

Endogenous Testosterone is Associated with Increased Striatal Response to Audience Effects during Prosocial Choices

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3 **Endogenous testosterone is associated with increased striatal**
4 **response to audience effects during prosocial choices**

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Abstract

The role of testosterone on cognitive functions in humans remains controversial. One recent hypothesis suggests that this steroid hormone advances social status. As being observed by others is known to modulate a range of behaviors because of image concerns, we hypothesized that such an audience effect might be an important component of status seeking that is under the control of testosterone. Thus, we investigated to which extent testosterone levels are associated with the effect of being observed during prosocial choices and the neural mechanisms underlying this effect. We enrolled twenty-four male participants, aged 22.47 ± 2.62 years, in an fMRI experiment to examine the relationship between testosterone levels and brain activity engaged in deciding whether to accept or reject monetary transfers to two types of organizations (a positively evaluated organization and a negatively evaluated organization) in presence or absence of an audience. When comparing the public to the private condition, the rate of acceptance increased for the positively evaluated organization, while the rate of rejection increased for the negatively evaluated one. Higher testosterone levels were linked to greater activation in the striatum in the public compared to the private condition, regardless of the organization type. These results indicate a relationship between testosterone levels and striatal activity induced by the audience effect. These findings provide new insights on the role of testosterone in human social behavior.

Keywords: Testosterone; Audience effect; Striatum; Social image; Charitable giving

65 **1. Introduction**

66 The steroid hormone testosterone has long been known to regulate the development of
67 physical masculinization (Renfree et al., 2002). Apart from its role in the body, there has been
68 growing interest in understanding testosterone-behavior relationships over the past decades
69 (Geniole and Carré, 2018; Hines, 2017). One traditional view on testosterone functions is that
70 it drives certain forms of aggression in both humans (Coccaro et al., 2007; Dabbs and
71 Hargrove, 1997; Räsänen et al., 1999) and non-human primates (Bouissou, 1983;
72 Giammanco et al., 2005). However, this traditional view of the role of testosterone in driving
73 aggression has been revisited in more recent theories and experiments (Archer, 2006;
74 Nadler et al., 2019). Recent studies emphasized its relation to status-enhancing behavior in
75 the form of prosocial or antisocial behavior, depending on the social contexts (Booth et al.,
76 2006; Dreher et al., 2016; Eisenegger et al., 2011; Mazur and Booth, 1998). For example,
77 higher levels of testosterone in both men and women have been associated with enhanced
78 social status (Rowe et al., 2004; Sellers, 2006) or increased spatial cognitive skills when
79 status is at play (Newman et al., 2005). Other behavioral results in men and women have also
80 emphasized the relationship between testosterone levels and social cooperation (Casto and
81 Edwards, 2016; Sanchez-Pages and Turiegano, 2010) or the choice of an interaction
82 strategy (domination vs. submission) in a social context (Inoue et al., 2017; van Honk et al.,
83 2014). In addition to these correlational evidence, recent behavioral studies tested to what
84 extent testosterone administration plays a causal role during social interactions. A single
85 dose of testosterone in women decreased trust but increased generosity in non-competitive
86 settings (Boksem et al., 2013), led to fair bargaining behavior (Eisenegger et al., 2010) and
87 motivated for reputable-status seeking, even when the resulting behaviors were
88 economically disadvantageous (van Honk et al., 2016). Similarly, these findings have been
89 extended to men. For example, exogenous testosterone administration in men has been

90 shown to increase not only the altruistic punishment of unfair offers, but also prosocial
91 behavior (positive reciprocity) in response to generous offers in a modified ultimatum game
92 (Dreher et al., 2016), social cooperation (van Honk et al., 2012), preferences for high-status
93 goods (Nave et al., 2018) and status-seeking motivation with unstable low social status
94 (Losecaat Vermeer et al., 2020).

95 However, a key element of social interactions in real-world settings is whether other
96 individuals can observe both the decisions made by the decision maker and their
97 consequences, which is in fact a neglected aspect of the aforementioned studies. Decisions
98 under observability can indeed be influenced by individuals' image concerns. In these
99 settings, individuals may focus on matching their in-group social values rather than raising
100 social status (Everett et al., 2015). Previous studies have found that individuals' behavior
101 can be influenced by the mere presence of others (Hamilton and Lind, 2016), suggesting
102 that the presence of an audience may be one of the dominant factors driving several social
103 enhancing behaviors (Bradley et al., 2018). Audience as a modulator of behavior has been
104 found in a diversity of species, including humans and nonhuman primates (Chib et al., 2018;
105 Sekiguchi and Hata, 2018). Given that the mere presence of an audience can promote
106 status-seeking behavior in our social life and testosterone has been shown to play an
107 important role in status-relevant behavior, understanding the extent to which testosterone
108 levels can be related to audience during prosocial decisions would greatly advance our
109 understanding of testosterone-behavior relationships. In particular, since testosterone is
110 involved in status-relevant behavior, one may expect that an audience should enhance its
111 relation with norm-compliant prosocial behavior. Moreover, identifying the underlying neural
112 mechanisms of the association between testosterone levels and audience in prosocial
113 behavior would provide important insights not only into the prosocial role of testosterone in
114 the context of social interactions, but also into the mechanisms underlying the

115 testosterone-status relationship. This matters particularly since testosterone has been shown
116 to be disrupted in psychiatric disorders (Li et al., 2020). In particular, children who have been
117 exposed to high concentrations of testosterone as a fetus would be more likely to exhibit
118 autistic traits (Mullard, 2009). Although previous research investigated the effect of audience
119 on prosocial behavior in autism, the relationship with testosterone remains to be investigated
120 (Izuma et al., 2011). Prior neuroimaging evidence pinpoints a brain network essential for
121 conducting prosocial decisions. This includes the striatum, anterior cingulate cortex (ACC),
122 ventromedial prefrontal cortex (vmPFC) and temporo-parietal junction (TPJ). This network is
123 recruited when expecting social rewards as well as when weighing monetary costs against
124 compliance with one's moral values, or when helping choices are made (Cutler and
125 Campbell-Meiklejohn, 2019; Qu et al., 2019). Yet, how the aforementioned network is
126 regulated by sex hormone is unknown, although an increasing effort has been devoted to
127 exploring how other hormones such as estrogen and oxytocin modulate prosocial behavior
128 (Kemp and Guastella, 2010; Zethraeus et al., 2009). Here, we explored the relationship
129 between endogenous testosterone levels and the neural mechanisms underlying prosocial
130 behavior in reaction to the presence or absence of an audience. To address this question,
131 we used the behavioral data from a donation experiment published by Qu et al. (2019). In
132 this experiment, participants had to decide whether to accept or reject monetary transfers to
133 two organizations (one positively evaluated, and the other negatively evaluated). Prosocial
134 behavior was characterized by two types of decisions: accepting a monetary transfer to a
135 positively evaluated organization at a personal cost, or foregoing personal monetary gains to
136 reject a transfer to an organization that they evaluated negatively. These decisions were
137 made in private or in public, depending on the trials. Decisions while being observed
138 required weighing the costs and benefits of accepting vs. rejecting the donation, plus the
139 expected (positive or negative) image sent to the observer. Such reasoning requests the

140 conversion of social and monetary rewards into a common currency for comparisons to be
141 made (Sescousse et al., 2015). In such settings, participants thus faced a moral dilemma:
142 either serving a good cause but at a personal monetary cost, or making money but betraying
143 ones' moral values. This design allows us to investigate whether testosterone is involved in
144 guiding prosocial vs. selfish decisions induced by the presence of an audience when
145 participants face a moral dilemma. Because weighing monetary costs against compliance
146 with one's moral values (Qu et al., 2019) and perceiving one's good reputation (Izuma et al.,
147 2008, 2010) have been reported to result in striatal activity, we hypothesize a positive
148 correlation between testosterone levels and striatal activation while making prosocial
149 decisions in reaction to the presence of an audience.

150

151

152 **2. Material and methods**

153 **2.1 Participants**

154 We summarize in this section the experimental design, all the details being developed in
155 Qu *et al.* (2019). Twenty-four healthy male participants, aged 22.47 ± 2.62 years, with no
156 history of neurological or psychiatric illness participated in the fMRI experiment. Three
157 participants were discarded from the analysis because of failure to collect testosterone data.
158 All participants were right-handed, as assessed by the Edinburgh Handedness Inventory
159 (Oldfield, 1971), and presented no symptoms of depression, as assessed by the 13-item
160 version of the Beck Depression Inventory (Beck and Beck, 1972). Informed consent was
161 obtained from every participant. The study was approved by the local ethics committee (CPP
162 Centre Léon Bérard).

163 **2.2 Pre-testing**

164 As described in our previous study (Qu *et al.*, 2019), a behavioral pilot study involving
165 48 healthy volunteers was performed at GATE-Lab, Lyon, to help with designing stimuli and
166 task procedures. To guide the selection of the organizations, we asked them to complete a
167 questionnaire after the presentation of brief descriptions and logo images of 14
168 organizations. Organizations with positive or negative valence were presented. For each
169 one, participants had to rate their feelings towards them on a scale from -10 to 10. The
170 organizations were presented in the questionnaire in a random order across participants.
171 Based on this pilot study, we chose for the fMRI experiment the two organizations that
172 received the worst (mean = -5.73, SD = 3.68) and the best (mean = 8.40, SD = 2.04) ratings.
173 They were a negatively evaluated organization (NEG ORG) ('Groupe d'Action Royaliste', –
174 an organization that aims at promoting the restoration of monarchy in France) and a
175 positively evaluated charity (POS ORG) ('Resto du coeur', a charity providing food to poor
176 people). Because the policy does not allow us to publish trademarked names, we have

177 changed the real names of these two organizations. GAR represents the NEG ORG and
178 RES (a symbol of heart) represents the POS ORG (a charity providing food to poor people)
179 (Fig 1).

180 **2.3 Experimental Task**

181 Our previous study (Qu et al., 2019) described that “we used a 2 × 2 within-participant
182 design, in which participants decided whether to accept or reject monetary transfers to the
183 two organizations. Depending on the blocks of decisions, the offers of transfer is concerned
184 with either the POS ORG or the NEG ORG. Decisions were made either in presence or
185 absence of observers (“public” vs. “private” conditions) (Fig 1). At the beginning of the
186 experiment, participants received an initial endowment of 14 Euros. During the experiment,
187 they were faced with successive offers involving a variable monetary payoff for themselves
188 and a variable payoff for the organization. When making decisions regarding the POS ORG,
189 participants had to decide whether to accept or reject monetary transfers to the organization
190 at a variable monetary cost to themselves, deducted from their initial endowment. When
191 making decisions regarding the NEG ORG, they had to decide whether to accept or reject
192 monetary transfers to the organization in exchange for a personal monetary payoff added to
193 their initial endowment. In the latter case, the only way for a participant to earn money was to
194 accept a donation to the NEG ORG, whereas in the former treatment, any donation to the
195 POS ORG involved a monetary loss for the participant. One crucial aspect is that in both
196 treatments, each organization would receive a donation; however, in one case such a
197 donation entails a moral cost for the individual (allowing the experimenter to send money to
198 the NEG ORG in order to earn money for oneself may violate one’s moral values), while in
199 the other case, the donation to the organization generates a moral benefit for the individual
200 (altruistically foregoing a personal gain to benefit the POS ORG may comply with one’s
201 moral values). Because we systematically varied the monetary cost of a moral decision, we

202 were able to identify the price elasticity of demand for moral actions. Intuitively, if participants
203 did not perceive some actions as immoral, they would display no elasticity to the moral cost
204 of choosing the self-serving action. The monetary stakes for the organizations and for the
205 participants varied independently across trials. In each trial, the organization's potential
206 gains ranged from 4 to 32 Euros, in increments of 4 Euros. Participants' potential payoffs (in
207 the case of the NEG ORG) or costs (in the case of the POS ORG) varied from 1 to 8 Euros,
208 in increments of 1 Euro. Each participant was therefore exposed to 64 different dilemmas.

209 Only one public decision and one private decision among all the trials were randomly
210 selected for payment at the end of the experiment. If the participant accepted the offer in the
211 randomly selected trial, the amount of the accepted transfer was sent to the organization
212 (the mean of the two amounts was used if the two trials concerned the same organization),
213 and the participant's endowment was increased or decreased based on his decision. If the
214 same organization happened to be randomly selected twice, then the organization received
215 the average transfer and the participant's endowment was adjusted based on the average of
216 the two decisions. If the participant rejected the offer in the randomly selected trials, nothing
217 was sent to the organization, and the participant's initial endowment was not modified.

218 The presence or absence of an observer (public versus private conditions) was
219 displayed on the screen in the following way. In private trials, a yellow frame surrounded the
220 offer, and a picture of a padlock was displayed at the top of the screen reminding
221 participants about the privacy of their decisions. In the public condition, a cyan frame
222 surrounded the offer, and a picture of the eyes of an observer was displayed above,
223 reminding participants that an independent observer would see their decisions. Indeed, cues
224 of being watched exert an influence on participants' behavior (Bateson et al., 2006). To
225 further stress the visibility of their choices in the public trials, participants knew that an
226 observer in the control room, to whom they were introduced prior to the experiment, would

227 see the participant's screen and therefore observe their public trials decisions; in the public
228 trials, the chosen alternative was highlighted for 1.5 s on the screen by expanding the font,
229 while the other option disappeared. In the private condition, no changes were made on the
230 screen after the response, assuring participants that nobody would be able to see their
231 choices from the scanner control room. Finally, at the end of the experiment, participants
232 had to declare in front of a video camera which decision they made in the randomly selected
233 trial for the public condition. Participants were told that decisions in the private condition
234 were recorded anonymously, guaranteeing that none of the experimenters could link a
235 participant's identity with his decisions. A person not affiliated with the experiment and
236 unaware of its content paid all participants. All the participants reported believing in the
237 manipulation.

238 For each possible combination of individual and organization payoffs, and for both
239 organizations, participants made two decisions, one in private and one in public. Participants
240 therefore made a total of 256 decisions, 128 related to the NEG ORG and 128 related to the
241 POS ORG. Each trial began with the presentation of an offer, which could either be accepted
242 or rejected by pressing the left or right button on a response pad. A fixation cross was
243 displayed during a random time interval (jitters), drawn from a uniform distribution between
244 2.5 and 6.5s. Participants were encouraged to make their decision within 3 s. After this delay,
245 a message was displayed on the screen to remind them to respond.

246 The scanning session was divided into 4 runs of 64 trials. The first two runs concerned
247 one organization and the last two concerned the other organization. Within the first run of
248 each organization, the first half of the trials was either public or private, with the opposite for
249 the subsequent run. The order of the private/public conditions in the second run mirrored the
250 order of these conditions in the first run. The order of presentation of the organizations and
251 of public/ private conditions was balanced across participants. Thirty-two dilemmas from the

252 64 possible combinations were presented in each run and each private/public condition. To
253 guarantee that the two pairs of runs of each organization were balanced with respect to the
254 payoffs for the individual and the organization, we assigned to one run the set of dilemmas
255 composed by the participant's odd potential payoffs and the 4, 12, 20, and 28 potential
256 amounts for the organization, while the other run was assigned the 32 remaining dilemmas
257 of the matrix. Within this criterion, the order of the 32 dilemmas was randomized.

258 Visual stimuli were back-projected on a screen located at the head of the scanner bed
259 and presented to the participants through an adjustable mirror located above their head. The
260 presentation of the stimuli was controlled by Presentation © software (Neurobehavioral
261 Systems), which also recorded trigger pulses from the scanner signaling the beginning of
262 each volume acquisition.”

263 **2.4 Procedures**

264 During a first interview (the pilot pre-testing), participants were asked to rate their
265 feelings toward each of 14 organizations on a scale ranging from -10 to 10. Based on this
266 pilot study, we chose for the fMRI experiment the two organizations that received the worst
267 and the best ratings. For the fMRI experiment, we selected only participants who rated the
268 POS ORG with a score greater than 0 and the NEG ORG with a negative score. The day of
269 the experiment, participants first received instructions about the experiment.

270 After receiving the instructions, participants did a few free practice trials of all conditions
271 in the control room of the fMRI and were allowed to ask questions. After the practice session,
272 participants were asked to read a description of the two organizations. Before entering the
273 fMRI room, they met with the independent observer. After scanning, the participants were
274 debriefed. Participants filled a post-experimental questionnaire asking whether they truly
275 perceived the different trials as independent, whether they believed in the difference

276 between private and public conditions, and whether they thought that the presence of the
277 observer had influenced their decisions.

278 **2.5 Testosterone Measurements**

279 In order to minimize the effect of circadian hormone rhythms, all sessions were
280 conducted between 1:45 PM and 3:45 PM. Prior to and after the scanning session, blood
281 samples were obtained to detect the levels of plasma testosterone for each participant.
282 Plasma total testosterone was used for the assay and was measured by a solid-phase,
283 competitive chemiluminescent enzyme immunoassay, IMMULITE 2000 (Diagnostic
284 Products Corporation, Los Angeles, CA). Intra- and inter-assay coefficients of variation were
285 7.2% and 8.2%, respectively. Such an assay had an analytical sensitivity of 0.5 nmol/L.
286 Corrections for incomplete recovery were made using 3H-labeled internal standards
287 (Déchaud et al., 1981; Rinaldi et al., 2001; Sabot et al., 1985). Free testosterone would be
288 more interesting to investigate, but we did not record sex-hormone binding globulin (SHBG)
289 allowing to compute free testosterone values. In spite of this, the measurement of total
290 testosterone has still been argued to be effective in exploring the potential link between
291 testosterone levels and neuropsychological functions in humans (Hua et al., 2016). In order
292 to control for other variables affecting testosterone levels, participants were asked to
293 practice little physical exercise during the appointment day and to refrain from any
294 caffeine-containing food or drinks and cigarettes from at least one hour before the
295 experiment started.

296 **2.6 Behavioral Analysis**

297 We characterized accepted trials in the POS ORG and rejected trials in the NEG ORG
298 as “prosocial selection”, as these two options permit to a positively evaluated charity to earn
299 money or avoid that a negatively evaluated organization receives money at a personal direct

300 or indirect cost to the participants (either through a reduction of the initial endowment or
301 through foregoing a potential gain). By contrast, the rejected trials in the POS ORG and the
302 accepted trials in the NEG ORG were both characterized as “selfish selection” because
303 these options increased or preserved the initial endowment. Our previous study (Qu et al.,
304 2019) has reported in detail the relationships between the parameters of the tasks and
305 participants’ decisions, identified by using random-effects logistic models for each
306 organization. Therefore, here we only report a brief and updated analysis of the main
307 findings after having excluded the three participants from our previous study for whom we
308 failed collecting hormones. A repeated-measures ANOVA on prosocial choices was
309 conducted, with audience condition (public vs. private) and organization type (POS vs. NEG
310 ORG) as within-participants factors. This is followed by Wilcoxon signed-rank tests for
311 post-hoc testing.

312 **2.7 fMRI Data Acquisition**

313 The details of the fMRI acquisition and analysis have been reported in Qu *et al.* (2019).
314 fMRI data was acquired on a 1.5 Tesla Siemens MRI scanner. The scanning was divided
315 into 4 sessions. Blood-oxygenation-level-dependent (BOLD) signal was measured with
316 gradient echo T2* weighted echo-planar images (EPIs). Twenty-six interleaved slices
317 parallel to the AC-PC line were acquired per volume (matrix 64*64, voxel size = 3.4*3.4*4
318 mm, TR=2500ms, TE=60ms). We used a manual shimming within a rectangular region
319 including the orbitofrontal cortex and the basal ganglia to improve the local field
320 homogeneity. A high-resolution T1-weighted structural scan was subsequently acquired for
321 each participant (matrix 256 × 256 × 176; voxel size = 1 × 1 × 1 mm; TR = 1,970 ms; TE =
322 3.93 ms; flip angle = 15).

323 **2.8 fMRI Pre-processing**

324 Data were pre-processed and analyzed using the SPM8 software package (Wellcome
325 Department of Imaging Neuroscience, London) implemented in Matlab 7.10 (Mathworks,
326 Natick, MA). The first four functional volumes of each session were removed to allow the
327 BOLD signal to reach a steady state. The remaining images were slice-timing corrected,
328 spatially realigned and unwarped to correct for motion artifacts. Unwarping was performed
329 based on phase maps calculated using the Fieldmap SPM toolbox. Then in order to
330 suppress the residual fluctuations due to interpolation errors from large motions, we used
331 the motion adjustment algorithm provided in the ArtRepair toolbox (Mazaika et al., 2009)
332 after a smoothing with a 4 mm full width at half maximum (FWHM) Gaussian kernel. This
333 method is an alternative to adding motion regressors to the design matrix. The scan artifacts
334 were then detected and repaired using both global intensity and scan-to-scan movement
335 with the Artifact Repair algorithm from the ArtRepair SPM toolbox.

336 For each participant, the structural image was co-registered to the mean functional
337 image, segmented into white and gray matter, and the gray matter was normalized to a
338 standard gray matter template distributed by SPM8. The transformation parameters
339 estimated in this step were applied to all functional images. Functional images were then
340 spatially smoothed with a 7 mm FWHM Gaussian kernel.

341 **2.9 fMRI Data Analysis**

342 As described in our previous study (Qu et al., 2019), at the single-participant level,
343 statistical analyses were performed using a GLM in which all regressors were modeled as
344 delta functions and convolved with a canonical hemodynamic response function (HRF). We
345 applied a high-pass filter with a cut-off of 128 s to the time series to remove low-frequency
346 noise and baseline drifts, and we used an AR(1) model plus white noise to correct for
347 temporal autocorrelation. Estimations were done in an explicit grey matter mask based on
348 the tissue probability map provided by SPM.

349 Since the current study aims at exploring the relationships between testosterone levels
350 and brain activity involved in the audience effect, we need to describe the analysis of
351 audience effects based on our previous study (Qu et al., 2019). Specifically, we focused on a
352 number of brain regions, such as those associated with making prosocial choices in the
353 charity condition and those engaged with an audience effect, regardless of organization
354 types or choices. We attempted to build a model including 8 regressors of interest at the time
355 of “offer onset” in separate conditions 2 (accepted trials vs. rejected trials) × 2 (private vs.
356 public) × 2 (POS vs. NEG ORG). We included the size of the potential gain for the
357 organization and the size of the potential gain or loss for the participant with two orthogonal
358 parametric regressors. Because little is known about the brain networks engaged when
359 being observed (i.e., in the public condition) compared to when making decisions in private,
360 regardless of the choice made, we performed two contrasts to test for the main effects of
361 audience and privacy: public > private, and private > public, regardless of the organization
362 types and participants’ choices. Given our specific a priori region of interest, we used small
363 volume correction (SVC) with a threshold of $P < 0.05$ (FWE corrected) based on our a priori
364 region of interest. The SVC was performed using a sphere with 10mm radius centering
365 around the coordinate of peak voxel in the left and right putamen (left: -16, 14, -10; right: 12,
366 10, -4) derived from a previous studies on audience effect (Izuma et al., 2010) and in the left
367 and right caudate nucleus ($x, y, z = -17, 6, 13$ and $x, y, z = 18, 6, 9$) derived from a previous
368 study where charitable donation was investigated (Moll et al., 2006). Please note that these
369 original coordinates in the Talairach space were transformed into the corresponding
370 coordinates in MNI space using GingerALE 2.3. Given that we ran four SVC tests restricted
371 to a single region, we have used a Bonferroni-corrected threshold of $0.05/4 = 0.013$,
372 accounting for the number of SVC tests.

373 For the correlational analysis between testosterone levels and striatal activity induced by
374 the public vs. private contrast for both organizations, we employed the averaged
375 testosterone levels between those measured prior to and after the scanning session in a
376 simple regression analysis. To illustrate the correlation between testosterone levels and the
377 patterns of activation, percentage signal changes were extracted in the functional ROIs of
378 interest (left caudate and left putamen) using the MarsBar toolbox
379 (<http://marsbar.sourceforge.net>).

380

381 **3. Results**

382 **3.1 Audience effects**

383 Our ANOVA analysis showed that there was a significant main effect of organization type
384 on prosocial choices ($F(1,20) = 7.50, p < 0.05$), whereas there was not a significant main
385 effect of audience condition on prosocial choices ($F(1,20) = 0.01, p > 0.05$). Moreover, there
386 was a significant interaction between them on prosocial choices ($F(1,20) = 8.79, p < 0.01$). A
387 Wilcoxon signed-rank test showed in the POS ORG, participants accepted significantly more
388 offers on average in the public (70%) as compared to the private condition (66%; Wilcoxon
389 $|Z| = 2.81, p < 0.01, r = 0.43$). In contrast, in the NEG ORG, participants accepted
390 significantly less offers on average in the public (43%) relative to the private condition (47%;
391 Wilcoxon $|Z| = 2.30, p < 0.05, r = 0.35$) (**Fig 2A**). This was further confirmed by color-coded
392 heatmaps of the probability of accepted donations for transfers to the POS ORG and the
393 NEG ORG, respectively (**Fig 2B**). These color-coded heatmaps clearly demonstrated that
394 participants were more willing to accept to donate to the POS ORG in public than in private
395 condition and were less willing to accept to donate to the NEG ORG in public than in private
396 condition.

397 **3.2 The link between testosterone, behavior and striatum**

398 We first analyzed the main effect of acceptance in the public compared to the private
399 condition, independently of the organization type. Striatal activity significantly increased in
400 public compared to private decisions (MNI [x y z] [-12 2 -2], $T = 3.66, p(\text{SVC}) < 0.05, \text{FWE}$)
401 (**Table 1**). In addition, regions such as the anterior cingulate cortex (ACC) (MNI[x y z] [0 23
402 34], $T = 5.65$), temporal parietal junction (TPJ) (MNI[x y z] [48 -25 25], $T = 4.34$) were also
403 active in public vs private decisions (**Table 1**). By contrast, in private vs public decisions, a
404 different brain network was found with only the occipital gyrus (MNI[x y z] [30 -82 -20], $T =$
405 4.45) being significantly engaged (**Table 1**). Given that our a priori hypothesis predicts a

406 positive correlation between testosterone levels and striatal signal during prosocial decisions
407 in presence of an audience, we performed a correlation analysis between testosterone
408 levels and BOLD responses for prosocial decisions made in public vs in private for both
409 types of organization. As predicted, our results revealed a positive relationship between
410 testosterone levels and striatal activity induced by prosocial decisions for public > private
411 condition (putamen: MNI[x y z] [-21 5 -11], $T=6.77$, $p(\text{SVC}) < 0.05$, FWE; caudate nucleus:
412 MNI[x y z] [-15 2 13], $T = 5.07$, $p(\text{SVC}) < 0.05$, FWE) (**Fig 3; Table 2**). The striatum, involved
413 in prosocial behavior in public, showed a correlation with endogenous testosterone levels.
414 By contrast, when looking at prosocial decisions made in private > in public for both types of
415 organization, we found no supra-threshold activations in the social image-related brain
416 network correlating with testosterone levels (**Table 2**). Meanwhile, to exclude potential
417 confounding effects caused by the salience of the public context *per se*, we have further
418 performed correlational analyses between testosterone levels and striatal activities induced
419 by prosocial decisions for public vs. implicit baseline and for private vs. implicit baseline.
420 These analyses failed to reveal significant correlations between them (**supplementary**
421 **Table 1 and 2**). Moreover, considering that our previous study has revealed that the
422 audience effect (public > private) for both prosocial choices and for selfish choices
423 commonly engaged a common brain network including the striatum (Qu et al., 2019), our
424 further correlation analysis revealed that similar results could also be observed for selfish
425 decisions for public > private condition (**supplementary Figure 1**). This provides further
426 evidence that such a relationship was not specific to prosocial decisions only but can also be
427 observed for selfish choices. Taken together, these results somewhat indicate that our
428 observation of a significant relationship between testosterone levels and audience-induced
429 striatal activities was not driven by the salience of the public context *per se*. Finally, to further
430 examine the potential relationship between testosterone levels and the difference in

431 prosocial decisions made in public vs. in private for each type of organization, we performed
432 a number of correlational analyses. However, we did not observe any significant relationship
433 between them (POS ORG: $r = -0.07$, $p = 0.78$; NEG ORG: $r = 0.18$, $p = 0.44$)
434 (**supplementary Figure 2**). Similarly, when exploring the possible link between striatal
435 activities in public vs. in private and the difference in prosocial decisions made in public vs.
436 in private for each type of organization, we found a significant relationship between them
437 neither for the POS ORG (putamen: $r = 0.02$, $p = 0.94$; caudate: $r = -0.18$, $p = 0.43$), nor for
438 the NEG ORG (putamen: $r = -0.16$, $p = 0.50$; caudate: $r = 0.03$, $p = 0.90$).
439

440 **4. Discussion**

441

442 The goal of the present study was to investigate the relationship between endogenous
443 testosterone levels and the neural correlates responsible for prosocial decisions in presence
444 of an audience, *i.e.*, when social image and status concerns may be activated. Our results
445 showed that striatal response correlated positively with endogenous testosterone levels in
446 the public condition as compared to the private condition, regardless of organization types.
447 That is, when being observed, a greater striatal activity correlated with testosterone levels.
448 This effect highlights the fact that audience facilitates prosocial decisions for both types of
449 organizations.

450 The striatum has been previously demonstrated to be one of the key brain areas
451 involved in reputation-based behaviors, such as charitable giving and decision making in
452 presence of a moral dilemma (Izuma, 2012; Izuma et al., 2010; Moll et al., 2006; Shenhav
453 and Greene, 2010). This brain region is also strongly involved in reward processing (Haber
454 and Knutson, 2009; Sescousse et al., 2013). To better understand the potential role of the
455 striatum in public prosociality, two interdependent processes need to be considered during
456 the process of reputation building. The first is the ability to create meta-representations of
457 oneself so as to achieve the desirable image benefit from a given social behavior. A second
458 process is the ability to overcome the conflict between the expected value of an option and
459 the value of the other, less appealing, options (cost-benefit trade-off). While the right
460 temporal parietal junction (TPJ) may contribute to each of these processes (Obeso et al.,
461 2018), the striatum may preferentially be engaged in the cost-benefit analysis of the
462 available options when image concerns are active (Izuma, 2012). This functional role of the
463 striatum in reputation-based processes may be linked to the value attributed to rewards as a
464 common denominator between prosocial behavior (monetary gains for the charity in the
465 POS ORG) and moral behavior (moral benefit of rejecting offers in the NEG ORG). This was

466 probably the case for both organizations when choices were made in public rather than in
467 private. In fact, Izuma *et al.* (2008, 2010) and Qu *et al.* (2019) have shown that making
468 donations while being observed and receiving monetary rewards both elicit striatal regions
469 activity. In addition, the striatum is known to be engaged upon recognition of acceptance
470 from others, *i.e.*, being liked by others (Davey *et al.*, 2010). The results of the current study
471 additionally reveal the neural mechanisms underlying the role of testosterone in public
472 prosociality when facing different moral dilemmas.

473 One important question is to identify the exact processes underlying the relationship
474 between testosterone levels and striatal activation. In our study, this process cannot be
475 attributed to the standard role of testosterone in reactive aggression. Yet, testosterone levels
476 have been shown to correspond with increased striatal activity related to monetary rewards
477 (Op de Macks *et al.*, 2011). Because striatal activity is engaged with different types of
478 rewards (Li *et al.*, 2015), including moral benefits, the observed correlation in the current
479 study could be proposed to reflect that testosterone potentiates striatal circuits functionality
480 to raise their reward functions, perhaps mediated through dopamine (Haber and Knutson,
481 2009). To sum up, our results could contribute to the understanding of the striatal functions
482 in contexts where social image is at play, and reveal a further striatal role in social
483 interactions, as testosterone levels might contribute to transform social image concerns into
484 generous or prosocial acts even for individuals that are not intrinsically prosocially
485 motivated.

486 Another possible contribution of the current findings to the literature relies on the
487 translation from women's to men's prosocial behavior in public. Previous studies have
488 shown the role of testosterone in status-enhancing behavior in women (Boksem *et al.*, 2013;
489 Eisenegger *et al.*, 2010; Mehta *et al.*, 2015; van Honk *et al.*, 2012; Zilioli *et al.*, 2014).
490 However, it should be noted that these actual effects observed after testosterone treatment

491 were induced by factors other than testosterone, since in the female brain aromatization to
492 estradiol could equally well mediate the behavioral effects. Also, testosterone administration
493 induces supra-physiological levels that are not representative for the actual natural level of
494 testosterone in the female brain. Our present study adds to the literature by showing how
495 natural testosterone is related to striatal activity during prosocial behavior induced by the
496 presence of an audience in men. This may suggest that the role of testosterone in social
497 behavior could be observed across sexes. However, several cognitive functions have been
498 proven different between men and women, as well as in temperament characteristics
499 (Borkenau et al., 2012a; Eagly, 2013). Men seem to show more of a variable pattern of
500 social characteristics than women such as in extraversion, or agreeableness levels,
501 suggesting that women have a less variable personality across the general population
502 (Borkenau et al., 2012b). These factors may induce sex differences in the interpretation of
503 social contexts. For example, sex differences were reported with regard to cortisol levels
504 disparity, which altered behavior differently in a competition context (Kivlighan et al., 2005).
505 As such, this raises an interesting question of whether our current findings in men would
506 extend to women.

507 **Limitations**

508 We acknowledge some limitations of our study. First, it included a relative small sample,
509 possibly tempering the strength of our conclusions. Replications with larger samples would
510 be welcome. Second, even though the present study had a strong prior hypothesis about the
511 striatum involved in the audience effect (Izuma et al., 2010; Moll et al., 2006), it will still be
512 useful to search for information about other brain regions since one region is unlikely to be
513 working all by itself. Third, although the measurement of total testosterone has been argued
514 to be effective in examining the relationship between testosterone and neuropsychological
515 function (Hua et al., 2016), further correlation with free testosterone would be needed to

516 avoid limiting testing correlation to total testosterone levels, which may overlook the
517 possibility of excessive bondage to either sex-hormone binding globulin (SHBG) or albumin
518 in the blood. Fourth, we used blood samples to measure testosterone levels, which may
519 have activated anticipatory stress leading to increased cortisol levels. Moreover, there is a
520 great deal of interaction within the endocrine system, so our understanding of the
521 relationship between testosterone levels and the audience effect on prosocial behavior
522 would benefit from the inclusion of more hormones in the same study. In particular, the
523 dual-hormone hypothesis posits that testosterone's role in status-motivated behavior is
524 modulated by concentrations of cortisol (Dekkers et al., 2019; Mehta and Josephs, 2010;
525 Mehta and Prasad, 2015). Due to the small sample size, we were not able to explore
526 potential interacting effects of testosterone and cortisol on the audience effect on prosocial
527 behavior. Fifth, the present study only concerns men. We chose to scan only men because
528 gender has been shown to affect prosocial behavior (Buckholtz et al., 2015; Croson and
529 Gneezy, 2009; FeldmanHall et al., 2015) and unethical behavior (Berns et al., 2012; Dreber
530 and Johannesson, 2008; FeldmanHall et al., 2012). Moreover, young women experience
531 hormonal modulations of the reward system (Andreoni and Vesterlund, 2001; Dreher et al.,
532 2007), which may affect the testosterone levels. In addition, there are known interactions
533 between the effects of audience and the observer's gender (kept constant in the present
534 experiment). For example, in women the mere presence of men can induce transient
535 decrements in cognitive efficiency and academic performances when confronted to math
536 tests despite similar performances when tested separately (Childs, 2012; Eckel and
537 Grossman, 1998). There is no doubt that future studies should investigate whether the
538 present findings extend to women. Sixth, although the present study provided novel insight
539 on the relationship between testosterone levels and audience effect on prosocial behavior
540 through striatal activity, it is only correlative evidence. Further investigations should explore

541 the causal role of testosterone on the audience effect, using exogenous testosterone
542 administration.

543
544 **5. Conclusion**
545

546 The current study provides initial, correlational neural evidence for prosocial image
547 seeking in the striatum that is regulated by testosterone. As such, we hope that future
548 research will build upon our study by replicating our results. These findings help with
549 shedding light on prior findings showing that testosterone is involved in social status seeking
550 in social endeavors. Our results constitute a good starting point for investigating the neural
551 mechanisms underlying the causal role of testosterone in human social behaviors. Exploring
552 the causal role of testosterone on the striatal activity induced by the audience effect by using
553 exogenous testosterone administration would be a natural extension.

554

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567

568 **Author contributions**

569
570 EM, MCV, LB and JCD contributed to the study concept and design. Testing and data
571 collection were performed by EM. EM, IO and YL performed the data analysis. YL drafted
572 the manuscript. IO, LB, MCV and JCD provided critical revisions of the manuscript for
573 submission. All authors approved the final version of the manuscript for submission.

574

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578 **References**

- 579 Andreoni, J., Vesterlund, L., 2001. Which is the fair sex? Gender differences in altruism. *The*
580 *Quarterly Journal of Economics* 116, 293-312.
- 581 Archer, J., 2006. Testosterone and human aggression: an evaluation of the challenge
582 hypothesis. *Neuroscience and biobehavioral reviews* 30, 319-345.
- 583 Bateson, M., Nettle, D., Roberts, G., 2006. Cues of being watched enhance cooperation in a
584 real-world setting. *Biol Lett* 2, 412-414.
- 585 Beck, A.T., Beck, R.W., 1972. Screening depressed patients in family practice. A rapid
586 technic. *Postgraduate Medicine* 52, 81-85.
- 587 Berns, G.S., Bell, E., Capra, C.M., Prietula, M.J., Moore, S., Anderson, B., Ginges, J., Atran,
588 S., 2012. The price of your soul: neural evidence for the non-utilitarian representation of
589 sacred values. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367,
590 754-762.
- 591 Boksem, M.A.S., Mehta, P.H., Van den Bergh, B., van Son, V., Trautmann, S.T., Roelofs, K.,
592 Smidts, A., Sanfey, A.G., 2013. Testosterone Inhibits Trust but Promotes Reciprocity.
593 *Psychological Science* 24, 2306-2314.
- 594 Booth, A., Granger, D.A., Mazur, A., Kivlighan, K.T., 2006. Testosterone and social
595 behavior. *Social Forces* 85, 167-191.
- 596 Borkenau, P., Hrebickova, M., Kuppens, P., Realo, A., Allik, J., 2012a. Sex Differences in
597 Variability in Personality: A Study in Four Samples. *Journal of personality*.
- 598 Borkenau, P., McCrae, R.R., Terracciano, A., 2012b. Do men vary more than women in
599 personality? A study in 51 cultures. *Journal of research in personality*.
- 600 Bouissou, M.F., 1983. Androgens, aggressive behaviour and social relationships in higher
601 mammals. *Hormone research* 18, 43-61.
- 602 Bradley, A., Lawrence, C., Ferguson, E.J.P.o.t.R.S.B.B.S., 2018. Does observability affect
603 prosociality? 285, 20180116.
- 604 Buckholz, J.W., Martin, J.W., Treadway, M.T., Jan, K., Zald, D.H., Jones, O., Marois, R.,
605 2015. From blame to punishment: disrupting prefrontal cortex activity reveals norm
606 enforcement mechanisms. *Neuron* 87, 1369-1380.
- 607 Casto, K.V., Edwards, D.A., 2016. Testosterone and reconciliation among women:
608 after-competition testosterone predicts prosocial attitudes towards opponents. *Adaptive*
609 *Human Behavior and Physiology* 2, 220-233.
- 610 Chib, V.S., Adachi, R., O'doherty, J.P.J.S.c., neuroscience, a., 2018. Neural substrates of
611 social facilitation effects on incentive-based performance. 13, 391-403.
- 612 Childs, J., 2012. Gender differences in lying. *Economics Letters* 114, 147-149.
- 613 Coccaro, E.F., Beresford, B., Minar, P., Kaskow, J., Geraciotti, T., 2007. CSF testosterone:
614 relationship to aggression, impulsivity, and venturesomeness in adult males with personality
615 disorder. *Journal of psychiatric research* 41, 488-492.
- 616 Croson, R., Gneezy, U., 2009. Gender differences in preferences. *Journal of Economic*
617 *literature* 47, 448-474.
- 618 Cutler, J., Campbell-Meiklejohn, D., 2019. A comparative fMRI meta-analysis of altruistic
619 and strategic decisions to give. *NeuroImage* 184, 227-241.

- 620 Dabbs, J.M., Jr., Hargrove, M.F., 1997. Age, testosterone, and behavior among female
621 prison inmates. *Psychosom Med* 59, 477-480.
- 622 Davey, C.G., Allen, N.B., Harrison, B.J., Dwyer, D.B., Yücel, M., 2010. Being liked activates
623 primary reward and midline self - related brain regions. *Human brain mapping* 31, 660-668.
- 624 Déchaud, H., Lejeune, H., Garoscio-Cholet, M., Mallein, R., Pugeat, M., 1981.
625 Radioimmunoassay of testosterone not bound to sex-steroid-binding protein in plasma.
626 *Clinical chemistry* 35, 1609-1614.
- 627 Dekkers, T.J., van Rentergem, J.A.A., Meijer, B., Popma, A., Wagemaker, E., Huizenga,
628 H.M., 2019. A meta-analytical evaluation of the dual-hormone hypothesis: Does cortisol
629 moderate the relationship between testosterone and status, dominance, risk taking,
630 aggression, and psychopathy? *Neuroscience & Biobehavioral Reviews* 96, 250-271.
- 631 Dreber, A., Johannesson, M., 2008. Gender differences in deception. *Economics Letters* 99,
632 197-199.
- 633 Dreher, J.-C., Dunne, S., Pazderska, A., Frodl, T., Nolan, J.J., O'Doherty, J.P., 2016.
634 Testosterone causes both prosocial and antisocial status-enhancing behaviors in human
635 males. *Proceedings of the National Academy of Sciences* 113, 11633.
- 636 Dreher, J.-C., Schmidt, P.J., Kohn, P., Furman, D., Rubinow, D., Berman, K.F., 2007.
637 Menstrual cycle phase modulates reward-related neural function in women. *Proc Natl Acad
638 Sci U S A* 104, 2465-2470.
- 639 Eagly, A.H., 2013. Sex differences in social behavior: A social-role interpretation.
640 Psychology Press.
- 641 Eckel, C.C., Grossman, P.J., 1998. Are women less selfish than men?: Evidence from
642 dictator experiments. *The economic journal* 108, 726-735.
- 643 Eisenegger, C., Haushofer, J., Fehr, E., 2011. The role of testosterone in social interaction.
644 *Trends Cogn Sci* 15, 263-271.
- 645 Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., Fehr, E., 2010. Prejudice and truth
646 about the effect of testosterone on human bargaining behaviour. *Nature* 463, 356-359.
- 647 Everett, J.A.C., Faber, N.S., Crockett, M., 2015. Preferences and beliefs in ingroup
648 favoritism. *Front Behav Neurosci* 9, 15-15.
- 649 FeldmanHall, O., Dalgleish, T., Evans, D., Mobbs, D., 2015. Empathic concern drives costly
650 altruism. *Neuroimage* 105, 347-356.
- 651 FeldmanHall, O., Dalgleish, T., Thompson, R., Evans, D., Schweizer, S., Mobbs, D., 2012.
652 Differential neural circuitry and self-interest in real vs hypothetical moral decisions. *Soc
653 Cogn Affect Neurosci* 7, 743-751.
- 654 Geniole, S.N., Carré, J.M., 2018. Human social neuroendocrinology: Review of the rapid
655 effects of testosterone. *Hormones and Behavior* 104, 192-205.
- 656 Giammanco, M., Tabacchi, G., Giammanco, S., Di Majo, D., La Guardia, M., 2005.
657 Testosterone and aggressiveness. *Medical science monitor : international medical journal of
658 experimental and clinical research* 11, RA136-145.
- 659 Haber, S.N., Knutson, B., 2009. The reward circuit: linking primate anatomy and human
660 imaging. *Neuropsychopharmacology* 35, 4-26.
- 661 Hamilton, A.F.d.C., Lind, F., 2016. Audience effects: what can they tell us about social
662 neuroscience, theory of mind and autism? *Culture and brain* 4, 159-177.

663 Hines, M., 2017. Gonadal Hormones and Sexual Differentiation of Human Brain and
664 Behavior.

665 Hua, J.T., Hildreth, K.L., Pelak, V.S., 2016. Effects of Testosterone Therapy on Cognitive
666 Function in Aging: A Systematic Review. *Cogn Behav Neurol* 29, 122-138.

667 Inoue, Y., Takahashi, T., Burriss, R.P., Arai, S., Hasegawa, T., Yamagishi, T., Kiyonari, T.,
668 2017. Testosterone promotes either dominance or submissiveness in the Ultimatum Game
669 depending on players' social rank. *Scientific Reports* 7, 5335.

670 Izuma, K., 2012. The social neuroscience of reputation. *Neuroscience research* 72, 283-288.

671 Izuma, K., Matsumoto, K., Camerer, C.F., Adolphs, R., 2011. Insensitivity to social
672 reputation in autism. *Proc Natl Acad Sci U S A* 108, 17302-17307.

673 Izuma, K., Saito, D.N., Sadato, N., 2008. Processing of social and monetary rewards in the
674 human striatum. *Neuron* 58, 284-294.

675 Izuma, K., Saito, D.N., Sadato, N., 2010. Processing of the incentive for social approval in
676 the ventral striatum during charitable donation. *J Cogn Neurosci* 22, 621-631.

677 Kemp, A.H., Guastella, A.J., 2010. Oxytocin: prosocial behavior, social salience, or
678 approach-related behavior? *Biological psychiatry* 67, e33-e34.

679 Kivlighan, K.T., Granger, D.A., Booth, A., 2005. Gender differences in testosterone and
680 cortisol response to competition. *Psychoneuroendocrinology* 30, 58-71.

681 Li, Y., Ramoz, N., Derrington, E., Dreher, J.-C., 2020. Hormonal responses in gambling
682 versus alcohol abuse: A review of human studies. *Progress in Neuro-Psychopharmacology
683 and Biological Psychiatry* 100, 109880.

684 Li, Y., Sescousse, G., Amiez, C., Dreher, J.C., 2015. Local morphology predicts functional
685 organization of experienced value signals in the human orbitofrontal cortex. *J Neurosci* 35,
686 1648-1658.

687 Losecaat Vermeer, A.B., Krol, I., Gausterer, C., Wagner, B., Eisenegger, C., Lamm, C.,
688 2020. Exogenous testosterone increases status-seeking motivation in men with unstable low
689 social status. *Psychoneuroendocrinology* 113, 104552.

690 Mazaika, P., Hoefft, F., Glover, G., Reiss, A.L., 2009. Methods and Software for fMRI
691 Analysis for Clinical Subjects. *Human Brain Mapping*.

692 Mazur, A., Booth, A., 1998. Testosterone and dominance in men. *The Behavioral and brain
693 sciences* 21, 353-363; discussion 363-397.

694 Mehta, P.H., Josephs, R.A., 2010. Testosterone and cortisol jointly regulate dominance:
695 Evidence for a dual-hormone hypothesis. *Hormones and behavior* 58, 898-906.

696 Mehta, P.H., Prasad, S., 2015. The dual-hormone hypothesis: a brief review and future
697 research agenda. *Current Opinion in Behavioral Sciences* 3, 163-168.

698 Mehta, P.H., van Son, V., Welker, K.M., Prasad, S., Sanfey, A.G., Smidts, A., Roelofs,
699 K.J.P., 2015. Exogenous testosterone in women enhances and inhibits competitive
700 decision-making depending on victory–defeat experience and trait dominance. 60,
701 224-236.

702 Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., Grafman, J., 2006. Human
703 fronto–mesolimbic networks guide decisions about charitable donation. *Proceedings of the
704 National Academy of Sciences* 103, 15623-15628.

705 Mullard, A., 2009. What is the link between autism and testosterone? *Nature*.

706 Nadler, A., Camerer, C.F., Zava, D.T., Ortiz, T.L., Watson, N.V., Carré, J.M., Nave, G.,
707 2019. Does testosterone impair men's cognitive empathy? Evidence from two large-scale
708 randomized controlled trials. *Proceedings of the Royal Society B: Biological Sciences* 286,
709 20191062.

710 Nave, G., Nadler, A., Dubois, D., Zava, D., Camerer, C., Plassmann, H., 2018. Single-dose
711 testosterone administration increases men's preference for status goods. *Nat Commun* 9,
712 2433.

713 Newman, M.L., Sellers, J.G., Josephs, R.A., 2005. Testosterone, cognition, and social
714 status. *Hormones and behavior* 47, 205-211.

715 Obeso, I., Moisa, M., Ruff, C.C., Dreher, J.-C.J.e., 2018. A causal role for right
716 temporo-parietal junction in signaling moral conflict. 7, e40671.

717 Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory.
718 *Neuropsychologia* 9, 97-113.

719 Op de Macks, Z.A., Moor, B.G., Overgaauw, S., Güroğlu, B., Dahl, R.E., Crone, E.A., 2011.
720 Testosterone levels correspond with increased ventral striatum activation in response to
721 monetary rewards in adolescents. *Developmental Cognitive Neuroscience* 1, 506-516.

722 Qu, C., Météreau, E., Butera, L., Villeval, M.C., Dreher, J.-C., 2019. Neurocomputational
723 mechanisms at play when weighing concerns for extrinsic rewards, moral values, and social
724 image. *PLOS Biology* 17, e3000283.

725 Räsänen, P., Hakko, H., Visuri, S., Paanila, J., Kapanen, P., Suomela, T., Tiihonen, J.,
726 1999. Serum testosterone levels, mental disorders and criminal behaviour. *Acta psychiatrica*
727 *scandinavica* 99, 348-352.

728 Renfree, M.B., Wilson, J.D., Shaw, G., 2002. The hormonal control of sexual development,
729 Novartis Foundation Symposium. Chichester; New York; John Wiley; 1999, pp. 136-156.

730 Rinaldi, S., Dechaud, H., Biessy, C., Morin-Raverot, V., Toniolo, P., Zeleniuch-Jacquotte, A.,
731 Akhmedkhanov, A., Shore, R.E., Secreto, G., Ciampi, A., Riboli, E., Kaaks, R., 2001.
732 Reliability and validity of commercially available, direct radioimmunoassays for
733 measurement of blood androgens and estrogens in postmenopausal women. *Cancer*
734 *epidemiology, biomarkers & prevention* : a publication of the American Association for
735 *Cancer Research*, cosponsored by the American Society of Preventive Oncology 10,
736 757-765.

737 Rowe, R., Maughan, B., Worthman, C.M., Costello, E.J., Angold, A., 2004. Testosterone,
738 antisocial behavior, and social dominance in boys: pubertal development and biosocial
739 interaction. *Biological psychiatry* 55, 546-552.

740 Sabot, J.F., Deruaz, D., Dechaud, H., Bernard, P., Pinatel, H., 1985. Determination of
741 plasma testosterone by mass fragmentography using [3,4-¹³C]testosterone as an internal
742 standard. *Journal of Chromatography* 339, 233-242.

743 Sanchez-Pages, S., Turiegano, E., 2010. Testosterone, facial symmetry and cooperation in
744 the prisoners' dilemma. *Physiology & behavior* 99, 355-361.

745 Sekiguchi, Y., Hata, T.J.B.P., 2018. Effects of the mere presence of conspecifics on the
746 motor performance of rats: Higher speed and lower accuracy.

747 Sellers, J.G., 2006. Testosterone and status seeking.

748 Sescousse, G., Caldú, X., Segura, B., Dreher, J.-C., 2013. Processing of primary and
749 secondary rewards: A quantitative meta-analysis and review of human functional
750 neuroimaging studies. *Neuroscience & Biobehavioral Reviews*.

751 Sescousse, G., Li, Y., Dreher, J.-C., 2015. A common currency for the computation of
752 motivational values in the human striatum. *Soc Cogn Affect Neurosci* 10, 467-473.

753 Shenhav, A., Greene, J.D., 2010. Moral judgments recruit domain-general valuation
754 mechanisms to integrate representations of probability and magnitude. *Neuron* 67, 667-677.

755 van Honk, J., Bos, P.A., Terburg, D., 2014. Testosterone and dominance in humans:
756 behavioral and brain mechanisms, *New frontiers in social neuroscience*. Springer, pp.
757 201-214.

758 van Honk, J., Montoya, E.R., Bos, P.A., van Vugt, M., Terburg, D., 2012. New evidence on
759 testosterone and cooperation. *Nature* 485, E4.

760 van Honk, J., Will, G.-J., Terburg, D., Raub, W., Eisenegger, C., Buskens, V., 2016. Effects
761 of Testosterone Administration on Strategic Gambling in Poker Play. *Scientific Reports* 6,
762 18096.

763 Zethraeus, N., Kocoska-Maras, L., Ellingsen, T., Von Schoultz, B., Hirschberg, A.L.,
764 Johannesson, M., 2009. A randomized trial of the effect of estrogen and testosterone on
765 economic behavior. *Proceedings of the National Academy of Sciences* 106, 6535-6538.

766 Zilioli, S., Mehta, P.H., Watson, N.V., 2014. Losing the battle but winning the war: uncertain
767 outcomes reverse the usual effect of winning on testosterone. *Biol Psychol* 103, 54-62.
768

769

770 **Figure Legends**

771 **Figure 1. Experimental design.** We used a 2x2 within-participant design, in which
772 participants decide to accept or reject the possibility of doing a costly good action for the
773 benefit of a positively evaluated organization (POS ORG) or avoiding a bad one which would
774 advantage both them and negatively evaluated organization (NEG ORG), either in presence
775 or absence of an audience (PUBLIC vs. PRIVATE). The amounts of the potential transfers to
776 the organizations and of the potential costs or payoffs to the participants were varied
777 independently across trials. In each trial, the organization potential gains ranged from 4 to 32
778 Euros, by steps of 4 Euros. The participants' potential payoffs (in the case of the NEG ORG)
779 or costs (in the case of the POS ORG) varied from 1 to 8 Euros, by steps of 1 Euro. This
780 manipulation resulted in 64 different dilemmas. Each trial began with the presentation of an
781 offer that the participant could either accept or reject by pressing the left button response or
782 the right button response, respectively. To further stress the presence of observers during
783 public trials, the chosen alternative was highlighted for 1.5s by expanding its characters,
784 while the other was disappearing. On the opposite, in the private condition, no changes were
785 shown after the response, ensuring the participant that nobody would be able to see their
786 choice. A fixation cross was eventually displayed during a random time interval.

787 **Figure 2. Behavioral results. (A) Decisions modulated by the presence of an audience.**
788 The participants' rate of acceptance was significantly increased when decisions were
789 observed in public than in private for the POS ORG. Similarly, for the NEG ORG,
790 participants were significantly more likely to reject the propositions in public than in private.
791 The results indicated that participants made status seeking behavior due to the presence of
792 an observer. POS ORG, positively evaluated organization; NEG ORG, negatively evaluated
793 organization. ** $p < 0.01$, * $p < 0.05$. Error bars represent standard errors of the mean. **(B)**
794 **Color-coded heatmaps of the probability of acceptance to donate for each dilemma of**

795 **the 8x8 monetary/moral gain/loss matrix.** Warmer colors indicate higher probability of
796 acceptance, whereas colder colors indicate lower probability of acceptance. One heatmap is
797 drawn for each type of organization and each audience condition.

798 **Figure 3. The correlation between testosterone levels and striatal activity.** Activation in
799 the striatum (putamen: MNI[x y z] [-21 5 -11], $T=6.77$, $p(\text{SVC}) < 0.05$, FWE; caudate nucleus:
800 MNI[x y z] [-15 2 13], $T = 5.07$, $p(\text{SVC}) < 0.05$, FWE) was positively correlated with
801 testosterone levels, regardless of the types of organization. The scatter plots indicate that
802 the striatum involved in decisions about transferring to the POS ORG and NEG ORG
803 respectively in public is particularly prominent in high-testosterone men. POS ORG,
804 positively evaluated organization; NEG ORG, negatively evaluated organization.

805 **Table Legends**

806 **Table 1.** Foci of activation relating to decisions made in public as compared to that made in
807 private and vice versa. All reported foci are thresholded at $p < 0.001$ voxel-wise uncorrected
808 with $p < 0.05$ FWE cluster-wise correction except for regions marked with the sign * which
809 survived at a SVC corrected threshold of $p < 0.05$, FWE.

810 **Table 2.** Foci of activation relating to the correlation between brain activity induced by
811 decisions made in public vs that made in private and the testosterone levels for both
812 organizations. All reported foci are thresholded at $p < 0.001$ voxel-wise uncorrected with $p <$
813 0.05 FWE cluster-wise correction except for regions marked with the sign * which survived at
814 a SVC corrected threshold of $p < 0.05$, FWE.

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816 **Supplemental materials:**

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819 **Supplementary Table 1.** Whole-brain correlations for analysis of the association between
 820 brain activity induced by prosocial decisions for public vs. implicit baseline and the
 821 testosterone levels for both organizations. All reported foci are thresholded at $p < 0.001$
 822 cluster-wise uncorrected ($k > 10$).

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Brain regions	L/R	MNI coordinates			T value
		x	y	z	
<i>Prosocial decisions: (public > implicit baseline) x testosterone levels</i>					
Middle temporal gyrus	R	51	-1	-23	5.12
Superior parietal gyrus	L	-15	-34	37	4.63
Posterior cingulate gyrus	L	-34	43	26	4.31
Superior parietal gyrus	R	15	-40	58	4.43
<i>Prosocial decisions: (implicit baseline > public) x testosterone levels</i>					
Lingual gyrus	L	-97	-5	64	4.81

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827 **Supplementary Table 2.** Whole-brain correlations for analysis of the association between
 828 brain activity induced by prosocial decisions for private vs. implicit baseline and the
 829 testosterone levels for both organizations. All reported foci are thresholded at $p < 0.001$
 830 cluster-wise uncorrected ($k > 10$).

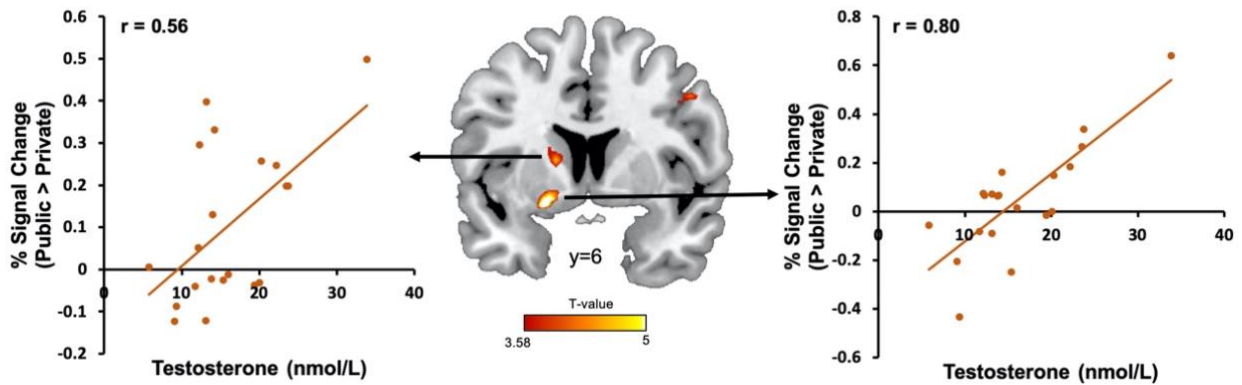
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Brain regions	L/R	MNI coordinates			T value
		x	y	z	
<i>Prosocial decisions: (private > implicit baseline) x testosterone levels</i>					
Postcentral gyrus	R	51	-10	52	5.14
Anterior insula	R	33	-1	-8	5.03
Middle frontal gyrus	L	-42	14	52	4.98
<i>Prosocial decisions: (implicit baseline > private) x testosterone levels</i>					
Lingual gyrus	L	-3	-82	-14	5.66
Cerebellum	L	-12	-37	-26	5.19
Midbrain	R	12	-19	-14	4.98

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Supplementary Figure 1. The scatter plot showing the relationship between

842 **testosterone levels and striatal activity induced by selfish decisions made in public >**

843 **private condition.** Whole-brain correlations for analysis of the association between brain

844 activity induced by selfish decisions made in public > private condition and the testosterone

845 levels for both organizations. Activation in the striatum (putamen: MNI[x y z] [-21 5 -11],

846 T=6.77, $p(\text{SVC}) < 0.05$, FWE; caudate nucleus: MNI[x y z] [-15 2 13], T = 5.07, $p(\text{SVC}) <$

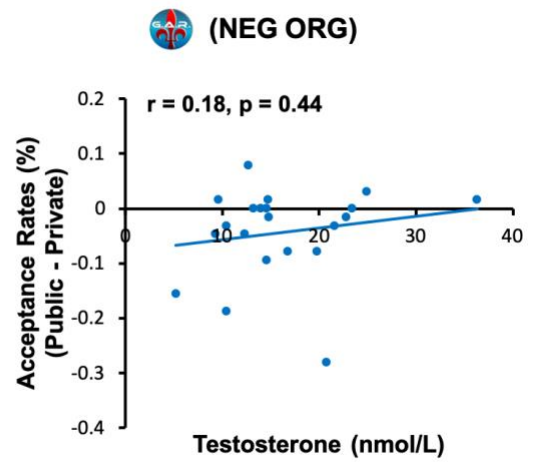
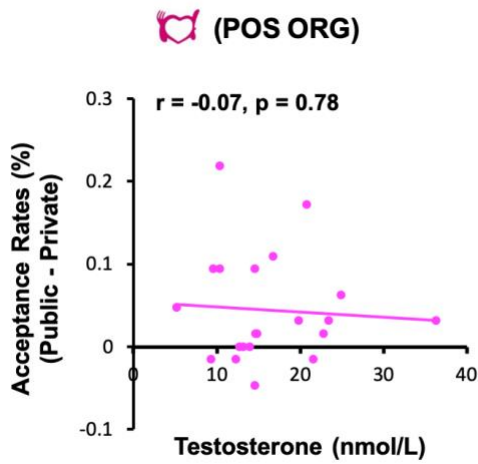
847 0.05, FWE) was positively correlated with testosterone levels, regardless of the types of

848 organization. The scatter plots indicate that the striatum involved in selfish decisions about

849 transferring to the POS ORG and NEG ORG respectively in public > in private is particularly

850 prominent in high-testosterone men.

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The supplementary Figure 2. The scatter plots showing the relationship between testosterone levels and the changes in acceptance rates in public vs. in private for each type of organization. There was not a significant relationship between them neither for the POS ORG (Left), nor for the NEG ORG (Right).