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Endogenous testosterone correlates with parochial altruism depending on decision strategy in relation to costly punishment

Luise Reimers [Equal first author, 1], **Eli Kappo** [1], **Lucas Stadler** [1], **Mostafa Yaqubi** [1], **Esther K Diekhof** [Corresp. Equal first author, 1]

[1] Faculty of Mathematics, Informatics and Natural Sciences, Department of Biology, Institute of Zoology, Neuroendocrinology and Human Biology Unit, Universität Hamburg, Hamburg, Deutschland

Corresponding Author: Esther K Diekhof
Email address: esther.diekhof@uni-hamburg.de

Testosterone plays a key role in shaping human social behavior. Recent findings have linked testosterone to altruistic behavior in economic decision tasks depending on group membership and intergroup competition. The preferential treatment of ingroup members, while aggression and discrimination is directed towards outgroup members, has been referred to as parochial altruism. Here we investigated in two consecutive studies, whether testosterone is associated with parochial altruism depending on individual tendency for costly punishment. In the first study, 61 men performed a single-shot ultimatum game (UG) in a minimal group context, in which they interacted with members of an ingroup and an outgroup. In the second study, 34 men performed a single-shot UG in a more realistic group context, in which they responded to the proposals of supporters of six political parties during the German election year 2017. Political parties varied in their social distance to the participants' favorite party as indicated by an individual ranking, which resulted in one ingroup (rank 1) and five outgroups of varying social distance (rank 6 referred to as the most distant outgroup). Participants also performed a cued recall task, in which they had to decide whether they had already encountered a face during the UG (old-new decision). In both studies, results showed a parochial pattern with higher rejection rates of outgroup than ingroup offers. Interestingly, higher salivary testosterone was associated with higher rejection rates related to unfair offers by the most distant outgroup, yet only in the group of self-oriented subjects (pro-selfs). Further, only the pro-selfs showed a memory advantage for unfair interaction partners in study 2, especially if those were ingroup members. The present findings suggest that the latent intergroup bias during decision-making, that was particularly visible in pro-selfs, may be related to endogenous testosterone. In line with previous evidence that already indicated a role of testosterone in shaping male parochial altruism in male soccer fans, these data underscore the general yet rather subtle role of testosterone also in other social settings.

Endogenous testosterone correlates with parochial altruism depending on decision strategy in relation to costly punishment

Luise Reimers[1,*], Eli Kappo[1], Lucas Stadler[1], Mostafa Yaqubi[1], **Esther K. Diekhof**[1,*]

[1]*Universität Hamburg, Faculty of Mathematics, Informatics and Natural Sciences, Department of Biology, Institute of Zoology, Neuroendocrinology and Human Biology Unit, Martin-Luther-King Platz 3, D-20146 Hamburg, Germany*

These authors contributed equally

Corresponding author:

Esther Diekhof

University of Hamburg

Zoological Institute

Neuroendocrinology Unit

Martin-Luther-King Platz 3

D-20146 Hamburg/ Germany

Tel.: +49-40-42838-3931

Email: esther.diekhof@uni-hamburg.de

Abstract

Testosterone plays a key role in shaping human social behavior. Recent findings have linked testosterone to altruistic behavior in economic decision tasks depending on group membership and intergroup competition. The preferential treatment of ingroup members, while aggression and discrimination is directed towards outgroup members, has been referred to as parochial altruism.

Here we investigated in two consecutive studies, whether testosterone is associated with parochial altruism depending on individual tendency for costly punishment. In the first study, 61 men performed a single-shot ultimatum game (UG) in a minimal group context, in which they interacted with members of an ingroup and an outgroup. In the second study, 34 men performed a single-shot UG in a more realistic group context, in which they responded to the proposals of supporters of six political parties during the German election year 2017. Political parties varied in their social distance to the participants' favorite party as indicated by an individual ranking, which resulted in one ingroup (rank 1) and five outgroups of varying social distance (rank 6 referred to as the most distant outgroup). Participants also performed a cued recall task, in which they had to decide whether they had already encountered a face during the UG (old-new decision).

In both studies, results showed a parochial pattern with higher rejection rates of outgroup than ingroup offers. Interestingly, higher salivary testosterone was associated with higher rejection rates related to unfair offers by the most distant outgroup, yet only in the group of self-oriented subjects (pro-selfs). Further, only the pro-selfs showed a memory advantage for unfair interaction partners in study 2, especially if those were ingroup members.

The present findings suggest that the latent intergroup bias during decision-making, that was particularly visible in pro-selfs, may be related to endogenous testosterone. In line with previous evidence that already indicated a role of testosterone in shaping male parochial altruism in male soccer fans, these data underscore the general yet rather subtle role of testosterone also in other social settings.

1. Introduction

Humans display a unique scale of prosocial behaviors such as cooperation and altruism. At the same time, the human history of conflicts and wars is unparalleled. This supposedly inconsistent behavior of ingroup favoritism and outgroup hostility has recently been referred to as *parochial altruism* (Choi and Bowles 2007). Empirical evidence for parochial altruism comes from several studies applying economic decision tasks (Baumgartner et al. 2012; Bernhard, Fischbacher, and Fehr 2006; Diekhof, Wittmer, and Reimers 2014; Fershtman and Gneezy 2001; Goette et al. 2012; Kubota et al. 2013; Reimers and Diekhof 2015). For instance, members of different indigenous language groups in Papua New Guinea have been shown to display a strong ingroup bias by punishing norm violators that treated members of their own group unfairly more often compared to situations, in which the "victim" was an outgroup member (Bernhard, Fischbacher, and Fehr 2006). In addition, this ingroup bias seems to be accompanied by a stronger tendency towards outgroup hostility in contexts that involve intergroup competition. In a group competition context, army platoon members punished members of other platoons than their own more harshly than in a neutral decision context, and even if the outgroup member was cooperative (Goette et al. 2012). This behavioral pattern has been explained with the prevalent intergroup conflicts in human ancestry. Since cooperation within the own group and successfully

competing against outgroups was crucial in terms of survival, these conflicts have been proposed to have led to the evolution of both altruism and parochialism (Bowles 2009; Choi and Bowles 2007).

Accumulating evidence has previously linked testosterone to economic decision making in social interactions, yet studies mostly revealed inconsistent results. For instance, some studies found that testosterone was associated with increased fairness preference and thus higher rejection rates in response to unfair proposals made in the context of an ultimatum game (UG) (Burnham 2007; Dreher et al. 2016; Eisenegger et al. 2010; Mehta and Beer 2010), which has been interpreted as an act of altruistic punishment as it involves the loss of the offered share. Others found the opposite, namely that testosterone administration may be related to increased greediness and selfishness as well as a reduced fairness preference in the UG, which was reflected by either reduced punishment of violations of the fairness norm or reduced generosity when being in the role of the UG proposer (Kopsida et al. 2016; Zak et al. 2009). Finally, some studies found no effect at all (Cueva et al. 2017; Zethraeus et al. 2009). However, the above-mentioned studies differed in their methodological approach: some investigated endogenous testosterone effects (Burnham 2007; Mehta and Beer 2010), while others tested the effect of testosterone administration (Cueva et al. 2017; Eisenegger et al. 2010; Kopsida et al. 2016; Zak et al. 2009; Zethraeus et al. 2009). Moreover, samples consisted either of men (Burnham 2007; Cueva et al. 2017; Dreher et al. 2016; Zak et al. 2009), or women (Eisenegger et al. 2010; Zethraeus et al. 2009) or were mixed (Kopsida et al. 2016; Mehta and Beer 2010). This made it difficult to discern the actual effect of testosterone on economic decisions in the UG, and well-designed replication studies are currently lacking.

As to the mechanism underlying parochial altruism, testosterone has recently been proposed to play an important role in mediating the effect of testosterone on decision-making in the UG and related economic decision tasks (Diekhof, Wittmer, and Reimers 2014; Reimers, Büchel, and Diekhof 2017; Reimers and Diekhof 2015). One recent study investigated the behavioral effects of endogenous testosterone by accounting for group membership and intergroup competition. Male soccer fans played the UG against other soccer fans of either their own favorite team (ingroup) or of other teams of varying enmity and social distance (outgroups) (Diekhof, Wittmer, and Reimers 2014). In the UG two players bargain about how to split an initial endowment (Güth, Schmittberger, and Schwarze 1982). Soccer fans with high testosterone levels offered more points to the ingroup and also rejected rather fair offers (40% of initial endowment), when these were made by an outgroup in a competitive relative to a neutral decision context, in which an additional group reward could be acquired (Diekhof, Wittmer, and Reimers 2014). A similar pattern of increased ingroup cooperation in the face of intensified intergroup competition was found in a prisoner's dilemma, another economic decision task measuring cooperation rates (Reimers and Diekhof 2015). Moreover, a recent neuroimaging study has provided first evidence for testosterone's action in the brain in a sample of male soccer fans playing the UG (Reimers, Büchel, and Diekhof 2017). The results indicate dissociable testosterone-brain correlations depending on individual tendency for costly punishment. In individuals with a more selfish (i.e., economically rational) strategy, which resulted in overall lower rejection rates in response to unfair offers of ingroup members, testosterone was positively correlated with activity in the anterior insula, a brain region implicated in processing negative emotions and norm violations (Civai et al. 2012; Sanfey et al. 2003) in the context of the UG, yet also with positive emotional affect in other contexts (e.g., Hennenlotter et al. 2005). In inequity averse individuals (i.e.,

subjects with strong fairness preference) high testosterone was predictive of increased activity in ventromedial prefrontal regions, which have previously been associated with monitoring of subjective reward value (Amodio and Frith 2006; Plassmann et al. 2008). This was observed in response to unfair outgroup proposers in a non-competitive context, when subjects played for their own outcome. Interestingly, the selfish players also showed a stronger tendency towards parochial altruism (higher rejection rates in response to unfair outgroup than ingroup offers), and even in absence of an intergroup competition. To sum up, the converging evidence from the three studies cited above suggests that testosterone could be one factor that modulates male parochial altruism in the context of economic decision making.

The above-mentioned studies tested male soccer fans, who maintain long-term rivalries to other teams and show a strong, genuine feeling of group affiliation that might even compare to a 'tribal identity' (Vugt and Park 2010). As such, soccer fans represent a natural social group with a strong emotional involvement that is suitable to study parochial altruism (Weisel and Böhm 2015). Here, we investigated whether testosterone similarly affects parochial altruism in artificially created groups (study 1) and in a more natural context of political party supporters during the election year 2017 (study 2), yet presumably without such a strong 'tribal identity' as observed in male soccer fandom. This was based on two reasons: first, we wanted to examine whether the link between testosterone and parochialism is stable enough to be observed in different social settings, i.e., whether the association found between testosterone in the minimal group study 1 could also be observed in the more realistic social setting of study 2. And second, the group commitment of soccer fans as well as the enmity to other teams can vary with the current position of the admired team in the league and the ongoing team competition can create a

stressor as is often observed in unstable hierarchies, which could have potentially obscured subtle parochial tendencies in our previous studies. By assessing the present participants in two rather stable group settings, i.e., either in the minimal group setting with a fixed group association (study 1) or during the German election year (study 2), we tried to control for these interfering variables.

In the first study, we conducted the UG experiment with male subjects that were divided into two groups according to their behavioral performance in a maze task that was completed directly before the UG. In the second study, we questioned participants about their political orientation using a ranking procedure through which we individually identified the favorite political party as well as the one most distant to the participant. Moreover, since memory for uncooperative group members was found to be enhanced in previous studies (Bell et al. 2012; Bell and Buchner 2009, 2012; Hechler, Neyer, and Kessler 2016; Howard and Rothbart 1980), we assessed cued recall performance in a surprise face memory task (old-new decision) that used the faces from the UG intermixing them with the same number of new faces. With this we wanted to assess whether there was indeed a memory advantage for ingroup members who showed schema-incongruent behavior in the UG, i.e., a norm violation through an unfair proposal, as suggested previously (e.g., Hechler, Neyer, and Kessler 2016), and whether this was associated with testosterone or strategy group.

Based on the results of our previous studies with soccer fans, we hypothesized that subjects with a high endogenous testosterone level would display enhanced parochial altruism in both studies. Further, as our recent neuroimaging study had observed dissociable correlations between testosterone and brain activity depending on the decision strategy regarding costly punishment

(Reimers, Büchel, and Diekhof 2017), we further tested whether individual decision strategy influenced the interaction between testosterone and parochialism in the two studies as well.

2. Material and Methods

2.1 Study 1

2.1.1 Participants

61 healthy male students (mean age ± SD: 24.95 ± 4.28 years) participated in this study. The participants were recruited via online advertisement on a campus website and by word of mouth. Only subjects that reported no drug or alcohol abuse, no chronic or psychiatric illness and did not take any form of medication, especially hormones, were included in this study. They were paid a show-up fee of 10 € for participation and were told that they could win even more money (up to 5 €) depending on their performance. This study was approved by the local ethics committee (*Aerztekammer Hamburg; Ethical Application Ref: PV3948*). All subjects gave written informed consent prior to participation.

2.1.2 Procedure – Minimal group study

Data collection took place from 2014 to 2015. Before the test day subjects were given instructions and were handed out five 2 ml polypropylene Eppendorf tubes for the saliva samples, which they had to collect themselves at home at the morning of the test day. They had to start with the first sample directly after waking up and then had to collect another four samples with 30 minutes in between. During the sampling period of 2 hours subjects were told to refrain

from eating, smoking and drinking anything but water. Directly after the first sample tooth brushing was allowed, however it had to be finished at least 15 minutes before the second sample, to prevent contamination by micro-bleeding.

Upon arrival at the test facility, the test procedure started with the group assignment, which was a pencil and paper maze task. This task was intended to create an artificial group formation that was unrelated to the experiment itself. Such a minimal group paradigm (MGP) has previously been shown to evoke ingroup favoritism and intergroup bias (Tajfel et al. 1971). Subjects went through the maze. After seven seconds time was stopped. Participants were instructed that, according to the distance they covered in the maze, they were assigned to one of the two teams. The two teams were named after two famous cartoon characters, which were used as the group icons in the following experiments. To make this group assignment even more authentic to the subjects, maze templates that showed the cut-off distance dividing the two teams were shown to the subjects. In reality, the group assignment was pre-determined by the experimenters to ensure an equal distribution among the two teams. For subjects who were supposed to be in the 'fast team' another template was used than for subjects who were assigned to the 'slow team'. After the group assignment, subjects were given written instructions that explained the rules of the UG (see (Diekhof, Wittmer, and Reimers 2014; Reimers, Büchel, and Diekhof 2017) for comparison).

The UG was designed as a computer-based experiment that was run using the Presentation software by NBS (Neurobehavioral Systems). A short training version was completed and all further questions were answered. Subsequently, the UG was played in the role of the responder (see below), followed by two questions asking about hypothetical offers in the role of the proposer. After that subjects completed the Barratt-Impulsiveness-Scale (BIS; Patton et al.,

1995) and answered several questions from the German socio-economic panel that measure trust, positive and negative reciprocity (Dohmen et al. 2008). Saliva samples were frozen at -20°C until further analysis.

2.1.3 Ultimatum Game in a minimal group context

One famous and often applied economic decision task is the UG (Güth, Schmittberger, and Schwarze 1982). In the UG two players, the proposer and the responder, interact in an economic exchange. The proposer has to make an offer about how to split a fixed sum of money (or experimental points) to the responder. If the responder accepts the offer, both players get paid according to the proposed share. But in case he rejects the offer, both players get nothing. Despite the costs, humans tend to offer equal to almost equal shares and tend to reject unfair offers lower than 20% (Güth, Schmittberger, and Schwarze 1982; Henrich et al. 2005).

Here we applied a computer-based intergroup version of the UG (intergroup-UG) that was similar to previously applied intergroup-UGs (Diekhof, Wittmer, and Reimers 2014; Reimers, Büchel, and Diekhof 2017). Yet in contrast to these previous studies, we will focus the analysis on the first session of the intergroup-UG here. In the first session of the intergroup-UG, subjects play for their personal reward and do not receive any further instructions regarding a competition between groups for an extra group bonus, which would be the case in the second session of the intergroup-UG. In our previous studies (see for example in (Diekhof, Wittmer, and Reimers 2014)), the first session was termed the “neutral context”, since there the group affiliation is not explicitly addressed as being important for the accomplishment of the task goal, i.e., one’s individual reward. In contrast, the second session was referred to as the “competitive context”, since there we also introduced the second task goal, which was to achieve an additional bonus in

form of a group reward for behavior that maximizes the outcome of the group. In that way, the "neutral context" of the first session of the intergroup-UG should reveal the latent parochial tendency of the person which is not enforced by an explicit instruction that refers to the group identity of the proposers (see also (Reimers, Büchel, and Diekhof 2017)). Moreover, the interpretation of the results from the competitive, second session of the intergroup-UG is not unproblematic. This is because the "neutral context" of session 1 always precedes the "competitive context" of session 2. Consequently, transfer effects cannot be ruled out from the naïve context of session 1 to the competition in session 2. For example, some subjects might, after short reflection, regret their use of costly punishment during session 1 and could switch to a more selfish-strategy, especially if they consider the group reward rather unlikely to achieve. This could be particularly the case in a study in which ingroup cohesion might be expected to be rather lax (as in study 1) or in which more than two teams are competing for the same group reward (like in study 2 below). In particular, when comparing the results from different studies for consistency this could increase the risk of a study-specific bias in the "competitive context" of session 2 that might obscure or contaminate the already subtle effect of testosterone on behavior.

In study 1, the first session consisted of 40 single-shot interactions, during which subjects faced either an ingroup or an outgroup proposer (i.e., 20 trials each). The proposers were always endowed with 10 points and half of their offers were either fair (i.e., 4 or 5 out of 10 points) or unfair (i.e., 1, 2, or 3 out of 10 points). Offer types and team membership of the proposers were pseudorandomized and counterbalanced for condition transitions. Fair offers contained either 4 points (2 trials/team) or 5 points (8 trials/team) out of 10 points, while unfair offers were determined as 1 point (4 trials/team), 2 points (4 trials/team) or 3 points (2 trials/team). This

means that 80% of unfair proposals offered 20% or less of the initial endowment in the present study. Since 20% is assumed to be the threshold at which subjects start to reject more and more unfair offers (Güth, Schmittberger, and Schwarze 1982; Henrich et al. 2005), a rejection rate equal to or exceeding 80% of all unfair offers, i.e., comprising those from both the in- and outgroup in our version of the intergroup-UG, was assumed to reflect a high degree of inequity aversion that was marked as the first individual decision strategy (inequity averse subjects). In contrast, rejection rates well below 80% were considered as reflecting a rather selfish motivation (individual decision strategy 2, pro-selfs) with the motivation to collect as many points as possible for oneself, yet a high tolerance for unfairness. Based on this classification, that was exclusively based on the experimental structure and referred to the percentage of highly unfair trials as cut-off value, participants were divided into the two strategy groups.

In the intergroup-UG the proposers were introduced with a photo and their first name including initials of the surname to increase authenticity. The photographs showed a frontal view of the face with a neutral expression. The pictures were taken from other male students of Hamburg University about five years before the present study. To control for familiarity, we asked all participants after the experiment whether they knew anyone, but this was not the case. The team membership was indicated by small team icons (i.e., the cartoon characters). To further emphasize the social nature of the task, subjects were told that the proposers were former participants and that participants of the present study would now decide about their payoff. However, all proposers and their offers were pre-determined by the experimenter.

Before starting the intergroup-UG, participants were instructed to decide about each offer according to their individual preference. As they were told in the instructions, each decision determined their additional payment and the accumulated points would be translated into Euros.

A total of 2.50 Euros was the maximum reward that could be accumulated in the first session. Subjects also performed the intergroup-UG in a "competitive context" (session 2) for the same reward and the additional chance to win a group bonus (see Diekhof et al., 2014 for comparison). The data from the second session were however not analyzed here, for reasons outlined above. After having completed the intergroup-UG (total duration of 30 minutes), subjects were asked to switch to the role of the proposer and to make two offers to an anonymous ingroup and outgroup member.

2.1.4 Analysis of hormonal parameters from human saliva

After having collected and frozen all samples, the saliva samples were thawed at 26°C and then vortexed and centrifuged at RCF 604 ×g in a common Eppendorf Minispin centrifuge for 5 minutes to discard mucus and other residuals. The five morning samples were pooled into one aliquot by extracting an equal volume of each sample and mixing them together. This was done to control for the pulsatile secretion pattern of testosterone and ensured that the morning peak concentration was captured by the pooled aliquot sample. Samples that looked contaminated (e.g., had no transparent color or contained traces of blood) were discarded. Testosterone concentrations in the aliquot samples were analyzed using two enzyme-linked immunosorbent assay (ELISA) kits by Demeditec Diagnostics (sensitivity = 2.2 pg/ml). The denoted intra-assay coefficient of variation is indicated as 6.58% at 90.8 pg/ml and the interassay variation is given as 7.4% at 74.3 pg/ml. All aliquots were assayed twice and two control samples, one with a low and another one with a high concentration, were included.

2.1.5 Statistical analyses of Study 1

316 Mean rejection rates in all experimental conditions, i.e., group membership of proposer (ingroup,
317 outgroup), and type of offer (fair, unfair), were calculated for each subject. The rejection rates
318 were then submitted to a repeated-measures ANOVA, to test whether they were affected by team
319 membership, offer type and endogenous testosterone level. Furthermore, we investigated
320 whether individual differences in the tendency to reject unfair offers (individual decision
321 strategy) were related to endogenous testosterone and parochial altruism in the UG. As described
322 above and following previous approaches (Reimers, Büchel, and Diekhof 2017), we applied a
323 rejection rate of 80% to unfair offers in general (i.e., independent of team membership) as the
324 cut-off mark between the two strategy groups. The rate of 80% represents the proportion of
325 extremely unfair offers (i.e., 10% and 20%) within all unfair trials. Thus, a rejection rate of 80%
326 and more suggests an increased propensity for inequity aversion and subsequent costly
327 punishment indicated by categorical rejection of both the extremely unfair and the moderately
328 unfair offers (i.e., 30% offers) from both groups. Pro-selfs displayed a higher degree of
329 parochialism with higher rejection rates in response to outgroup offers as compared to ingroup
330 offers (rejection rate [mean ± SEM]: fair ingroup offers = 2.76% ± 1.30%; fair outgroup offers =
331 13.79% ± 4.42%; unfair ingroup offers = 27.93% ± 4.80%; unfair outgroup offers = 51.72% ±
332 6.12%; fair offers: $Z = -2.97$, $p = 0.003$; unfair offers: $Z = -3.08$, $p = 0.002$) (Fig. 1). However,
333 this might have primarily been the consequence of the strategy group assignment and the overall
334 higher rejection rates in inequity averse subjects (see (Reimers, Büchel, and Diekhof 2017) for
335 comparison) and will therefore not be subject of further discussion. For examination of the
336 influence of endogenous testosterone, subjects were divided into two groups according to their
337 testosterone level using median-split (see for example (Diekhof, Wittmer, and Reimers 2014) for
338 a similar approach). The testosterone median was calculated separately within the two strategy

groups, since we wanted to achieve an equal distribution of the testosterone groups in the two decision strategies. After that the data were then combined resulting in a low testosterone group (n = 30, mean ± SEM = 115.75 ± 3.34 pg/ml) and a high testosterone group (n = 30, mean ± SEM = 183.63 ± 5.92). We opted for the statistical approach of median-split of testosterone since the mean rejection rates of unfair offers in the intergroup-UG often display a rather limited range of variability, since subjects only receive few offers of a certain category and from one group, and represent non-parametric data (see (Diekhof, Wittmer, and Reimers 2014)).

In case of a significant Mauchly-test for sphericity in the ANOVA, results were reported using the Greenhouse-Geisser-corrected values. When significant effects were detected in the ANOVA, post-hoc comparisons were performed with the Wilcoxon-Test in case of repeated measures, and with the Mann-Whitney U-Test for independent data. Values of $p < 0.05$, two-tailed, were considered as significant. If necessary, p-values were corrected for multiple testing using the Bonferroni correction.

2.2 Study 2

2.2.1 Subjects

34 healthy male students (mean age ± SD: 25.06 ± 4.46 years) participated in the second study. The subjects were recruited via online advertisement on a campus website and by word of mouth. Participants reported no drug or alcohol abuse, and were free of any chronic illness including disorders of the hormone system as well as psychiatric or neurological disorders. They were also free of medication. A participation fee and an additional monetary reward related to the points acquired during the intergroup-UG were paid (see Study 1). All subjects gave written

informed consent and the study was approved by the local ethics committee (*Aerztekammer Hamburg*).

2.2.2 Procedure of political supporter study

Key to participation in study 2 was an interest in politics, which was assessed by the GermanScale for Political Interest (the PIKS questionnaire; (Otto and Bacherle 2011)). The PIKS questionnaire was sent by e-mail to the potential participant. The five questions on political interest and involvement were to be answered on a 5-point-Likert-scale, possible options ranging from 5, "applies fully", to 1, "doesn't apply at all", resulting in a mean PIKS-score (± SD) of 4.14 (± 0.59) for all participants. To determine group affiliation, the participants were additionally asked to rank the 6 political parties, which had a chance to win seats in the German parliament (*Bundestag*) according to their preference in the upcoming vote. The rating was thereby to be based on the shared values a participant held with the parties. The political parties comprised the four mainstream parties, i.e., the *SPD (Social Democrats)*, the *CDU (Christian Democrats)*, the *Greens*, and the *FDP (Free Liberals)*, as well as two parties from the extreme left and right wing, i.e., *The Left* and the *AfD (Alternative for Germany)*, which all succeeded to acquire seats in the German Bundestag in 2017. The rating procedure was carried out with attention to privacy of the participant in order to avoid social pressure and to rule out bias from the experimenter's side. Based on the political ranking, the participants were ascribed an affiliated ingroup (ranked as 1), while all other parties were considered as outgroups with varying degree of social distance depending on their rank. The party with a ranking of 6 was considered as the most distant outgroup. For subsequent analyses, these individual ranks were used. Otherwise the procedure of study 2 closely matched the one employed in study 1, including

the same questionnaires and saliva sampling procedure. Data collection took place in 2017. The complete experiment lasted about 1 hour and 15 minutes in total, which included the two sessions of the UG (see above) followed by a short distraction period and a face memory task.

2.2.3 Ultimatum game in a political context

The structure or the intergroup-UG strongly resembled the one of the minimal group study (approximate total duration of 30 minutes), starting with participants in the role of the responder and finally switching to the role of the proposer. Yet, in contrast to study 1, proposals came from 6 different groups that comprised the supporters from the 6 political parties. Again, each proposer was indicated by a unique photograph. The photographs were taken from the anonymous experimental picture stock of the department as well as from other universities. The pictures to be used in the game had previously been tested for approachability, making sure that none of the faces evoked a biased response in the participants. The approachability test was performed in an independent sample of 30 students, male and female, who rated each of the faces on a seven-point Likert-scale answering the question: “Would you ask this stranger for directions?”. Based on the rating, three faces remained unused in the experiment due to an extraordinary mean approachability rating, the others were equally distributed into the categories of (un)fairness and political inclination by approachability.

The first, unbiased session of the intergroup-UG comprised 48 single-shot computer game interactions with an apparently real, but actually fictional opponent indicated by the unique photograph. In an introductory text, participants were falsely informed about a nation-wide study in which other students had already participated, whose pictures, proposals and party affiliation participants were about to see in the game. From each political party 4 offers were considered as

(rather) fair (with two proposers offering either 4 or 5 points of 10), while the remaining 4 offers were unfair and included one offer of 1 point and 2 points, each, as well as 2 offers of 3 points. This resulted in a different threshold for determination of the individual decision strategy in study 2. Here, only 50% of the unfair proposals offered 20% or less of the initial endowment. This is why a mean rejection rate equal to or exceeding 50% across all unfair offers of the 6 ranks was assumed to reflect a high degree of inequity aversion (individual decision strategy 1; see study 1 above). In contrast, rejection rates well below 50% were considered as reflecting a rather selfish motivation. Based on this study-specific thresholding participants were divided into the two strategy groups in order to achieve maximum comparability with study 1.

2.2.4 Cued recall task (memory for faces)

In the second study we also wanted to test (1.) whether the different strategy groups differed in their overall ability to recollect the identity of faces from previous interactions, in particular unfair ingroup members, (2.) whether they showed a differential recollection for persons who treated them unfair or fair on previous trials, and (3.) whether recollection ability varied in relation to testosterone level. Similar procedures have already been employed in studies using related paradigms like the dictator game and demonstrated a memory advantage during recollection of the identity of unfair interaction partners, particularly for those from the ingroup (Hechler, Neyer, and Kessler 2016). The face memory task followed a short distraction period, in which participants filled out several questionnaires including the Trust and Reciprocity questionnaire (Dohmen et al. 2008) and a demographic questionnaire. In addition, they were asked to see themselves as player A in an UG and make their own proposals to future opponents. These proposals were to be made to 6 hypothetical future players B, portrayed as grey

anonymous silhouettes, each of whom was stated to be favoring one of the aforementioned 6 political parties. Offers were allowed to range between 1 and 5 points. Another assignment consisted of the same proposal task with a variation: instead of the UG, the participants were playing a dictator game, in which none of the anonymous partners would be able to reject their offer.

The subsequent cued recall task was presented to the participants by surprise. The 48 faces used in the two sessions of the UG were pseudorandomized and mixed with 48 new faces which had been selected from the same database and tested for approachability as stated above. Appearing one after another like in the UG, none of the faces were juxtaposed with any information. Instead, participants were asked to indicate with a button press whether the face was known or unbeknownst to them (old vs. new decision). Each trial ended with the subject's decision. The aim of this face memory task was to assess individual memory for unfair opponents in relationship with the ingroup-outgroup dynamic (Hechler, Neyer, and Kessler 2016).

2.2.5 Hormone analysis

The analysis of saliva samples followed the procedure described above (see study 1 above).

2.2.6 Statistical analyses

Here, we investigated whether individual differences in the tendency to reject unfair offers in general (individual decision strategy) were related to endogenous testosterone and parochial altruism (rejection of unfair outgroup offers) in the UG. Subjects who were considered inequity averse exhibited rejection rates clearly above 50% (n = 19, rejection rate of unfair offers [mean ± SEM] = 76.9% ± 3.53%), whereas selfish subjects (pro-selfs), who appeared to be more focused

on personal reward maximization, rejected by far less than 50% of unfair offers (n = 15, rejection rate unfair offers [mean ± SEM] = 23.7% ± 5.14%). 50% was the study-specific threshold that dissociated between moderately unfair and highly unfair offers, as described above. Following the logic from study 1, we assessed the nonparametric correlation between individual testosterone level and either the rejection of unfair offers made by the most distant outgroup (rank 6) or the average rejections made in interactions with unfair outgroup partners (mean rejection rates for unfair offers made by ranks 2 to 6). Through this, we wanted to ascertain that differences in social distance in study 1 and 2 would not confound the data.

Study 2 also incorporated a cued recall task, in which we wanted to examine differences in the ability to recollect previously encountered face identities as a function of their unfairness and social distance as well as in relation to testosterone and the two strategy groups. For this purpose we analyzed the hit rates for recalling the unfair proposers from rank 1 (ingroup) and rank 6 (most distant outgroup).

3. Results

3.1 Results of Study 1

Replicating previous results (Diekhof, Wittmer, and Reimers 2014; Reimers, Büchel, and Diekhof 2017; Reimers and Diekhof 2015) a clear tendency towards parochialism was found. A 2 ("team": ingroup, outgroup) x 2 ("offer": unfair, fair) x 2 ("testosterone group": high, low) repeated-measures ANOVA revealed a significant two-way interaction between "team" and "offer" ($F_{1, 58} = 4.34$; $p = 0.042$; partial $eta^2 = 0.07$) and we also found a main effect of "team" ($F_{1, 58} = 9.41$; $p = 0.003$; partial $eta^2 = 0.14$) as well as of "offer" ($F_{1, 58} = 189.51$; $p < 0.001$;

partial eta^2 = 0.77). Further, we identified a statistical trend for a differential effect of the high and low testosterone group on the rejection rates that was expressed by a three-way interaction of "testosterone group" x "team" x "offer" ($F_{1, 58}$ = 3.33; p = 0.073; partial eta^2 = 0.054). Post-hoc comparisons showed that rejection rates were significantly higher in interactions with outgroup members than with ingroup members. This was true for both the fair as well as the unfair offers ($p<0.01$). Yet, there was no differential pattern in the post-hoc tests that supported the interaction. In fact, there was a numerical difference in the delta of rejections between unfair and fair ingroup offers (57.7 ± 4.74%) and the delta of the respective outgroup offers (63.44 ± 4.27%), but this difference was not significant in the Wilcoxon test (p = 0.103). Mann-Whitney-U-Tests also did not yield significant results when directly comparing rejection rates of subjects with high and low testosterone. Yet, when considering the high testosterone group alone, the Wilcoxon test revealed that subjects in this group rejected unfair outgroup offers significantly more often than ingroup offers (rejection of unfair ingroup offers [mean ± SEM] = 64.67% ± 6.96%; rejection of unfair outgroup offers = 80.67% ± 4.47%; Z = -2.48; $p < 0.025$, *Bonferroni-corrected threshold*). When participants got the chance to make a proposal themselves, offers made to ingroup members were significantly higher than the ones made to outgroup members (Z = -4.0; $p < 0.001$; proposal ingroup [mean ± SEM]: 4.1 ± 0.14 points, proposal outgroup: 3.38 ± 0.18 points).

In a second step, following our previous approach that takes into account the decision strategy of an individual, i.e., an inequity averse vs. a self-interested strategy [18], we tested separately whether the rejection rates within each strategy group were related to endogenous testosterone. The two strategy groups were well matched and did not differ in questionnaire scores (i.e., BIS, trust, positive and negative reciprocity) and were comparable with regard to mean age and

testosterone level both on the group level and when comparing the high and low testosterone groups between strategies ($p > 0.31$). Yet after separating the data according to strategy groups, only the ANOVA in the group of pro-selfs revealed a trend-wise three-way interaction between "team" x "offer" x "testosterone group" ($F_{1, 26} = 3.68$; $p = 0.066$; partial $eta^2 = 0.124$), which was absent in inequity averse subjects ($F_{1, 30} = 0.17$; $p = 0.681$; partial $eta^2 = 0.006$). The three-way interaction had also reached trend-level in the ANOVA of the whole group as reported above. Post-hoc comparisons showed that pro-selfs with a high testosterone level rejected unfair outgroup offers significantly more often than pro-selfs with a low testosterone level ($U = 47.5$, $p = 0.019$; mean rejection rate [mean ± SEM] high testosterone group = 65.0% ± 7.39%, $n = 14$; low testosterone group = 35.71% ± 8.43%, $n = 14$) (see Fig. 1). In inequity averse subjects, however, testosterone apparently had no influence on the rejection rates, which could however also be related to the higher rejection rates. In addition to that, this apparent link between high testosterone and enhanced parochialism was further substantiated by the correlation between testosterone and the bias for parochialism in the reaction to unfair offers made by the outgroup (i.e., the parochialism bias was defined as the difference in treating unfair outgroup and ingroup proposals and was calculated by subtracting the unfair ingroup rejection rate from unfair outgroup rejection rate). In subjects with high testosterone this bias was greater in selfish participants than in inequity averse subjects (parochialism bias [mean ± SEM]: pro-selfs = 33.57% ± 10.09%; inequity averse subjects = 0.63% ± 2.95%; $U = 43.00$, $p = 0.003$) (see Fig. 2). Moreover, we found a significant positive correlation between individual testosterone level and the rejection rates of unfair outgroup offers in pro-selfs (Spearman' s Rho = 0.534, $p = 0.003$, $n = 29$) (see Fig. 3). Again, this link was absent in the inequity averse subjects (Spearman' s Rho = -0.141, $p = 0.441$, $n = 32$), who displayed only low variability in their rejection rates supposedly

also as a consequence of a ceiling effect of rejection rates in this group. Overall, the association between the variable rejection rates of the pro-selfs and individual differences in testosterone levels provided further support for the view that testosterone might fine-tune behavioral responses related to parochial altruism, which becomes particularly visible in individuals with a loose fairness norm and also fits with previous observations regarding testosterone-associated differences in brain physiology between strategies (Reimers, Büchel, and Diekhof 2017). Finally, being in the 'fast' or 'slow team' had no effect on the rejection rates, which was tested by re-running the first ANOVA including the subject's artificial team membership. Also when directly comparing rejection rates of the 'fast' and 'slow team' with a Mann-Whitney U Test, no significant differences emerged ($p > 0.227$).

3.2 Results of Study 2

Study 2 was intended to examine whether the results related to parochial altruism could also be found in a natural group context (supporters of political parties tested during the German election year 2017). First of all, we found that the political preferences of our student sample were clearly oriented towards the left wing parties (SPD, The Greens, The Left), which was also reflected by the mean ranking across participants (lower mean ranks indicate more favorable rating (mean ± sem): SPD = 2.44 ± 0.23, The Left = 2.94 ± 0.29, The Greens = 2.97 ± 0.23, CDU = 3.06 ± 0.22, FDP = 4.03 ± 0.23, AfD = 5.56 ± 0.20). Moreover, in line with study 1 and our previous results (Diekhof, Wittmer, and Reimers 2014; Reimers, Büchel, and Diekhof 2017; Reimers and Diekhof 2015) we found a significant two-way interaction ($F_{3.69, 121.78} = 2.81$; $p = 0.032$; partial $eta^2 = 0.079$) in the repeated-measures ANOVA with the factors rank of "political preference" (6 ranks) and "offer" (unfair, fair). This was also reflected by a significant linear trend with

increasing social distance, as determined by an univariate ANOVA with the independent factor ”rank” and the dependent variable ”mean rejection rate for unfair offers” ($F_{1,203} = 9.94$; $p = 0.002$). When comparing rejection rates between the most extreme cases, i.e., the first rank (one’s favorite political party, which will be referred to as ‘ingroup’) and the last rank (the 6th rank, which is associated with the least liked party with the most distant political values in the ranking, referred to as the ‘most distant outgroup’) we found significantly enhanced rejection rates for outgroup offers, both in the context of fair and unfair offers ($p<0.002$). In the comparison of the ingroup (rank 1) with the other ranks, we also documented two significant differences in the treatment of unfair offers by supporters of distant political parties ranked as 4 and 5, whose rejection was also more frequent ($p \leq 0.002$) (see Fig. 4, which displays the rejections rates related to unfair offers independent of strategy). All these differences survived the Bonferroni corrected threshold of 0.01. This means, that the design of study 2 was also suitable to show parochialistic tendencies amongst the supporters of political parties.

More importantly, the question was whether these parochialistic tendencies and in particular parochial altruism may be also be related to endogenous testosterone and the decision strategy as already documented in study 1. For simplicity and to compare study 2 (six groups) in an adequate way to study 1 (two groups), we subdivided the sample according to decision strategy (pro-selfs vs. inequity averse subjects) and analyzed the impact of testosterone on mean rejection rates of unfair outgroup offers made by the most distant outgroup (rank 6) separately in the two strategy groups. In line with study 1, a significant positive correlation emerged between testosterone and the rejection rates of the most distant outgroup (rank 6) that was restricted to the group of pro-selfs (Spearman’s Rho = 0.632; $p = 0.011$) (Fig. 3). Interestingly, if the data of the rejection of unfair offers from the most distant outgroups from the two studies were combined

($n_{pro\text{-}selfs}$ = 42) the p-value decreased drastically (Spearman's Rho = 0.578; p = 0.00006) suggesting a similar direction and strength of the correlation across studies. In the inequity averse sub-sample of study 2, no significant correlation could be found (Spearman's Rho = 0.035; p = 0.886), which corresponds to the result of study 1.

Since it is possible that differences in social distance between the outgroup used in study 1 (arbitrary group assignment) and the 6th rank of study 2 (most antagonistic political party) could have somehow confounded the correlations, we re-calculated the correlation between testosterone and the mean rejection rates for unfair offers averaged across the 5 political outgroups ranging from rank 2 to 6. Again, only pro-selfs showed a significant positive association between the average outgroup rejections and testosterone (Spearman's Rho = 0.657; p = 0.008; n = 15), while inequity averse subjects did not (Spearman's Rho = 0.157; p = 0.521; n = 19). In that way, the data from this second, independent sample tested in a different social setting underscore the theory that testosterone might support parochial altruism in subjects who are more interested in personal reward (pro-selfs), yet who apparently also have a more flexible fairness norm. These behavioral differences emerged despite the fact that in study 2, likewise to study 1, the two strategy groups did not differ in questionnaire scores (i.e., BIS, trust, positive and negative reciprocity) and were comparable in age and mean testosterone level (all comparisons p > 0.24).

We also examined the proposals made to anonymous political supporters of the 6 different parties. Proposals were made to future interaction partners to be encountered in either an UG or a dictator game context. For simplicity we only looked at the proposals made to the ingroup (rank 1) and the most distant outgroup (rank 6). In both the UG and the dictator game subjects clearly differentiated between the two groups and this was independent of the strategy group (UG:

592 $proposal_{rank1}$ ± = 4.6 ± 1.3 points ; $proposal_{rank6}$ ± = 3.0 ± 0.3 points; Z = - 3.87, p < 0.001; DG:
593 $proposal_{rank1}$ ± = 3.6 ± 0.3 points; $proposal_{rank6}$ ± = 1.4 ± 0.2 points; Z = - 4.18, p < 0.001).
594 However, there was no correlation between the generosity of the proposals and testosterone
595 when considering the complete sample. Only in the subgroup of pro-selfs we found a positive
596 relationship with the amount offered to an ingroup member during the DG (Spearman's Rho =
597 0.588; p = 0.021; n = 15).
598 Finally, in study 2 subjects performed a surprise cued recall task that was similar to the one used
599 by (Hechler, Neyer, and Kessler 2016). However, in our task version the group identity of the
600 faces shown was not indicated during the memory test, but participants were shown without any
601 notion of group identity. It has been suggested that there may be a memory advantage for
602 individuals of one's own group, especially if they exhibited schema-incongruent behavior (e.g.,
603 behaved unfairly) (Hechler, Neyer, and Kessler 2016). In order to assess this, we performed a
604 repeated-measures ANOVA on the trials showing previously unfair persons with factor "group
605 membership" (ingroup and most distant outgroup) and the between-subjects factor "strategy
606 group" (pro-selfs and inequity averse participants). This yielded a trend-wise interaction between
607 the factors ($F_{1, 32}$ = 3.43; p = 0.073; partial eta^2 = 0.1), which was reflected by an almost
608 significant difference in the recall of unfair ingroup members between strategy groups with a
609 memory advantage in pro-selfs (correct recall: $mean_{pro\text{-}selfs}$ ± sem = 62.78 ± 7.62%; $mean_{inequity}$
610 $_{averse}$ ± sem = 43.42 ± 6.58%; U = 86.5, p = 0.051, two-tailed). The recall of unfair ingroup
611 members was further positively correlated with individual testosterone level in pro-selfs
612 (Spearman's Rho = 0.534; p = 0.040; n = 15) as was the recall of unfair treatment averaged over
613 all ranks (Spearman's Rho = 0.626; p = 0.013; n = 15). There was no memory advantage in
614 relation to testosterone for unfair members of the most distant outgroup (rank 6) (Spearman's

Rho = 0.347; p = 0.205; n = 15). In contrast, inequity averse subjects showed no memory advantage for unfair proposers in relation with testosterone (p>0.34). This suggests that only in pro-selfs the recollection of unfair proposers and especially those from one's own group may have been associated with endogenous testosterone and that they also had a slight bias towards better recollection of ingroup proposers who violated the fairness norm.

3.3 Comparison of the results from study 1 and 2

In order to compare the results of the two studies, that were based on the same rationale concerning the influence of testosterone on parochial altruism, yet differed in the social setting that created the group affiliation (artificial vs. natural), we compared both the behavioral data as well as the demographics that included scores from two self-report questionnaires. For simplicity, we only compared the delta of the rejection rates in response to the (most distant) outgroup and the ingroup as an indicator of the parochialism bias in the UG.

First, the degree of parochialism bias in the pro-selfs did not significantly differ between studies. Further, parochialist tendencies as reflected by increased rejection of unfair outgroup offers were supposedly related to endogenous testosterone and occurred independent of the social setting in which subjects were tested, as already indicated before (see Fig. 3).

Contrasting these findings, a differential decision pattern emerged in inequity averse subjects between the studies. While in inequity averse subjects from study 1 the parochialism bias (delta of unfair outgroup rejection rates minus unfair ingroup rejection rates) was not significantly different from zero, neither regarding the whole sample nor when subdividing the sample by the median of testosterone (all comparisons: p>0.70; see Fig. 2), in study 2 the bias was significantly enhanced from zero in inequity averse subjects and this effect was independent of testosterone

(low testosterone (mean ± sem) = 34.17 ± 10.57 ; Z = -2.38, p = 0.017, n = 10; high testosterone (mean ± sem) = 22.22 ± 10.58; Z = -2.12, p = 0.034, n = 9). This differential treatment of the in- and outgroup by the inequity averse sample in the two studies was also evident in the direct comparison. The inequity averse participants from study 2 had a significantly higher bias value than those from study 1, which was again independent of testosterone (both comparisons: $p \leq 0.023$).

Secondly, we also compared the demographics and questionnaire scores between the two studies and separately for the two strategy groups. The selfish subjects from both studies were comparable with regard to age, BIS score, and endogenous testosterone level. Yet, they differed significantly in the scores for trust, positive and negative reciprocity from the German socio-economic panel (Dohmen et al. 2008). Accordingly, pro-selfs from study 1 showed significantly lower scores in trust and positive reciprocity than pro-selfs from study 2 (study 1: trust = 7.07 ± 0.35; positive reciprocity = 4.04 ± 0.2; study 2: trust = 8.29 ± 0.45; positive reciprocity = 10.29 ± 0.35; both comparisons $p < 0.04$), whereas the score for negative reciprocity was significantly higher in study 1 (study 1: negative reciprocity = 8.79 ± 0.38; study 2: negative reciprocity = 5.57 ± 0.42; $p < 0.001$). Like the pro-selfs, the inequity averse subjects from the two studies were also comparable with regard to age, and endogenous testosterone level. Further, in line with the results of the pro-selfs we found increased ratings of negative reciprocity from the German socio-economic panel in study 1 (study 1 = 8.53 ± 0.32; study 2 = 5.47 ± 0.32; $p < 0.001$). In contrast and like in pro-selfs, the scores for trust and positive reciprocity were significantly lower in inequity averse subjects from study 1 (study 1: trust = 7.31 ± 0.27; positive reciprocity = 4.31 ± 0.17; study 2: trust = 8.63 ± 0.34; positive reciprocity = 10.79 ± 0.32; both comparisons $p < 0.005$). In addition to that, inequity averse individuals from study 1 showed higher BIS scores

indicating increased impulsiveness (study 1 = 65.3 ± 1.76; study 2 = 59.32 ± 1.64; p = 0.026). To sum up, the self-reports of subjects from study 1 indicated higher distrust as well as an increased preference for retaliation of negative effects (negative reciprocity) that one had experienced, while participants from the second study showed a higher preference for returning a favor (positive reciprocity). This suggests that subjects from the two studies might have shown a general difference in the way to treat other humans in socio-economic interactions, which was independent of the decision strategy.

Although, we had no direct hypothesis regarding a connection, the differences between the scores from the trust and reciprocity questionnaire, whose trait of 'negative reciprocity' might be related to spitefulness, from the two studies suggested a possible relation of these traits with rejection rates in the UG, particularly as these were different. This led us to assess their association with the parochialism bias (delta of unfair outgroup rejection rates minus unfair ingroup rejection rates). For this we correlated individual scores with the delta across studies (n=90). We found a positive correlation with positive reciprocity (Spearman's Rho = 0.243; p = 0.019) and a negative one with negative reciprocity (Spearman's Rho = -0.244; p = 0.019) (*p<0.025; Bonferroni-corrected threshold*). These correlations apparently stemmed from the group of inequity averse subjects from both studies (n = 51; positive reciprocity: Spearman's Rho = 0.549; p < 0.001; negative reciprocity: Spearman's Rho = - 0.483; p < 0.001) as they were not evident in the pro-selfs (p>0.66).

4. Discussion

The aim of this research was to test whether an artificial group formation (study 1) and a natural group affiliation (study 2) would both install a sufficient group commitment to measure

individual differences in parochial altruism in the intergroup-UG and to investigate how these differences are related to circulating testosterone and individual decision strategy. In study 1, the subjects were divided into two artificial groups according to the distance they had covered in a maze task after seven seconds. For study 2, we tested supporters of political parties in the German election year of 2017 who showed a strong interest in politics and had a clear favorite party as well as reservations of varying degree towards the other parties competing in the election. The subjects of both studies acted as responders in a computer-based intergroup-UG with single-shot interactions and offers of varying degrees of unfairness. In the end, participants switched to the role of the proposer and had to decide about hypothetical offers to either members of their own group or the other group(s). Moreover, study 2 also included a cued recall task to assess memory for previously unfair proposers.

As hypothesized and in line with previous studies (Diekhof, Wittmer, and Reimers 2014; Reimers, Büchel, and Diekhof 2017), a marked pattern of parochial altruism was evident with higher rejection rates in outgroup than in ingroup interactions in both studies, which was even reflected by a linear trend for increased social discounting with increasing social distance in study 2 corresponding to the results of earlier studies (e.g., Strombach et al. 2015). Such rejections could indicate the willingness to forgo points in order to punish outgroup members, which would reflect an altruistic motive. An alternative view would interpret this behavior as spiteful rather than altruistic, with the aim to minimize other's payoffs in order to equalize relative gain between the interaction partners (Jensen 2010). It has been assumed that spiteful individuals see others as competitors whose gains negatively affect their own utility (Espín et al. 2015). Yet, it is not clear why spitefulness should necessarily follow a parochial pattern. We observed that our participants, and especially those with the otherwise selfish motive of reward

maximization (the pro-selfs), had a clear preference to minimize the payoff of unfair outgroup members, yet not the one of unfair ingroup members. This indicates that rejections benefited the relative gain of the ingroup, but clearly harmed the outgroup at their own expense. Moreover, when being in the role of the UG proposer all subjects in general offered more points to ingroup than to outgroup members in both studies, which again contributed more to the relative gain of ingroup partners. Finally, in study 2 subjects indicated a reduced preference for negative reciprocity and therefore supposedly a reduced tendency for decisions motivated by spite. In contrast to that, they were more trusting and had a higher preference for positive reciprocity. Still, the subjects of study 2 exhibited a similar tendency for altruistic punishment of unfair decisions as those in study 1, which might argue against the assumption that spitefulness (or negative reciprocity) was the major driving force of decisions across studies (but also see discussion of discrepant findings between the two studies below, which indicated that at least one sub-sample from study 1 could have been motivated by spite).

Moreover, when looking at the findings of study 1 we found that the minimal group formation task elicited parochial altruism in the same manner as did previous studies with natural groups (e.g., ethnic groups as in Fershtman and Gneezy 2001, or the sample tested in study 2). The minimal group formation task resembled previously applied methods of assigning subjects to different groups according to their performance on a meaningless task (like in a task that required the estimation of the number of presented dots). Given previous evidence indicating that even such minimal conditions for group assignment promote an intergroup bias (Brewer 1979; Tajfel et al. 1971; Volz, Kessler, and Cramon 2009), we expected to find a similar pattern. But note that alternative methods to create group identity have also revealed conflicting findings

731 indicating that norm violations committed by ingroup members are punished more often (e.g.,
732 McLeish and Oxoby 2007; Mendoza et al., 2014). Although costly punishment has been
733 proposed to sustain group cooperation (e.g., Fehr and Gächter 2002) and may thus be expected to
734 occur more often in response to unfair ingroup members, we found previously that our version of
735 the intergroup-UG particularly provoked increased punishment of unfair outgroup members by
736 young healthy men, even when our participants played for themselves without a direct intergroup
737 competition (Diekhof, Wittmer, and Reimers 2014; Reimers, Büchel, and Diekhof 2017).
738 What is nevertheless interesting to note in study 2 is the memory advantage for ingroup members
739 that committed a norm-violation, i.e., previously made an unfair proposal, which became
740 apparent in self-oriented subjects in the cued recall task. Interestingly, memory performance was
741 thereby positively correlated to endogenous testosterone level in the same subjects. This is
742 reminiscent of the finding by Reimers et al. (Reimers, Büchel, and Diekhof 2017), who also
743 demonstrated an increased neural sensitivity for unfair ingroup offers in the group of pro-selfs,
744 and this was indicated by increased activation of the anterior insula that scaled with individual
745 testosterone. Given this evidence, we speculate that in both studies the pro-selfs may have
746 exhibited increased attention towards unfair proposals made by ingroup members, as reflected by
747 an increased engagement of the anterior insula n (Reimers, Büchel, and Diekhof 2017) and
748 indicated by a better memory for the respective norm-violators in study 2. This would also be in
749 line with previous studies showing that schema-incongruent information in a social setting may
750 lead to a memory advantage (Bell and Buchner 2012; Hechler, Neyer, and Kessler 2016). Yet, it
751 is interesting to note that we only found evidence for this in subjects who clearly differentiated
752 between their own group and the members of other groups (i.e., pro-selfs who rejected less of the
753 unfair offers made by ingroup members). This may indicate that despite the acceptance of an

unfair offer, the pro-selfs were more attentive for norm-violations within their own group, which might become important on a second interaction with the same person.

4.1 Decision strategy and testosterone level are associated with parochial altruism across studies

Following the separation of two strategy groups that was based on the classification already used in our previous study (Reimers, Büchel, and Diekhof 2017), we naturally found behavioral differences between subjects categorized as self-oriented players and subjects who displayed a reduced tolerance for unfairness. These differences in behavior could reflect an increased altruistic tendency in the inequity averse group, as has been previously assumed (Reimers, Büchel, and Diekhof 2017) since these subjects displayed a heightened tendency to punish unfair proposers at one's own expense. Yet, one may also argue that the response of this group was caused less by an altruistic, but more by the spiteful and antisocial motive to not begrudge the other player his higher share (Jensen 2010). For this reason, in the present research project we opted for the more neutral term of 'inequity aversion', which describes the fact that this group of subjects did not tolerate any of the highly unfair offers and also showed a reduced tolerance for the moderately unfair offers on a general basis, indiscriminate of in- or outgroup offers. Inequity averse behavior was found in both studies of the present research despite a different percentage of the highly unfair offers of 1:9 or 2:8 points (i.e., 80% of highly unfair offers in study 1 and 50% in study 2) and a different number of intergroup interactions (2 groups in study 1 and 6 groups, of which 5 were considered as outgroups of varying social distance). The pro-selfs, on the other hand, displayed a stronger tendency towards parochial altruism in the two studies with higher rejection rates of outgroup than ingroup offers, despite an overall lax fairness norm. This

777 difference in parochial tendency between the two strategy groups replicates previous data
778 pointing to the same effect of decision strategy on parochialism. It is yet to be considered a
779 probable consequence of the strategy group assignment based on the mean rejection rates of
780 unfair offers in the neutral session that naturally resulted in significant group differences in this
781 decision context, particularly when considering the ceiling effect in rejection rates of the inequity
782 averse group (Reimers, Büchel, and Diekhof 2017). Interestingly, the pattern of rejection rates
783 observed in pro-selfs (ingroup < outgroup) also conforms to the Social Identity Theory (Tajfel
784 1982) as well as to a recent findings that demonstrated that people may be more tolerant to social
785 norm violating behaviors executed by ingroup members (Wang et al. 2017). Yet, as already
786 mentioned above, the memory advantage for unfair ingroup proposers may also indicate an
787 increased attention for these unexpected norm-violations that might result in future consequences
788 on a second encounter with the respective person.
789 Most importantly, in the pro-selfs of both studies endogenous testosterone was associated with
790 an increased propensity towards outgroup hostility. Selfish participants with a high testosterone
791 level rejected unfair outgroup offers significantly more often than pro-selfs with a low level also
792 in comparison to ingroup offers in study 1 (Fig. 2). This was further highlighted by a significant
793 positive correlation between individual testosterone level and the rejection rate for unfair
794 outgroup offers in both studies (Fig. 3). These results suggest that testosterone might be one
795 important physiological factor that could promote parochial altruism and might not necessarily
796 be related to the sensitivity for unfairness *per se*. Further, based on the present data a strategy-
797 dependent effect of testosterone in shaping the behavioral response to unfairness could be
798 proposed, that may be particularly pronounced in subjects with an otherwise lax fairness norm,
799 i.e., pro-selfs. Recent neuroimaging findings further substantiate this view by pointing out that

testosterone affects brain activity associated with parochial altruism differentially depending on the decision strategy of an individual (Reimers, Büchel, and Diekhof 2017). One might speculate that variations in strategies might predispose individuals to different behavioral default impulses so that specific neural circuits are activated to inhibit this initial urge to reject an unfair proposal, but at the same time enhance attention to proposer identity, and testosterone might play a role in these compensatory neural processes.

Important to note, the present findings represent correlational evidence and placebo-controlled administration studies are required to probe for the causal link between testosterone and parochial altruism. Previous studies that administered testosterone provide first evidence for a causal effect of testosterone on decision making in the UG (e.g., Dreher et al. 2016; Eisenegger et al. 2010; Kopsida et al. 2016; Zak et al. 2009). However, these studies did not account for effects of social context such as group membership of the interaction partner, which might explain their inconsistent findings regarding the behavioral effect of testosterone (i.e., antisocial vs. prosocial, see Introduction). Thus, an interesting avenue for future research will be to investigate exogenous testosterone effects on altruistic punishment in the context of intergroup interactions.

4.2 Discrepancies between the present findings on the testosterone-parochialism associations and previous observations made in the context of soccer fandom

The present results on testosterone differ from those of our previous study that had tested a group of male soccer fans (Diekhof, Wittmer, and Reimers 2014). There, the positive relationship between testosterone and parochial altruism was observed when soccer fans transitioned from the first (neutral) session to the competitive part of the intergroup-UG (session 2), during which

groups explicitly competed for an additional group bonus. Diekhof et al. (2014) thereby observed that, firstly, the relative enhancement of rejections of rather fair outgroup offers (4:6) was stronger in soccer fans with a high testosterone level. Secondly, the same subjects showed an increased parochialism bias, but only during the competition, whereas there was no such relationship in the first session of the intergroup-UG. Finally, when being in the role of a proposer, soccer fans with high testosterone made more generous proposals to members of their ingroup. In contrast, in the present two studies the effect of testosterone on the parochialism bias already occurred in session 1 and was restricted to the group of pro-selfs, who subsequently also offered less to outgroup members when they had higher than average testosterone. However, the previous and present behavioral studies differ in some important aspects. While in the previous study (Diekhof, Wittmer, and Reimers 2014) participants faced proposers of four different sports teams (i.e., the soccer ingroup, a neutral soccer outgroup, an unknown cricket outgroup and a disliked soccer outgroup), three of whom were competing in the German soccer league (*Bundesliga*), the present research either used two different artificially created team identities (i.e., ingroup and outgroup) in study 1 or employed a natural group of German voters with high political interest in study 2 that included six different political groups, which ran in the election. These differences in the groups under research might have led to different degrees of group commitment, as demonstrated previously by Weisel and Böhm (Weisel and Böhm 2015). Despite the use of natural groups in both study 2 and the study by Diekhof et al. (Diekhof, Wittmer, and Reimers 2014), who were all competing for a desired resource, either for seats in the German *Bundestag* or a high *Bundesliga* ranking, we assume that soccer fandom evokes a much stronger emotional group affiliation than being a supporter of a certain political party prior to an important election in Germany, even though this was not explicitly tested here. Compared

to these natural social settings, even less emotional commitment may be assumed in a member of a minimal group that was based on the performance in a simple reaction time task like in study 1, although this assumption is again speculative since it was not tested here. As already discussed in detail by Weisel and Böhm (Weisel and Böhm 2015), the election campaigns of the different mainstream parties in Germany (*SPD, Greens, CDU* and *Free Liberals*) are less emotional than for example in the United States (US). As Weisel and Böhm (Weisel and Böhm 2015) put it, the political discourse in Germany is mild and the mainstream parties are not as polarized as for example the Democrats and Republicans in the US. Also, many voters may consider them to have more in common than in separation. Only parties on the extreme right or left wing may be considered as distinct, which was also demonstrated here by the ranking of the extreme right wing party, the *AfD*. Of the 34 participants in study 2, 28 categorized the extreme right as rank 6, and another 3 did so as rank 5. In contrast to interactions between political voters in real life, the context of soccer fandom is characterized by a high degree of enmity between teams and normally the affiliation with one's own team is very strong and emotional, that it may often resemble a tribal identity (Vugt and Park 2010). Our previous study only tested subjects who strongly agreed with statements like "*soccer is my life*" and who owned not only season tickets for matches of their favorite team, but also went to away matches and owned fan merchandise like bedclothes with a team logo (Diekhof, Wittmer, and Reimers 2014). Further, a soccer season comprises 34 weeks of a year with games every weekend, while an election for the German *Bundestag* happens only every 4 years and the hot phase of the election campaign comprises only a handful of weeks directly before the election. This requires a constant engagement with the success of one's favorite team as well as real life interactions with other supporters of one's team as well as those from rival teams (please note that subjects were asked for their degree of

soccer fandom in (Diekhof, Wittmer, and Reimers 2014), as described above). Weisel and Böhm (Weisel and Böhm 2015) found less outgroup hate in supporters of political parties than in soccer fans in an economic game which is sensitive for the different aspects of parochialism. When comparing the parochialism bias (i.e., the subtraction of the rejection rate in response to unfair ingroup from unfair outgroup offers) of the present two and our previous behavioral soccer study (Diekhof, Wittmer, and Reimers 2014), we see that the minimal group study 1 had the lowest value (mean ± standard deviation = 10.67 ± 27.61), which was also significantly different from the bias found in study 2 (mean ± standard deviation = 24.0 ± 33.19) and the one documented by Diekhof et al. (Diekhof, Wittmer, and Reimers 2014) (mean ± standard deviation = 23.33 ± 35.57). Yet, in contrast to Weisel and Böhm (Weisel and Böhm 2015) we did not find a difference in the parochialism bias between political supporters during the election year and the hardcore soccer fans, which might be related to the fact that the politically most distant outgroup in most participants comprised the extreme right party that opposes many moral values shared by the other parties. Further adding to this, the majority of subjects in study 2 (77.6%) indicated a party from the left wing (*SPD, The Left, The Greens*) as their favorite party (rank 1), which may be most distant from the extreme right wing. Nevertheless, we still speculate that the emotional engagement might have been highest in the hardcore soccer fans, which could be the reason why we had been unable to observe the rather subtle effect of testosterone on behavior during the non-competitive context of the UG in the first soccer study. Interestingly, Diekhof et al. (Diekhof, Wittmer, and Reimers 2014) found a positive association between testosterone and the parochialism bias during the competition, when subjects got the chance to win an additional group bonus, which required them to forego personal reward in order to maximize the number of points accumulated for their group. This suggests that the subtle effect of endogenous

testosterone might be influenced by the social ramifications in which a group is built, and this could explain discrepant findings between studies. In the two studies here, the testosterone-behavior association became only visible in selfish subjects, who apparently have a rather flexible fairness norm, and the association occurred in the unbiased part of the UG, in which subjects were not explicitly instructed to pay attention to the group affiliation of an interaction partner. Nevertheless, this result emerged across the different social settings of study 1 and 2, which may point to a valid, but small effect of testosterone on latent behavioral parochialism during socio-economic interactions outside of the context of soccer fandom.

4.3 Differences in parochialism bias of inequity averse subjects of study 1 and 2

The results of study 1 and 2 did not always concur. When looking at the groups of inequity averse participants, findings were less consistent than those documented in pro-selfs. In fact, the inequity averse participants from study 1 did not show a parochialism bias at all, but exhibited comparably high rejection rates in response to both unfair ingroup and outgroup offers. On the contrary, in study 2 the bias was clearly evident, but independent of testosterone (see Fig. 2). This differential response pattern might have been related to differences in personality traits. For one thing, the participants of study 1 showed a higher degree of negative reciprocity, which comprised the increased tendency for retaliation or to harm someone who has previously harmed oneself, while the tendency to return a favor (positive reciprocity) and the trust in strangers was reduced in comparison of subjects from study 2. For another, the inequity averse sub-sample from study 1 was also more impulsive. Impatience as an aspect of impulsiveness has previously been shown to influence decisions in the UG. In particular, spitefulness in the UG may be driven by an increased impatience, which would result in increased rejections of unfair offers as well as

reduced proposals in general (Espín et al. 2015). While the former could be documented for the inequity averse sub-sample of study 1, the latter could not be found. Yet, the personality profile with increased negative reciprocity in combination with heightened impulsivity in this sub-sample, clearly points in the direction of increased spitefulness as a motive for the exceedingly high rejection rates that did not show any indication of parochialism. Interestingly, we also found a negative correlation between the parochialism bias in inequity averse subjects and negative reciprocity (as well as a positive correlation with positive reciprocity), suggesting more equal rejection rates for unfair ingroup and outgroup members in subjects with high negative reciprocity. So at least in this sub-group, we could speculate about a spiteful rather than altruistic motive for increased overall rejections in the UG (Espín et al. 2015; Marlowe et al. 2011), which however needs to be replicated by future studies.

4.4 Outlook and limitations

The present studies identified a single hormone as a correlate of parochial altruism in the intergroup-UG. However, testosterone may not be the only hormonal factor involved in ingroup favoritism and outgroup hostility. There is recent evidence for other hormonal systems to play a role in shaping parochial altruism. For instance, the neuropeptide oxytocin has been shown to drive parochial altruism in men during economic interactions (De Dreu et al. 2010). The steroid hormones testosterone and estrogen have been shown to modulate the expression of the neuropeptides oxytocin and vasopressin (Liening and Josephs 2010; Soares et al. 2010), which are both involved in a variety of social behaviors (Bos et al. 2012). Thus, the effects of testosterone on parochial altruism in the pro-selfs might have been mediated through alterations in oxytocin expression.

Another hormone that might potentially influence testosterone's effects on social behavior is cortisol. A growing number of studies provide evidence for the *dual-hormone hypothesis*, which states that the effects of testosterone on status-related behavior, such as dominance, depend on the levels of cortisol (Mehta and Josephs 2010). In fact, a recent study has provided initial evidence for the dual-hormone hypothesis in the context of an UG showing that a rise in testosterone was associated with increased acceptance rates of unfair offers in individuals with decreased cortisol levels (Mehta et al. 2015). Therefore, future studies on the role of testosterone in shaping intergroup behavior should aim to further elucidate the effects of these other potentially relevant hormones as well as hormonal interactions.

An aspect that currently remains unknown, as it was not in the focus of the present study, is the impact of genetic predispositions on individual differences in parochial altruism. For instance, a genetic polymorphism in the androgen receptor gene, the CAG tandem repeat length, is associated with the sensitivity for circulating androgens such as testosterone (Chamberlain, Driver, and Miesfeld 1994). Subjects with a more selfish tendency have been reported to show a tendency towards shorter repeat lengths and thus supposedly increased androgen sensitivity (Reimers, Büchel, and Diekhof 2017), which would help to explain the present findings.

Finally, the expression of parochial altruism may not only be driven by physiological factors, but may further be shaped and could even be intensified by cultural ramifications like gender or racial stereotypes, socially preferred or sanctioned behaviors and long-standing rivalries between groups. Yet, by thoroughly assessing the physiological basis of parochial altruism we might be better able to formulate hypotheses that address the potential interaction between physiological and cultural factors that may collectively lead to prevailing intergroup bias and may fuel racism across the globe.

5. Conclusion

In conclusion, the present findings show that high levels of testosterone are linked to behavioral patterns of parochial altruism depending on individual decision strategy. Extending previous data that demonstrated an association between testosterone and parochial altruism in soccer fans (Diekhof, Wittmer, and Reimers 2014; Reimers, Büchel, and Diekhof 2017; Reimers and Diekhof 2015), the present study revealed a comparable relationship in artificially created groups and supporters of political parties. Based on the concordant findings of study 1 and 2, it may be assumed that the previously observed effect of testosterone on parochial altruism represents an evolutionary conserved neurobiological mechanism that is highly relevant and thus also detectable in minimal group contexts as well as natural social settings outside the context of soccer fandom. In sum, our results add further evidence to the modulatory role of testosterone in shaping parochial altruism and point to potential future avenues for research aiming to understand the neuroendocrinology underlying this prevalent human behavior.

6. Author contributions

LR and ED designed the experiments. Data collection was performed by LS, EK and MY. All authors analyzed the data. ED and LR wrote the first draft of the paper and all authors contributed in revising and finalizing the manuscript.

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9. Figure legends

Figure 1: Mean rejection rates of unfair offers in the ultimatum game depend on decision strategy and endogenous testosterone in study 1. The subgroup of pro-selfs with high endogenous testosterone (n = 14) displayed an enhanced intergroup bias as indicated by the significantly higher rejection rates of unfair outgroup compared to ingroup proposals. In contrast to that, the inequity averse participants did not differentiate between in- and outgroup proposals and rejected unfair offers frequently irrespective of team identity and endogenous testosterone. *p < 0.025, *Bonferroni-corrected*.

Figure 2: Parochialism bias varies with decision strategy and endogenous testosterone in study 1. The subgroup of pro-selfs with high endogenous testosterone (n = 14) displayed a significant parochialism bias in comparison to those with low testosterone (n = 14) and compared to zero. *p < 0.05.

Figure 3: Testosterone was positively correlated with outgroup hostility in pro-selfs in both studies. Higher endogenous testosterone was significantly associated with higher rejection rates related to unfair outgroup offers (study 1: Spearman' s Rho = 0.473, p = 0.010, n = 29; study 2: Spearman's Rho = 0.632, p = 0.011, n = 15). In contrast to that, no significant correlation was found in inequity averse participants (not shown here).

Figure 4: Rejection rates for unfair offers increase with increasing social distance of political party supporters in study 2. A significant difference is observed between the first

rank, i.e. supporters of one's favorite political party, and the last three ranks of the distant outgroups ($p \leq 0.002$).

Figure 1

Mean rejection rates of unfair offers in the ultimatum game depend on decision strategy and endogenous testosterone in study 1.

The subgroup of pro-selfs with high endogenous testosterone (n = 14) displayed an enhanced intergroup bias as indicated by the significantly higher rejection rates of unfair outgroup compared to ingroup proposals. In contrast to that, the inequity averse participants did not differentiate between in- and outgroup proposals and rejected unfair offers frequently irrespective of team identity and endogenous testosterone. *p < 0.025, *Bonferroni-corrected*.

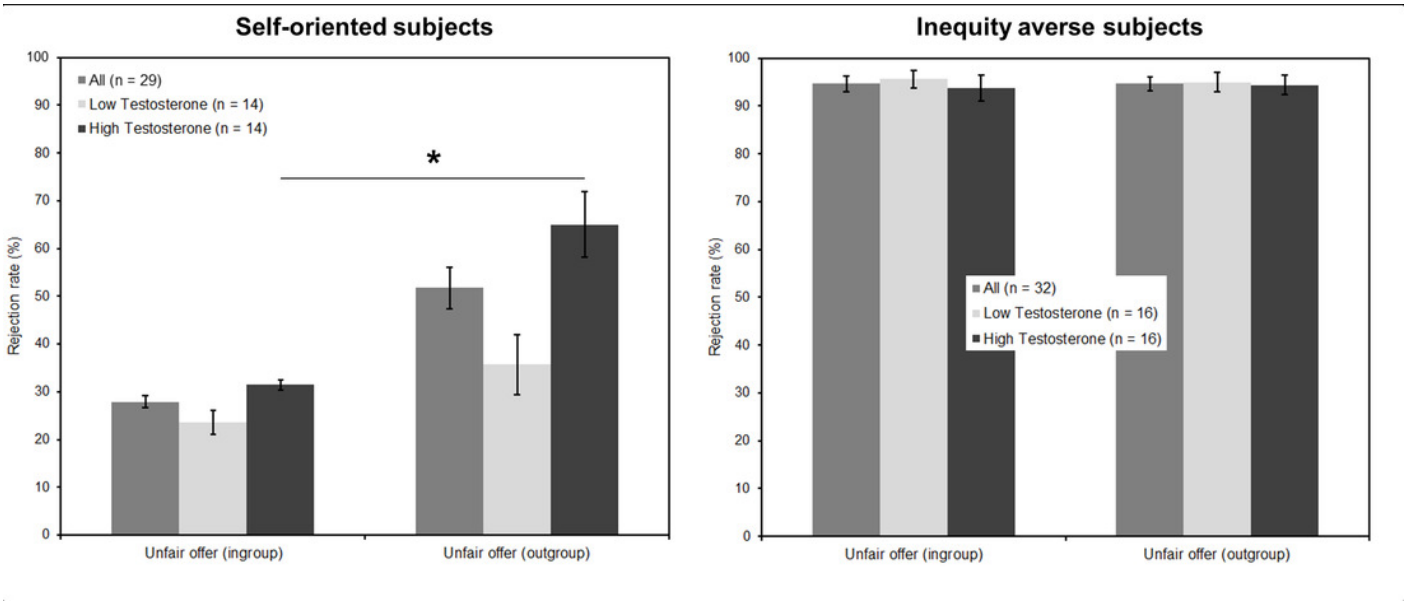

Figure 2

Parochialism bias varies with decision strategy and endogenous testosterone in study 1.

The subgroup of pro-selfs with high endogenous testosterone (n = 14) displayed a significant parochialism bias in comparison to those with low testosterone (n = 14) and compared to zero. *$p < 0.05$.

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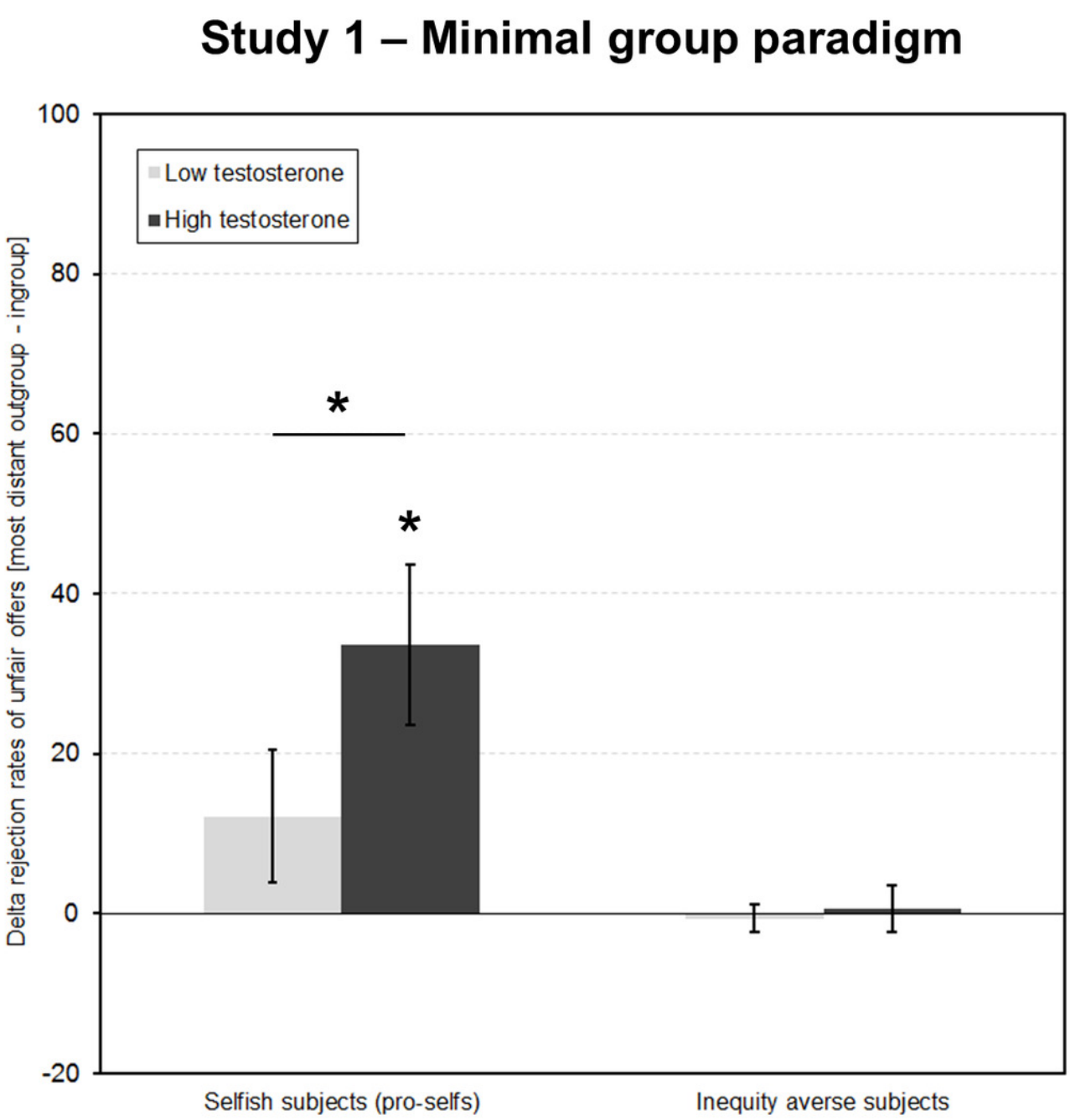

Figure 3

Testosterone was positively correlated with outgroup hostility in pro-selfs in both studies

Higher endogenous testosterone was significantly associated with higher rejection rates related to unfair outgroup offers (study 1: Spearman' s Rho = 0.473, p = 0.010, n = 29; study 2: Spearman's Rho = 0.632, p = 0.011, n = 15). In contrast to that, no significant correlation was found in inequity averse participants (not shown here).

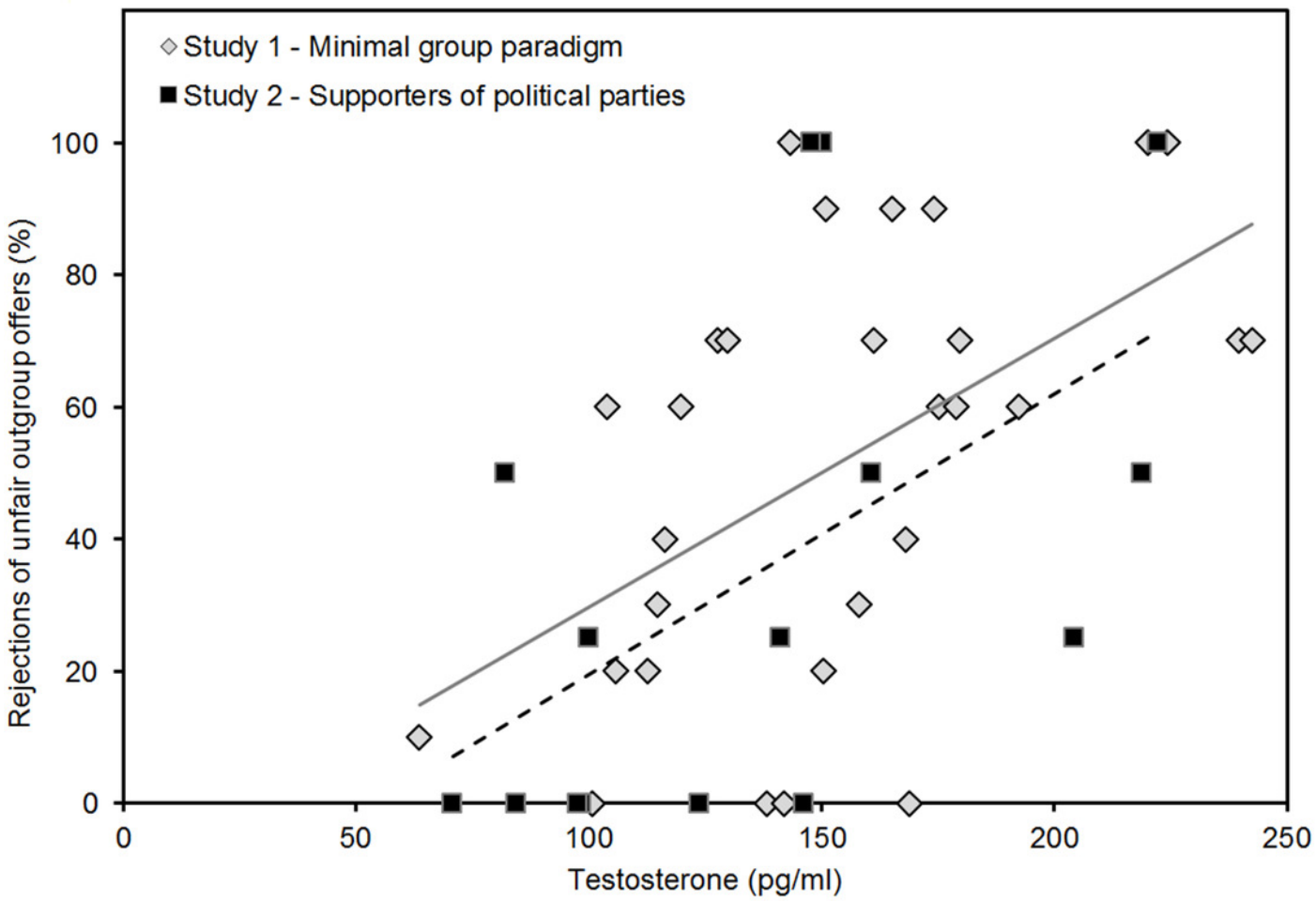

Figure 4

Rejection rates for unfair offers increase with increasing social distance of political party supporters in study 2.

A significant difference is observed between the first rank, i.e. supporters of one's favorite political party, and the last three ranks of the distant outgroups ($p \leq 0.002$).