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Original Article

Who is the fairest of them all? The independent effect of attractive features and self-perceived attractiveness on cooperation among women[☆]

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ABSTRACT

The present paper analyzes the extent to which attractiveness-related variables affect cooperative behavior in women. Cooperativeness is evaluated through a Prisoner's Dilemma Game (PDG). We consider several morphometric variables related to attractiveness: *fluctuating asymmetry* (FA), *waist–hip ratio* (WHR), *body mass index* (BMI) and *facial femininity* (FF). These variables have been shown to predict human behavior. We also include as a control variable a score for *self-perceived attractiveness* (SPA). We test differences in these variables according to behavior in the PDG. Our results reveal that low-FA women cooperate less frequently in the PDG. We also find that women with lower WHR are more cooperative. This result contradicts the expected relation between WHR and behavior in the PDG. We show that this effect of WHR on cooperation operates through its influence on the expectation that participants hold on the cooperative intent of their counterpart. In addition, we show that the effect of attractive features on cooperation occurs independently of the participants' perception of their own appeal. Finally, we discuss our results in the context of the evolution of cooperative behavior and under the hypothesis that attractiveness is a reliable indicator of phenotypic quality.

1. Introduction

Human cooperation is an undeniably appealing phenomenon that has attracted substantial attention from scientists (Hammerstein, 2003). One line of research on cooperative behavior has obtained important insights by using strategic games (e.g. Mulford, Orbell, Shatto, & Stockard, 1998; Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005; Millet & Dewitte, 2006; Takahashi, Yamahishi, Tanida, Kiyonari, & Kanazawa, 2006; Van den Bergh & Dewitte, 2006; Burnham, 2007; Zaatari & Trivers, 2007; Zak et al., 2009; Zethraeus et al., 2009; Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010; Sanchez-Pages & Turiegano, 2010, 2013, Lovejoy, Catellier, Evans, Lohiser, & Chiu, 2013). In strategic games, participants face simplified social situations in the laboratory and receive rewards depending on their decisions as well as those of other participants. Because these studies use controlled environments, the behavior displayed by subjects is easily measurable and replicable.

In the present study, we define cooperation as an individual behavior aimed to maximize collective interest rather than pure self-interest. One way of evaluating cooperation with strategic games is through the Prisoners' Dilemma (PDG henceforth). The PDG is a strategic game in which collective welfare and self-interest are in stark conflict. Standard Game Theory postulates that individuals act following their self-interest only and should hence not cooperate in the PDG, even though such behavior eventually leads to a loss in collective welfare. Early experimental studies demonstrated that such prediction is only partially fulfilled. Even in one-shot situations, and when playing against complete strangers, humans tend to cooperate in the PDG in sizeable rates (see Marwell & Ames, 1981 and Dawes & Thaler, 1988, among many). Undoubtedly, it is of a great interest to explore which individual factors, if any, cause some individuals to be more prone to cooperate than others.

Several recent papers describe the effect of physiology-related variables on human behavior in economic experiments (Kosfeld et al., 2005; Millet & Dewitte, 2006; Van den Bergh & Dewitte, 2006; Burnham, 2007; Zaatari & Trivers, 2007; Apicella et al., 2008; Zak et al., 2009; Zethraeus et al., 2009; Eisenegger et al., 2010). However, few studies have focused on the relationship between individual features and cooperative behavior in two-person interactions like the PDG (Mulford et al., 1998; Takahashi et al., 2006; Sanchez-Pages & Turiegano, 2010; Lovejoy et al., 2013). Even smaller is the number of these studies focusing exclusively on women. This gap in the literature is rather unsatisfactory given the important physiological differences, especially the endocrine, that exist between sexes (for exceptions see Buser, 2012; Pearson & Schipper, 2013).

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In the present paper, we investigate the relationship between cooperation among women in the PDG and a number of physiology-related variables with well-established effects on human behavior. These variables are facial fluctuating asymmetry, facial femininity, waist–hip ratio and body mass index.

Fluctuating asymmetry (FA) is a variable with a physiological basis and linked to individual's fitness. It can be defined as a departure from symmetry in traits that are symmetrical at the population level (Van Dongen & Gangestad, 2011). FA is considered to be the result of developmental instability, reflecting the ability of an organism to maintain a stable development of its morphology and to overcome possible external perturbations (Møller & Swaddle, 1997; Thornhill & Gangestad, 2006; Van Dongen & Gangestad, 2011). Consequently, it has been described as linked to individual fitness in many species (Møller, 1997; Møller & Thornhill, 1998). In humans, there exists a positive average effect of FA on a variety of outcomes, from hormone levels to health problems. These effects are robust, especially those related to reproduction (Van Dongen & Gangestad, 2011). FA has also been related to human behavior (Furlow, Gangestad, & Armijo-Prewitt, 1998; Manning & Wood, 1998; Pound, Penton-Voak, & Brown, 2007; Zaatari & Trivers, 2007; Holtzman, Augustine, & Senne, 2011; Muñoz-Reyes, Gil-Burmann, Fink, & Turiegano, 2012). In particular, FA has been studied in relation to cooperative behavior in males. Results show that low-FA males (more symmetric) cooperate less often in the PDG (Sanchez-Pages & Turiegano, 2010). FA is also a determinant of behavior in the ultimatum game (Zaatari & Trivers, 2007; Zaatari, Palestis, & Trivers, 2009; Sanchez-Pages & Turiegano, 2013). In both the PDG and in the ultimatum game (UG henceforth), symmetrical men (with lower FA) tend to be less pro-social. Personality measurements corroborate this finding (Holtzman et al., 2011). One possible explanation for the lack of pro-sociality of symmetrical males is their higher capability to obtain resources by themselves, which reduces their need to obtain help from others. An additional aspect related to the link between FA and fitness is that a low FA is considered to be an attractive feature in many human populations (reviewed in Johnston, 2006; Kościński, 2007; Little, Jones, & DeBruine, 2011; Thornhill & Gangestad, 1999; Van Dongen & Gangestad, 2011).

Another morphometric feature described as an indicator of fitness is the waist–hip ratio (WHR), which results from dividing the waist perimeter by the hip perimeter. This measure is strongly influenced in women by hormone levels during puberty, which in turn determine the differential allocation of fat between sexes (Kirschner & Samojlik, 1991; Björntorp, 1997; Lev-Ran, 2001). Since the distribution of fat is very different between males and females, WHR can be considered as a secondary sexual characteristic in women. The standard values of WHR in Caucasian female populations range from 0.67 to 0.80 (Marti et al., 1991). WHR is associated with both health and fertility. Women with ratios around 0.70 present optimal estrogen levels (Jasieńska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004) and are less likely to develop serious illness, such as diabetes, cardiovascular disorders and ovarian cancer (reviewed in Singh, 2002). Regarding fertility, women with values of WHR of 0.80 or higher have significantly lower pregnancy rates than women with lower values, independently of their body mass index (Singh, 2002). In addition, it has been pointed out that women with a low WHR present an ideal fat distribution in terms of fertility (Swami & Tovée, 2007). The link of this feature to fertility and resistance to illness is to be expected, given that secondary sex characteristics are linked to fitness in many species (Møller & Alatalo, 1999).

WHR is related to another physiological indicator of health in humans, the body mass index (BMI) (Tovée, Reinhardt, Emery, & Cornelissen, 1998; Tovée, Maisey, Emery, & Cornelissen, 1999, Flegal, Kit, Orpana, & Graubard, 2013), also linked to reproductive potential. Extreme values of BMI have a negative impact on fertility (Reid & Van Vugt, 1987; Kaplan, 1990; Brown, 1993; Lake, Power, & Cole, 1997). Given its association with both health and fertility, many researchers have proposed BMI as a primary measure of female attractiveness (Tovée et al., 1999), although it is commonly recorded as a nutritional marker. The World Health Organization considers the range 18.50–24.99 as standard for adults. Values under 18.50 are considered underweight, between 25 and 30 as overweight, and equal to or above 30 as obese.

Both WHR and BMI are important indicators of female attractiveness. Although related, they display relatively independent effects. Controlling for BMI, women with a WHR around 0.70 are classified as the most attractive by men of most cultures, including Western Caucasian societies (Singh, Dixson, Jessop, Morgan, & Dixson, 2010). Still, the optimal value in terms of attractiveness ranges from 0.60 to 0.80 across different human populations (Marlowe, Apicella, & Reed, 2005; Dixson, Dixson, Morgan, & Anderson, 2007). Individuals exhibiting a remarkable deviation in their WHR (for example, women with high WHR and men with low WHR) are commonly seen as less attractive by the opposite sex (Pazhoohi & Liddle, 2012). BMI also influences individual attractiveness. Low values within the standard range, i.e. around 20, are those typically regarded as more appealing (Tovée et al., 1998, Tovée et al., 1999).

Another variable related with both phenotypic quality and attractiveness is the degree of facial sexual dimorphism. Facial femininity (FF henceforth) in women positively correlates with disease resistance (Thornhill & Gangestad, 2006), estrogen levels and fertility (Law Smith et al., 2006). Some authors have proposed FF as an individual indicator of the historical energy balance and the capacity to allocate energy for reproduction (Gangestad & Scheyd, 2005). Sexual dimorphism in facial features depends on sexual hormones levels during puberty (Johnston, 2006). Sexual development in female faces entails certain noticeable modifications, such as thickening of the lips and thinning of the cheekbones (Johnston, 2000). Hormone levels in puberty (Berenbaum & Beltz, 2011) and, more specifically, the degree of masculinity/femininity of the face, have proven to have an effect on adult behavior (Apicella et al., 2008; Carré, McCormick, & Mondloch, 2009; Pound, Penton-Voak, & Surridge, 2009; Stirrat & Perrett, 2010, 2012; Haselhuhn & Wong, 2012), although most of these studies have been performed in men. More importantly, the degree of masculinity/femininity has been described as a good predictor of attractiveness both in women and men (reviewed in Johnston, 2006; Kościński, 2007; Little et al., 2011; Thornhill & Gangestad, 1999).

Attractiveness affects human behavior both in individuals' everyday life and in the laboratory (e.g., Mulford et al., 1998; Langlois et al., 2000; Takahashi et al., 2006; Wilson & Eckel, 2006). This could bring up a potential confound: the observed effects of attractiveness-related features on behavior may operate directly or indirectly, that is, by determining perceived attractiveness which subsequently affects behavior. In order to control for this possibility, we included a score of self-perceived attractiveness (SPA henceforth) as an additional variable. The effect of SPA on cooperation has already been explored. Results show that women who find themselves attractive are less cooperative in the PDG (Mulford et al., 1998). In general, individuals who consider themselves attractive are also considered as such by others (Feingold, 1992; Marcus & Miller, 2003; Weeden & Sabini, 2007). Hence, the SPA score allows us to test whether the fitness-related variables we consider influence cooperative behavior directly or through their effect on self-perceived attractiveness.

Our main hypothesis is that women who display features associated with higher fitness—low FA, high FF and low WHR—cooperate less often in the PDG. We base this hypothesis on previous results indicating that men showing higher fitness are less prone to behave pro-socially (Zaatari & Trivers, 2007; Zaatari et al., 2009; Sanchez-Pages & Turiegano, 2010; Holtzman et al., 2011). The standard explanation for these results is based on the idea that cooperative behavior is a tool to receive future help from others. Thus, high-fitness individuals, who enjoy a greater capacity to obtain resources by themselves, need to resort to cooperative behavior less often (Zaatari & Trivers, 2007). According to our hypothesis, women with a low WHR (controlling for BMI) and a high FF should show less cooperative behavior in the PDG. We also expect to find a positive effect of FA on cooperation, meaning that we expect symmetric women to cooperate less often. This result has already been found for males (Sanchez-Pages & Turiegano, 2010), and there is no reason to expect the influence of FA on behavior to be sex dependent.

We are also interested in whether the effects of these variables on cooperation are mediated by attractiveness. One plausible hypothesis might be that these features solely influence cooperative behavior through attractiveness because high-fit individuals are perceived as more attractive and also feel more attractive themselves. This can be very important since attractive people tend to receive benefits from others without the expectation of costly reciprocation. Under this hypothesis, the attractiveness of high-fit individuals accustoms them to receive benefits which lead them to behave less pro-socially. In the present study, we can examine this hypothesis by analyzing whether the effect of FA, WHR and FF on cooperative behavior depends on SPA. Still, we conjecture that these variables do not exclusively operate through attractiveness. This is because high-fit individual is more capable of obtaining resources independently of whether they receive them from others who consider her as attractive. So, as a second hypothesis, we postulate that all these three features exert their effect on cooperation independently of SPA. Such result would imply that the biological determinants behind the studied features (such as developmental stability and hormone levels) wield their influence on behavior regardless of whether the individual considers herself as attractive or not.

2. Methods

2.1. Design and performance of experiments

Experiments were performed at the Faculty of Sciences of the UAM (Madrid, Spain). Participants were recruited among the student population few weeks before the semester exams in the spring and autumn of 2012. Recruitment was made by means of advertisement billboards and e-mail (sent by non-teaching staff) as the UAM ethical committee requires. In total, 176 White Spanish females took part in this study.

Participants played the PDG within a set of different tests (not considered in the current paper). In the PDG, subjects have to choose between two possible strategies: "cooperate" or "defect." If the two players choose "cooperate" they both get 90 points, if both choose "defect" each one gets 30 points. If they choose different actions, the one who cooperates gets 10 points and the one who defects obtains 160 points. The exchange rate used in the experiment was 100 points = 1€. Under the standard game-theoretical approach "defect" is a dominant strategy because it is the strategy that maximizes the individual benefit regardless of the decision of the counterpart. In addition to playing the PDG, participants were asked to guess the decision of their opponent (expected behavior, or EB). This variable has been shown to be a strong determinant of behavior in the PDG (Sanchez-Pages & Turiegano, 2010). Participants played a single round of the PDG. They were informed that they were playing against another female participant from a previous session. They did not know anything else about their counterpart. Subjects knew that their decisions would affect participants of a future session in the same way. The experiment was run employing the Z-Tree 3.2.10 software (Fischbacher, 2007). Each participant was allocated a computer terminal. Experimental sessions had less than 20 subjects each. Participants received a show-up fee (5€) and a variable reward dependent on the decisions taken in the different games implemented in the experiment. Final payment was 13.25 $\pm$ 0.08€ (avg $\pm$ SEM) per person (PDG average payment was 0.87 $\pm$ 0.04€). Prior to the experiment, participants were informed that their final payment would depend on their decisions in several items of the study, but not in all of them. Few weeks after the experiment, subjects were informed about the exact payment procedure.

At the end of each experimental session, pictures of each participant were taken to prospectively measure individual FA and FF. Their height, weight, and both waist and hip perimeter were measured in order to estimate BMI and WHR. Participants also provided some personal data by filling up a questionnaire (age, current studies, ethnic group, sexual orientation, SPA). All data remained completely anonymous as required by the ethical committee of the UAM.

2.2. Measurement of morphometric variables

Three full frontal facial color photographs were taken of each participant, at 3 meters of distance and under standardized light conditions with the zoom completely opened in order to avoid distortion of the facial shape. Participants were asked to remove any facial adornment, to pose with a neutral expression and to look directly into the camera. To measure FA from these images, the shape of each face was defined by manually setting 39 predetermined *Landmarks* (LMs). These 39 points can be unambiguously identified in each photo (Fig. 1). The LMs were placed twice by two of the authors in order to detect possible placement errors. LMs were located employing the TPS software (by F.J. Rohlf, available at http://life.bio.sunysb.edu/morph/).

To calculate the FA of each image, we compared the LMs of each face and its mirror image (Klingenberg, Barluenga, & Meyer, 2002). The asymmetry of a bilateral object can be partially attributed to directional asymmetry (differences in the population between average right and left size) and partially to FA (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 image using the Procrustes ANOVA method (Klingenberg & McIntyre, 1998). This decomposition was performed with the Morpho J software (available at http://www.flywings.org.uk/MorphoJ_page.htm). As an individual measure of symmetry we used the Mahalanobis distance, which avoids the effect of correlation between variables (Rodríguez-Salazar, Álvarez-Hernández, & Bravo-Nuñez, 2001). We thus employed a value of FA that is highly independent of the selected LMs. To control for the potential error in the LMs placement, FA computation in Morpho J requires two sets of LMs for each face (each set placed by a different researcher). Error in LM positioning was not significant (Procrustes ANOVA, error SS = 9297×10^{-3}, $df = 13{,}172$, $F = 0.006$, $p = 0.989$).

We estimated facial femininity (FF) by measuring the Procrustes distance between each participant's average face and a masculine reference face. The masculine reference face was built from the images of 100 males belonging to the same age and population as the subjects of study. Participants' average face was obtained as an average of the three captured pictures and their mirror images. The use of symmetrical average faces for comparison with the masculine reference face avoids any undesired effect of individual symmetry in the measure of FF.

We computed the WHR by dividing the waist perimeter by the hip perimeter of each participant and trying to minimize the error caused by clothes. Waist perimeter was measured in the lower girth region of the natural waist, generally right above the umbilicus. Hip perimeter was measured in the wider point of the gluteus. During measurements, participants stood feet together, loosen arms, normal breath, and with their body weight uniformly distributed. In order to estimate BMI, the weight and height of each participant were measured barefoot and without heavy clothing. A female researcher took these measurements from each participant privately and just once.

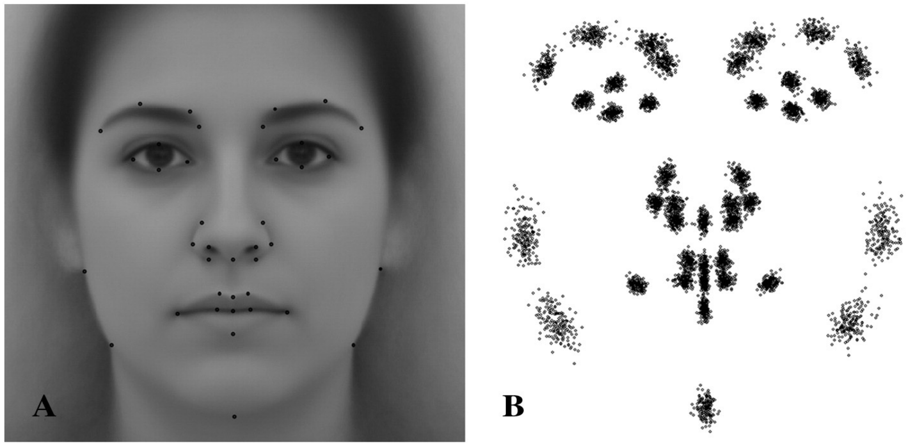

Fig. 1. Example of landmarks placement.

2.3. Self-perceived attractiveness (SPA)

To obtain SPA, each participant reported an estimation of its own attractiveness in a 1 to 7 Likert-like scale, being 1 the lowest score and 7 the maximum, assessed as deviations of the population average. Participants who consider themselves on the average were advised to score themselves with 4.

2.4. Statistical analyses

We tested for the normality of all variables by means of the Shapiro–Wilk test. For those variables not normally distributed, we performed the usual logarithmic transformations. However, both SPA and BMI were resistant to that transformation. To analyze the results, we employed (non-parametric) Spearman rho (σ) for correlations, two-tailed Student t tests for the normally distributed variables and Mann–Whitney test for SPA and BMI. We also employed logistic regressions to analyze the simultaneous effect of several variables on our dichotomous dependent variable ("Cooperate" or "Defect"). We employed SPSS 15.0 (SPSS Inc.) in all the statistical analyses.

3. Results

Table 1 presents the summary statistics of all the variables considered. First, we analyzed how the physiological variables relate to SPA. As expected, SPA correlates negatively with WHR, BMI and FA (Table 2). Although our measure of FF did not correlate with SPA, it negatively correlates with WHR. This is quite remarkable given that both features are strongly influenced by hormone levels during puberty. Age did not correlate with any of the morphometric variables or with SPA, although it must be noted that the age range of our subjects was very narrow. Although WHR and BMI do not show a significant correlation in our data, we followed the literature and controlled for BMI in any further analysis including WHR.

Regarding behavior in the PDG, 31.30% ($n = 55$) of the 176 participants did not cooperate, a fraction consistent with results previously observed in the literature. We also tested for differences in behavior according to the expectation that participants had on the behavior of their counterpart. There was a strong and significant association between the behavior of a participant and the behavior she expected from her counterpart ($\chi^2 = 42.718$, $p < 0.001$). Of the participants who expected their counterpart to cooperate ($n = 123$), 83.74% ($n = 103$) of them cooperated, whereas of the other 53 participants who expected their counterpart to defect, 66.04% ($n = 35$) defected.

Next, we analyzed the relationship between behavior in the PDG (cooperate or defect) and the individual variables considered (Table 1). Results reveal that those subjects who defected displayed a higher WHR and a lower FA than those who cooperated. In addition, and in line with the literature, participants who defected perceived themselves as attractive (high SPA). Age, FF and BMI were not significantly different between participants who cooperated and those who defected.

We performed a set of logistic regressions in order to test simultaneously the effect of these variables on cooperation in the PDG (Table 3). In an initial analysis, we included all the morphometric variables plus age (first row of Table 3). We observed that WHR and FA were statistically significant. Note that the coefficients associated to these variables are negative and positive respectively. In other words, participants with low WHR and high FA tended to cooperate more in the PDG. Next we built a simpler model excluding age and FF given that they were not significant (second row of Table 3). In this model, the variables FA and WHR remained significant. In the following model (third row of Table 3) we included the variable

Table 1
Summary statistics for the entire subject population and according to choice in the PDG.

	Total	Defect ($n = 55$)	Cooperate ($n = 121$)	
Age (yr)	21.42 ± 0.19	21.31 ± 0.31	21.48 ± 0.24	$t_{174} = -0.419$; $p = 0.675$
WHR	0.7198 ± 0.003	0.7300 ± 0.006	0.7152 ± 0.004	$t_{174} = 2.184$; $p = 0.030$
BMI	22.746 ± 0.291	23.294 ± 0.592	22.497 ± 0.326	$U = 3000$; $N_1 = 55$ $N_2 = 121$; $p = 0.296$
FA	4.248 ± 0.038	4.101 ± 0.065	4.3155 ± 0.046	$t_{174} = -2.631$; $p = 0.009$
FF	8.318 ± 0.131 × 10^{-2}	8.238 ± 0.204	8.354 ± 0.166	$t_{174} = -0.412$; $p = 0.681$
SPA	4.313 ± 0.071	4.564 ± 0.132	4.198 ± 0.083	$U = 2666.5$; $N_1 = 55$ $N_2 = 121$; $p = 0.024$

Mean ± SEM. For statistics analysis, the natural logarithm of WHR was employed.

Table 2
Spearman rho correlation between considered variables.

	Ln(WHR)	BMI	FA	FF	Age
SPA	$\sigma_{176} = -0.255$; $p = 0.001$	$\sigma_{176} = -0.190$; $p = 0.011$	$\sigma_{176} = -0.178$; $p = 0.018$	$\sigma_{176} = -0.070$; $p = 0.357$	$\sigma_{176} = 0.084$; $p = 0.265$
Ln(WHR)		$\sigma_{176} = 0.118$; $p = 0.119$	$\sigma_{176} = 0.235$; $p = 0.002$	$\sigma_{176} = -0.217$; $p = 0.004$	$\sigma_{176} = 0.027$; $p = 0.720$
BMI			$\sigma_{176} = 0.106$; $p = 0.162$	$\sigma_{176} = -0.129$; $p = 0.087$	$\sigma_{176} = 0.117$; $p = 0.124$
FA				$\sigma_{176} = -0.046$; $p = 0.546$	$\sigma_{176} = 0.040$; $p = 0.602$
FF					$\sigma_{176} = 0.042$; $p = 0.577$

SPA (which correlates with both WHR and FA) in order to test whether the effect of the morphometric variables on the decision in the PDG depends on how attractive participants find themselves. In that model, all SPA, WHR and FA were significant. High values of SPA and WHR led to defection, whereas high values of FA led to cooperation. Hence, the physiological variables FA and WHR remained significant after including SPA in the logistic regression model. It is remarkable that both a low SPA and a low WHR relate with a tendency to cooperate considering that WHR negatively correlates with attractiveness. Women who see themselves as relatively unattractive cooperate more often, but women with low WHR—an attractive feature—tend to be more cooperative as well.

Finally, we included the variable expected behavior (EB) which has been described to strongly affect participants' decision in the PDG (fourth row of Table 3). The resulting model confirmed this finding: When participants expected their counterpart to cooperate, they were more inclined to cooperate. It is worth noting that the significance of FA and SPA barely changed after the inclusion of EB. This result suggests that the effect of FA and SPA on behavior in the PDG does not operate through EB. However, the inclusion of EB in the model rendered WHR non-significant at the 95% confidence level. This leads us to conclude that the effect of WHR on cooperation operates mostly through its influence on the expectation that subjects hold on the behavior of their counterpart. In fact, there were no significant differences in FA ($t_{174} = -1.104$; $p = 0.312$) nor SPA ($U = 3001.5$; $N_1 = 53$, $N_2 = 122$; $p = 0.374$) between those who expected their counterpart to cooperate and those who expected the opposite. But there were significant differences in WHR between the two groups ($t_{174} = 2.519$; $p = 0.013$): those participants who expected their opponent to cooperate displayed lower ratios (0.715 ± 0.004) than those who expected defection (0.732 ± 0.006).

4. Discussion

The goal of the present study is to analyze the existing relationship between cooperative behavior in women and a set of individual characteristics previously categorized as indicators of phenotypic quality (high fitness), that are also known to be related with female attractiveness.

Of the studied variables, FA and WHR showed an effect on the decision to cooperate. Even more interestingly, and in line with our second hypothesis, their effect seems to be independent of the perception that individuals have of their own attractiveness. This is shown by the fact that FA and WHR maintained their significance after controlling for SPA. This independent effect of the physiological variables and SPA on participants' cooperative behavior in the PDG is undoubtedly the more outstanding result of our study.

Several studies reveal an association between behavior and fitness-related features, particularly symmetry, in humans (Furlow et al., 1998; Manning & Wood, 1998; Pound et al., 2007; Muñoz-Reyes et al., 2012), and more specifically in relation to cooperative or prosocial behavior (Zaatari & Trivers, 2007; Zaatari et al., 2009; Sanchez-Pages & Turiegano, 2010; Holtzman et al., 2011). Nevertheless, to date, no study had explored whether the effect of symmetry (or other physiological variables) works through the self-perception of personal attractiveness. A plausible explanation of the observed effect of FA on cooperative behavior might be that a symmetric person should feel more attractive and, therefore, more entitled to obtain resources autonomously due to the benefits conferred by attractiveness (reviewed in Langlois et al., 2000; Mulford et al., 1998). Our results, however, cast doubts on this explanation. The effect of FA on cooperation is independent of the effect of self-perceived attractiveness given that the effect of phenotypic quality on women's behavior

Table 3
Estimation of the probability of cooperation in the PDG: Logistic models.

Variables in the model	Model				Variable				
	−2LL	Likelihood ratio test	*df*	*p*	Variables	Coef	Wald	*df*	*p*
Ln(WHR), BMI, FA, FF, age	202.882	15.741	5	0.008	Constant	−7.246	5.657	1	0.017
					Ln(WHR)	−8.394	6.008	1	0.014
					BMI	−0.023	0.229	1	0.632
					FA	1.137	9.551	1	0.002
					FF	−0.113	0.001	1	0.991
					Age	0.048	0.467	1	0.494
Ln(WHR), BMI, FA	203.360	15.262	3	0.002	Constant	−6.210	5.951	1	0.015
					Ln(WHR)	−8.284	6.043	1	0.014
					BMI	−0.020	0.176	1	0.675
					FA	1.125	9.475	1	0.002
SPA, Ln(WHR), BMI, FA	191.849	26.773	4	<0.001	Constant	−3.089	1.263	1	0.261
					SPA	−0.715	10.410	1	0.001
					Ln(WHR)	−11.407	9.736	1	0.002
					BMI	−0.056	1.280	1	0.258
					FA	1.085	8.194	1	0.004
EB, SPA, Ln(WHR), BMI, FA	157.962	60.660	5	<0.001	Constant	−2.776	0.754	1	0.385
					EB	2.293	29.791	1	<0.001
					SPA	−0.671	7.572	1	0.006
					Ln(WHR)	−7.649	3.414	1	0.065
					BMI	−0.096	2.865	1	0.091
					FA	1.127	6.315	1	0.012

Expected behaviour of the opponent (EB) was coded as 1 if cooperation was expected and 0 if defection was expected.

remains significant after controlling for self-perception of attractiveness. While remarkable, the independent effect of these two factors is not entirely unexpected. Results observed in studies with males reveal that although men who find themselves attractive tend to cooperate more (Mulford et al., 1998, but see Takahashi et al., 2006), highly symmetrical males cooperate less often (Sanchez-Pages & Turiegano, 2010). This occurs even though attractiveness and symmetry are correlated (reviewed in Johnston, 2006; Kościński, 2007; Little et al., 2011; Thornhill & Gangestad, 1999; Van Dongen & Gangestad, 2011). The basis of this intriguing relationship between FA and behavior, triggered independently of SPA, could be explained by an unconscious self-adjustment of behavior to its expected consequences based on previous experience. It has been described that several animal behaviors adjust to mathematical models based on their cumulative rate of success and failure despite animals do not use such models consciously (Dugatkin & Reeve, 2000). The link between symmetry and a low tendency to cooperate might be due to other individual characteristics which could be associated to FA, such as self-confidence or perceived self-sufficiency (the estimation of the own ability to obtain resources). As a matter of fact, symmetry is correlated with several personality traits, like neuroticism, agreeableness and openness to experience, the last two negatively (Fink, Neave, Manning, & Grammer, 2005; Holtzman et al., 2011). This association might be behind the link we observe between low FA and a weaker tendency to cooperate. Even though we find these questions quite interesting, they are beyond the scope of this study.

Independently of the mechanism behind it, the link we find between FA and cooperative behavior in women is to be expected given the results already found in men. More symmetrical males are less pro-social in the PDG (Sanchez-Pages & Turiegano, 2010) and in the UG (Zaatari & Trivers, 2007), and display fewer pro-social personality traits (Holtzman et al., 2011). Considering their higher phenotypic quality (Thornhill & Gangestad, 2006), low-FA individuals depend less on maintaining a good relationship with their social environment, and, hence, are not prone to sacrifice personal benefits in order to favor others (Zaatari & Trivers, 2007). This explanation (already proposed in Mulford et al., 1998) also fits with the relationship between attractiveness and cooperative behavior described in this paper under the hypothesis that attractiveness is a valid indicator of fitness (Langlois et al., 2000). We do not want to imply that the need for resources was behind participants' behavior in our experiment. We rather suggest that their different capabilities in obtaining resources and their experiences when sharing them might have shaped subjects' daily behavior and made them more or less pro-social independently of their short-term needs.

The independence between the effects of attractive-related physiological features and of SPA is evident in the case of WHR (once controlled for BMI). Even though low WHR scores are associated with attractiveness in women (Singh et al., 2010), we show that low WHR values associate with cooperative behavior. This result is unexpected if one exclusively focuses on the relationship between WHR and attractiveness. It confirms our conclusion that the effect of the attractive-related variables on cooperation does not operate exclusively through their influence on SPA. A likely explanation for this result stems from the positive association we found between a high WHR and the belief in the defection of the opponent. The effect of WHR on EB seems to be the strongest determinant of participants' behavior. Table 3 shows that EB explains individual behavior in the PDG better than any other variable (also in Mulford et al., 1998; Sanchez-Pages & Turiegano, 2010). That is, a high WHR is associated with a tendency to believe that the opponent will not cooperate, and this belief leads to defection. The relationship we observe between high WHR and the belief on the counterpart's defection is to be expected, especially given the associations already described in healthy women between this variable and different distrustful behaviors, such as hostility (Kaye, Folsom, Jacobs, Hughes, & Flack, 1993), low self-perceived social status (Adler, Epel, Castellazzo, & Ickovics, 2000), and social anxiety (Landén et al., 2004). This may suggest that WHR, beyond of its relationship with fitness (Singh, 2002; Jasieńska et al., 2004; Swami & Tovée, 2007), may be indicating "desirability as a social partner" which, in turn, leads to women showing higher values (low desirability) to behave distrustfully in social interactions because of their previous experiences.

The FF of the participants had no significant effect on the propensity to cooperate in the PDG. Although the degree of sexual differentiation of the face has a well-known association with several behaviors, to date, most of the studies on this issue have focused only in men (Apicella et al., 2008; Pound et al., 2009; Stirrat & Perrett, 2010, 2012). These studies employ the ratio between facial width and height (both in men and women) as a measure of masculinization/feminization. This feature was initially described as dimorphic between sexes (Weston, Friday, & Lio, 2007; Carré & McCormick, 2008), but has recently been questioned as such (Kramer, Jones, & Ward, 2012; Lefevre et al., 2012). In any case, in studies which included female participants, this measure of masculinity (or femininity) showed no effect on the propensity to engage in deception or cheating during a negotiation (Haselhuhn & Wong, 2012), nor in dominance (Carré & McCormick, 2008). However, the same measure showed an effect on male behavior under the same experimental conditions. Therefore, our results are consistent with those stating that facial sexual dimorphism may influence behavior in men but not in women. It might be argued that we are not measuring facial femininity properly, but the strong correlation between FF and WHR substantiates the robustness of our femininity measure (see Table 2). This correlation is in line with the relationship previously observed between facial and body attractiveness when measured separately, which confirms that these two variables are valid indicators of fitness (Thornhill & Grammer, 1999). Although both FF and WHR are related to estrogen levels, it is remarkable that they do not have the same effect on cooperative behavior. This fact suggests that considering the stage of development in which the feminizing effect of hormones occurs is important in order to ascertain its effects on a specific behavior. Obviously, additional experiments and physiological studies are needed to deepen our understanding of this result.

Regarding our first hypothesis, of the three variables related to fitness, only FA displayed the expected effect on cooperation, while FF showed no effect and WHR yielded the opposite. However, the effect of SPA fits with our hypothesis if one considers it as a reliable signal of fitness (Langlois et al., 2000). In summary, two variables confirmed our expectations and two did not. It is very interesting that WHR and FA, which are strongly correlated (see Table 2) and linked to fitness, have opposite effects on cooperative behavior. The strong correlation between them and their correlation with SPA confirm them as measures of phenotypic quality, like facial and body attractiveness (Thornhill & Grammer, 1999), facial and voice femininity (Feinberg et al., 2005) and symmetry and sexual dimorphism (Little et al., 2008). The fact that their effects on behavior in the PDG follow different directions suggests that they relate to different kinds of high-fit features (Singh, 2002; Gangestad & Scheyd, 2005; Swami & Tovée, 2007; Van Dongen & Gangestad, 2011). That aside, this contradiction also casts doubts on the idea that the motivation to cooperate is only related to the possibility of obtaining resources from others through reciprocation. This is only one of the possible, and not mutually exclusive, motivations of pro-social behavior (social norms and ethical beliefs are also obvious factors). The mixed results obtained here demonstrate the difficulty of associating any behavior to a single motivation.

Let us remark that the present study is one of the few analyzing pro-social behavior solely in women. In a public good game played only by females, Buser (2012) found that contributions were higher during the menstrual phase of the menstrual cycle and that those participants with a lower 2D/4D ratio contributed less. Nevertheless, there exists a vast literature comparing behavior between men and women in strategic games (reviewed in Balliet, Li, Macfarlan, & Van Vugt, 2011). Results show consistently that men and women act differently depending on the sex of their counterpart in social dilemmas. The lowest levels of cooperation are usually found in setups where only women participate. While in mixed-sex interactions women tend to be more cooperative, men tend to be more cooperative in same-sex interactions (Croson & Gneezy, 2009; Balliet et al., 2011). Under an evolutionary perspective, these differences are usually attributed to the advantage of males when forming coalitions aimed to obtain resources in hunting and war. This difference between men and women could in turn mediate the effect of SPA, WHR and FA when women face mixed-sex instead of single-sex strategic interactions.

To conclude, and beyond the interest of the results obtained and their implications, it is important to remark that this study, as many others, was performed using exclusively a university population within a Western culture. For this reason, before generalizing results to the human species, it would be needed to extend the experiments to a major range of ages and socio-cultural strata, including a wider range of ethnicities. This is particularly necessary when considering WHR given that its association with numerous features relies partially on the ethnicity of the subjects (Kaye et al., 1993). However, we can conjecture what could be the effect of fitness-related variables on cooperative behavior in non-Western industrialized societies. As it has been described (Henrich, Heine, & Norenzayan, 2010), people in many of these societies behave more in line with the predictions of Standard Game Theory. Following this pattern, one should expect less people to cooperate in the PDG in non-industrialized societies. Therefore, under the assumption that cooperative behavior is a tool to receive future help from others, only extremely low-fit individuals (showing remarkable unadaptative values in these variables) should cooperate often in these societies. Of course, this can only be elucidated by performing comparable experiments in other societies.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2013.11.005.

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