Testosterone, Facial Symmetry and Cooperation in the Prisoners’ Dilemma

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Abstract:

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

Keywords: Testosterone, Cooperation, Prisoners’ dilemma, Fluctuating asymmetry, Facial masculinity, 2D:4D.
1. Introduction

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

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

There is also a wide body of literature linking these three variables with typically masculine features and behaviours. 2D:4D is a predictor of the degree of expression of
sexually dimorphic and other sex-hormone mediated traits, like visuo-spatial ability or
left hand preference, and some behaviors like increased aggressiveness or
competitiveness [24-27]. In men, circulating T has been linked to behaviours like
acquisition of status, aggression, sensation-seeking or interest in sex [8,28-30]. Finally,
the degree of masculinity has been shown to have an effect on male behaviour [20,31]
but, above all, it has been described as a good predictor of male attractiveness [32-34].
Evidence shows that more attractive people behave differently [35-39]. However, it is
important to bear in mind that masculinity is not the only factor determining male
attractiveness [40-42].

Fluctuating asymmetry (FA) is a departure from symmetry in traits that are
symmetrical at the population level [43]. It is considered to be the result of
developmental instability. It thus reflects the ability of the organisms to maintain a
stable development of their morphology and to overcome possible perturbations. This
ability is thought to be affected by genetic and environmental factors. Many studies
show a link between symmetry and genetic quality [44]. In humans, facial symmetry
has been proposed as a cue for heritable fitness benefits [45,46], and it is widely
considered as attractive [47,48]. Some studies have found that FA positively correlates
with facial masculinity [49-51]. This suggests that both characteristics subtly indicate
genetic quality. Still, many other studies find no correlation between them [52-54]. FA
can be thus related to human behaviour in many different ways, since it is expected that
the genetic quality of individuals has an impact on behaviour [55-58]. In general,
symmetrical men (with low FA) tend to be less cooperative and more competitive. This
behavior is believed to be due to their superior phenotypic quality, which increases their
likelihood of winning conflicts and reduces their need to receive help from others [58].
In this study, we examine the effect of proxies for T exposure in utero and during puberty, of current levels of T and of FA on how human males play a one-shot symmetric Prisoner Dilemma Game (PDG). The effects of some of these variables have been previously tested in different economic experiments, like the ultimatum game [58-60], public good games [61], the dictator game [62] and risk-taking in an investment game [31]. Formally, the symmetric PDG is a special case of the public good game with two players and two available actions: “Cooperate” (equivalent to a full contribution) and “Defect” (equivalent to no contribution). The outcome obtained by the players when both defect is worse for each of them than the outcome they would have obtained if both of them had cooperated. When the players choose different actions, the one who cooperated receives a very low payoff, while the defector obtains a very high payoff. “Defect” is thus a dominant strategy in this game, that is, it is the best strategy for both participants regardless of whatever their opponent does. However, it is well known that humans tend not to follow this rule. There is substantial experimental evidence showing that humans are willing to cooperate and trust others in the one-shot PDG [63,64].

We expect high FA males to cooperate more in the PDG, in line with some previous results [38,58,60]. As FA is a marker of genetic quality, high symmetric people have less need for receiving help from others, reducing their interest in mutual reciprocity. In the same line, as high T is also considered to be a marker of genetic quality, we expect the three T-related variables (2:4 finger ratio, Facial Masculinity and current T level) to have a positive impact on defection rates. Effects in this direction have been previously observed in other games [61]. However, it has been pro-social behaviour has also been observed in people with low 2D:4D [61,62]. Because of this, it is difficult to predict specifically what will be the sign of the effect on the PDG of the
exposure to high T at these three different stages [31], although it is likely that 2D:4D will display some effect [61].

2. Methods

2.1. Participants

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

2.2. Experimental procedure

The experiments were performed employing the z-Tree 3.2.10 software for Economics Experiments [65]. The experiments were run in sessions with less than 20 subjects. In order to avoid unexpected effects on participants’ behaviour [59] all the experiments were tracked by the (male) authors. Before each session, all subjects were carefully instructed about the experiment and their photographs, hand-scans and saliva samples were taken. All the subjects filled a questionnaire asking their age, ethnicity, sexual orientation and degree. This study was part of a larger one that included several
other items. Apart from the show-up fee (£5 in Edinburgh, 5€ in Madrid), subjects were
told that their final payment would depend upon their choices in several but not all of
the items in the questionnaire. They were informed of which ones counted for payment
only after the experiment concluded. Each experimental session took about an hour.
Subjects were paid privately in cash after the session and after they filled the
corresponding official receipt.

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

2.3. Masculinity and FA Measurement

Full frontal facial colour photographs were taken of all participants with an
Olympus E-500 digital camera with resolution 3264x2448 in JPEG format under
standardized light conditions. The camera distance was kept constant at 3m and the
zoom was completely opened to avoid slight optical distortion of true facial shape.
Participants were asked to remove any facial adornment, to pose with a neutral
expression and to look directly into the camera. We took three images of each
participant in order to choose the best one for our purposes. Facial measures, as
masculinity or FA, were calculated from the photographs using geometric
morphometric tools [66]. The shape of each face was defined by manually setting 39
predetermined points called landmarks (LM). These 39 points (Figure 1) were chosen because they can be unambiguously identified in every photo. This ensures that they mark positions which rigorously correspond, in a biological or perceptual ground, to the same position in every face [67]. The LMs were placed twice, once by each author, which makes possible to assess any measurement error.

We employed these LMs to calculate the Procrustes distance between pairs of rotated and scaled images [67] using the TPS software package (by F.J. Rohlf, see http://life.bio.sunysb.edu/morph/). To calculate the asymmetry of each image, we compared the LM position of each face and a mirror-image of the same one, measuring the Procrustes distance between both LM positions [68]. FA can be understood as a deviation of the “perfect” symmetry or, as it is commonly considered, as an individual deviation from the average (directional) asymmetry. In this context the asymmetry of a bilateral object is attributable partially to directional asymmetry (differences in the population between average right and left size) and partially to fluctuating asymmetry (deviation of each individual’s asymmetry from the overall average asymmetry). We obtained FA by decomposing the Procrustes distance between each image and its mirror reflecting in directional and fluctuating asymmetry by employing the Procrustes ANOVA method. The latter method characterizes the shape of an object (the faces) as a single geometric object. Because calculation of Procrustes coordinates is based on the algebra of sums of squares, individual deviations from the average shape can be partitioned in different components, as happens in the conventional ANOVA [69]. The classic ideas of fluctuating and directional asymmetry are applied using this alternative approach [70], where directional asymmetry corresponds to the variation introduced by the variable “side of the object”, while FA corresponds to the variation explained by the interaction between side and individual. To compute the FA of each individual we
employed Morpho J software (by C. P. Klingenberg. See http://www.flywings.org.uk/MorphoJ_page.htm). The FA values obtained correlate strongly with the total asymmetry calculated for each face (r=0.982, p<0.001).

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

2.4. Digit Ratio Measurement

Participants' right hands were scanned with an Hp psc 2110 scanner with a resolution of 600x1200 ppi. The second and fourth digits were measured from the centre of the flexion crease proximal to the palm to the top of the digit. This is a commonly accepted way to calculate 2D:4D [31,61,67]. To measure the fingers both authors independently placed a LM in each of the described positions and both lengths were measured afterwards. The placing of LMs and the measures were done with the appropriate utility of the TPS morphometric free software package. The two
measurements of 2D:4D were highly correlated ($r = 0.96$, $p < 0.001$, $N = 147$). The measure employed in the analysis was their average. In some cases, it was necessary to repeat the hand scanning because the image was unsuitable for correct measuring. We measured lengths in pixels up to two decimal places.

2.5. Salivary T Measurement

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

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

3. Results

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

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

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

In order to simultaneously evaluate the effect of all the variables on cooperative behaviour we built a logistic regression model including City as a control variable, FA, and Masculinity. We also included 2D:4D and its second order term, in order to
correctly account for the non-linear effect of this variable [61]. The resulting model was significant (see Table 2). We found a highly significant effect of FA on cooperation. That is, men with higher FA levels tend to cooperate more in the PDG. We also found a significant effect of 2D:4D and its second term, positive and negative respectively, implying that men with intermediate values of 2D:4D are more likely to cooperate. Moreover, the model including solely 2D:4D and its second order term was also significant (see Table 2). These both effects can be roughly observed if we divided the sample into blocks. When we divide the sample in two equal-sized blocks according to FA, participants who presented high values of FA cooperated more often (61.12%) than low FA participants (45.34%). On the other hand, if the sample is divided in three equal-sized blocks according to 2D:4D, it is possible to observe that participants who showed an intermediate value of 2D:4D (the intermediate third of them) tend to cooperate more often (67.35%), whereas participants with low or high values cooperate less frequently (45.10% and 46.81% respectively).

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

Another variable that can affect cooperation is the expected behaviour of the counterpart (EB). This variable is strongly significant (see Table 2) and its inclusion in our model renders City and FA insignificant, implying that these two variables are somehow related to EB. The participants who thought that the other part will cooperate
show higher FA than the rest ($t_{45}=2.011, p=0.046$) while no differences were found in City ($\chi^2_{1}=3.183, p=0.074$).

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

4. Discussion

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

No previous studies have attempted to explore the link between FA and cooperation, although the relevance of FA in other behaviours is well known [55-58]. On the other hand, very few studies have analyzed the effect of T on cooperation, although its effects on human behaviour have been extensively investigated.
The closest contributions to ours have studied the effect of these two variables on the Ultimatum Game [58-60,75]. The Ultimatum Game (UG) is not normally considered as a game of cooperation because it does not contain a fundamental tension between social and private incentives. Still, some authors have used it as an approximation to the cooperative interactions that occur during hunting [76]. Under this interpretation, a dominant individual tries to obtain the cooperation of another one in order to hunt, and proposes a division of the expected catch. The non-dominant individual can accept or reject that proposal. Rejection means that no catch is obtained.

Note that, contrary to what happens in the PDG, social and private incentives are aligned when the second individual has to make a choice.

In the UG, males with low 2D:4D (presumably exposed to high T/E ratio in utero) have higher minimum acceptable offers, although there is no described relation between this variable and the offers made [59,60]. On the other hand, males with low FA (that is, more symmetric) make lower offers, although there is no described relation between this variable and the likelihood of rejection [58]. Our results are in line with these studies, as FA affects males’ behaviour in the PDG by influencing the estimation that players have about the choice of the other player, similarly to what occurs in the UG (where symmetry affects offers, which in turn are an indirect measure of the expected probability of acceptance). Symmetric males thus tend to believe that their counterpart will defect and behave accordingly. This is in line with previous studies that have observed that symmetric males tend to cooperate less frequently because of their superior phenotypic quality [58]. Given their higher ability in obtaining resources, males with low FA do not need to be, nor look as cooperative as males with high FA, and then cooperate less. This is however at odds with other experiments in which more attractive subjects trust others more in a Trust Game [39]. This can be explained if we
bear in mind that attractiveness does not only depend on FA [34] and that in that experiment the subject pool was composed by males and females, and they tend to evaluated attractiveness attending to different features [77]. In any case the PDG and the Trust Game are very different games. In the Trust Game, as the second players acts after the first have trusted (or not), “leading by example” can have an important effect. This is not possible in the PDG because it is simultaneous. Symmetric males may then trust because of their self-confidence and because they may attempt to obtain higher status by leading cooperation.

We also find that individuals with lower 2D:4D, (exposed to higher T level in utero) tend to defect more, in the same line as in the UG [59,60]. This does not coincide completely with the results obtained in studies that explored the relationship between individual characteristics and contributions in a public good game [61]. They find that individuals which did not cooperate or behaved altruistically (that is, they contributed more than what the social norm dictates) show high 2D:4D, although these effects were not statistically significant in men. In our experiment, cooperation is just a dichotomous variable while in the public good game cooperation is a spectrum (i.e., the amount of the contribution). Our experimental design is thus simpler and can offer cleaner results but this comes at the price of limiting the richness of possible behaviours. We find, as these authors do, that low 2D:4D subjects are less likely to behave altruistically (tend to cooperate less often in our game). However, their conjecture that subjects with low 2D:4D tend to adhere to social norms cannot explain our results, since defecting is unlikely to be the social norm in PDG. In our case, self-sufficiency in obtaining resources can explain the behaviour of subjects with low 2D:4D. This point of view is in line with another study on cooperation in which more attractive males tended to cooperate less [38]. As we have already mentioned, we cannot assume that our more
symmetric or masculine subjects will be identified as the more attractive because this is a trait affected by many other variables [34]. In any case, our results go in the same direction as those.

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

In our study, two other variables that could potentially affect cooperative behaviour, like facial masculinity and current T, display no effect. It is well known that the current level of T is linked to aggressiveness and status-seeking behaviour [8,28]. In addition, facial masculinity might have shown an effect as it is considered as a signal of genetic fitness according to the “immunocompetence handicap hypothesis” [79]. We have found no relationship between these variables and cooperation in the PDG. Hence, based on these lacks of effect we conclude that cooperation in PDG is not understood as a challenge [29,80] and that the aversion to a possible breakdown of cooperation cannot be equated to the standard concept of risk aversion [31]. It is interesting that the exposure to T in some periods of life seems to have an impact on certain types of
behaviour, like risk aversion [31], but not in others, like the ones we investigate in this study. This suggests that exposure to T influences behaviour in very diverse ways. The different effects of the levels of T during development and the links between the behaviours that seem to be affected by the hormone also deserve further experiments. To perform such studies it would be necessary to test the same pool of subjects in different economic experiments after controlling for all these variables. In the same line, to ensure that developmental instability is behind facial FA, it will be necessary complement further data on cooperation and FA with measures in some others bilateral traits. In addition, it would be necessary to extend the experiments by employing women and non-students as subjects, enlarging thus the range of age and occupations.

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5. References


[75] Zaatari D, Palestis BG, Trivers R. Fluctuating asymmetry of responders affects offers in the ultimatum game oppositely according to attractiveness or need as perceived by proposers. Ethology 2009;115:627-632.


### Tables

| 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 |

**Table 1.**

*Mean values of variables in the total population and according to participants’ choice*

- a Data are the mean (±SD)
- b In our whole population, 69 individuals defected and 78 cooperated.
- c Salivary T was only measured in the experimental sessions performed in Madrid, where 28 individuals defected and 47 cooperated.
### Variables in the model

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### Logistic models for the whole sample and for the Spanish subjects.

The variables included are 2D:4D (second to fourth finger ratio) FA (fluctuating asymmetry), Masculinity (facial masculinity), Current T (current salivary T) and EB (expected behaviour of the counterpart).
Figures

Figure 1.

Landmarks placement.

A) An average face with the 39 landmarks placed. B) All 147 landmarks configurations superimposed after Procrustes Fit. These coordinates are the basis for all FA calculations.