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3 **Endogenous testosterone is associated with increased striatal**
4 **response to audience effects during prosocial choices:**
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6 Yansong Li^{a,b#}, Elise Météreau^{c,d}, Ignacio Obeso^{c,d,e}, Luigi Butera^f, Marie Claire Villeval^g and
7 Jean-Claude Dreher^{c,d#}
8

9 ^a Reward, Competition and Social Neuroscience Lab, Department of Psychology, School of
10 Social and Behavioral Sciences, Nanjing University, Nanjing 210023, China

11 ^b Institute for Brain Sciences, Nanjing University, Nanjing 210023, China

12 ^c Neuroeconomics, Reward and decision making' group, Cognitive Neuroscience Center, CNRS
13 UMR 5229, Bron, France

14 ^d Université Claude Bernard Lyon 1, Lyon, France

15 ^e HM Hospitales – Centro Integral en Neurociencias HM CINAC, Móstoles, Madrid, Spain

16 ^f Copenhagen Business School, Denmark

17 ^g Univ Lyon, CNRS, GATE (UMR 5824), Ecully 69130, France
18
19

20 **Running Title:** Testosterone and striatal response to audience effects
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23
24 **#Correspondence:**

25 Yansong Li, Ph.D
26 Reward, Competition and Social Neuroscience Lab
27 Department of Psychology & Institute for Brain Sciences
28 Nanjing University
29 Nanjing, China
30 Telephone: 0086-025-89680958
31 Fax: 0086-025-89680950
32 Email: yansongli@nju.edu.cn
33

34 Jean-Claude Dreher, Ph.D
35 Neuroeconomics Lab,
36 Institut des Sciences Cognitives Marc Jeannerod, CNRS
37 67 Bd Pinel, 69675 Lyon
38 France
39 Tel: +33 (0)4 37 91 12 38
40 Fax:+33 (0)4 37 91 12 10
41 Email: dreher@isc.cnrs.fr
42

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

66 **1. Introduction**

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

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

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

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

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

151

152

153 **2. Material and methods**

154 **2.1 Participants**

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

164 **2.2 Pre-testing**

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

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

181 2.3 Experimental Task

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

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

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

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

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

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

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

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

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

264 **2.4 Procedures**

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

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

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

279 **2.5 Testosterone Measurements**

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

297 **2.6 Behavioral Analysis**

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

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

313 **2.7 fMRI Data Acquisition**

314 The details of the fMRI acquisition and analysis have been reported in Qu *et al.* (2019).
315 fMRI data was acquired on a 1.5 Tesla Siemens MRI scanner. The scanning was divided
316 into 4 sessions. Blood-oxygenation-level-dependent (BOLD) signal was measured with
317 gradient echo T2* weighted echo-planar images (EPIs). Twenty-six interleaved slices
318 parallel to the AC-PC line were acquired per volume (matrix 64*64, voxel size = 3.4*3.4*4
319 mm, TR=2500ms, TE=60ms). We used a manual shimming within a rectangular region
320 including the orbitofrontal cortex and the basal ganglia to improve the local field
321 homogeneity. A high-resolution T1-weighted structural scan was subsequently acquired for
322 each participant (matrix 256 × 256 × 176; voxel size = 1 × 1 × 1 mm; TR = 1,970 ms; TE =
323 3.93 ms; flip angle = 15).

324 **2.8 fMRI Pre-processing**

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

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

342 **2.9 fMRI Data Analysis**

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

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

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

381

382 **3. Results**

383 **3.1 Audience effects**

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

398 **3.2 The link between testosterone, behavior and striatum**

399 We first analyzed the main effect of acceptance in the public compared to the private
400 condition, independently of the organization type. Striatal activity significantly increased in
401 public compared to private decisions (MNI [x y z] [-12 2 -2], $T = 3.66, p(\text{SVC}) < 0.05, \text{FWE}$)
402 (**Table 1**). In addition, regions such as the anterior cingulate cortex (ACC) (MNI[x y z] [0 23
403 34], $T = 5.65$), temporal parietal junction (TPJ) (MNI[x y z] [48 -25 25], $T = 4.34$) were also
404 active in public vs private decisions (**Table 1**). By contrast, in private vs public decisions, a
405 different brain network was found with only the occipital gyrus (MNI[x y z] [30 -82 -20], $T =$
406 4.45) being significantly engaged (**Table 1**). Given that our a priori hypothesis predicts a

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

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

440

441 **4. Discussion**

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

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

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

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

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

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

508 **Limitations**

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

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

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

544
545 **5. Conclusion**

546 The current study provides direct correlational neural evidence for prosocial image
547 seeking in the striatum that is regulated by testosterone. These findings help with shedding
548 light on prior findings showing that testosterone is involved in social status seeking in social
549 endeavors. Our results constitute a good starting point for investigating the neural
550 mechanisms underlying the causal role of testosterone in human social behaviors. Exploring
551 the causal role of testosterone on the striatal activity induced by the audience effect by using
552 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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577

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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.** Foci of activation relating to the correlation between brain activity
820 induced by prosocial decisions for public vs. implicit baseline and the basal testosterone
821 levels for both organizations. All reported foci are thresholded at $p < 0.001$ cluster-wise
822 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.** Foci of activation relating to the correlation between brain activity
 828 induced by prosocial decisions for private vs. implicit baseline and the basal testosterone
 829 levels for both organizations. All reported foci are thresholded at $p < 0.001$ cluster-wise
 830 uncorrected ($k > 10$).

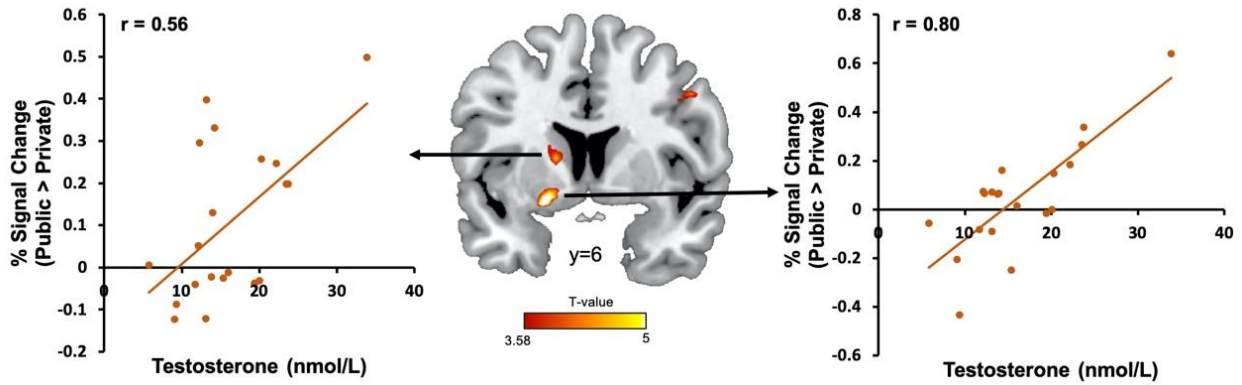
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Brain regions	L/R	MNI coordinates			T value
		x	y	z	
<i>Prosocial decisions: (private > implicit baseline) x testosterone levels</i>					
Postcentral gyrus	R	51	-10	52	5.14
Anterior insula	R	33	-1	-8	5.03
Middle frontal gyrus	L	-42	14	52	4.98
<i>Prosocial 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 testosterone levels and striatal activity induced by selfish decisions made in public > private condition. Activation in the striatum (putamen: MNI[x y z] [-21 5 -11], T=6.77, $p(\text{SVC}) < 0.05$, FWE; caudate nucleus: MNI[x y z] [-15 2 13], T = 5.07, $p(\text{SVC}) < 0.05$, FWE) was positively correlated with testosterone levels, regardless of the types of organization. The scatter plots indicate that the striatum involved in selfish decisions about transferring to the POS ORG and NEG ORG respectively in public > in private is particularly prominent in high-testosterone men.