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Fluctuating asymmetry and behavior in the ultimatum game in Jamaica☆

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Abstract

The ultimatum game measures cooperative tendencies in humans under experimental conditions. One individual can split money between oneself and another, while the other has the option of accepting or rejecting the offer, with each player receiving the accepted split or nothing if the split is rejected. We studied the association of players' degree of symmetry [fluctuating asymmetry (FA)] with behavior in the ultimatum game. Symmetrical males were expected to be less cooperative and, thus, make lower offers (while being more likely to reject unfair offers). In a population of young adult Jamaicans, who are well-characterized for bodily symmetry, we found that symmetrical males made significantly lower offers than asymmetrical ones ($p < .001$), but found no effect on rejection rates (perhaps due to a very small sample size). No significant association of symmetry and game playing was found in women, but women with a higher body mass index made less generous offers ($p < .05$).

Keywords: Cooperation; Ultimatum game; Fluctuating asymmetry

1. Introduction

The ultimatum game is an experimental tool for measuring cooperation between two individuals (Camerer, 2003; Guth & Schmittberger, 1982). It is simple, grants real monetary rewards, and can be applied crossculturally. The game is often played a single time by a proposer and a responder. The proposer is given an amount of money to split with another—usually anonymous—individual. The proposer proposes a split, and if the responder accepts the offer, the two split the money accordingly. If Player 2 rejects it, neither player receives any money. There is no further interaction between the two individuals. Responders should be happy with whatever they are given as long as it is not zero, and so proposers are expected to make very low offers and keep a large portion of the money. But this is not what research shows. Offer modes and medians are 40–50% of the endowment, offer means are 30–40%, and offers below 20% are usually rejected even when this amounts to the loss of half a day's pay (Camerer, 2003).

In most research studies, the game is played anonymously, which is a useful device for excluding the effects of previous and subsequent interactions. Some researchers assume that behavior displayed in these games evolved to fit one-shot, anonymous interactions, even though these are without any other benefit to inclusive fitness, including later return effects (Fehr & Henrich, 2003; Gintis, Bowles, Boyd, & Ferh, 2003). We shall return to this view later. Our own view is that the ultimatum game measures individuals' implicit cooperative and punitive tendencies, as well as their sense of injustice (hence rejection of low offers)—all selected to function in a world of repeated interactions. The nonexperimental world is a world in which repeat interactions are, with rare exceptions, the norm (Trivers, 2004). An unfair action can, in principle, be immediately countered with physical or verbal attack and—on the somewhat longer term—immediate cessation of any cooperative or altruistic acts. So it would be surprising if the behavior uncovered in one-shot anonymous encounters (in which there is no chance of repeat interactions) were to have evolved to function only in precisely this very rare circumstance.

In either case, it is of interest to know whether individual variables are associated with variations in behavior in such games, and we chose to see whether an important measure of biological quality—an individual's degree of fluctuating

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asymmetry (FA)—had any effect on an individual's behavior in the ultimatum game. That is, what is the effect of a proposer's FA on the size of offers made, and what is the effect of a responders' FA on offer values that are rejected?

FA is a widely used measure of biological quality because it measures an important underlying variable, the degree of developmental stability, which is an organism's ability to reach an adaptive end point despite ontogenetic perturbations (Møller, 2006; Møller & Swaddle, 1997; Polak, 2003). The more symmetrical individuals are (low FA), the better is the rest of their phenotype. Symmetry has strong positive associations with ability to cope with a wide range of developmental stressors, with resistance to parasites, immune strength, ability to escape predators, speed, strength, and mental acuity. Not surprisingly, low FA (symmetry) has a strong positive effect on attractiveness in a wide range of species, including humans. These correlations suggest that individuals may be able to functionally adapt to their own degree of FA. We were curious to know whether such effects might be uncovered by using the ultimatum game on a population of 13- to 20-year-old Jamaicans who were well characterized for the degree of bodily FA in both 1996 and 2002 (Trivers, Manning, Thornhill, Singh, & McGuire, 1999).

We predicted that more symmetrical men would be more likely to make small offers (and, in turn, reject relatively larger ones) because their superior phenotypic quality increases their ability to gain access to resources anyway (without cooperation), eg, via physical aggression. Put another way, we expect more asymmetrical men to benefit relatively more from cooperative interactions and, therefore, to make more generous offers (in order to induce a more cooperative relationship with the other party). This assumes that people act in the ultimatum game as if they were embedded in a world of repeated interactions (Burnham & Johnson, 2006; Hagen & Hammerstein, 2005; Trivers, 2004, 2005).

Symmetrical men (but not women) are more likely to participate in fights, to start them, and to have a high opinion of their ability to win fights (self-reports: Furlow, Gangestad, & Armijo-Prewitt, 1998). Symmetry is also positively associated with aggression in boys (but not girls), using a paper-and-pencil test of aggressive tendencies (Manning & Wood, 1998) or teachers' records of actual aggression in Jamaica (Trivers, unpublished data). This bias makes sense if, as expected, more symmetrical males (low FA) are more likely (via their superior phenotype) to win fights. This has been shown in insects (Thornhill, 1992) and crabs (Sneddon & Swaddle, 1999), but not in birds (Dufour & Weatherhead, 1998; Swaddle & Witter, 1995). Aggression may permit a male to seize resources from another without offering any cooperative benefit in return.

More recently, Takahashi, Yamagishi, Tanida, Kiyonari, and Kanazawa (2006) have shown that in four other economic games, male defectors are judged (from photos) to be physically more attractive than male cooperators, while no such effect is found in females. They propose that physically attractive men are able to turn this attractiveness into reproductive opportunities with low parental investment (requiring little cooperation), while unattractive males will achieve their reproductive success via parental investment, for which cooperation with others is important. Hence, the latter will be more cooperative than the former. Since low-FA individuals (of both sexes) are consistently viewed as more attractive than high-FA individuals (Brown et al., 2005; Gangestad, Thornhill, & Yeo, 1994; Hughes, Harrison, & Gallup, 2002; Thornhill & Gangestad, 1999), their argument gives predictions congruent to our own.

It is unclear whether superior phenotypic quality in females translates into superior access to resources. Certainly there is no evidence that low-FA females are more aggressive. Nor is it obvious that greater physical attractiveness would make cooperation less important in women. Since no predictions were obvious for women, none was made.

2. Method

2.1. Participants

One hundred fifty-three Jamaican young adults (84 males and 69 females; mean age=15.93 years; S.D.=1.67; mode=15; range=13–20) from the Southfield district of St. Elizabeth parish participated in the ultimatum game study in March 2004. Participants were members of the Jamaican Symmetry Project, which is a long-term study of FA in rural Jamaican children (Trivers et al., 1999).

2.2. Morphometric measurement

Morphometric measurements were collected in 1996 and 2002 (wrists, ankles, elbows, third digit, fourth digit, fifth digit, and feet) with vernier calipers (0.01 mm accuracy). Digits were measured from the basal crease on the ventral surface of the hand up to the tip of the digit. To establish repeatability levels, each trait was measured twice and then averaged (Trivers et al., 1999). Bilateral trait measurements were found to be reliable indicators of between-subject differences and to reflect true FA rather than biologically significant directional asymmetry. Relative composite FA was calculated by subtracting the length of the right side of the trait from the left (L–R) corrected for trait size (Palmer & Strobeck, 1986), we summed the absolute values across all traits. FA in 1996 strongly predicts FA in 2002 ($p<.0001$; $r^2=.16$).

There were 112 children missing at Time 2 of the current study (39%). Ignoring missing values can yield biased estimates and inferences (Engels & Diehr, 2003; Jones, 1996; Laird, 1988). Missing values for 2002 were replaced by the average of two missing value replacement methodologies: Last Observation Carried Forward (LOCF) and Expectation Maximization (EM). These methods are accepted for missing value replacement in longitudinal studies

when data are missing randomly (EM preferred; Enders, 2001) or nonrandomly (LOCF preferred; Engels & Diehr, 2003). It appears that data in the Jamaican Symmetry Project are missing at random. Specifically no variable was associated with "missingness" at Time 2. Importantly, FA in 1996 was not related to whether an individual had missing FA data in 2002 ($r=-.04$, $p=.50$). Since we cannot rule out nonrandom missing values due to unmeasured factors, both EM and LOCF methods were used in the current study. After missing values had been replaced, the sum for all trait averages was calculated to yield a composite FA measure between the two time periods.

Height and weight measurements were used to calculate body mass index (BMI) and then averaged across 1996 and 2002 for inclusion as a covariate in the models as body size correlated with FA (Manning, 1995; Trivers et al., 1999). BMI was square root transformed due to a slight positive skew in distribution.

Friendliness was measured in 2000 by collecting peer ratings of friendliness. All subjects rated photographs of their peers for degree of "friendliness" on a Likert scale ranging from 1 (*very unfriendly*) to 5 (*very friendly*). Friendliness was included in this study to determine whether individual differences in this variable are positively related to ultimatum game offers. In addition, we wanted to assess the independent association between FA and offers when sociability was held constant.

2.3. The ultimatum game

Each participant played two ultimatum games, one as a proposer and another as a responder, with approximately half-an-hour delay between the two games, during which participants were engaged in other research. The games were played anonymously, and the players were matched randomly. Subjects were told that they could be matched with any of their peers, whether male or female. The players were asked to split 1000 Jamaican dollars (US$16), equivalent to about 2 days of wages at the low end of the scale. Game instructions assured subjects that they would be collecting their share in real money at the end of the games, as indeed they did.

2.4. Data analyses

Data were analyzed using SPSS version 13. The primary hypothesis was tested using simultaneous multiple regression in which offers in the ultimatum game were regressed on background variables (i.e., age, sex, mean BMI over the 6-year period, and friendliness scores) and composite relative FA. We used this analytic method to test whether FA correlated with ultimatum game offers independent of background variables included in the model. To test whether the effects of FA were equivalent across the sexes, we added a Sex by FA interaction term to the model. The interaction term was formed so that sex was multiplied by the FA of the player (Aiken & West, 1991; Jaccard & Turrisi, 2003).

3. Results

3.1. Descriptive statistics

In this sample, the mean offer was 341.91 (out of 1000) Jamaican dollars (S.D.=168.62). Due to a negative skew in offers, reflected data were square root transformed and then reflected back to meet the assumption of normality. The modal offer was a 50:50 split ($n=49$). Out of the 153 games played, there were 15 rejections. Offers rejected ranged from 0 to 300 Jamaican dollars. Friendliness differed between the sexes, whereby females were friendlier than males [$t(108)=4.62$, $p<.001$]. Due to this baseline sex difference, friendliness was included as a covariate. No other sex differences were found among study variables.

3.2. FA and ultimatum game offers

The squared multiple correlation for the entire model was 0.31, which was statistically significant [$F(7,77)=4.40$, $p<.01$; Table 1]. The standardized regression coefficient for male FA (0.59) was the association between male FA and offers. FA had a significant positive effect on the size of

Table 1
Raw standardized coefficients, t values, and ∂r^2 values from standard regression in which an ultimatum game offer was regressed on age, BMI, FA of the player, sex interaction terms for FA, and BMI of the player for male-versus-female main effect models

	Ultimatum game offer (female offer model)					Ultimatum game offer (male offer model)				
	B	S.E. *B*	*b*	*t*	∂r^2	*B*	S.E. *B*	*b*	*t*	∂r^2
Age	0.09	0.07	−0.26	1.22	.02	–	–	–	–	–
Sex	−1.77	1.11	−1.35	−1.60	.04	–	–	–	–	–
BMI	−0.06	0.03	−0.26	−2.12*	.06	−0.02	0.04	−0.09	−0.49	.00
BMI×Sex	0.04	0.05	0.55	0.78	.01	–	–	–	–	–
FA	0.69	3.14	0.04	0.22	.00	9.31	1.95	0.59	4.76**	.25
FA×Sex	8.62	3.66	1.03	2.35*	.07	–	–	–	–	–
Friendliness	0.11	0.11	0.12	1.04	.02	–	–	–	–	–
Constant	2.70	1.02	–	2.65*	–	–	–	–	–	–

"Female offer model" sex was dummy coded such that 0=*female* and 1=*male*.
"Male offer model" sex was dummy coded such that 0=*male* and 1=*female*.
Both models: $R^2=.31$, $p<.001$, $F(7,77)-4.40$.
* $p<.05$.
** $p<.01$.

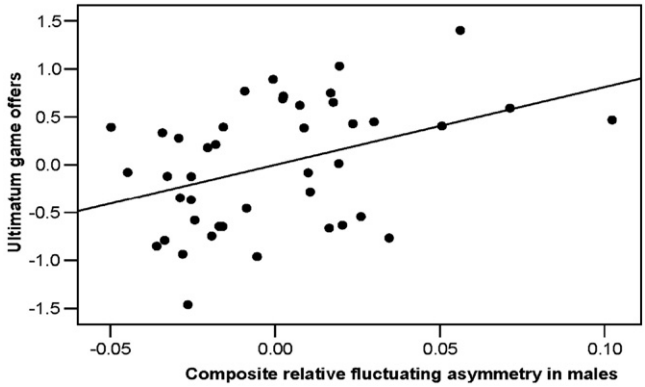

Fig. 1. Male FA and ultimatum game offers. Partial regression plot (age, body size, and friendliness entered as covariates) depicting a positive relationship between a male player's composite relative FA and higher offers in the ultimatum game. Residual ultimatum game offer=2.70+9.31×residual male FA.

offer in males (t=4.76, p<.001). The squared semipartial positive correlation between FA and offers was 0.25, indicating that changes in male FA accounted for 25% of the variance in ultimatum game offers (Fig. 1).

An unexpected association was uncovered in young women. Female BMI negatively correlated with ultimatum game offers (standardized regression coefficient=−0.26, t=−2.12, p<.05), accounting for 6% of offers in the ultimatum game (Table 1). However, male BMI was not related to offers (semipartial r^2=.00, p=.59). In other words, women who were larger for their height made lower offers. Neither female FA nor any other variable was related to offers (all ts <1.61; all ps >.07) (Table 1).

3.3. FA and ultimatum rejections

Very few individuals rejected offers (n=15; i.e., <10%) and so a parametric statistical model cannot be conducted to test whether FA correlated with the amount rejected. We ran Spearman rank correlations, but FA was not significantly related to the amount rejected (Spearman r=−.07, p>.05).

4. Discussion

It has been argued that variations in economic experimental behavior within and across groups cannot be explained in terms of individual variables (Henrich et al., 2005), but rather they should be explained in terms of cultural and economic institutions and local notions of fairness (Henrich et al., 2001, 2005). We join previous research in showing that individual characteristics can bias behavior in economic games. Among traits that had effects on behavior in the ultimatum game were age (Hoffmann Tee, 2006; Murnighan & Saxon, 1998), race (Eckel & Grossman, 2002), 2:4 digit ratio (Van den Bergh & Dewitte, 2006), and testosterone levels (Burnham & Johnson, 2006). While previous work found no effect on offers of (self-evaluated) attractiveness (Solnick & Schweitzer, 1999), male attractiveness (as evaluated by others) has recently been shown to be (negatively) associated with cooperative tendencies in four other economic games (Takahashi et al., 2006).

Our results are the first to find a significant difference between the sexes in the ultimatum game, not as independent variables themselves but in their interaction with an individual's degree of FA. Previous studies failed to show a difference between the sexes on average offer values in the ultimatum game (Eckel & Grossman, 2002; Solnick, 2001). As we predicted, males with low FA make lower offers than males with high FA, but no association was observed in females.

Males appear to adopt different strategies depending on their phenotypic quality. Given their superior ability in obtaining resources, especially in situations involving aggression, low-FA males do not have to be, nor appear to be, as cooperative as higher-FA males. Alternatively, as Takahashi et al. (2006) suggest, being less attractive, high-FA males may be oriented toward long-term relationships with high paternal investment, which benefit preferentially from cooperative relationships with both sexes.

The two sexes appear to develop different strategies in response to an important biological trait. We suggest that the strategy shift revealed in a one-trial ultimatum game is the result of an underlying long-term strategy. Because a relatively generous offer may be the first in a series of reciprocal cooperative exchanges, those more likely to benefit from such exchanges act more generously on the first move.

An alternate explanation would posit that what we are observing is a tendency towards "strong reciprocity" varying with FA, where the latter is an entity imagined to be favored by group selection to function precisely in anonymous single-shot encounters with no reverberating effects (Gintis et al., 2003). Perhaps one can argue that it is better for the group if low-FA individuals have their natural superiority in expected reproductive success augmented by relatively unfair exchanges in their own favor, but then why is this effect seen only in males, not females? In addition, as Burnham and Johnson (2006) point out, all failures to cooperate in the ultimatum game are disadvantageous to the group (since no one gains any resources), so it remains obscure how one would interpret behavior in this game on the assumption that it evolved to fit anonymous, one-shot encounters.

It would be interesting to run ultimatum games in which the sex of the responder (or of the proposer) is revealed to the other. Do high-FA males still make more generous offers when sex and the FA of their partner are revealed? Likewise, it would be interesting to see how FA affects behavior in other economic games, such as the public goods game. Experiments along these lines are now underway in Lebanon and Jamaica. Finally, it would be useful to have simultaneous measures of physical attractiveness, aggression, and FA on the same sample in the

ultimatum game so as to differentiate alternative hypotheses for the effects observed.

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References

Aiken, L. S., & West, S. G. (1991). *Multiple regression: Testing and interpreting interactions*. Thousand Oaks: Sage Publications.

Brown, W. M., Cronk, L., Grochow, K., Jacobson, A., Popovic, C. K., & Trivers, Z. (2005). Dance reveals symmetry especially in young men. *Nature*, *438,* 1148–1150.

Burnham, T. C., & Johnson, D. D. P. (2006). The biological and evolutionary logic of human cooperation. *Analyse and Kritik*, *27,* 113–135.

Camerer, C. F. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton: Princeton Univ. Press.

Dufour, K. W., & Weatherhead, P. G. (1998). Bilateral symmetry and social dominance in captive male red-winged blackbirds. *Behavioral Ecology and Sociobiology*, *42,* 71–76.

Eckel, C. C., & Grossman, P. J. (2002). Sex differences and statistical stereotyping in attitudes toward financial risk. *Evolution and Human Behavior*, *23,* 281–295.

Enders, C. K. (2001). A primer on maximum likelihood algorithms available for use with missing data. *Structural Equation Modeling*, *8,* 128–141.

Engels, J. M., & Diehr, P. (2003). Imputation of missing longitudinal data: A comparison of methods. *Journal of Clinical Epidemiology*, *56,* 968–976.

Fehr, E., & Henrich, J. (2003). Is strong reciprocity a maladaption? On the evolutionary foundations of human altruism. In P. Hammerstein (Ed.), *Genetic and cultural evolution of cooperation* (pp. 55–82). Cambridge, MA: MIT Press.

Furlow, B. F., Gangestad, S. W., & Armijo-Prewitt, T. (1998). Fluctuating asymmetry and human violence. *Proceedings of the Royal Society of London B*, *265,* 1–6.

Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, *15,* 73–85.

Gintis, H., Bowles, S., Boyd, R., & Fehr, E. (2003). Explaining altruistic behavior in humans. *Evolution and Human Behavior*, *24,* 153–172.

Guth, W., & Schmittberger, R. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior and Organization*, *3,* 367–388.

Hagen, E. H., & Hammerstein, P. (2005). Game theory and human evolution: A critique of some recent interpretations of experimental games. *Theoretical Population Biology*, *69,* 339–348.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., & McElreath, R. (2001). In search of *Homo economicus*: Behavioral experiments in 15 small-scale societies. *American Economic Review*, *91,* 73–78.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., Alvard, A., Barr, A., Ensminger, J., Henrich, N. S., Hill, K., Gil-White, F., Gurven, M., Marlowe, F. W., Patton, J. Q., & Tracer, D. (2005). "Economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*, *28,* 795.

Hoffmann, R., & Tee, J. -Y. (2006). Adolescent–adult interactions and culture in the ultimatum game. *Journal of Economic Psychology*, *27,* 98–116.

Hughes, S. M., Harrison, M. A., & Gallup, G. G. (2002). The sound of symmetry: Voice as a marker of developmental instability. *Evolution and Human Behavior*, *23,* 173–180.

Jaccard, J., & Turrisi, R. (2003). *Interaction effects in multiple regression*. (2nd ed.). Thousand Oaks: Sage Publications.

Jones, M. P. (1996). Indicator and stratification methods for missing explanatory variables in multiple linear regression. *Journal of the American Statistical Association*, *91,* 222–230.

Laird, N. M. (1988). Missing data in longitudinal studies. *Statistics in Medicine*, *7,* 305–315.

Manning, J. T. (1995). Fluctuating asymmetry and body-weight in men and women—Implications for sexual selection. *Ethology and Sociobiology*, *16,* 145–153.

Manning, J. T., & Wood, D. (1998). Fluctuating asymmetry and aggression in boys. *Human Nature*, *9,* 53–65.

Møller, A. P. (2006). A review of developmental instability, parasitism and disease. *Infection, Genetics and Evolution*, *6,* 133–140.

Møller, A. P., & Swaddle, J. P. (1997). *Developmental stability and evolution*. Oxford: Oxford University Press.

Murnighan, J. K., & Saxon, M. S. (1998). Ultimatum bargaining by children and adults. *Journal of Economic Psychology*, *19,* 415–445.

Palmer, A. R., & Strobeck, C. (1986). Fluctuating asymmetry: Measurement, analysis, patterns. *Annual Review of Ecology and Systematics*, *17,* 391–421.

Polak M. (Ed.). *Developmental instability: Causes and consequences*. New York: Oxford University Press; 2003.

Sneddon, L. U., & Swaddle, J. P. (1999). Asymmetry and fighting performance in the shore crab *Carsinus maenas*. *Animal Behaviour*, *58,* 431–435.

Solnick, S. J. (2001). Gender differences in the ultimatum game. *Economic Inquiry*, *39,* 189–200.

Solnick, S. J., & Schweitzer, M. (1999). The influence of physical attractiveness and gender on ultimatum game decisions. *Organizational Behavior and Human Decision Processes*, *79,* 199–215.

Swaddle, J. P., & Witter, M. S. (1995). Chest plumage, dominance and fluctuating asymmetry in female starlings. *Proceedings of the Royal Society of London B*, *260,* 219–223.

Takahashi, C. T., Yamagishi, S. T., Tanida, S., Kiyonari, T., & Kanazawa, S. (2006). Attractiveness and cooperation in social exchange. *Evolutionary Psychology*, *4,* 300–314.

Thornhill, R. (1992). Fluctuating asymmetry, interspecific aggression and male mating tactics in two species of Japanese scorpionflies. *Behavioral Ecology and Sociobiology*, *30,* 357–363.

Thornhill, R., & Gangestad, S. (1999). The scent of symmetry: A human sex pheromone that signals fitness? *Evolution and Human Behavior*, *20,* 175–201.

Trivers, R. (2004). Mutual benefits at all levels of life. *Science*, *304,* 964–965.

Trivers, R. (2005). Reciprocal altruism: 30 years later. In C. P. van Schaik, P. M. Kappeler (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 67–83). Berlin: Springer-Verlag.

Trivers, R., Manning, J. T., Thornhill, R., Singh, D., & McGuire, D. (1999). Jamaican Symmetry Project: Long-term study of fluctuating asymmetry in rural Jamaican children. *Human Biology*, *71,* 417–430.

Van den Bergh, B., & Dewitte, S. (2006). Digit ratio (2D:4D) moderates the impact of sexual cues on men's decisions in the ultimatum game. *Proceedings of the Royal Society of London B*, *273,* 2091–2095.