

# Testosterone Inhibits Trust but Promotes Reciprocity

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## Abstract

The steroid hormone testosterone has been associated with behavior intended to obtain or maintain high social status. Although such behavior is typically characterized as aggressive and competitive, it is clear that high social status is achieved and maintained not only through antisocial behavior but also through prosocial behavior. In the present experiment, we investigated the impact of testosterone administration on trust and reciprocity using a double-blind randomized control design. We found that a single dose of 0.5 mg of testosterone decreased trust but increased generosity when repaying trust. These findings suggest that testosterone may mediate different types of status-seeking behavior. It may increase competitive, potentially aggressive, and antisocial behavior when social challenges and threats (i.e., abuse of trust and betrayal) need to be considered; however, it may promote prosocial behavior in the absence of these threats, when high status and good reputation may be best served by prosocial behavior.

## Keywords

social, social cognition, social interaction, neuroendocrinology, decision making, hormone, context, status, trust, testosterone

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It has long been recognized that the steroid hormone testosterone contributes significantly to social behavior. Prevailing folk theories about how testosterone is related to people's actions in the social environment typically focus on how it leads to increased aggression toward others. However, systematic experimentation is beginning to reveal that although this hormone is indeed related to how people behave in their interactions with others, the relationship between testosterone and decision making is a complex one. One persuasive set of data has shown that testosterone is associated with dominance behavior—that is, actions intended to obtain or maintain high social status (Mazur & Booth, 1998). Endogenous and exogenous testosterone are positively associated with social rank and dominance behavior of some primates (Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2006; Sapolsky, 1991) as well as humans, both male and female (Cashdan, 1995; Mazur & Booth, 1998). Maintaining dominance and a high-status position requires an increased sensitivity to impending social threats and aversive events, particularly events that

might actually challenge high social status. Previous research has shown that testosterone concentrations correlate with this type of increased vigilance for status threats (Archer, 2006; van Honk et al., 1999).

This *challenge hypothesis* states that testosterone aids the organism in preparing for and facing socially challenging situations, such as competing for mates or responding to challenges to dominance (Wingfield, Hegner, Dufty, & Ball, 1990). Although this hypothesis was originally proposed to account for the role of testosterone in birds (and is not unchallenged in that field; Goymann, 2009), testosterone may play a similar role in competitive behavior in both men and women (Edwards, Wetzel, & Wyner, 2006). For example, Booth, Shelley, Mazur, Tharp, & Kittok (1989) monitored a university

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men's tennis team throughout a season and measured saliva testosterone concentrations on multiple occasions. Testosterone concentrations were higher on match days than on the days before and after. It is noteworthy that such effects are also consistently observed in competitions of a less physically demanding nature, such as chess or domino tournaments (for a review, see Salvador, 2005), which suggests that physical exertion per se cannot account for these findings. Indeed, even physiological reactions to implicit cues of social challenge and threat have been shown to covary with testosterone concentrations. For example, endogenous testosterone concentrations have been found to be positively correlated with attentional biases toward angry facial expressions (van Honk et al., 1999), and testosterone administration increased cardiac responses to angry faces (van Honk, Tuiten, & Hermans, 2001). Likewise, participants who received a single dose of testosterone gave lower trustworthiness ratings to facial photographs than did those in whom testosterone was not administered (Bos, Terburg, & van Honk, 2010). This effect was particularly strong in subjects who normally displayed high levels of trust, which suggests that testosterone may adaptively increase vigilance for social threats, presumably to better prepare people for competition for both status and valuable resources (Eisenegger, Haushofer, & Fehr, 2011).

Thus, previous findings support the notion that testosterone stimulates a concern for status, which increases competitive behavior, particularly in socially challenging situations. In the absence of these challenges or perceived threats to dominance, however, testosterone seems largely unrelated to social behavior (Wingfield et al., 1990), presumably because competitiveness and aggression are no longer needed to promote social status (Carré, Putnam, & McCormick, 2009; Zak et al., 2009). In converging evidence from studies of nonhuman primates, associations between testosterone concentrations and aggressive dominance behavior in baboons are observed only when the social hierarchy is unstable and resources are uncertain or scarce; during periods of stability and plentiful resources, these associations are not observed (Sapolsky, 1991; see also Mehta, Jones, & Josephs, 2008).

Indeed, in a nonthreatening context, competitive or aggressive behavior may even have detrimental effects on reputation and social standing. In these circumstances, dominance and high status may be better served by displaying prosocial behavior (Anderson & Kilduff, 2009; Milinski, Semmann, & Krambeck, 2002). Whereas a person concerned with reputation and status might handle potential social threat in the environment with vigilance, dominance, competition, and reduced prosociality, that person, during times of peace and stability, might maintain and increase social status through prosocial behavior. This is an important distinction, and it strongly suggests that more subtle explorations of the effects of

testosterone in decision-making behavior are required, in which the specific context of the interaction being studied is carefully considered.

In the experiment reported here, we tested this context-dependent model of testosterone's role in social decision making by using an anonymous one-shot trust game (Berg, Dickhaut, & McCabe, 1995), in which each participant plays the game only once (i.e., has "one shot") in each role. Decision making was tested both in the presence of social threat (decisions to trust) and the absence of social threat (decisions to reciprocate trust of an unequivocally prosocial interaction partner). We used a double-blind randomized control design with real monetary stakes. In the trust game, a player (the investor) decided how much of an endowment to invest in a partner (the trustee). Once transferred, this money was tripled by the experimenter, and the trustee then had the opportunity to return some of this money to the investor but was not required to do so. If the trustee honored trust and returned, for example, half of the money received, both players ended up with a higher monetary payoff than the original endowment. However, the trustee could also abuse trust and, for example, keep the entire amount, which would leave the investor with a payoff that was lower than the original endowment.

The decision to trust involves the potential social threat of one's trust being abused. Substantial evidence exists to show that humans find abuse of trust highly aversive (Bohnet & Zeckhauser, 2004; Fehr & Schmidt, 2006). This type of betrayal is likely to be damaging to one's reputation, and thus the investor is confronted with a potential threat to his or her status. We hypothesized that testosterone increases vigilance toward such threats and would thereby motivate behavior that would reduce the chances of incurring this betrayal. Therefore, we predicted that investors in the testosterone-treatment group would invest lower amounts than those in the placebo-treatment group (i.e., they would be less trusting).

The task was designed so that trustees always received the maximum amount from the investor (i.e., the investor was the vulnerable one), and therefore, the decision to reciprocate was clearly devoid of social or financial threat. Nevertheless, the trustee was also confronted with a dilemma: There was an obvious temptation not to reciprocate and thereby maximize personal monetary outcome. In general, not reciprocating trust may be beneficial in the short term but is likely to incur long-term costs by damaging a person's reputation and discouraging other people from trusting that person during future encounters. Therefore, the motivation of whether to reciprocate trust is guided not only by maximizing personal outcome but also by a motivation to maintain a positive social image (Fehr & Gintis, 2007). When other people show high trust and the participant is in control of the outcome of the interaction, there is no threat of

betrayal and associated damage to one's social status. Therefore, we predicted that under these circumstances, testosterone would not stimulate aggressive competitive behavior (as would be indicated by low levels of reciprocity). Instead, we expected that testosterone would be related to higher levels of reciprocal behavior, because it may be considered beneficial to one's good reputation to display high levels of reciprocity (Anderson & Kilduff, 2009), which demonstrates an important prosocial aspect to testosterone in the context of social interactions.

In this experiment, we were interested in the specific effects of testosterone on social decision making. However, decisions to trust may also have a nonsocial component: To trust, investors must assess and overcome the potential risk of monetary loss. Although the notion that trust decisions are closely associated with individual sensitivity to risk has not found broad empirical support (Trautmann & Vieider, 2012), some effects of testosterone on risk attitudes have been reported (e.g., Apicella et al., 2008; but see, e.g., Zethraeus et al., 2009). Therefore, we separately assessed participants' nonsocial-risk attitudes and examined whether these attitudes could mediate an effect of testosterone on trust. In addition, although empirical work has focused mainly on the potential overlap between trust decisions and risky-gamble decisions (uncertain outcomes with known probabilities), trust may in fact be more similar to decisions made under conditions of ambiguity (uncertainty with unknown probabilities). When one decides to trust, the probability that this trust will be reciprocated is unknown, which makes it more analogous to an ambiguous decision than to a risky one, and therefore, we also separately assessed ambiguity tolerance.

## Method

### *Participants*

Participants were 54 healthy female volunteers (age range = 18–30 years, mean age = 21.6,  $SD = 2.4$ ) recruited at Radboud University Nijmegen. To control for fluctuating androgen concentrations during the menstrual cycle, we included only women who were taking hormonal contraceptives. Participants had no history of psychiatric, neurological, or endocrine disease and were not current users of corticosteroids. Before the experiment, they gave written informed consent to participate. The local ethics committee approved the protocol for this study. All participants received monetary compensation, which consisted of a base payment of €50.

### *Task and measures*

**Trust game.** Participants played a one-shot trust game for real monetary stakes with an anonymous partner.

Each participant played once as an investor and once as a trustee, always in that order. Investors received €20 each and were asked to decide how much to keep and how much to invest in a partner. Investors were told that the invested amount would be tripled and sent to the trustee. The investor's task ended here. The participant then switched to the role of trustee. The trustee would decide how much of a tripled investment to return to the investor (note that trustees were told that the investment came from another participant). However, trustees always received €60 (a tripled investment of the full €20). We manipulated the investment received by trustees in this way to make sure that all trustees received the same high offer, which signaled high trust on the part of the investor. The trustee had to decide how much to return to the investor, knowing that she would be able to keep the remainder for herself. The trustee's task ended at this point.

The percentage of the (tripled) investment that the trustee chose to return was used to calculate the payment of the next investor. For example, if the new investor invested €12, and the previously tested trustee had returned 50%, the investor would earn €8 (the amount of the original €20 not invested) plus €18 (50% of €36, the tripled investment of €12) for a total of €24. Payment for a trustee consisted of the part of the €60 that each trustee decided to keep for herself.

**Risk-tolerance measure.** We elicited tolerance for risk by presenting each participant with 18 choices one by one in a random order. For each choice, participants selected either a 50% chance of earning €30 (and a corresponding 50% chance of earning nothing) or a sure payoff. This sure payoff, which was different for each pair of options, ranged from €1.50 to €28.50. When considering very small sure payoffs (e.g., €1.50), most participants should prefer to take the gamble (i.e., a 50% chance of winning €30); for very large sure payoffs (e.g., €28.50), most participants should prefer the certain option to the gamble. We calculated the tolerance for risk as the percentage of gambles chosen in the task; a risk tolerance of 50% corresponded to risk neutrality, lower values indicated risk aversion, and higher values indicated risk seeking. A randomly selected pair of options was used to determine participants' payoff for this task. For example, if a participant, given the options of a sure €12 or a 50% chance of winning €30, chose the sure €12, that amount would be paid to her; if she chose the gamble, a random number generator would determine whether she would be paid €30 or €0.

**Ambiguity-tolerance measure.** To measure ambiguity tolerance, we used a probability-matching procedure (Kahn & Sarin, 1988). As in our elicitation of risk preferences, we offered participants 18 choices from a list. Each

choice included an ambiguous option (an unknown probability of winning €30 or €0) and a risky option (a known probability of winning €30 or €0; e.g., a 20% chance of winning €30); each risky option had the same potential monetary outcome (winning €30 or €0) but offered a different probability of winning (between 5% and 95%). When the known probability of winning the risky option is very small, most participants prefer the ambiguous option; when the probability of winning the risky option is very large, most prefer the risky option. We calculated ambiguity tolerance as the percentage of times that the participant chose the ambiguous option. A randomly selected choice set was used to determine participants' payoff for this task. For example, if a participant given the option between a 20% chance of winning €30 (the risky option) or an unknown chance of winning €30 (the ambiguous option) chose the risky option, a random number generator (between 0 and 1) would determine whether she would be paid €30 (if the random number was 0.2 or smaller) or €0 (if the random number was greater than 0.2). If the participant chose the ambiguous option, a random number generator (between 0 and 1) would first determine the probability of winning (between 0 and 1), and a second random number would then determine whether she would be paid €30 or €0 (analogous to the risky option).

## Procedure

**Substance administration.** Participants self-administered a single dose of a testosterone or placebo solution sublingually in a double-blind design. The former consisted of 0.5 mg of testosterone suspended in a clear solution with 0.5 mg of hydroxypropyl- $\beta$ -cyclodextrin, 0.005 ml of 96% ethanol, and distilled water. The presence or absence of testosterone was the only difference between the testosterone and placebo solutions. Previous research in which 0.5 mg of testosterone was administered sublingually in women established the time course of changes in serum testosterone concentrations as well as physiological and psychological changes in response to sexual stimuli (Tuiten et al., 2000). This research showed that this dose and route of administration in women results in a tenfold increase in serum testosterone concentrations 15 min after administration; serum testosterone concentrations return to baseline 90 min after administration. However, physiological and psychological effects of 0.5 mg of testosterone are not observed until 3.5 to 6 hr after administration (Tuiten et al., 2000). Several studies have corroborated that, in women, sublingual administration of 0.5 mg of testosterone has a robust effect 4 to 6 hr later on a variety of cognitive, emotional, and behavioral tasks (see Bos, Panksepp, Bluthé, & van Honk, 2012). The pharmacokinetics of this testosterone-administration technique (appropriate

dosage and time course) remains unknown in men, which is why we recruited only women for this study. The protocol for our study was built on this well-established body of research; participants self-administered testosterone or a placebo approximately 4.5 hr before behavioral testing started.

**Testosterone saliva measurement.** Endogenous baseline testosterone concentrations were measured in saliva before participants administered testosterone or a placebo (Liening, Stanton, Saini, & Schultheiss, 2010). We collected 2.5 ml of saliva from each participant using a sterile polypropylene microtubule. After the behavioral tasks were complete, saliva samples were shipped on dry ice to Clemens Kirschbaum's laboratory in Dresden, Germany. Saliva samples were analyzed in duplicate for testosterone concentrations with a double-antibody luminescence immunoassay kit (RE62031; IBL International, Hamburg, Germany). This kit can detect concentrations of testosterone as low as 1.8 pg/ml. Saliva control samples with known concentrations of testosterone—one high value and one low value—were included on each assay. The average interassay coefficient of variation, calculated from the mean values for the high and low control samples on each assay plate, was 6.48%, and the average intraassay coefficient of variation was 8.56%. As expected, baseline testosterone concentrations were not significantly different in the two treatment groups (testosterone group:  $M = 23.6$  pg/ml,  $SEM = 2.9$ ; placebo group:  $M = 22.2$  pg/ml,  $SEM = 2.8$ ),  $t(52) = 0.33$ , n.s. In addition, there was no correlation between baseline testosterone concentrations and investor or trustee decisions in the trust game in either the placebo group or the testosterone group. Baseline testosterone concentrations also did not interact with treatment condition in predicting trust-game decisions. Finally, even after we controlled for baseline testosterone concentrations, our main analyses still revealed effects of treatment on decisions to trust and decisions to reciprocate trust. Overall, these analyses indicate that baseline testosterone concentrations before testosterone or placebo administration did not account for our findings.

**Behavioral testing.** The experimental tasks were presented on a computer with a 15-in. screen that was running Presentation software (Version 14.9; Neuro-behavioral Systems, Albany, CA). The tasks were self-paced and lasted for an average of approximately 10 min.

**Postexperiment questionnaire.** Participants filled out a short questionnaire that consisted of closed-ended questions about the experiment, such as whether they thought they had received testosterone or a placebo, whether they enjoyed the task, whether they believed they would actually make money, and whether they

believed their decisions had real consequences for other people. The results showed that 80% of the participants thought they had received a placebo. Of the 20% who thought they had received testosterone, only 55% were correct, which means that their guesses were at chance level,  $\chi^2(1, N = 11) = 0.23$ , n.s.

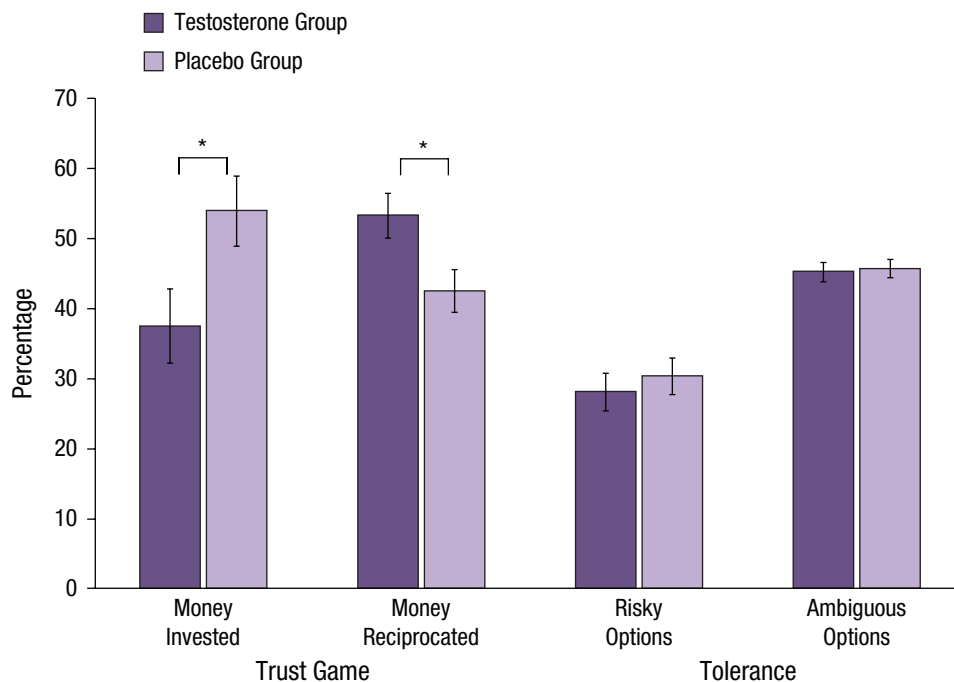
### Statistical analyses

There were some significant interrelations between our measures. We found trust to be related to age,  $r(51) = .29$ ,  $p < .05$  (older people trusted more than younger people did), and we also observed a marginally significant correlation between trust and tolerance for risk,  $r(51) = .26$ ,  $p = .06$ . Therefore, data were entered into univariate analyses of variance that included treatment as a fixed factor and baseline testosterone concentration and age as covariates. In addition, to control for potential confounding effects of treatment condition on nonsocial decision making, we included risk and ambiguity tolerance as covariates of trust in our analyses. Three participants reported on their post-experiment questionnaires that they did not believe that they had interacted with real

people in the trust game, they did not believe they had responded to decisions made by others, and they did not believe that their choices had real consequences for others. These three participants (one from the placebo group and two from the testosterone group) were therefore excluded from our analyses of decision making in the trust game.

### Results

Figure 1 provides a graphic overview of the results. Testosterone had a significant effect on the decisions of participants when they played as an investor in the trust game: Whereas participants who received the placebo invested an average of 54% ( $SEM = 5.0$ ) of their €20, participants who received testosterone invested significantly less, on average 38% ( $SEM = 5.3$ ) of their €20,  $F(1, 47) = 4.32$ ,  $p < .05$ ,  $R^2 = .16$ . Conversely, when they played as trustees, participants who received testosterone reciprocated significantly more of the €60 entrusted to them (53%,  $SEM = 3.2$ ) than did participants who received a placebo (43%,  $SEM = 3.0$ ),  $F(1, 47) = 6.11$ ,  $p < .05$ ,  $R^2 = .14$ . These effects were independent: Including



**Fig. 1.** Results for the trust game and tolerance measures as a function of participant group. For the trust game, the graph shows the percentage of the original endowment that the investor gave to the partner and the percentage of the tripled investment that was returned to the investor. For the tolerance measures, the graph shows the percentage of risky options chosen and ambiguous options chosen. Data bars represent estimated marginal means; error bars indicate standard errors of the mean. An asterisk indicates a significant difference between groups ( $*p < .05$ ).

reciprocity as a covariate in the model predicting trust showed that testosterone treatment predicted decreased trust independently of reciprocity,  $F(1, 46) = 6.56, p < .05, R^2 = .21$ . Conversely, including trust in the model predicting reciprocity showed that testosterone predicted increased reciprocity independently of willingness to trust,  $F(1, 46) = 8.39, p < .01, R^2 = .19$ . Finally, testosterone treatment significantly decreased the willingness to trust independently of tolerance for risk or ambiguity,  $F(1, 45) = 4.47, p < .05, R^2 = .17$ . We observed no between-group differences in either risk tolerance,  $F(1, 50) = 0.36, n.s.$ , or ambiguity tolerance,  $F(1, 50) = 0.77, n.s.$

## Discussion

In the experiment reported here, we investigated the effects of testosterone on social decision making. We hypothesized that testosterone, via its role in assessing and responding to status-related challenges, would have different effects on social choices depending on the presence or absence of challenges or threats. Specifically, we argued that in the context of social challenge, testosterone would be associated with competitive, potentially antisocial behavior, whereas in the absence of such challenges, testosterone would not invoke such competitive responses and might even enhance prosocial behavior.

The findings confirmed our predictions. Specifically, we found that testosterone decreased trust independently of any effects of treatment on risk or ambiguity tolerance. These findings are in agreement with previous results associating testosterone concentrations with decreased prosocial behavior in terms of both increased rejections of unfair offers by responders in the ultimatum game (Burnham, 2007; Güth, Schmittberger & Schwarze, 1982) and lower offers by proposers (Zak et al., 2009; but see Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010). Conversely, testosterone increased reciprocity: When trust was placed in participants, those who had received testosterone repaid this trust more generously than those who had received a placebo, which unequivocally shows that testosterone can stimulate prosocial behavior, even in anonymous economic-exchange settings such as a one-shot trust game.

Testosterone has been previously associated with actions directed at obtaining or maintaining high social status, and it has been proposed that it plays an important role in facing challenges to dominance (Archer, 2006; Mazur & Booth, 1998; Wingfield et al., 1990). Indeed, research has shown that testosterone concentrations correlate with increased vigilance for status threats (van Honk et al., 1999, 2001) and that they change how people assess potential threats to status (Archer, 2006; Bos et al., 2010). We argue that this mechanism may underlie the decreased levels of trust observed in participants who

were given testosterone rather than a placebo in the present experiment. The potential betrayal of one's trust can be interpreted as a clear threat to one's status, and testosterone may play a vital role in focusing players' attention on the consequences of this abuse of trust. The lack of any significant difference between the general risk attitudes of the testosterone and placebo groups strongly suggests that the diminution of trust cannot be explained by any fundamental change in risk attitudes per se.

In the absence of challenge or perceived threats to dominance, testosterone has been found to be largely unrelated to motivating competitive behavior (Sapolsky, 1991; Wingfield et al., 1990). Rather, in these circumstances, dominance and high status may be better served by displaying prosocial behavior (Milinski et al., 2002). Although this may be especially the case in humans, even in other primate societies, high-ranking individuals have been observed sharing resources to maintain the top position in the social ranking (Mitani & Watts, 2001). A good reputation (i.e., being perceived as honest, authentic, generous, and trustworthy) is of crucial importance for acquiring or maintaining high social status (Anderson & Kilduff, 2009; Fehr & Schmidt, 2006), and the expression and repayment of trust is an important social signaling mechanism that influences both competitive and cooperative behavior (Fehr & Fischbacher, 2003). Consequently, we found that participants who had been given testosterone reciprocated trust significantly more than those who had received a placebo.

In summary, testosterone's effect on the underlying motivation to obtain or maintain high status and dominance may stimulate behaviors that can be considered either antisocial or prosocial. Crucially, this effect depends on the context in which such behaviors are displayed: Testosterone may mediate competitive and potentially aggressive and antisocial behavior when social challenges and threats need to be confronted and handled, but it can also induce prosocial behavior in the absence of these threats, when high status and good reputation are best served by positive behavior. This provides a more nuanced account than the traditional view of testosterone as being involved in purely aggressive and antisocial behavior. This view has received only mixed empirical support; many studies of humans have failed to find effects of testosterone on aggressive and norm-violating behavior (see Archer, 2006) or even norm-compliant behavior (van Honk, Montoya, Bos, van Vugt, & Terburg, 2012; Wibral, Dohmen, Klingmüller, Weber, & Falk, 2012). Indeed, behavioral effects of testosterone reported in the literature are often inconsistent and plagued by small effect sizes when the behaviors' context is not considered (for reviews, see Bos et al., 2012; Eisenegger et al., 2011).

A similar observation has been made regarding the effects of oxytocin, a hormone that is often considered to be antagonistic to testosterone. Testosterone is traditionally associated with increased aggressive and antisocial behavior, whereas oxytocin is traditionally associated with increased empathic prosocial behavior (e.g., Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005). Effects of oxytocin on behavior are often small and inconsistent as well (Bartz, Zaki, Bolger, & Ochsner, 2011); a number of studies have linked oxytocin with antisocial sentiments and behavior, such as envy and schadenfreude (Shamay-Tsoory et al., 2009), and antisocial behavior toward out-group members (De Dreu et al., 2010). Likewise, our findings show that testosterone does not always stimulate aggressive and antisocial behavior; it may also increase prosocial behavior. Therefore, classifying the impact of these hormones on social behavior and decision-making in terms of anti- or prosocial behavior may be too much of a simplification. Instead, these hormones are likely to regulate relatively broad social motivations (e.g., a motivation to affiliate or dominate) that alter the basic processing of social challenges, which in turn could produce a wide variety of behavioral effects that could be qualified as either anti- or prosocial, depending on the situational context (see also Bartz et al., 2011; Bos et al., 2012).

Some degree of caution should be taken with interpreting findings from the present experiment (and virtually all other testosterone-administration studies to date): Although administration of 0.5 mg of testosterone results in reliable physiological and psychological changes, such dosage in women results in serum testosterone concentrations that far exceed the natural range (Tuiten et al., 2000). Therefore, although our experiment provides one clear account of the relationship between testosterone, on the one hand, and trust and reciprocity, on the other, whether variations in serum testosterone concentrations within the natural physiological range similarly affect decisions involving trust and reciprocity remains an open question. It will be important in future research to develop feasible administration techniques that induce changes in serum testosterone concentrations that are within the normal biological range to complement the extant body of research. On a similar note, we showed that testosterone affects trust and reciprocity in women, but we left open the question of whether similar effects would be observed in men. Indeed, previous findings suggest that administration of testosterone could differentially affect social decision making in men and women (Eisenegger et al., 2010; Zak et al., 2009). Therefore, future studies should corroborate the present findings in men.

### Author Contributions

M. A. S. Boksem and P. H. Mehta contributed equally to this work. M. A. S. Boksem and P. H. Mehta designed the research with assistance from B. Van den Bergh, S. T. Trautmann, A.

Smidts, K. Roelofs, and A. G. Sanfey. P. H. Mehta organized the research, and P. H. Mehta and V. van Son performed the research. M. A. S. Boksem analyzed the data and wrote the manuscript. A. Smidts, K. Roelofs, and A. G. Sanfey assisted in writing the manuscript.

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### Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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