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Two Studies on the Interplay between Social Preferences and Individual Biological Features

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1 **Two Studies on the Interplay between Social Preferences and Individual Biological**

2 **Features**

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4 Running headline: Biological features and social preferences

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20   **ABSTRACT**

21   Biological features and social preferences have been studied separately as factors

22   influencing human strategic behaviour. We run two studies in order to explore the interplay

23   between these two sets of factors. In the first study, we investigate to what extent social

24   preferences may have some biological underpinnings. We use simple one-shot distribution

25   experiments to attribute subjects one out of four types of social preferences: Self-interested

26   (SI), Competitive (C), Inequality averse (IA) and Efficiency-seeking (ES). We then

27   investigate whether these four groups display differences in their levels of facial

28   Fluctuating Asymmetry (FA) and in proxies for exposure to testosterone during phoetal

29   development and puberty. We observe that development-related biological features and

30   social preferences are relatively independent. In the second study, we compare the relative

31   weight of these two set of factors by studying how they affect subjects' behaviour in the

32   Ultimatum Game (UG). We find differences in offers made and rejection rates across the

33   four social preference groups. The effect of social preferences is stronger than the effect of

34   biological features even though the latter is significant. We also report a novel link between

35   facial masculinity (a proxy for exposure to testosterone during puberty) and rejection rates

36   in the UG. Our results suggest that biological features influence behaviour both directly and

37   through their relation with the type of social preferences that individuals hold.

38

39   *Keywords*: Testosterone; Ultimatum Game; Fluctuating Asymmetry; Facial masculinity;

40   2D:4D; Social preferences.

1. Introduction

In the last few years, experimental methods have been used to explore how biological features relate to individual behaviour in strategic situations. These laboratory experiments have employed a number of simple games long-studied in Experimental Economics (Smith, 1987). These games embody simplified social interactions in which the payoffs that subjects obtain depend both on their own decisions and the decisions of others. These experiments generate results which are easily measurable, quantifiable and replicable. The biological features studied in this literature include the impact of hormones and their receptors (Kosfeld et al., 2005; Burnham, 2007; Zak et al., 2007; Crockett et al., 2008; Knafo et al., 2008; Zak et al., 2009; Eisenegger et al., 2010), genetic differences (Wallace et al., 2007; Cesarini et al., 2008), neural factors (Fehr & Rangel, 2011), and the effect of developmental instability, proxied by Fluctuating Asymmetry (Zaatari & Trivers, 2007; Zaatari et al., 2009; Sanchez-Pages & Turiegano, 2010).

These studies have also shed new light on the wide array of results in economic experiments showing that many individuals care strongly about the whole distribution of income and not only about their own material payoff. This class of concerns receive the name of *social preferences* in Economics. Social preferences have been extensively studied and include inequality aversion (Fehr & Schmidt, 1999; Bolton & Ockenfels, 2000; Binmore & Shaked, 2010), joint welfare maximization (Charness & Rabin, 2002), and competitive preferences (Frank, 1987; Charness & Grosskopf, 2001). Social preferences have been studied extensively in Psychology under the rubric of Social Value Orientation (for reviews see Balliet, et al., 2009 and Murphy & Ackerman, 2012)

65   Research in Experimental Economics typically uses observed choices to uncover

66   unobservable individual heterogeneity in social preferences. This is called the *revealed*

67   *preference* approach. On the other hand, research in Biology uses individual heterogeneity

68   (in physiological features, for instance) to explain observed differences in behaviour. The

69   present paper aims at building a bridge between these two approaches. To this end, we run

70   two studies. The first one explores the extent to which individual biological features and

71   social preferences are independent of each other. The second study explores, within the

72   same population, the relative importance of these two sets of variables in strategic

73   interactions by relating them to behaviour in the Ultimatum Game (UG henceforth).

74

75   *Study 1*

76   In the first step of this study, we use a set of one-shot distribution experiments to

77   classify subjects into one of the main four types of social preferences described in the

78   Experimental Economics literature (Engelmann & Strobel, 2004): Self-interested (SI),

79   Competitive (C), Inequality averse (IA) and Efficiency-seeking (ES). These four types of

80   social preferences translate into different behaviours in economic interactions. SI subjects

81   are mainly interested in maximizing their own payoff. The ES subjects are interested in

82   maximizing the total benefits obtained by all participants, even at their own expense. IA

83   subjects are interested in minimizing the disparity in the distribution of income

84   independently of whether this disparity is in their favour or not. Finally, C subjects are

85   interested in minimizing unfavourable inequality and in maximizing favourable inequality,

86   even at the expense of some material payoff.

87

88   Once classified, we study whether subjects who hold different social preferences

89   display differences in several biological features. The biological features which we consider

90   here are facial Fluctuating Asymmetry (FA, henceforth), and two proxies for testosterone

91   exposure in utero and during puberty, the second to fourth digit ratio (2D:4D) and facial

92   masculinity, respectively. We have chosen these variables because they have showed to

93   influence a number of behaviours (e.g. tendency to cooperate, competitiveness), which are

94   affected by social preferences as well. Their impact on adult behaviour operates through

95   their effect on nervous system development (Bates, 2007; Berenbaum & Beltz 2011).

96

97   FA refers to minor non-directional deviations from bilateral symmetry (Palmer &

98   Strobeck, 1986). It is considered to be the result of developmental instability. Many studies

99   show a link between symmetry and individual fitness, both in non-humans (Møller, 1997;

100 Møller, 2006), and in humans (Van Dongen & Gangestad, 2011). Facial symmetry has been

101 proposed as a cue of heritable fitness benefits (Scheib et al., 1999; Little & Jones, 2006).

102 Regarding human behaviour, low FA is linked to individuals who are more self-confident,

103 prone to behave aggressively (Furlow et al., 1998; Manning & Wood, 1998; Benderlioglu

104 et al., 2004) and less cooperatively (Sanchez-Pages & Turiegano, 2010).

105

106   Testosterone (T) is a steroid hormone which promotes behaviours aimed at

107 increasing reproductive success in males, such as risk-taking (Mazur & Booth, 1998)

108 aggression (Archer, 2006), sensation-seeking (Roberti, 2004) and interest in sex (Rupp &

109 Wallen, 2007). T levels have been described to correlate with general fitness, reproductive

110 success and status (Mazur & Booth, 1998; Bribiescas, 2001; Zitzmann & Nieschlag, 2001;

111 Muehlenbein & Bribiescas, 2005). In addition, T exerts organizational effects on the brain

112   during phoetal sexual differentiation (Morris et al., 2004), and during puberty (Sisk et al.,

113   2003). Exposure to T in these critical periods is considered to have an effect on brain

114   structures and, therefore, on adult male behaviour (Berenbaum & Beltz 2011). We use

115   2D:4D and facial masculinity as proxies for the level of exposure to the hormone in these

116   two developmental stages. Evidence indicates that 2D:4D negatively correlates with

117   prenatal testosterone (Lutchmaya et al., 2004; Zheng & Cohn, 2011). Low 2D:4D subjects

118   are also less likely to behave altruistically (Millet & Dewitte, 2006; Sanchez-Pages &

119   Turiegano, 2010). But, as 2D:4D is related to dispositional dominance, low ratios associate

120   as well with pro-social behaviour in certain contexts (Millet, 2011). On the other hand,

121   many masculine facial features develop during puberty under the action of testosterone

122   (Enlow, 1996). Facial masculinity has been shown to affect human male behaviour

123   (Apicella et al., 2008; Pound et al., 2009). Finally, given that some authors have linked

124   facial masculinity to male attractiveness (Johnston, 2006; Rhodes, 2006), we conjecture

125   that facially masculine men might behave similarly to attractive men (Takahashi et al.,

126   2006; Wilson & Eckel, 2006).

127

128   To the best of our knowledge, no previous study has investigated the link between

129   the social preferences considered in Economics and the biological features considered in

130   the present work (but see Yamagishi et al., 2012). Hence, our conjectures on the existence

131   of differences in biological features across social preference groups or on the direction of

132   these differences (if any) cannot be strongly substantiated by previous results. Still, related

133   evidence suggests that subjects less interested in their relative position in the income

134   distribution (SI and ES) should show lower levels of facial masculinity given the relation

135   described between testosterone and status-seeking behaviour (Mazur & Booth, 1998;

136 Josephs et al., 2006). We predict a similar pattern for 2D:4D (Millet & Dewitte, 2006)

137 although we expect IA subjects, who are the most interested in implementing an egalitarian

138 distribution of income, to show the lowest levels (Van den Bergh & Dewitte, 2006; Millet

139 & Dewitte, 2009). Regarding FA, individuals less interested in joint welfare (SI and C) are

140 expected to display lower levels of FA since more symmetric individuals are less interested

141 in cooperation given that they need less support from their peers (Zaatari & Trivers, 2007;

142 Sanchez- Pages & Turiegano, 2010). This difference in FA is expected to be greatest

143 between SI an ES subjects, as SI subjects do not care about the outcome received by others

144 whereas ES subjects care mostly about joint welfare.

145

146 *Study 2*

147   In the second study, we compare the relative importance of individual biological

148 features and social preferences in strategic interactions by looking at subjects' behaviour in

149 the UG. In this experiment, two players have to divide a sum of money. The first player

150 proposes how to divide the sum between the two players. The second player can either

151 accept or reject this proposal. A rejection implies that both players receive nothing.

152 Acceptance implies that the money is split according to the proposal. This game is well

153 suited for our purposes because of two reasons. First, it is well-known that behaviour in the

154 UG departs substantially from the standard economic prediction of own income

155 maximization. Pure self-interest dictates that responders should accept any positive offer

156 and that proposers should make the lowest possible offer. However, low offers are often

157 rejected and the vast majority of offers range between 30% and 50% of the sum to be

158 distributed (Roth, 1995). The second reason is that the UG has been widely employed in the

159 study of the effects of hormones on behaviour (Kosfeld et al., 2005; Burnham, 2007; Zak et

7

160 al., 2007; Crockett et al., 2008; Zak et al., 2009; Zethraeus et al., 2009; Eisenegger et al.,

161 2010), and of development-related variables, like FA (Zaatari & Trivers, 2007; Zaatari et

162 al., 2009) and 2D:4D (Van den Bergh & Dewitte, 2006).

163

164   In the role of responders, we expect SI and ES subjects to accept lower offers than

165 the rest of participants; the SI group because they prefer any positive amount of money to

166 nothing, and the latter because rejection entails the loss of the whole amount to be

167 distributed. On the other hand, C subjects should reject low offers more often because

168 acceptance would leave them significantly worse off than the proposer. IA subjects should

169 reject low offers too in order to avoid a high disparity in the earnings of the two

170 participants. In the role of proposers, we expect IA and ES subjects to make higher offers

171 than the rest, given that IA agents care strongly about equality and that ES subjects can

172 reduce the risk of rejection (that would lead to the whole sum being wasted) by doing so.

173 This leads us to expect that the offers made by SI and C subjects should be lower in average

174 than those made by IA and ES.

175

176   In addition to the relationships already described in the literature between biological

177 features and behaviour in the UG, (Van der Bergh & Dewitte, 2006; Zaatari & Trivers,

178 2007), we also expect participants who reject low offers to show higher facial masculinity.

179 We base this prediction on 1) the link between masculine features and self-sufficiency

180 (Muehlenbein & Bribiescas, 2005), and 2) the higher rejection rates of unfair splits

181 displayed by males with higher testosterone levels (Burnham, 2007), and 3) the known

182 effect of facial attractiveness, which partially relates to masculinity, on reciprocity (Wilson

183 & Eckel, 2006). Finally, in the role of proposers, we expect participants exposed to low

8

184   levels of testosterone during development (with higher 2D:4D or lower facial masculinity)

185   to make higher offers. This hypothesis is based on the interpretation of fairness in the UG

186   as an expression of cooperation (Page et al., 2000) and on the relationship between

187   cooperation and exposure to testosterone during development (Millet & Dewitte, 2006;

188   Sanchez-Pages & Turiegano, 2010).

189

190   **2. Methods**

191

192   *Preliminaries*

193   The two studies we report here were performed successively in Madrid in the winter

194   of 2009. A total of 152 self-declared white male subjects participated, distributed in 10

195   morning sessions with less than 20 subjects each. Participants were recruited by e-mail. All

196   of them filled a short questionnaire asking their age, discipline of study, ethnicity and

197   sexual orientation. Subjects were students at the Universidad Autónoma de Madrid (UAM),

198   mostly from the School of Biological Sciences. Ages varied from 17 to 30, 20.34±0.17yr;

199   av±SEM). Participants gave their written consent to the use of their data. The experiment

200   was approved by the Ethics Committee of the UAM.

201

202   Subjects were seated at partitioned computer terminals to ensure they could not

203   interact with each other. All subjects were carefully instructed about the rules of the

204   experiment. The experiment was conducted via computers employing the z-Tree 3.2.10

205   software for Economics Experiments (Fischbacher, 2007). Subjects were informed that

206   their payment could reach around 9€ and it was going to depend on some of the choices

207   they were about to make, although they did not know which ones specifically. Hence, all

208   decisions mattered for participants. Actual payments were computed based on all their

209   decisions except for their choice as proposers in the UG. We informed subjects of this

210   payment method a few weeks after the experimental sessions finished in order to avoid

211   information spreading. Payoffs during the experiment were expressed in points, and

212   participants knew that the exchange rate was 100p=2€. At the end of each session, subjects

213   were paid privately in cash. The average amount paid was 8.43±0.43€ (av±SD), including a

214   show-up fee (5€). The experimental sessions took about 30 minutes. No female was present

215   during the sessions nor the process of data collection in order to avoid any moderating

216   effects of sexual cues on participants' behaviour (Van der Bergh & Dewitte, 2006).

217

218   *Measurement of individual biological features*

219   Photographs of the participants and scans of their hands were taken before each

220   session. We took high-resolution full frontal facial colour photographs of all participants

221   with an Olympus E-500 digital camera. The photos were taken in homogeneous conditions

222   (soft light, fixed distance of the camera, completely opened zoom to avoid any optical

223   distortion). Participants were asked to remove any facial adornment and to pose with a

224   neutral expression. We tried to minimize any distortion caused by the rotation of the head

225   by asking subjects to look directly into the camera, and by correcting their position if

226   necessary (instead of using a more osteological standardization, such as the Frankfort

227   Horizontal). We took three images of each participant.

228

229   The shape of each face was defined by manually setting 39 landmarks (LM) which

230   can be unambiguously identified in every photo (Sanchez-Pages & Turiegano, 2010) by

231   using the TPS morphometric free software (by F.J. Rohlf, see

232   http://life.bio.sunysb.edu/morph/). We employed these LMs to calculate facial masculinity

233   and FA using the Morpho-J free software (by C. P. Klingenberg. See

234   http://www.flywings.org.uk/MorphoJ_page.htm). The LMs were placed twice, once for

235   each researcher, allowing the software to quantify digitizing error through Procrustes

236   ANOVA analysis (Klingenberg & McIntyre 1998; Klingenberg et al. 2002).

237

238   Individual FA was calculated employing a Procrustes ANOVA analysis

239   (Klingenberg & McIntyre 1998; Klingenberg et al. 2002). We placed LMs in two photos of

240   each subject in order to control for any error in the photo taking process. We thus

241   quantified two measurement errors, in photo taking and the digitizing error. There was a

242   significant directional asymmetry in the sample, that is, the mean asymmetry was

243   significantly different from zero (the main effect of mirroring is significant in the

244   Procrustes ANOVA; $F=4.34$ $df=37$ $p<0.001$). Individual FA scores correspond to the

245   Procrustes distance between the original and mirrored copies of the landmark configuration

246   of each individual after correcting for directional asymmetry (Klingenberg & McIntyre,

247   1998; Schaefer et al., 2006).

248

249   Facial masculinity was measured by calculating the Procrustes distance between the

250   LM configuration of each male average image and a reference female face (Sanchez-Pages

251   & Turiegano, 2010). The reference female face was obtained by averaging 50 images of

252   white self-reported female students and their mirror images. Each male average face was

253   obtained from two photos of each participant and their mirror images. We employed this

254   protocol in order to avoid any perturbation in this measurement caused by the asymmetry of

255   males faces compared to the female reference face. An advantage of this method is its

256   independence from age and ethnic differences (given the appropriate reference group).

257

258   Participants' right hands were scanned with a CanoScan LiDE70 high-resolution

259   scanner. The second and fourth digits were measured from the centre of the flexion crease

260   proximal to the palm to the top of the digit. This is a commonly accepted method to

261   calculate 2D:4D (Fink et al., 2005; Millet & Dewitte, 2006; Apicella et al., 2008). The

262   fingers were measured twice (once by each author) employing the appropriate utility of the

263   TPS morphometric free software. Both measures highly correlated ($r = 0.985$, $p < 0.001$

264   and $N = 152$). The variable employed in the analyses was the average of both measures.

265

266   *Study 1*

267   In the first study, we measured social preferences with a sequence of two-choice

268   questions presented to subjects, our Social Preferences Test (SPT). Answering to a

269   sequence of questions is a method commonly employed when measuring social preferences

270   (Van Lange et al., 1997).The choices in the SPT were two distributions of points between

271   the subject and a counterpart. Subjects were told that this counterpart was a participant in

272   future experimental sessions. In the first pair of choices, subjects had to choose between

273   distribution A= {20, 30} and distribution B= {30, 80}, where the first figure indicates the

274   number of points allocated to the subject making the choice. These distributions displayed

275   inequality unfavourable to the subject. In the second pair of distributions, the inequality

276   was favourable to the subject, who was asked to choose between distribution C= {70, 10}

277   and D= {60, 50}. These two pairs of distributions are such that the four possible different

278   profiles of choices correspond to four different types of social preferences. The choice {B,

279 C} corresponds to SI subjects, that is, those mostly interested in maximizing the amount of

280 points they receive. The choice {B, D} corresponds to ES subjects, that is, those interested

281 in maximizing the total sum of points. The choice {A, D} corresponds to IA subjects

282 because those choices yield the most egalitarian distribution of points within each pair.

283 Finally, we attribute the remaining choice to C subjects, that is, those interested in

284 minimizing unfavourable inequality and in maximizing favourable inequality, even at the

285 expense of some material payoff.

286

287   Our SPT was designed along the same lines as the well-established Triple-

288 Dominance Measure of Social Value Orientation (SVO) (Van Lange et al., 1997). This

289 measure presents subjects with nine questions, each containing three distributions of

290 income. Each of these three items corresponds to a primary SVO: prosocial, individualistic

291 and competitive. A subject who picks six or more items corresponding to one of these

292 SVOs is classified as such. Hence, the Triple-Dominance measure of SVO may leave

293 unclassified a non-negligible fraction of subjects (Eek & Gärling, 2006). We designed our

294 SPT in order to classify all participants. This *efficiency* property (Murphy et al., 2011) is

295 important, especially when subjects are paid for their choices. More importantly, the SPT

296 permits a finer classification of subjects: the Triple-Dominance Measure of SVO contains

297 no item in which the subject experiences unfavourable inequality, and therefore it cannot

298 distinguish between IA and ES subjects, classifying both of them as prosocial. In addition,

299 the SPT is simple and provides clear economic incentives. Still, given that the SPT is based

300 on a small number of questions, we checked its validity by comparing it to the Triple-

301 Dominance Measure of SVO.

302   We ran this robustness study at UAM in the fall of 2011 and 2012. A total of 106

303   self-declared white males subjects (age 20.85±0.19yr) were presented with the nine items

304   of the Triple-Dominance Measure of SVO and the two choices of our SPT. Subjects were

305   informed that they would be paid for the eleven options they chose. Results of this study

306   showed a high degree of consistency between the Triple-Dominance Measure of SVO and

307   the SPT. The SPT produced a classification which coincided with the SVO measure for

308   90.4% of the subjects that the SVO test classified (12 out of the 106 subjects were left

309   unclassified by the SVO). Let us reiterate that subjects classified as either IA or ES in the

310   SPT are classified as prosocial in the Triple-Dominance Measure of SVO. In February

311   2013, we checked the reliability of our SPT by asking these participants to answer again the

312   SPT through e-mail (but without a payment). We recruited 79 of the initial 106 participants.

313   Of these participants, 84.8% (n=67) did not change of SPT group. The more stable group

314   was SI (94.4% of the initial SI maintained this classification). The most frequent change in

315   group was between IA and EM (3 of the 13 initial IA became classified as EM).

316

317   *Study 2*

318   In the second study, participants took part in four one-shot UGs. Participants were

319   asked to make choices in both roles, as responders and as proposers. In order to avoid

320   competitive effects within each group of participants, subjects were playing each time

321   against a participant not present in the room. As proposers, subjects could offer any integer

322   amount of points between 0 and 100p to a future participant. As responders, they played

323   three times; they were told that they were playing against three previous participants. Each

324   time they had to accept or reject a different offer: a low offer (15p), an intermediate offer

325   (30p) and a high offer (50p). The order of these three offers was randomly chosen in each

326   session. Given that subjects had to make an offer to a future participant as proposers, it was

327   natural for them to receive offers from previous participants in the role of responders. We

328   chose this design over asking subjects for their minimal acceptable offer because that

329   design makes less clear for subjects how choices determine payments. The high offer (50p)

330   served as a control to ensure that subjects understood the experiment. All subjects accepted

331   that offer, so we will not include it in any further analysis.

332

333   *Statistical analyses*

334   Table 1 provides summary statistics of the morphological variables we employ. We

335   tested the normality of these variables with the Kolmogorov-Smirnov test. Masculinity and

336   2D:4D are normally distributed. We log transformed FA after multiplying the measure by

337   100 (in order to avoid negative values which could complicate the interpretation of its

338   effects). Offer was resistant to any transformation into normality, so when performing any

339   analysis with this variable we used non-parametric methods. To analyze the results we

340   employed ANOVA and student-t test for differences in normally distributed variables,

341   Kruskal-Wallis H for non-normally distributed variables (i.e., Offer) and chi square test

342   when comparing nominal variables. When analyzing correlation between variables, we

343   used the non-parametric Spearman ρ. We also employed logistic regressions to analyze

344   simultaneously the effect of several independent variables on our dichotomous dependent

345   variables (acceptance or rejection of the low and medium offers). These analyses were

346   made following the recommendations in Kleinbaum & Klein (2002). First, the effects of

347   individual variables were analyzed independently. New variables were subsequently added

348   to these models. We do not report results on interactions between variables because they

349   were not significant. We employed SPSS15 in all our statistical analysis.

15

350   **3. Results**

351

352   *Study 1*

353   In the first study, we classified the 152 subjects according to their answers in the

354   SPT. The most common social preference group among our participants was SI (51.32%,

355   n=78), followed by C (23.03%, n=35), ES (20.39%, n=31), and finally IA (5.26%, n=8).

356   There were statistically significant differences (Chi square test, χ^2_3=9.208, p=0.027)

357   between subjects who were studying Economics (n=55) and those who were studying

358   Biology (n=81); the former type of students displayed a higher proportion of SI subjects

359   (SI=61.8%; ES=21.8%; C=16.4%; IA=0%) whereas the latter displayed a higher proportion

360   of C subjects (SI=44.4%; ES=18.5%; C=27.2%; IA=9.9%).

361

362   Next we analyzed how biological features varied across these groups (Figure 1). We

363   found no significant differences in 2D:4D (ANOVA, $F_{148, 3}$=0.746, p=0.527) nor in facial

364   masculinity ($F_{148, 3}$=0.579, p=0.630). We also found that, as we initially conjectured, SI

365   subjects show lower levels of FA than ES subjects (t test, t_{107}=2.043, p=0.043). Differences

366   are not significant across all four groups ($F_{148, 3}$=2.056, p=0.109), although they follow the

367   predicted pattern (see Figure 1).

368

369   *Study 2*

370   In the role of proposers, the average offer made across all subjects was 44.84 points.

371   We found significant differences in the average offer across groups (Kruskal-Wallis test,

372   H_3=9.598, p=0.022). Figure 1.C shows that SI and C subjects make lower offers on average

373   than the ES and IA subjects as predicted. Neither 2D:4D (Spearman correlation coefficient,

374   ρ_{152}=0.031, p=0.702), facial masculinity (ρ_{152}=-0.032, p=0.692) nor FA (ρ_{152}=-0.065,

375   p=0.430) show a significant correlation with the offer for the entire subject pool.

376

377   Regarding their behaviour as responders, 31.57% of subjects rejected the medium

378   offer whereas 58.55% rejected the low offer. There were significant differences in rejection

379   rates across the SPT groups, both for the medium (Chi square test, χ^2_3=11.261, p=0.010)

380   and the low offer (χ^2_3=9.944, p=0.019). Figure 1 shows that, as expected, SI and ES agents

381   accept both offers more often, whereas C subjects reject them more frequently.

382

383   As the first step in the simultaneous analysis of the importance of biological features

384   and social preferences, we analyzed the effect of the former set of factors on responders'

385   behaviour (see Table 2 for p-values and statistics). Participants who rejected the low offer

386   had higher facial masculinity than those who accepted it. We found no differences in FA

387   between subjects who accepted or rejected the low offer, in line with previous results in the

388   literature (Zaatari & Trivers, 2007). We found no significant differences in 2D:4D either,

389   although average digit ratios followed the pattern (lower ratios in participants who rejected

390   the offer) previously reported in the literature (Van den Bergh & Dewitte, 2006). We

391   performed the same analysis for the medium offer and we found identical patterns for the

392   three variables, although none of the differences were statistically significant ("medium

393   offer" row in Table 2).

394

395   Finally, we evaluated simultaneously the effect of all variables on acceptance rates

396   by running a logit regression analysis (Table 3). The analysis of the low offer showed a

397   significant effect of the SPT classification in the same direction as in the results described

398   above. Facial masculinity had a negative impact on the acceptance rate of the low offer.

399   The logit analysis of the medium offer yielded that the SPT classification had a significant

400   impact on acceptance rates, whereas no biological variable was found to have a significant

401   effect (lower half of Table 3).

402

403   **4. Discussion**

404

405   Inequality aversion and efficiency concerns on the one hand (Fehr & Schmidt, 1999;

406   Charness & Rabin, 2002; Engelmann & Strobel, 2004), and exposure to hormones and

407   proxies for developmental instability on the other (Kosfeld, et al., 2005; Van den Bergh &

408   Dewitte, 2006; Burnham, 2007; Zaatari & Trivers, 2007; Zak et al., 2007; Apicella et al.,

409   2008; Crockett et al., 2008; ; Zak et al., 2009; Eisenegger et al., 2010), can explain why the

410   behaviour observed in economic experiments departs from the predictions of standard

411   economic theory. In this paper, we offer a systematic attempt at linking social preferences,

412   individual biological features and strategic behaviour.

413

414   In a first study, we found that these two sets of explanations are related only to some

415   extent. Two different social preference groups, SI and ES, which account for 71.71% of the

416   subject pool, displayed differences in FA, a biological feature that has been shown to affect

417   behaviour in economic games. No significant differences were found in facial masculinity

418   or 2D:4D across social preference groups. The link between social preferences and

419   individual biological differences would thus seem of relatively low importance, at least

420   under our measure of social preferences. We measured social preferences by means of the

18

421 SPT, a set of one-shot distribution experiments whose results are highly consistent with the

422 widely-used Triple- Dominance Measure of SVO (Van Lange et al., 1997). This measure is

423 also highly reliable. The STP is more efficient than the Triple- Dominance Measure of

424 SVO since it classifies all subjects, and it is also finer since it can single out inequality

425 averse subjects. Both the SPT and SVO are designed to shut down strategic concerns such

426 as reciprocity that could potentially confound with purely distributional concerns. However,

427 none of these two measures can rule out that subjects may have reputation-management

428 concerns when making one-shot distributional choices (Trivers, 2004). Another weakness

429 of both measures is their limited statistical power resulting from their use of a categorical

430 classification instead of a continuous one. We cannot rule out that the SPT does not have

431 the statistical power required to detect subtle but yet important biological effects. In our

432 future research, we plan to investigate further this issue by using the Slider Measure

433 developed by Murphy et al. (2011) given its higher statistical power.

434

435   In the second study, we looked at the effect of social preferences (measured by the

436 SPT) and individual biological features in behaviour in the UG. The four SPT groups

437 behaved differently in both roles, as we had predicted (see Figure 1B, C). As a matter of

438 fact, social preferences measured with the SPT seem to have a stronger effect on behaviour

439 than the biological features studied here. When we include both the SPT classification and

440 the set of physiologically-based variables in the analysis of acceptance rates (see Table 3),

441 the former is always significant, whereas the latter is significant only for the low offer. This

442 suggests that the importance of biological features might be crowded out by financial

443 incentives. In the role of proposers, there are differences in the amount offered by the four

444 groups, but there is no correlation between the offer made and any biological feature we

445   considered. These results suggest that social considerations have an effect at least as strong

446   as biological features (Eisenegger et al., 2010; Salvador, 2005). This conclusion, however,

447   can apply to neutral contexts only. Previous studies have shown that modest situational

448   cues can alter the relationship between biological features and the behaviour of males in the

449   UG (Van den Bergh & Dewitte, 2006). This is consistent with results showing that

450   behaviour in the UG rests on a balance between phylogenetically older structures, involved

451   in automatic reactive emotional responses (amygdala), and the neocortical areas, which

452   have a richer future representation (frontal cortex and insula) (Gospic et al., 2011). While

453   biological characteristics are important in the emotional response to a challenge, they are

454   less important in the evaluation of long-term consequences. The presence of situational

455   cues inducing stronger emotional responses (Van den Bergh & Dewitte, 2006; Millet &

456   Dewitte, 2009) might enhance the influence of biological features on strategic behaviour.

457

458   But the effect of social preferences and biological features cannot be completely

459   decoupled. Biological features have an effect on behaviour through social preferences. We

460   obtained that SI and ES subjects have different levels of FA and also make different offers

461   in the UG. This suggests that the positive link between FA and offers in the UG observed in

462   Zaatari & Trivers (2007) could be attributed to two specific subsets of the population, one

463   interested in maximizing efficiency and another purely self-interested. Probably, this

464   correlation between FA and the offer in the UG for just a part of the subject pool rather than

465   for the entire sample constitutes our major departure from the previous literature. However,

466   there are three important differences between Zaatari & Trivers (2007) and our work that

467   make comparisons difficult. First, the vast majority of their subjects were teenagers (mean

468   age= 15.93 years; S.D.=1.67; mode=15; range=13–20) while ours were young adults (our

469   subjects ages varied from 17 to 30, with a mean of 20.34±0.17 years and a mode of 20).

470   This is an important difference that is even more relevant at the light of 1) the described

471   effects of T on behaviour in the UG (Burnham, 2007) and 2) that teenagers suffer rapid

472   changes in T levels (Buchanan et al., 1992; Sisk & Zehr, 2005). Another main difference is

473   that these authors measured asymmetry in several body characteristics, and attributed them

474   entirely to FA. In our analysis, we measured FA separating it from any possible directional

475   asymmetry (Schaefer et al., 2006). Third, these authors obtained the result linking low FA

476   to low offers after a statistical correction of the so-called background variables (age, sex,

477   body mass index and friendliness scores). We did not control for these measures (except for

478   age) and this adds another source of non-comparability.

479

480   The present paper also shows the influence of facial masculinity on behaviour.

481   Facial masculinity is a proxy for exposure to testosterone during puberty (Enlow, 1996).

482   This variable is an objective measure, in contrast with often-used measures of masculinity

483   based on subjective scores. Objective measures of facial masculinity have been rarely used

484   in behavioural research (Apicella et al., 2008; Carré & McCormick, 2008; Pound et al.,

485   2009) and, with the exception of Sanchez-Pages & Turiegano (2010), they have not been

486   used to study strategic behaviour. The immuncompetence handicap hypothesis states that

487   masculine traits signal inmunnocompetence and developmental stability (Folstad & Karter,

488   1992). In this line, perceived facial masculinity correlates both with health (Rhodes et al.,

489   2003) and strength (Fink et al., 2007) in young males. Therefore, men with more masculine

490   faces seem to be more capable of resisting physiological stress and, to some extent, could

491   be said to show higher phenotypic quality.

492

493   Our results for the UG seem plausible if one considers the game, as some authors do

494   (Page et al., 2000), as an approximation to the problem of dividing the expected catch in

495   hunting, where rejection means a refusal to cooperate. Given that males seem to adopt

496   different behavioural strategies depending on their phenotypic quality (Zaatari & Trivers,

497   2007; Apicella et al., 2008), more masculine males might not need to be as cooperative as

498   less masculine males because their greater ability to gain access to resources. This

499   hypothesis has also been proposed as an explanation of why more facially masculine males

500   tend to take more risks (Apicella et al., 2008) and why they show increases in circulating

501   testosterone after a success (Pound et al., 2009). Alternatively, as less masculine males are

502   less attractive to females (Johnston, 2006), their behaviour tends to be more cooperative in

503   order to signal their willingness to deliver high paternal investment and, therefore, their

504   interest in long-term relationships (Takahashi et al., 2006).

505

506   The present paper aimed to integrate the different approaches used in Economics on

507   the one side and Physiology on the other. Economic behaviour is based on the concept of

508   preferences, which are revealed through individual choices. In Biology, some fundamental

509   individual characteristics, like hormone levels (during development and in adults), have

510   been described to have an impact on behaviour. Our two studies were designed to combine

511   these two approaches and also to evaluate their relative importance. Clearly, the interplay

512   between these two sets of explanations is a very complex issue that deserves further tests

513   and analyses.

514

515

516

525

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781   **Figure Legends**

782

783   **Figure 1**

784   **Differences across behavioural types**

785   A) Differences in the individual features studied.

786   B) Differences in the rejection rates for the low and medium offers

787   C) Differences in the offers made.

788   FA was transformed into Ln(100xFA). Different statistical test were applied depending on

789   the characteristics of the variables studied (t test, χ^2 test and Kruskal-Wallis H test

790   respectively). * for $p<0.05$, ** for $p<0.01$.

791

792   **Table 1:** Summary statistics.
793

	Average	SD	Max	Min
Facial masculinity	0.089	0.022	0.154	0.042
Fluctuating Asymmetry	0.035	0.014	0.084	0.016
2D:4D finger ratio	0.962	0.030	1.049	0.897
N	152	152	152	152

794
795

796   **Table 2:**

797   Average individual features according to participants' response to the two offers.

		n	Fluctuating Asymmetry Ln(100 x FA)	Facial masculinity	2D:4D finger ratio
Low offer	Reject	89	0.036±0.014	0.093±0.022	0.960±0.030
	Accept	63	0.034±0.014	0.084±0.022	0.964±0.030
			$t_{150}=1.183$ p=0.239	$t_{150}=2.453$ p=**0.015**	$t_{150}=-0.792$ p=0.430
Medium offer	Reject	48	0.036±0.015	0.092±0.022	0.958±0.029
	Accept	104	0.035±0.014	0.088±0.022	0.964±0.031
			$t_{150}=0.232$ p=0.817	$t_{150}=0.895$ p=0.372	$t_{150}=-1.155$ p=0.250

798

799

Table 3:

801   Logistic models for the rejection rates in the low and medium offers.

802

Offer	MODEL				VARIABLE				
	-2LL	Likelihood Ratio Test	df	p	variables	coef	Wald	df	P
Low	189.589	16.659	6	0.011	Constant	-3.039	0.283	1	0.595
					2D:4D	5.310	0.817	1	0.366
					Masculinity	-17.409	4.425	1	**0.035**
					FA	-0.380	0.588	1	0.443
					SP		8.256	3	**0.041**
					ES	-0.548	1.481	1	0.224
					C	-1.277	7.270	1	**0.007**
					IA	-1.077	1.560	1	0.212
Medium	177.137	12.454	6	0.053	Constant	-5.169	0.718	1	0.397
					2D:4D	6.966	1.238	1	0.266
					Masculinity	-5.248	0.410	1	0.522
					FA	0.081	0.026	1	0.872
					SP		10.064	3	**0.018**
					ES	0.030	0.003	1	0.953
					C	-1.084	6.183	1	**0.013**
					IA	-1.647	4.355	1	**0.037**

803
804
805   Logistic regressions for the low and medium offers. The models reported include the
806   variables 2D:4D, fluctuating asymmetry (FA), facial masculinity (Masculinity) and social
807   preferences (SP). The latter variable has four possible categories: Efficiency Seeker (ES),
808   Competitive (C), Inequality Averse (IA) and Self Interested (the reference group). A series
809   of models were run by including one additional variable at a time. We report only the last
810   of these models.
811