



Edinburgh School of Economics
Discussion Paper Series
Number 192

*Testosterone, Facial Symmetry and
Cooperation in the Prisoners' Dilemma*

Santiago Sánchez-Pagés
Edinburgh University

Enrique Turiegano
Universidad Autónoma de Madrid

Date
2009

Published by
School of Economics
University of Edinburgh
30 -31 Buccleuch Place
Edinburgh EH8 9JT
+44 (0)131 650 8361
<http://edin.ac/16ja6A6>



THE UNIVERSITY *of* EDINBURGH

1 Testosterone, Facial Symmetry and Cooperation in the Prisoners' Dilemma

2

3 Santiago Sanchez-Pages¹ and Enrique Turiegano²

4

5 ¹: *Edinburgh School of Economics, University of Edinburgh, EH8 9JT, UK.*

6 ²: *Departamento de Biología, Universidad Autónoma de Madrid, 28049, Madrid, Spain.*

7

8

9 Correspondence: S. Sanchez-Pages, Edinburgh School of Economics. 31 Buccleuch

10 Place, EH8 9JT, Edinburgh, United Kingdom. +44 131 651 3005 (e-mail:

11 ssanchez@staffmail.ed.ac.uk).

12

13 **Abstract:**

14 Recent research has analyzed how individual characteristics, like the exposure to
15 different hormones and symmetry, affect decision-making and strategic behaviour. The
16 present article investigates the effect of symmetry, of exposure to testosterone (T) in
17 utero and during puberty and of current T on cooperation in a Prisoners' Dilemma
18 Game (PDG). T is a hormone with well known effect on males' behaviour, and that
19 promotes activities that seek to increase reproductive success. Fluctuating Asymmetry
20 (FA) reflects the ability of the organism to maintain a stable development and it is
21 usually employed as a variable reflecting genetic quality (low FA values are thought to
22 signal higher genetic quality). Our results show that subjects with intermediate levels of
23 second to fourth digit ratio (a proxy of exposure to T in utero) and with high FA
24 cooperate more often in the PDG. We also observe that the latter effect is due to the fact
25 that FA has an impact on subjects' expectations about the behaviour of their counterpart
26 in the game. These results reinforce the described link between markers related to
27 genetic quality and cooperative behaviour. This possible linkage of individual condition
28 and pro-social behaviour in humans clearly merits further attention.

29

30 *Keywords:* Testosterone, Cooperation, Prisoners' dilemma, Fluctuating asymmetry,

31 Facial masculinity, 2D:4D.

32

33 **1. Introduction**

34 Testosterone (T) is a steroid hormone which determines in males of different
35 species their development, their reproductive physiology and several behaviours [1-4].
36 In general, T affects males by promoting behaviours that seek to increase reproductive
37 success, like an increased territorial aggressiveness [5,6], competitiveness [7] or a
38 stronger status-seeking drive [8].

39 In mammals, T exerts organizational effects on the brain during foetal sexual
40 differentiation [9] and during puberty [10]. These critical periods of exposure may
41 affect adult male behaviour, in addition to the current level of T. Thus, in order to fully
42 understand the influence of T in adult male behaviour, it is essential to take into account
43 the exposure to the hormone during these critical periods. There are some measures in
44 adult men that can proxy for T exposure in utero and during puberty. These are,
45 respectively, the second to fourth digit ratio (2D:4D; the ratio between the length of
46 index, or second digit, and ring finger, or fourth digit) and facial masculinity. Plenty of
47 evidence indirectly suggests that 2D:4D negatively correlates with foetal T [11-13] and
48 the existence or a significant negative association between 2D:4D and fetal
49 testosterone/estradiol ratio (T/E ratio) [14]. On the other hand, many masculine facial
50 features develop during puberty under the influence of T [15,16]. Most studies have
51 found no correlation between these variables and the current T level, although some
52 controversy remains. 2D:4D seems unrelated to current T in normal adults [17] and to
53 facial metric measures of masculinity [18,19]. Sexually dimorphic facial traits are not
54 associated either with current T [20], but there is some evidence of a link between
55 perceived masculinity and current T [21,22] and 2D:4D [23].

56 There is also a wide body of literature linking these three variables with typically
57 masculine features and behaviours. 2D:4D is a predictor of the degree of expression of

58 sexually dimorphic and other sex-hormone mediated traits, like visuo-spatial ability or
59 left hand preference, and some behaviors like increased aggressiveness or
60 competitiveness [24-27]. In men, circulating T has been linked to behaviours like
61 acquisition of status, aggression, sensation-seeking or interest in sex [8,28-30]. Finally,
62 the degree of masculinity has been shown to have an effect on male behaviour [20,31]
63 but, above all, it has been described as a good predictor of male attractiveness [32-34].
64 Evidence shows that more attractive people behave differently [35-39]. However, it is
65 important to bear in mind that masculinity is not the only factor determining male
66 attractiveness [40-42].

67 Fluctuating asymmetry (FA) is a departure from symmetry in traits that are
68 symmetrical at the population level [43]. It is considered to be the result of
69 developmental instability. It thus reflects the ability of the organisms to maintain a
70 stable development of their morphology and to overcome possible perturbations. This
71 ability is thought to be affected by genetic and environmental factors. Many studies
72 show a link between symmetry and genetic quality [44]. In humans, facial symmetry
73 has been proposed as a cue for heritable fitness benefits [45,46], and it is widely
74 considered as attractive [47,48]. Some studies have found that FA positively correlates
75 with facial masculinity [49-51]. This suggests that both characteristics subtly indicate
76 genetic quality. Still, many other studies find no correlation between them [52-54]. FA
77 can be thus related to human behaviour in many different ways, since it is expected that
78 the genetic quality of individuals has an impact on behaviour [55-58]. In general,
79 symmetrical men (with low FA) tend to be less cooperative and more competitive. This
80 behavior is believed to be due to their superior phenotypic quality, which increases their
81 likelihood of winning conflicts and reduces their need to receive help from others [58].

82 In this study, we examine the effect of proxies for T exposure in utero and
83 during puberty, of current levels of T and of FA on how human males play a one-shot
84 symmetric Prisoner Dilemma Game (PDG). The effects of some of these variables have
85 been previously tested in different economic experiments, like the ultimatum game [58-
86 60], public good games [61], the dictator game [62] and risk-taking in an investment
87 game [31]. Formally, the symmetric PDG is a special case of the public good game with
88 two players and two available actions: “Cooperate” (equivalent to a full contribution)
89 and “Defect” (equivalent to no contribution). The outcome obtained by the players
90 when both defect is worse for each of them than the outcome they would have obtained
91 if both of them had cooperated. When the players choose different actions, the one who
92 cooperated receives a very low payoff, while the defector obtains a very high payoff.
93 “Defect” is thus a dominant strategy in this game, that is, it is the best strategy for both
94 participants regardless of whatever their opponent does. However, it is well known that
95 humans tend not to follow this rule. There is substantial experimental evidence showing
96 that humans are willing to cooperate and trust others in the one-shot PDG [63,64].

97 We expect high FA males to cooperate more in the PDG, in line with some
98 previous results [38,58,60]. As FA is a marker of genetic quality, high symmetric
99 people have less need for receiving help from others, reducing their interest in mutual
100 reciprocity. In the same line, as high T is also considered to be a marker of genetic
101 quality, we expect the three T-related variables (2:4 finger ratio, Facial Masculinity and
102 current T level) to have a positive impact on defection rates. Effects in this direction
103 have been previously observed in other games [61]. However, it has been pro-social
104 behaviour has also been observed in people with low 2D:4D [61,62]. Because of this, it
105 is difficult to predict specifically what will be the sign of the effect on the PDG of the

106 exposure to high T at these three different stages [31], although it is likely that 2D:4D
107 will display some effect [61].

108

109 **2. Methods**

110 *2.1. Participants*

111 The experiment was carried out in Edinburgh and Madrid. 160 students
112 participated in the experimental sessions. We discarded answers from non-white
113 students because we calculated facial masculinity by comparing each student
114 photograph with an average image obtained from 50 photos of white female students
115 (the most common racial group in our subject pool). In total, we employed 147 self-
116 reported white students, 78 in Spain and 69 in Scotland. They were aged from 17 to 30,
117 with the Spanish students (21.04 ± 2.45 ; mean \pm SD) being significantly older ($t_{145} = 4.534$,
118 $p < 0.001$) than the Scottish (19.52 ± 1.39). Based on self reports, 139 subjects were
119 heterosexuals and 8 were homosexual. Written consent was obtained from all
120 participants and the collection of photographs, hand-scans and saliva was approved by
121 the relevant ethics committees at each institution.

122

123 *2.2. Experimental procedure*

124 The experiments were performed employing the z-Tree 3.2.10 software for
125 Economics Experiments [65]. The experiments were run in sessions with less than 20
126 subjects. In order to avoid unexpected effects on participants' behaviour [59] all the
127 experiments were tracked by the (male) authors. Before each session, all subjects were
128 carefully instructed about the experiment and their photographs, hand-scans and saliva
129 samples were taken. All the subjects filled a questionnaire asking their age, ethnicity,
130 sexual orientation and degree. This study was part of a larger one that included several

131 other items. Apart from the show-up fee (£5 in Edinburgh, 5€ in Madrid), subjects were
132 told that their final payment would depend upon their choices in several but not all of
133 the items in the questionnaire. They were informed of which ones counted for payment
134 only after the experiment concluded. Each experimental session took about an hour.
135 Subjects were paid privately in cash after the session and after they filled the
136 corresponding official receipt.

137 The PDG that subjects played was a one-shot game with two available strategies,
138 “Cooperate” and “Defect”. If the two players choose “Cooperate” they both get 90
139 points, if both defect they both get 30 points. If they choose different actions, the one
140 who cooperates gets 10 points and the one who defects obtains 160 points. Hence both
141 players choosing “Defect” constitutes the unique Nash Equilibrium of the PDG. This
142 strategy profile is also a Dominant Strategy Equilibrium, since “Defect” is a dominant
143 strategy for both players. Subjects were asked which strategy they believed that their
144 hypothetical counterpart would choose and also which action they would take.

145

146 *2.3. Masculinity and FA Measurement*

147 Full frontal facial colour photographs were taken of all participants with an
148 Olympus E-500 digital camera with resolution 3264x2448 in JPEG format under
149 standardized light conditions. The camera distance was kept constant at 3m and the
150 zoom was completely opened to avoid slight optical distortion of true facial shape.
151 Participants were asked to remove any facial adornment, to pose with a neutral
152 expression and to look directly into the camera. We took three images of each
153 participant in order to choose the best one for our purposes. Facial measures, as
154 masculinity or FA, were calculated from the photographs using geometric
155 morphometric tools [66]. The shape of each face was defined by manually setting 39

156 predetermined points called landmarks (LM). These 39 points (Figure 1) were chosen
157 because they can be unambiguously identified in every photo. This ensures that they
158 mark positions which rigorously correspond, in a biological or perceptual ground, to the
159 same position in every face [67]. The LMs were placed twice, once by each author,
160 which makes possible to assess any measurement error.

161 We employed these LMs to calculate the Procrustes distance between pairs of
162 rotated and scaled images [67] using the TPS software package (by F.J. Rohlf, see
163 <http://life.bio.sunysb.edu/morph/>). To calculate the asymmetry of each image, we
164 compared the LM position of each face and a mirror-image of the same one, measuring
165 the Procrustes distance between both LM positions [68]. FA can be understood as a
166 deviation of the “perfect” symmetry or, as it is commonly considered, as an individual
167 deviation from the average (directional) asymmetry. In this context the asymmetry of a
168 bilateral object is attributable partially to directional asymmetry (differences in the
169 population between average right and left size) and partially to fluctuating asymmetry
170 (deviation of each individual’s asymmetry from the overall average asymmetry). We
171 obtained FA by decomposing the Procrustes distance between each image and its mirror
172 reflecting in directional and fluctuating asymmetry by employing the Procrustes
173 ANOVA method. The latter method characterizes the shape of an object (the faces) as a
174 single geometric object. Because calculation of Procrustes coordinates is based on the
175 algebra of sums of squares, individual deviations from the average shape can be
176 partitioned in different components, as happens in the conventional ANOVA [69]. The
177 classic ideas of fluctuating and directional asymmetry are applied using this alternative
178 approach [70], where directional asymmetry corresponds to the variation introduced by
179 the variable “side of the object”, while FA corresponds to the variation explained by the
180 interaction between side and individual. To compute the FA of each individual we

181 employed Morpho J software (by C. P. Klingenberg. See
182 http://www.flywings.org.uk/MorphoJ_page.htm). The FA values obtained correlate
183 strongly with the total asymmetry calculated for each face ($r=0.982$, $p<0.001$).

184

185 The masculinity of the faces was measured calculating the Procrustes distance
186 between the LMs of the male half-faces (where only 22 LM keep placed) and the LMs
187 of a female half-face obtained by averaging 50 images of female students. With this
188 protocol, each male presented two masculinity distances, one for each hemi-face. The
189 measure of masculinity employed in the analyses is the average of these two distances.
190 We employed hemi-faces to calculate the masculinity in order to avoid incorporating the
191 measure of the symmetry of the face indirectly (given that the female average image is
192 completely symmetrical). To perform this protocol we randomly chose one of the two
193 possible sets of LMs (one placed by each author). Both LMs configurations are strongly
194 correlated ($r=0.998$, $p<0.001$). Masculinity understood as the difference in shape
195 between standard male and female faces has been widely employed in order to generate
196 feminized and masculinized faces [71,72].

197

198 *2.4. Digit Ratio Measurement*

199 Participants' right hands were scanned with an Hp psc 2110 scanner with a
200 resolution of 600x1200 ppi. The second and fourth digits were measured from the
201 centre of the flexion crease proximal to the palm to the top of the digit. This is a
202 commonly accepted way to calculate 2D:4D [31,61,67]. To measure the fingers both
203 authors independently placed a LM in each of the described positions and both lengths
204 were measured afterwards. The placing of LMs and the measures were done with the
205 appropriate utility of the TPS morphometric free software package. The two

206 measurements of 2D:4D were highly correlated ($r = 0.96$, $p < 0.001$, $N = 147$). The
207 measure employed in the analysis was their average. In some cases, it was necessary to
208 repeat the hand scanning because the image was unsuitable for correct measuring. We
209 measured lengths in pixels up to two decimal places.

210

211 *2.5. Salivary T Measurement*

212 Current T was measured from saliva provided only by the subjects in Madrid,
213 following the protocol suggested by previous studies [73]. Saliva samples were taken
214 from each participant 30 minutes upon arrival in order to be sure that they have not
215 eaten, drunk or brushed their teeth just before saliva sampling. All samples were
216 collected between 11:00 and 13:00, and participants were asked to spit through a straw
217 into a saliva sampling device (SALI-TUBES 100, DRG). No significant differences in T
218 concentrations were found between subjects as a function of the hour in which the
219 samples were collected. Saliva samples were immediately centrifuged, frozen and stored
220 at -20°C . At the end of the collection period, all samples were assayed employing T
221 assays commercially available kits (Salivary T ELISA kit from DRG Diagnostics). Two
222 kits were employed successively, and the sample concentrations used in the analyses are
223 the averages of the duplicates. Inter-assay coefficients of variation were 14.26% and the
224 intra-assay coefficient of variation was 10.87%. One of the saliva samples was
225 discarded because it presented visible blood contamination. We were unable to obtain
226 measures from two other subjects because there was not enough volume of sample to
227 duplicate the measure.

228

229 *2.6. Statistics*

230 We tested the normality of all our variables with the Kolmogorov-Smirnov test.
231 Salivary T and 2D:4D are normally distributed, but we had to log transform FA and
232 masculinity after multiplying them by 100 (in order to avoid negative values that could
233 interfere with the interpretation of their effects). To analyze the results we employed
234 two-tailed Student-t tests. We also employed logistic regressions to analyze the effect of
235 several independent variables on our dichotomous dependent variable (“Cooperate” or
236 “Defect”). We employed SPSS12 for all the statistical analyses.

237

238 **3. Results**

239 Table 1 presents descriptive statistics for each variable. The t tests show that
240 participants in each city do not differ in 2D:4D ($t_{145}=0.263$, $p=0.793$), FA ($t_{145}=0.657$,
241 $p=0.512$) or facial masculinity ($t_{145}=1.426$, $p=0.156$). There exist age differences
242 between both groups (see methods). We have found that Spanish subjects cooperate
243 more often (62.82%) than the Scottish (42.03%; $\chi^2_1=6.355$, $p=0.012$). City was therefore
244 used as a control variable in all further analyses.

245 No correlation was found between any combination of the three variables (FA,
246 masculinity and 2D:4D) and age, except for a significant correlation between
247 masculinity and FA ($r=0.320$, $p<0.001$).

248 Table 1 provides average measures of participants depending on whether they
249 chose “Cooperate” or not, and the significance of the differences across these two
250 groups. Participants who cooperated had significantly higher FA values than those who
251 did not.

252 In order to simultaneously evaluate the effect of all the variables on cooperative
253 behaviour we built a logistic regression model including City as a control variable, FA,
254 and Masculinity. We also included 2D:4D and its second order term, in order to

255 correctly account for the non-linear effect of this variable [61]. The resulting model
256 was significant (see Table 2). We found a highly significant effect of FA on
257 cooperation. That is, men with higher FA levels tend to cooperate more in the PDG. We
258 also found a significant effect of 2D:4D and its second term, positive and negative
259 respectively, implying that men with intermediate values of 2D:4D are more likely to
260 cooperate. Moreover, the model including solely 2D:4D and its second order term was
261 also significant (see Table 2). These both effects can be roughly observed if we divided
262 the sample into blocks. When we divide the sample in two equal-sized blocks according
263 to FA, participants who presented high values of FA cooperated more often (61.12%)
264 than low FA participants (45.34%). On the other hand, if the sample is divided in three
265 equal-sized blocks according to 2D:4D, it is possible to observe that participants who
266 showed an intermediate value of 2D:4D (the intermediate third of them) tend to
267 cooperate more often (67.35%), whereas participants with low or high values cooperate
268 less frequently (45.10% and 46.81% respectively).

269 As FA and masculinity correlates, we built a model excluding masculinity given
270 that we found no differences in masculinity between those participants who cooperated
271 and those who did not (see Table 2). In order to account for possible interactions
272 between the variables (FA, 2D:4D, masculinity), we run several models including
273 interacting terms but none of them were significant (not shown).

274

275 Another variable that can affect cooperation is the expected behaviour of the
276 counterpart (EB). This variable is strongly significant (see Table 2) and its inclusion in
277 our model renders City and FA insignificant, implying that these two variables are
278 somehow related to EB. The participants who thought that the other part will cooperate

279 show higher FA than the rest ($t_{145}=2.011$, $p=0.046$) while no differences were found in
280 City ($\chi^2_1=3.183$, $p=0.074$).

281 Salivary T levels were only measured for the Spanish subjects, and not for all of
282 them ($n=75$). Salivary T did not correlate with 2D:4D ($r=-0.146$, $p=0.210$), facial
283 masculinity ($r=0.069$, $p=0.555$) nor FA ($r=-0.087$, $p=0.465$). We found no differences
284 in Salivary T levels between participants who cooperated and those who did not (see
285 Table 1). A model including only these 75 participants displays exactly the same
286 features as the model that included all the participants, that is, the positive effect of FA
287 on cooperation and that subjects with intermediate 2D:4D values tend to be more
288 cooperative (see Table 2). The model that includes Salivary T is also statistically
289 significant, but not the variable itself.

290

291 **4. Discussion**

292 The objective of this study is to analyze the relationship between cooperative
293 behaviour in the PDG and a set of individual characteristics, some of them related to the
294 exposure to T during life. Our results show a link between two of these characteristics,
295 FA and 2D:4D, and cooperative behaviour. Participants who showed an intermediate
296 value of 2D:4D tend to cooperate more often, while the participants with high FA also
297 cooperate more. These results are in line with the results obtained in other studies
298 [38,58-60]. We found no relationship between cooperation in the PDG and current
299 (salivary) T nor facial masculinity (our proxy for T exposure during puberty).

300 No previous studies have attempted to explore the link between FA and
301 cooperation, although the relevance of FA in other behaviours is well known [55-58].
302 On the other hand, very few studies have analyzed the effect of T on cooperation,
303 although its effects on human behaviour have been extensively investigated

304 [8,24,28,31,74]. The closest contributions to ours have studied the effect of these two
305 variables on the Ultimatum Game [58-60,75]. The Ultimatum Game (UG) is not
306 normally considered as a game of cooperation because it does not contain a fundamental
307 tension between social and private incentives. Still, some authors have used it as an
308 approximation to the cooperative interactions that occur during hunting [76]. Under this
309 interpretation, a dominant individual tries to obtain the cooperation of another one in
310 order to hunt, and proposes a division of the expected catch. The non-dominant
311 individual can accept or reject that proposal. Rejection means that no catch is obtained.
312 Note that, contrary to what happens in the PDG, social and private incentives are
313 aligned when the second individual has to make a choice.

314 In the UG, males with low 2D:4D (presumably exposed to high T/E ratio in
315 utero) have higher minimum acceptable offers, although there is no described relation
316 between this variable and the offers made [59,60]. On the other hand, males with low
317 FA (that is, more symmetric) make lower offers, although there is no described relation
318 between this variable and the likelihood of rejection [58]. Our results are in line with
319 these studies, as FA affects males' behaviour in the PDG by influencing the estimation
320 that players have about the choice of the other player, similarly to what occurs in the
321 UG (where symmetry affects offers, which in turn are an indirect measure of the
322 expected probability of acceptance). Symmetric males thus tend to believe that their
323 counterpart will defect and behave accordingly. This is in line with previous studies that
324 have observed that symmetric males tend to cooperate less frequently because of their
325 superior phenotypic quality [58]. Given their higher ability in obtaining resources,
326 males with low FA do not need to be, nor look as cooperative as males with high FA,
327 and then cooperate less. This is however at odds with other experiments in which more
328 attractive subjects trust others more in a Trust Game [39]. This can be explained if we

329 bear in mind that attractiveness does not only depend on FA [34] and that in that
330 experiment the subject pool was composed by males and females, and they tend to
331 evaluated attractiveness attending to different features [77]. In any case the PDG and the
332 Trust Game are very different games. In the Trust Game, as the second players acts after
333 the first have trusted (or not), “leading by example” can have an important effect. This
334 is not possible in the PDG because it is simultaneous. Symmetric males may then trust
335 because of their self-confidence and because they may attempt to obtain higher status by
336 leading cooperation.

337 We also find that individuals with lower 2D:4D, (exposed to higher T level in
338 utero) tend to defect more, in the same line as in the UG [59,60]. This does not coincide
339 completely with the results obtained in studies that explored the relationship between
340 individual characteristics and contributions in a public good game [61]. They find that
341 individuals which did not cooperate or behaved altruistically (that is, they contributed
342 more than what the social norm dictates) show high 2D:4D, although these effects were
343 not statistically significant in men. In our experiment, cooperation is just a dichotomous
344 variable while in the public good game cooperation is a spectrum (i.e., the amount of
345 the contribution). Our experimental design is thus simpler and can offer cleaner results
346 but this comes at the price of limiting the richness of possible behaviours. We find, as
347 these authors do, that low 2D:4D subjects are less likely to behave altruistically (tend to
348 cooperate less often in our game). However, their conjecture that subjects with low
349 2D:4D tend to adhere to social norms cannot explain our results, since defecting is
350 unlikely to be the social norm in PDG. In our case, self-sufficiency in obtaining
351 resources can explain the behaviour of subjects with low 2D:4D. This point of view is
352 in line with another study on cooperation in which more attractive males tended to
353 cooperate less [38]. As we have already mentioned, we cannot assume that our more

354 symmetric or masculine subjects will be identified as the more attractive because this is
355 a trait affected by many other variables [34]. In any case, our results go in the same
356 direction as those.

357 Another interesting result is that individuals with high 2D:4D, that is, those less
358 exposed to T in utero, tend to cooperate less often. This result has not been observed in
359 any previous analysis and it is thus difficult explain within the domain of usual
360 explanations. Unlike FA, 2D:4D has no impact on the behaviour that players expect
361 from their counterparts. Hence, the lack of cooperation of these subjects cannot be
362 attributed to their beliefs. This is an interesting result that we plan to explore properly in
363 our future research. The significant differences in cooperation rates between Edinburgh
364 and Madrid show that behaviour in PDG, as most human behaviours, is strongly
365 affected by cultural constraints. But the biological features also have an important
366 effect. Biological individual characteristics remain strongly significant after we control
367 for cultural differences in our logistic model, and also when we restrict the analysis to
368 only the Spanish subjects (see Table 2).

369 In our study, two other variables that could potentially affect cooperative
370 behaviour, like facial masculinity and current T, display no effect. It is well known that
371 the current level of T is linked to aggressiveness and status-seeking behaviour [8,28]. In
372 addition, facial masculinity might have shown an effect as it is considered as a signal of
373 genetic fitness according to the “immunocompetence handicap hypothesis” [79]. We
374 have found no relationship between these variables and cooperation in the PDG. Hence,
375 based on these lacks of effect we conclude that cooperation in PDG is not understood as
376 a challenge [29,80] and that the aversion to a possible breakdown of cooperation cannot
377 be equated to the standard concept of risk aversion [31]. It is interesting that the
378 exposure to T in some periods of life seems to have an impact on certain types of

379 behaviour, like risk aversion [31], but not in others, like the ones we investigate in this
380 study. This suggests that exposure to T influences behaviour in very diverse ways. The
381 different effects of the levels of T during development and the links between the
382 behaviours that seem to be affected by the hormone also deserve further experiments.
383 To perform such studies it would be necessary to test the same pool of subjects in
384 different economic experiments after controlling for all these variables. In the same line,
385 to ensure that developmental instability is behind facial FA, it will be necessary
386 complement further data on cooperation and FA with measures in some others bilateral
387 traits. In addition, it would be necessary to extend the experiments by employing
388 women and non-students as subjects, enlarging thus the range of age and occupations.

389

390 **ACKNOWLEDGMENTS**

391

392 The authors acknowledge the financial support of the Abbey/Santander Research Fund
393 and thank I. Monedero, M. Pita and M. Losada for their help with the experiments, J.
394 Marugan and C.P. Klingenberg for their help with Geometric Morphometry and FA
395 measures and to R. Forshaw for her constructive comments on the paper.

396 **5. References**

- 397 [1] Wingfield JC, Hegner RE, Dufty J, Ball GF. The "challenge hypothesis":
398 theoretical implications for patterns of T secretion, mating systems, and breeding
399 strategies. *Am Nat* 1990;136:829-846.
- 400 [2] Oliveira RF, Ros AFH, Gonçalves DM. Intra-sexual variation in male reproduction
401 in teleost fish: A comparative approach. *Horm Behav* 2005;48:430-439.
- 402 [3] Woolley SC, Sakata JT, Crews D. Evolutionary insights into the regulation of
403 courtship behavior in male amphibians and reptiles. *Physiol Behav* 2004;83:347-
404 360.
- 405 [4] Fusani L. Testosterone control of male courtship in birds. *Horm Behav*
406 2008;54:227-233.
- 407 [5] Wingfield JC. A continuing saga: the role of Testosterone in aggression. *Horm*
408 *Behav* 2005;48:253-255; discussion 256-258.
- 409 [6] Soma KK, Scotti ML, Newman AEM, Charlier TD, Demas GE. Novel
410 mechanisms for neuroendocrine regulation of aggression. *Front Neuroendocrinol*
411 2008;29:476-489.
- 412 [7] Edwards DA. Competition and Testosterone. *Horm Behav* 2006;50: 681-683.
- 413 [8] Mazur A, Booth A. Testosterone and dominance in men. *Behav Brain Sci*
414 1998;21:353-363.
- 415 [9] Morris JA, Jordan CL, Breedlove SM. Sexual differentiation of the vertebrate
416 nervous system. *Nat Neurosci* 2004;7:1034-1039.
- 417 [10] Sisk CL, Schulz K, Zehr J. Puberty: A finishing school for male social behavior.
418 *Ann NY Acad Sci* 2003;1007:189-198.

- 419 [11] Manning J, Scutt D, Wilson J, Lewis-Jones D. The ratio of 2nd to 4th digit length:
420 a predictor of sperm numbers and concentrations of testosterone, luteinizing
421 hormone and oestrogen. *Hum Reprod* 1998;13:3000-3004.
- 422 [12] Cohen-Bendahan CC, van de Beek C, Berenbaum SA. Prenatal sex hormone
423 effects on child and adult sex-typed behavior: methods and findings. *Neurosci*
424 *Biobehav R* 2005;29:353-384.
- 425 [13] McIntyre M. The use of digit ratios as markers for perinatal androgen action.
426 *Reprod Biol Endocrin* 2006;4:10.
- 427 [14] Lutchmaya S, Baron-Cohen S, Raggatt P, Knickmeyer R, Manning JT. 2nd to 4th
428 digit ratios, fetal testosterone and estradiol. *Early Hum Dev* 2004;77:23-28.
- 429 [15] Enlow D, Hans M. *Essential of facial growth*. Philadelphia: WB Saunders
430 Company; 1996.
- 431 [16] Kasperk C, Helmboldt A, Börcsök I, Heuthe S, Cloos O, Niethard F, et al. Skeletal
432 site-dependent expression of the androgen receptor in human osteoblastic cell
433 populations. *Calcified Tissue Int.* 1997;61:464-473.
- 434 [17] Hönekopp J, Bartholdt L, Beier L, Liebert A. Second to fourth digit length
435 ratio:2D:4D;and adult sex hormone levels: New data and a meta-analytic review.
436 *Psychoneuroendocrinology* 2007;32:313-321.
- 437 [18] Koehler N, Simmons LW, Rhodes G. How well does second-to-fourth-digit ratio
438 in hands correlate with other indications of masculinity in males? *Proc Biol Sci*
439 2004; 271 Suppl 5:S296-S298.
- 440 [19] Burriss R, Little A, Nelson E. 2D:4D and sexually dimorphic facial characteristics.
441 *Arch Sex Behav* 2007;36:377-384.
- 442 [20] Pound N, Penton-Voak IS, SurrIDGE AK. Testosterone responses to competition in
443 men are related to facial masculinity. *Proc Biol Sci* 2009;276:153-159.

- 444 [21] Penton-Voak IS, Chen JY. High salivary testosterone is linked to masculine male
445 facial appearance in humans. *Evol Hum Behav* 2004;25:229-241.
- 446 [22] Roney JR, Hanson KN, Durante KM, Maestripieri D. Reading men's faces:
447 women's mate attractiveness judgments track men's T and interest in infants. *Proc*
448 *Biol Sci* 2006;273:2169–2175.
- 449 [23] Neave N, Laing S, Fink B, Manning JT. Second to fourth digit ratio, testosterone
450 and perceived male dominance. *Proc Biol Sci* 2003;270:2167-2172.
- 451 [24] Manning J. Digit ratio: a pointer to fertility, behavior, and health. New Brunswick
452 (NJ): Rutgers University Press; 2002.
- 453 [25] Putz DA, Gaulin SJC, Sporter RJ, McBurney DH. Sex hormones and finger length:
454 What does 2D:4D indicate? *Evol Hum Behav* 2004;25:182-199.
- 455 [26] Hines M. Prenatal testosterone and gender-related behaviour. *Eur J Endocrinol*
456 2006; 155:S115-S121.
- 457 [27] Hampson E, Ellis C, Tenk C. On the relation between 2D:4D and sex-dimorphic
458 personality traits. *Arch Sex Behav* 2008;37:133-144.
- 459 [28] Roberti JW. A review of behavioral and biological correlates of sensation seeking.
460 *J Res Pers* 2004;38:256-279.
- 461 [29] Archer J. T and human aggression: an evaluation of the challenge hypothesis.
462 *Neurosci Biobehav Rev* 2006;30:319-345.
- 463 [30] Rupp HA, Wallen K. Relationship between testosterone and interest in sexual
464 stimuli: The effect of experience. *Horm Behav* 2007;52:581-589.
- 465 [31] Apicella CL, Dreber A, Campbell B, Gray PB, Hoffman M, Little AC.
466 Testosterone and financial risk preferences. *Evol Hum Behav* 2008;29:384-390.
- 467 [32] Thornhill R, Gangestad SW. Facial attractiveness. *Trends Cogn Sci* 1999;3:452-
468 460.

- 469 [33] Johnston VS. Mate choice decisions: the role of facial beauty. *Trends Cogn Sci*
470 2006;10:9-13.
- 471 [34] Rhodes G. The evolutionary psychology of facial beauty. *Annu Rev Psychol*
472 2006;57:199-226.
- 473 [35] Mulford M, Orbell J, Shatto C, Stockard J. Physical attractiveness, opportunity,
474 and success in everyday exchange. *Am J Sociol* 1998;103:1565-1592.
- 475 [36] Langlois JH, Kalakanis L, Rubenstein AJ, Larson A, Hallam M, Smoot M.
476 Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychol Bull*
477 2000;126:390-423.
- 478 [37] Kanazawa S, Kovar JL. Why beautiful people are more intelligent. *Intelligence*
479 2004;32:227-243.
- 480 [38] Takahashi C, Yamagishi T, Tanida S, Kiyonari T, Kanazawa S. Attractiveness and
481 cooperation in social exchange. *Evol Psych* 2006;4:315-329.
- 482 [39] Wilson RK, Eckel CC. Judging a book by its cover: Beauty and expectations in the
483 trust game. *Polit Res Q* 2006;59:189-202.
- 484 [40] Penton-Voak I, Jacobson A, Trivers R. Populational differences in attractiveness
485 judgements of male and female faces: Comparing British and Jamaican samples.
486 *Evol Hum Behav* 2004;25:355-370.
- 487 [41] Buss D. Strategies of human mating. *Psychol Top* 2006;15:239-260.
- 488 [42] Ellison PT. Beauty: In the gonads of the beholder - and the beheld. *Horm Behav*
489 2008;53:11-13.
- 490 [43] Valen LV. A study on fluctuating asymmetry. *Evolution* 1962;16:125-142.
- 491 [44] Møller AP. Developmental stability and fitness: a review. *Am Nat* 1997;149:916-
492 932.

- 493 [45] Scheib JE, Gangestad SW, Thornhill R. Facial attractiveness, symmetry and cues
494 of good genes. *Proc Biol Sci* 1999;266:1913-1917.
- 495 [46] Little AC, Jones BC. Attraction independent of detection suggests special
496 mechanisms for symmetry preferences in human face perception. *Proc Biol Sci*
497 2006;273:3093-3099.
- 498 [47] Perrett DI, Burt DM, Penton-Voak IS, Lee KJ, Rowland DA, Edwards R.
499 Symmetry and human facial attractiveness. *Evol Hum Behav* 1999;20:295-307.
- 500 [48] Little AC, Apicella CL, Marlowe FW. Preferences for symmetry in human faces in
501 two cultures: data from the UK and the Hadza, an isolated group of hunter-
502 gatherers. *Proc Biol Sci* 2007;274:3113-3117.
- 503 [49] Gangestad SW, Thornhill R. Facial masculinity and fluctuating asymmetry. *Evol*
504 *Hum Behav* 2003;24:231-241.
- 505 [50] Brown WM, Price ME, Kang J, Pound N, Zhao Y, Yu H. Fluctuating asymmetry
506 and preferences for sex-typical bodily characteristics. *Proc Nat Acad Sci*
507 2008;105:12938-12943.
- 508 [51] Little AC, Jones BC, Waitt C, Tiddeman BP, Feinberg DR, Perrett DI, et al.
509 Symmetry is related to sexual dimorphism in faces: data across culture and
510 species. *PLoS ONE* 2008;3:e2106.
- 511 [52] Penton-Voak IS, Jones BC, Little AC, Baker S, Tiddeman B, Burt DM, et al.
512 Symmetry, sexual dimorphism in facial proportions and male facial attractiveness.
513 *Proc Biol Sci* 2001;268:1617-1623.
- 514 [53] Koehler N, Simmons LW, Rhodes G, Peters M. The relationship between sexual
515 dimorphism in human faces and fluctuating asymmetry. *Proc Biol Sci* 2004;271
516 Suppl 4:S233-236.

- 517 [54] Van Dongen S, Ten Broek CMA, Galis F, Wijnaendts LCD. No association
518 between fluctuating asymmetry in highly stabilized traits and second to fourth digit
519 ratio (2D:4D) in human fetuses. *Early Hum Dev* 2009;85:393-398.
- 520 [55] Furlow B, Gangestad SW, Armijo-Prewitt T. Developmental stability and human
521 violence. *Proc Biol Sci* 1998;265:1-6.
- 522 [56] Manning J, Wood D. Fluctuating asymmetry and aggression in boys. *Hum Nat*
523 1998;9:53-65.
- 524 [57] Pound N, Penton-Voak IS, Brown WM. Facial symmetry is positively associated
525 with self-reported extraversion. *Pers Individ Differ* 2007;43:1572-1582.
- 526 [58] Zaatari D, Trivers R. Fluctuating asymmetry and behavior in the ultimatum game
527 in Jamaica. *Evol Hum Behav* 2007;28:223-227.
- 528 [59] Van den Bergh B, Dewitte S. Digit ratio (2D:4D) moderates the impact of sexual
529 cues on men's decisions in ultimatum games. *Proc Biol Sci* 2006;273:2091-2095.
- 530 [60] Burnham TC. High-T men reject low ultimatum game offers. *Proc Biol Sci*
531 2007;274:2327-2330.
- 532 [61] Millet K, Dewitte S. Second to fourth digit ratio and cooperative behavior. *Biol*
533 *Psychol* 2006;71:111-115.
- 534 [62] Millet K, Dewitte S. The presence of aggression cues inverts the relation between
535 digit ratio (2D:4D) and prosocial behaviour in a dictator game. *Brit J Psychol*.
536 2009;100:151-162.
- 537 [63] Marwell G, Ames RE. Economists free ride, does anyone else? : Experiments on
538 the provision of public goods, IV. *J Public Econ* 1981;15:295-310.
- 539 [64] Dawes RM, Thaler RH. Anomalies: Cooperation. *J Econ Perspect* 1988;2:187-197.
- 540 [65] Fischbacher U. z-Tree: Zurich toolbox for ready-made economic experiments. *Exp*
541 *Econ* 2007;10:171-178.

- 542 [66] Bookstein FL. Morphometric tools for landmark data: geometry and biology.
543 Cambridge University Press; 1991.
- 544 [67] Fink B, Grammer K, Mitteroecker P, Gunz P, Schaefer K, Bookstein FL, et al.
545 Second to fourth digit ratio and face shape. 2005; *Proc Biol Sci* 272:1995-2001.
- 546 [68] Klingenberg CP, Barluenga M, Meyer A. Shape analysis of symmetric structures:
547 quantifying variation among individuals and asymmetry, *Evolution* 2002;56:1909-
548 1920.
- 549 [69] Klingenberg CP, McIntyre GS. Geometric morphometrics of developmental
550 instability: analyzing patterns of fluctuating asymmetry with procrustes methods.
551 *Evolution* 1998;52:1363-1375.
- 552 [70] Schaefer K, Lauc T, Mitteroecker P, Gunz P, Bookstein FL. Dental arch
553 asymmetry in an isolated Adriatic community. *Am J Phys Anthropol*
554 2006;129:132-142.
- 555 [71] Perrett DI, Lee KJ, Penton-Voak I, Rowland D, Yoshikawa S, Burt DM, et al.
556 Effects of sexual dimorphism on facial attractiveness. *Nature* 1998;394:884-887.
- 557 [72] Penton-Voak IS, Perrett DI, Castles DL, Kobayashi T, Burt DM, Murray LK, et al.
558 Menstrual cycle alters face preference. *Nature* 1999;399:741-742.
- 559 [73] Granger DA, Shirtcliff EA, Booth A, Kivlighan KT, Schwartz EB. The "trouble"
560 with salivary T. *Psychoneuroendocrinology* 2004;29:1229-1240.
- 561 [74] Coates JM, Herbert J. Endogenous steroids and financial risk taking on a London
562 trading floor. *Proc Nat Acad Sci* 2008;105:6167-6172.
- 563 [75] Zaatari D, Palestis BG, Trivers R. Fluctuating asymmetry of responders affects
564 offers in the ultimatum game oppositely according to attractiveness or need as
565 perceived by proposers. *Ethology* 2009;115:627-632.

- 566 [76] Page KM, Nowak MA, Sigmund K. The spatial ultimatum game. *Proc Biol Sci*
567 2000;267:2177-2182.
- 568 [77] Marcus DK, Miller RS. Sex differences in judgments of physical attractiveness: A
569 social relations analysis. *Pers Soc Psychol Bull* 2003;29:325-335.
- 570 [78] Folstad I, Karter AJ. Parasites, bright males, and the immunocompetence
571 handicap. *Am Nat* 1992;139:603.
- 572 [79] Mehta PH, Josephs RA. Testosterone change after losing predicts the decision to
573 compete again. *Horm Behav* 2006;50:684-692.

574

575

Tables

576

	TOTAL^a	Defect	Cooperate		
Age (yr)^b	20.327±2.115	20.014±1.898	20.603±2.337	$t_{145}=-1.661$	p=0.099
2:4 finger ratio^b	0.962±0.030	0.965±0.036	0.959±0.025	$t_{145}=1.097$	p=0.274
Fluctuating Asymmetry^b	0.035±0.013	0.032±0.012	0.037±0.014	$t_{145}=-2.473$	p=0.015
Facial masculinity^b	0.098±0.022	0.098±0.024	0.098±0.020	$t_{145}=-0.055$	p=0.956
Salivary T (pg/ml)^c	135.997±26.124	132.322±28.057	138.186±24.954	$t_{73}=-0.940$	p=0.351

577

578 **Table 1.**579 ***Mean values of variables in the total population and according to participants' choice***580 ^a Data are the mean (±SD)581 ^b In our whole population, 69 individuals defected and 78 cooperated.582 ^c Salivary T was only measured in the experimental sessions performed in Madrid, where 28

583 individuals defected and 47 cooperated.

584

Variables in the model	MODEL				VARIABLE				
	-2LL	Likelihood Ratio Test	df	p	variables	coef	Wald	df	P
<i>2D:4D, (2D:4D)²</i>	193.048	10.186	2	0.006	Constant	-414.551	7.308	1	0.007
					2D:4D	865.059	7.392	1	0.007
					(2D:4D) ²	-450.728	7.466	1	0.006
<i>2D:4D, (2D:4D)², FA, Masculinity, City</i>	179.952	23.282	5	<0.001	Constant	-441.869	7.101	1	0.008
					2D:4D	921.353	7.198	1	0.007
					(2D:4D) ²	-480.065	7.287	1	0.007
					FA	1.464	7.048	1	0.008
					Masculinity	-0.806	0.892	1	0.345
City	0.859	5.593	1	0.018					
<i>2D:4D, (2D:4D)², FA, City</i>	180.858	22.376	4	<0.001	Constant	-447.523	165.366	1	0.007
					2D:4D	929.505	342.558	1	0.007
					(2D:4D) ²	-484.184	177.413	1	0.006
					FA	1.317	0.528	1	0.013
					City	0.810	0.357	1	0.023
<i>2D:4D, (2D:4D)², FA, City, EB</i>	120.438	82.796	5	<0.001	Constant	-557.024	7.007	1	0.008
					2D:4D	1165.062	7.122	1	0.008
					(2D:4D) ²	-607.991	7.220	1	0.007
					FA	0.959	2.444	1	0.118
					City	0.672	2.111	1	0.146
					EB	-3.307	41.259	1	<0.001
<i>2D:4D, (2D:4D)², FA</i>	90.766	12.179	3	0.007	Constant	-582.708	5.329	1	0.021
					2D:4D	1208.706	5.379	1	0.020
					(2D:4D) ²	-627.815	5.446	1	0.020
					FA	1.709	5.781	1	0.016
<i>2D:4D, (2D:4D)², FA, Current T</i>	86.483	12.623	4	0.013	Constant	-572.817	4.432	1	0.035
					2D:4D	1181.555	4.426	1	0.035
					(2D:4D) ²	-612.624	4.459	1	0.035
					FA	1.860	6.514	1	0.011
					Current T	0.014	1.884	1	0.170

ALL PARTICIPANTS

MADRID

585

586 **Table 2.**587 *Logistic models for the whole sample and for the Spanish subjects.*

588 The variables included are 2D:4D (second to fourth finger ratio) FA (fluctuating

589 asymmetry), Masculinity (facial masculinity), Current T (current salivary T) and EB

590 (expected behaviour of the counterpart).

591 **Figures**

592

593 **Figure 1.**

594 *Landmarks placement .*

595 A) An average face with the 39 landmarks placed. B) All 147 landmarks configurations

596 superimposed after Procrustes Fit. These coordinates are the basis for all FA

597 calculations.

598