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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  $22.47 \pm 2.62$  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  $22.47 \pm 2.62$  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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576

577

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## 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	
<b><i>Prosocial decisions: (public &gt; implicit baseline) x testosterone levels</i></b>					
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
<b><i>Prosocial decisions: (implicit baseline &gt; public) x testosterone levels</i></b>					
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 ( $k > 10$ ).

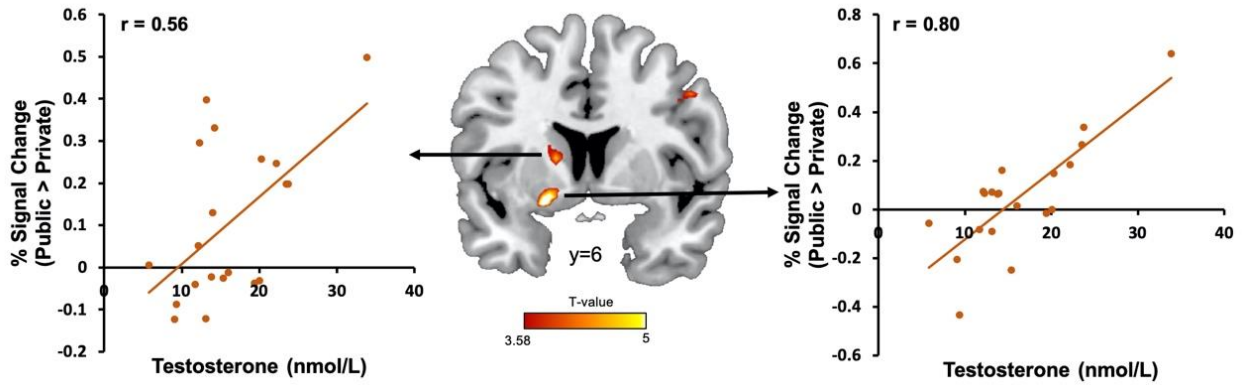
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Brain regions	L/R	MNI coordinates			T value
		x	y	z	
<b><i>Prosocial decisions: (private &gt; implicit baseline) x testosterone levels</i></b>					
Postcentral gyrus	R	51	-10	52	5.14
Anterior insula	R	33	-1	-8	5.03
Middle frontal gyrus	L	-42	14	52	4.98
<b><i>Prosocial decisions: (implicit baseline &gt; private) x testosterone levels</i></b>					
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.**