan (~$18), plus a bonus payment of 0~20 Chinese Yuan (~$3) depending on the decisions they made during the task.

2.2. Testosterone administration

The testosterone administration followed the protocol of Eisenegger, von

Eckardstein, Fehr, & von Eckardstein (2013) and Wu et al. (2019). All sessions started at 12:30 and lasted approximately 4 hours. Participants in the testosterone group received a single dose of testosterone gel, containing 150mg of testosterone [Androgel®, Bayer (Schweiz) AG, Zürich, Switzerland]. Participants in the placebo group received a colorless hydroalcoholic gel. A male research assistant, who was blind to the study's purpose, applied the gel to the participants' shoulders and upper arms. According to the established pharmacokinetics data (Eisenegger et al., 2013), the serum testosterone levels peak around three hours after testosterone administration, therefore we conducted the behavioral task at that time point.

2.3. Prosocial learning task

The prosocial learning task was adapted from Lockwood et al. (2016). There were three recipients in the prosocial learning task, i.e., the self, the other and the computer. For the self condition, participants played for themselves and received rewards they obtained. For the other condition, participants were told that the rewards they obtained would belong to someone else. For the computer condition, the rewards participants earned would not be awarded to either themselves or someone else. Each recipient condition had 3 blocks and there were 16 trials in a block. Thus, there were 144 trials in total, lasting for around 25 minutes. Each block had two different symbols, with one being associated with a high probability (75%) of reward and the other being associated with a low probability (25%) (see Figure 1). Each block began with an instruction screen indicating for whom the participants were playing, lasting

for 2000 ms (Figure 1A). Then the participants were presented with two symbols and they were asked to choose one of them. The selected symbol was highlighted for 300 ms, followed by a delay (2500 ms). The outcome was shown for 250 ms. After that, a randomly jittering fixation was shown for 2000-4000 ms. The order of the self, the other, and the computer conditions were randomized across subjects. The contingency between symbols and rewards was fixed in each trial.

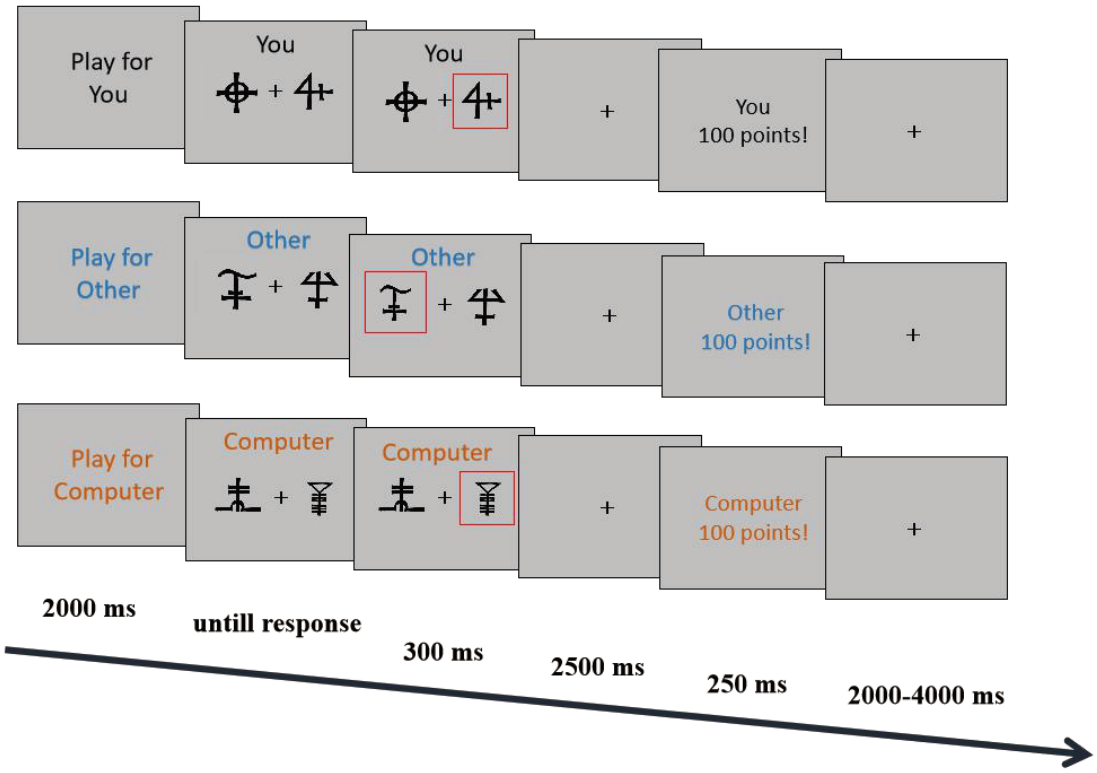

Figure 1. The prosocial learning task

2.4. Model fitting

The Rescorla-Wagner (RW) model (Miller, Barnet, & Grahame, 1995) reveals the updating expected value of stimuli or actions in trial-by-trial learning. The learning rate α controls the degree to which the current expected value $Q_{t+1}(a)$ is

updated by prediction error (PE). PE refers to the difference between the expected value $Q_t(a)$ and the received reward outcome $R_t(a)$ in the previous trials. Next, the SoftMax link function is employed to transfer the expected values $Q_t(a)$ to the probability that the participants choose the available action in trial *t*.

$$Q_{t+1}(a) = Q_t(a) + \alpha \cdot (R_t - Q_t(a)) \quad (1)$$

$$p_t(a|Q_t(a) = \frac{1}{1+e^{-\beta\ (\mathrm{Q_t(a)})}} \quad (2)$$

The null model assumes that participants have random choices meaning there is no learning occurring in the task. We first defined and calculated the trial-by-trial information of the participants, including their choice (1 for high probability reward symbol, 0 for low probability reward symbol) and the outcome. Learning performance is calculated as the average of a participant's choice over the total trials of each condition. A higher learning performance means that participants chose more high-reward symbols. Then, we fitted participants' choices with the RW model using the R package "hBayesDM" (Ahn, Haines, & Zhang, 2017) and the null model in R 4.1.3 and Rstan and obtained the learning rate based on the trial-by-trial choice and outcome of participants. The parameters of all models' fitting were set as: Iteration times = 8000, Markov chain = 4, warmup times = 4000, thinning parameter = 1.

2.5 Model comparison and prediction accuracy

We compared the RW model to the null model using the leave-one-out cross-validation information criterion (LOOIC). The winning model would have a lower

LOOIC score. In addition, we used simulated data based on the winning model's estimated parameters to calculate the prediction accuracy of the winning model using the R package "MLmetrics"(Yan, 2016).

2.6 Statistical analysis of behavioral data

We used two-way ANOVAs (MANOVA function; bruceR package (Bao, 2021)) to examine differences between treatment and recipient in the learning rate. We used a robust linear mixed-effects model (rlmer function; robustlmm package (Koller, 2016) for the trial-by-trial choices including trial number to examine whether participants could learn for all three recipients (Cutler et al., 2021). Data in this study and analysis scripts are available on the project's open science framework at https://osf.io/3u82k/.

3. Results

3.1. Validation of the reward learning task

First, participants in both groups were able to learn to obtain rewards for all recipients (see Figure 2A), as the learning performance was significantly above chance level in the three recipient conditions (all *ts*> 6.14, all *ps* < .001). Second, the number of trials had a significant effect in predicting trial-by-trial performance for each recipient and treatment group combination (all *Zs* > 3.21, *p*s < .001), confirming the validity of the paradigm. These patterns were comparable to a previous report (Lockwood et al., 2016), suggesting the task effectively induced prosocial learning.

3.2. Effects of testosterone on prosocial learning

A two-way ANOVA was performed to analyze the effects of treatment and recipient on the learning rate. The main effect of treatment (F (1, 354) = 93.70, p < .001, η^2 = 0.21) was significant such that the learning rate of the testosterone group was faster than that of the placebo group (M_D = 0.09, p < .001). The main effect of recipient (F (2, 354) =28.77, p < .001, η^2 = 0.14) was also significant, indicating that there was significant pairwise differences among the three recipients. Specifically, the learning rate of the self condition was faster than the learning rate of the other condition and the computer condition (α_{self} vs. α_{other} : M_D = 0.06, p < .001; α_{self} vs. $\alpha_{computer}$: M_D = 0.06, p < .001). Importantly, the interaction between treatment and recipient was significant (F (2, 354) = 8.53, p < .001, η^2 = 0.05; Figure 2C). The simple effect analysis revealed that there was self-advantage in the placebo group, as the learning rate of the self condition was significantly faster than the other condition (α_{self} vs. α_{other} : M_D = 0.11, SE = 0.02, t = 6.54, p < .001, d = 1.20) and the computer condition (α_{self} vs. $\alpha_{computer}$: M_D = 0.11, SE = 0.02, t = 6.60, p < .001, d = 1.21), while there was no significant difference between the other condition and the computer condition (α_{other} vs. $\alpha_{computer}$: M_D = 0.001, SE = 0.02, t = 0.06, p = .95, d = 0.01). In the testosterone group, the learning rate of other was comparable to the learning rate of self (α_{self} vs. α_{other} : M_D = 0.01, SE = 0.02, t = 0.70, p = .98, d = 0.13) and learning rate for the self condition and the other condition were both faster than the computer condition (α_{self} vs. $\alpha_{computer}$: M_D = 0.07, SE = 0.02, t = 3.87, p = .005,

$d = 0.71$; α_{other} vs. $\alpha_{computer}$: $M_D = 0.05$, $SE = 0.02$, $t = 3.12$, $p < .001$, $d = 0.56$), indicating the increase of learning rate in the other condition. We also calculated the simple effect of the group difference of the learning rate across conditions. The results showed that the mean difference of the learning rate between groups was the highest in the other condition ($\alpha_{testosterone}$ vs. $\alpha_{placebo}$: MD = 0.14, SE = 0.02, $t = 8.57$, $p < .001$, $d = 1.57$). The group difference was also significant in the self condition ($\alpha_{testosterone}$ vs. $\alpha_{placebo}$: MD = 0.05, SE = 0.02, $t = 2.73$, $p = .007$, $d = 0.50$) and the computer condition ($\alpha_{testosterone}$ vs. $\alpha_{placebo}$: $M_D = 0.09$, $SE = 0.02$, $t = 5.46$, $p < .001$, $d = 0.99$). Furthermore, the prosocial learning rate (i.e., α_{other} - α_{self}) of the testosterone group was significantly higher than that of the placebo group (MD = 0.1, SE = 0.02, $t = 4.78$, $p < .001$, $d = 0.87$; Figure 2D).

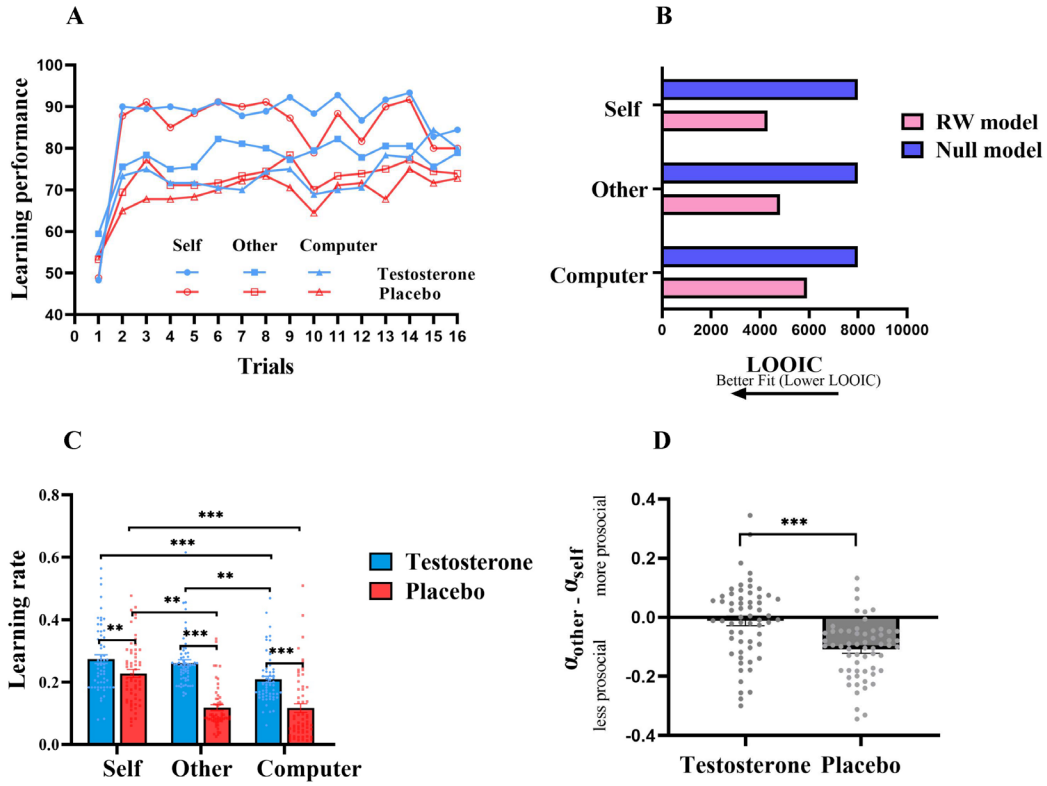

Figure. 2. (A) Placebo and testosterone groups' learning curves with learning performance of the three recipients. (B) Leave-one-out cross-validation information criterion (LOOIC) for the RW models and null models fitted to the self, other, and computer condition. (C) Learning rate of treatment in each condition, error bars represent standard errors. (D) Mean difference between α_{other} and α_{self} under each group, error bars represent standard errors. *p <.05, ** p < .01, ***p <.001.

3.3. Information about model fitting

The R-hat values obtained for the model parameters of the RW model and null model were close to 1.00, and visual examination of the MCMC chains confirmed the mixing of MCMC sampling, suggesting the models fit well.

3.4. Model comparison and model prediction accuracy

The RW model outperformed the null model (the leave-one-out cross-validation information criterion, $LOOIC_{self\_RW} = 4300.8$; $LOOIC_{other\_RW} = 4813.5$; $LOOIC_{computer\_RW} = 5911.0$), thus the winning model was the RW model (see Figure 2B). Then, we calculated the RW model's prediction accuracy by using the R package "MLmetrics" (Yan, 2016), and the prediction accuracy reached 79%.

4. Discussion

The present study combined testosterone administration with reinforcement learning in a prosocial learning task. Participants exhibited significantly higher learning performance than the chance level, indicating a successful learning process. This was also supported by the results of model comparison such that the RW model which described the reinforcement learning process was the winning model in all conditions (rather than the null model which assumed no learning occurring in the task). More importantly, we found that testosterone increased the learning rate for others ($d = 1.20$), to the extent that it was comparable to learning for oneself ($d = 1.21$). In addition, both the learning rate for others and the learning rate for oneself were significantly higher than learning rate for the computer in the testosterone group. The effect sizes of these results were relatively large ($d > 0.8$), indicating the robustness of the results. Taken together, these results demonstrated that the testosterone group exhibited more prosocial behavior by weighing or paying more

attention to others' outcomes.

Previously, the effects of testosterone on prosocial behavior have been found in contexts in which self-interest was always coupled with other-interest such that self-gain was associated with other-loss, for instance, in the UG (Dreher et al., 2016; Eisenegger et al., 2010), Trust Game (Boksem et al., 2013) and donation task (Wu et al., 2020). In our study, participants obtained reward for others (i.e., prosocial behavior) whereby the self-interest was independent of other-interest. Thus, testosterone can promote more prosocial behavior even when individuals cannot get any reward from such behavior. These findings corroborate the social status hypothesis, according to which testosterone promotes status-seeking prosocial behavior when it is appropriate for the social context (Eisenegger et al., 2011).

We also found that testosterone administration increased the overall learning rates across the three recipient conditions, suggesting participants in the testosterone group were more sensitive to the reward and thus enhanced reinforcement learning in general. It has to be noted that although the mean difference of learning rate between groups in the other condition was the largest, the mean difference of learning rate between groups in the self and computer condition also reached a significant level. A possible reason is that testosterone enhanced the reward sensitivity in the study. Testosterone has been found to be positively correlated with reward sensitivity (van Honk et al., 2004). For instance, in economic decision-making, individuals with higher testosterone levels show more risk-taking behavior in pursuit of rewards

(Apicella et al., 2008; Stanton, 2011). This result is also consistent with previous studies showing an association between testosterone and reinforcement learning (Kohne & Diekhof, 2022; Morris et al., 2015). It is well established that the reinforcement learning process is implemented through dopaminergic signaling in the ventral striatum (Costa, Dal Monte, Lucas, Murray, & Averbeck, 2016; Jocham, Klein, & Ullsperger, 2011) and testosterone receptors are located on dopamine neurons projecting to the ventral striatum (Creutz & Kritzer, 2004; Wood, 2008). Hence, one potential channel of testosterone-induced reinforcement learning is through the dopaminergic system. Future studies could explore how testosterone influences reinforcement learning through the dopaminergic system by taking into account the interaction between dopamine and testosterone or by focusing on how testosterone affects the reward circuit of the brain.

Some issues warrant further discussion. First, we only focused on the activational effects of testosterone in the current study. According to the testosterone exposure model, the effects of testosterone can be divided into activational effects (i.e., short-term exposure, temporary and reversible psychological effects) and organizational effects (i.e., long-term exposure during development, physiological effects) (Falter, Arroyo, & Davis, 2006). Future studies could shed light on both the activational effects and organizational effects of testosterone on prosocial learning. Second, previous research has shown the interaction between testosterone and other hormones in modulating human behavior. In particular, the dual hormone hypothesis proposed that cortisol can jointly regulate human behavior with testosterone (Mehta &

Josephs, 2010; Mehta & Prasad, 2015). It is worth exploring the role of cortisol in future testosterone administration studies. Third, the testosterone gel administration protocol in the current study required participants to wait for three hours for testosterone levels to peak. Recent work using testosterone nasal spray administration showed that behavioral and neural responses of testosterone effects were detectable within an hour (Bird et al., 2016; Carré et al., 2017). We encourage future work to better characterize the time course of testosterone administration. Lastly, the current study did not include the manipulation check of the testosterone level. Although we followed the testosterone gel administration protocol from previous studies(Eisenegger et al., 2013; Wu et al., 2019), testosterone was found to be prone to transference (Wolthuis, A., & de Vreeze, J., 2005; Stahlman et al., 2012), for instance, causing abnormal testosterone level in the placebo group, and this could affect the result. Future pharmacological studies should consider the transference of testosterone and the importance of manipulation check.

In summary, by using exogenous testosterone administration and prosocial learning task, we found that testosterone could facilitate the prosocial behavior when there was no conflict between self- and other-interests. Moreover, testosterone also enhanced the reward sensitivity, highlighting the role of testosterone in reward processing and decision-making.

Author contributions

XW and YW designed the study. XW collected and analyzed the data. XW, JL and

YW wrote the first version of the paper, JH and YN provided critical revisions. All authors approved the final version for submission.

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