INDIVIDUAL BIOLOGICAL TRAITS AND BEHAVIOR IN ECONOMIC GAMES IN TWO POPULATIONS: LEBANON AND JAMAICA

by

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ABSTRACT OF THE DISSERTATION

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Individuals are expected to adopt different cooperative strategies depending on their ability to obtain resources and this is likely to have an effect on cooperative interactions. Some traits of the interacting party could also affect an individual's willingness to b initiate a series of benefit exchanges. Economic games have been a successful experimental tool in measuring cooperative behavior in interactions involving two or more people. The ultimatum game measures cooperative behavior in an interaction between two individuals. One individual can split money between him or herself and another, while the other has the option of accepting or rejecting the offer. Cross-cultural research showed variation in offer size and rejection rates.

Another game used in anthropological research is the public goods game. Here, a group of three or more are allocated an amount of money, from which they can make a

contribution to their group's account. Money in the public account is doubled and divided over all group members. This is followed by a punishment option, where subject could pay to punish another group member. Research using both games is reviewed in chapter two.

This research investigates variations within individuals in two societies, Lebanon and Jamaica, by looking at some biological traits, facial and bodily symmetry, second-to-fourth digit ratio, waist-to-hip ratio and the degree of relatedness shared between the interacting individuals, among other individual traits.

Subjects increase offers when playing with an anonymous close relative, rather than a more distant relative or a member of their community (chapter three). Males with higher bodily asymmetry make higher offers (chapter four). Males with higher digit ratio made higher contributions to a public account (chapter five). Furthermore, females with low digit ratio are more likely to punish while those with high digit ratio tend to invest more in their punishment (chapter five). Younger and more symmetrical females make higher offers (chapter six). Finally, responding to partner's degree of facial symmetry, subjects either adopt an empathetic approach and offer more to an asymmetrical opposite-sexed partner, or express their attraction towards the more symmetrical partner and make a higher offer (chapter seven).

Acknowledgement and dedication

I would like to dedicate my dissertation to my brother, Khaldoun, a man with endless love and support.
I would like to especially thank my adviser Lee Cronk for time, efforts and support so generously given on so many levels over many years. Warmest thanks and appreciation to Robert Trivers for welcoming me to the Jamaican Symmetry Project which made much of this research possible and for encouragement and support throughout. Sincerest thanks and gratitude to Brian Palestis for statistical analysis and consultation and also to David Feinberg (and Luca Morino) for help with statistical analysis. Many thanks to Ryne Palombit and Dominic Johnson for serving on my committee and for helpful comments.

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Chapter one: Introduction: Cooperative and punitive behavior

In an innovative paper, Brosnan and de Waal (2003) show that the brown capuchin monkey (*Cebus paella)* appears to have a "sense of fairness". Monkeys were first paired and trained to perform an exchange task. When given a token, a monkey is supposed to give it back to the experimenter in order to receive a reward, in the form of either a cucumber or a grape. Partners who made the exchange either received the same reward (a cucumber), or a better reward (a grape), for the same work or, in some cases, for performing no work at all. If monkeys witness a conspecific receiving a grape, a more attractive reward than a cucumber, for equal effort, monkeys gradually refuse to perform their task for a cucumber. This negative reaction is even more amplified when a conspecific receives a reward for performing no effort at all. In some funny situations, the monkey even throws the cucumber back in the experimenter's face. This behavior could mean that monkeys have some sense of fairness and they expect equal labor to result in equal reward.

Notions of fairness obviously dominate human interactions with relatives and with non-relatives. They could entice people to act fairly, to respond positively to acts done to them they perceive as fair and to respond negatively to acts they perceive as unfair. Because of variation in ecology and cultural practices, notions of fairness are expected to vary across groups. But what about within-group variations? Do individual traits correlate with certain cooperative or punitive patterns? What could these traits be? What about strategy shifts? Do individuals change their cooperative strategies according to whom

they are interacting with, e.g. relative versus non-relative, attractive versus unattractive or perhaps by context? This project sets out to address these questions among others.

Altruistic behavior and cooperation

My research uses insights from two disciplines – theory from evolutionary theory and methodology from behavioral economics -to investigate altruistic behavior. Altruistic behavior is one that benefits another organism while being detrimental to the organism performing the behavior, in that it inflicts some costs on the organism and its reproductive success (Trivers 1971). So why would an individual diminish its own resources and increase them for another? This puzzle is partly solved with Hamilton's theory of kin selection, which explains altruistic behavior for related kin. Individuals contribute genetically to future generations both directly, by personally reproducing, and indirectly, by helping their relatives to reproduce (Hamilton 1964). Natural selection is likely to favor traits that lead individuals to help out their relatives as a factor of the degree of relatedness they share. Reciprocal altruism is another system of cooperation partly explaining this puzzle for unrelated individuals. It is the trading of altruistic acts between two organisms in which the benefit is larger than the cost so that over time both enjoy a net benefit (Trivers 1971). Finally, indirect reciprocity also helped explain altruistic behavior between non-kin. Selection might favor individuals that behave altruistically towards others if there is a third party watching who might be more likely to cooperate with one as a result back (Alexander 1987; Nowak & Sigmund 1998a, b).

While using evolutionary theory to explain cooperation, I borrow methods from experimental and behavioral economics. Behavioral economics studies cooperative behavior by putting two or more individuals in simple experimental situations where they can cooperate, defect (refrain from cooperating) and/or punish others, all with precise monetary consequences. Two major studies popular in this line of research are the ultimatum game (UG) and the public goods game (PGG) (Camerer 2003a, b).

In the ultimatum game, two people split an amount of money. One person makes an offer from the allocated amount to the other. If the other person agrees, the money is split accordingly. If not, nobody received any money. As for the public goods game, subjects make contributions to a common account from which a return benefit could be obtained. Sometimes, this is followed by a punishment stage, where subjects would pay a cost in order to punish non-contributors. A thorough review and discussion of these games will follow in the next chapter.

Anthropological research using behavioral economics has been growing to study western and non-western societies. Many researchers including both economists and anthropologists argue that variations in cooperative behavior within and across groups cannot be explained in terms of variables about the individuals. They believe variations can only be explained in terms of cultural and economic institutions and local or group notions of fairness (Henrich et al. 2005). Some advocates of this approach have recently formulated a group-selection theory arguing that humans evolved to act altruistically – not just *apparently* altruistically –with no long-term return benefit to their acts, and in

this view such behavior cannot be explained by kin selection, reciprocal altruism or indirect reciprocity (Gintis et al. 2003). They also argue that this predisposition so strong enough to make these acts quite frequent in everyday interactions. Strong reciprocity comes in the form of (1) costly cooperation or rewarding group members for abiding by group norms, and (2) costly punishment of non-cooperators or norm-violators (Fehr & Fischbacher 2004a, 2004b). Proponents of strong reciprocity rely on results from economic games and models to support their theory, and they believe that because games are one-shot anonymous situations lacking any return benefit, traits about the individual are not an important in determining the outcome of games. By contrast, this dissertation tests the alternative hypothesis that individuals vary in their cooperative behavior and that some of the variation could be due to biological traits of individuals, e.g. fluctuating asymmetry. These experiments appear to trigger an internal mechanism selected to operate in a world of repeated interaction. These one-shot anonymous games with no long term effects do not make up the majority of our interactions. And these games can be very helpful in measuring our general sense of fairness and cooperative tendancies.

My work investigates the human tendencies to initiate cooperation, reciprocation and punishment – experimentally measured by economic games – as they vary with an individual's biological traits and with traits of the interacting party. I explore the evolutionary significance of human patterns of helping, and of the different relevant individual traits that would have been favored by natural selection. Particularly, I look at subjects' own biological traits, their partner's biological traits, as well as at interactions between these traitis of both parties in two populations Lebanon and Jamaica. An

individual is hypothesized to modify its cooperative behavior according to some major biological traits about itself sex, fluctuating asymmetry (FA), waist-to-hip-ratio (WHR), and second-to-fourth digit ratio (2D:4D) and according to some qualities of the person they are interacting with, sex, facial symmetry, attractiveness and degree of relatedness. This is best tested with experimental economic games in that they provide an opportunity to measure cooperative and punitive behavior.

Why fluctuating asymmetry?

Fluctuating asymmetry (FA) is a good measure of phenotypic and genotypic quality as it measures an important underlying variable – the degree of developmental stability – which is an organism's ability to reach an adaptive end point despite environmental perturbations (Van Valen 1962; Møller 2006). The more symmetrical an individual is (low FA), the higher the quality of its phenotype overall. Symmetrical individuals have been shown to be better at resisting parasites, at coping with developmental stress, and at physical and mental abilities (Møller & Swaddle 1997; Polak 2004; Møller 2006). They have also been shown to be more aggressive (males), and attractive, which biases mate choice in both sexes. These correlations will be reviewed in more detail in chapter four. The question here is whether such biological characteristics could influence an individual's cooperative and punitive behavior. This leads to precise and testable predictions: would an individual adapt its cooperative strategies based on its phenotypic quality, measured in terms of FA? Would the sexes adopt different strategies according to their degree of FA? If physically stronger males in terms help out weaker in an act of

need-based altruism, then males with high FA would make lower offers in an ultimatum games. If weaker give to stronger to curry favor, high FA males are likely to make higher offers. When interacting with a female, her degree of FA in interaction with the male's FA could bias both individuals' cooperative behavior. High FA males might be intimidated by a low FA female and decide they are better off not squandering on resources. When interacting with low FA females rather than high FA females, low FA males might decide to be more cooperative. All these predictions will be tackled throughout different sections of this dissertation.

Why waist-to-hip ratio (WHR)?

Waist-to-hip ratio (WHR) is a major biological trait for human females. Lower WHR is associated with better survival, higher fecundity and higher attractiveness (Singh 1993a, 1993b, 1995). It is likely to have an effect on a female's cooperative behavior, being a measure of her reproductive value as perceived by males. To this end, I tested whether, for example, high WHR females would be less cooperative, or less likely to punish in a generalized context. Perhaps being of lesser reproductive quality, high WHR females do not have access to a lot of resources and so would rather keep resources to self rather than invest in an act beneficial to another, or would rather not squander resources on punishment. Would low WHR females exhibit the reverse behavior?

Why Second-to-fourth digit ratio?

Second-to-fourth digit ratio (2D:4D) reflects prenatal exposure to testosterone (Manning 2002). Digit ratios in males are negatively correlated with perceived masculinity, dominance, physical ability and aggression. Thus, digit ratio is expected to influence cooperative behavior. Males with low ratios are expected to be less cooperative than those with high ratios, and females to show a similar effect. Since individuals with lower ratios have better physical abilities, they are expected to be better in obtaining resources and so would benefit less from a system of benefit exchange than those with lesser physical abilities (i.e. high digit ratio). Furthermore, individuals with lower digit ratio, by being more aggressive, are expected to be more prone to punishment when cheated out of an interaction.

What about degree of relatedness?

If individuals are selected to help relatives because of returned inclusive fitness benefits, then such preferences are likely to vary according to degree of relatedness. My research tests the effect of the degree of relatedness on cooperative behavior in segmentary descent groups in Lebanon.

Why Lebanon and Jamaica?

Lebanon is a natural experimental setting to study the effect of relatedness on cooperative behavior. This is because some areas have a clan system, a group of paternally individuals that can go up to 25,000 members. Clan members interact regularly and degrees of relatedness are common knowledge for all. Jamaica is a good place to study

the effects of FA on cooperative behavior. Youngsters in Jamaica are shown to be more symmetrical than their age peers in the UK (Trivers et al. 1999).

Dissertation in brief

This dissertation is divided into eight chapters. In the second chapter, I will review the results of three major types of economic games: the ultimatum game, the dictator game and the public goods game. The third chapter describes my field research exploring possible effects of degrees of relatedness on cooperation using both ethnographic information and economic experimentation in the Beqaa' Valley of Lebanon, home to partilineal clan systems and segmentary descent groups. In the fourth chapter, fieldwork shifts to Jamaica and research questions shift to a major biological variable, fluctuating asymmetry and its possible effects on cooperative and punitive behavior between two individuals. Chapter five expands biological traits to include 2D:4D on the same Jamaican population, but this time to study cooperation and punishment in groups of four rather than of two. In chapter six, I explore correlations between traits like WHR, 2D:4D and facial symmetry on offer values and rejection rates on a group of school children in Lebanon. Chapter seven combines both field sites, Lebanon and Jamaica, where Jamaican subjects were set up to play with Lebanese subjects (photographs) to test any effects of partner's attractiveness and degree of symmetry on cooperative and punitive behavior. The last chapter sums up and explores these results in a comprehensive way.

My dissertation explores whether biological traits like FA or 2D:4D have any effects on cooperative and punitive behavior in economic games. It tests for within group variation and explores whether and how subjects adjust cooperative tendencies based on their individual traits (e.g. FA) and/or that of the individual they are interacting with.

Chapter two: Games and cooperation

I. Introduction: Game theory and animal behavior

Game theory was developed and used mostly by economists up until 1973, when John Maynard Smith used it to explain when and why some animals (e.g. fish) fight with each other. His idea was to treat behaviors as strategies that have been evolved just like physical traits evolve. In this sense, a well-adapted population will adopt the "best" strategy as any mutants following a different strategy will have lower reproductive success and die out. This "best" or optimal strategy is called evolutionary stable strategy or ESS.

Evolutionary biologists have now very much adopted game theory to formulate and test hypotheses about animal behavior, e.g. aggression, hunting, foraging, or cooperative behavior. It is mostly used to study situations in which the best strategy of one player depends on the actions of another. Figuring out what potential payoff an organism receives from a particular interaction is essential to predicting animal behavior. For non-human animals, the benefit gained from adopting a strategy are often clearly identifiable (at least in theory) as it usually includes something like more food, a higher rank in the social hierarchy, or reduced competition for mates (Pool 1995). Game theoretical models can explain, predict and test cooperative behavior. For naked mole rats (*Heterocephalus glaber)*, only one queen and three breeding males reproduce and the remaining 80 members of the colony, despite the high risk of being eaten by snakes, do all the digging

and clearing of tunnels. Anon-breeding individual still wants to stay alive, and not just because it can continue to serve the queen. When the queen or top males die, the worker may move up the hierarchy and become reproductive. This, therefore, creates a conflict of interests: the queen wants all colony members to work as hard as possible, while her subjects would want to slack off to stay alive and have the chance to reproduce. Using a quantitative game theory model, it was predicted that a worker's best strategy should depend on two factors: relatedness to the queen and likelihood of becoming a reproducing member.

Thus, conflicts of interest occur mostly between the queen and the larger workers or her more distant kin. Experiments confirmed this prediction: the same workers the queen has to shove to get back to work are the ones to become lazy with her removal (Pool 1995). Whether game theory explains more variation in behavior of non-human animals then humans is controversial. The application of game theory to animal behavior could always be made more complex by factors like large group size and multiple-interaction reciprocity among others.

Classical economists have addressed decision-making and used game theory to model economic human behavior. This interest flourished with the introduction of behavioral and experimental economics. Economists used to think that people behave according to what seems rational in a situation. Formalized in precise mathematical analysis, classic economic theory predicts subjects will act to maximize monetary rewards in a class of games (that being the rational thing to do).

Game theoretic predictions of economic behavior are based on two models that are not mutually exclusive (Gintis 2000a) (Henrich et al. 2005). The exogenous model argues that an individual's preferences are determined by group membership and communal notions of fairness. The endogenous model, however, posits that an individual's preferences come from his/her personal history and the nature of the current interaction itself.

Behavioral economics contradicted classical theory in that it shows that subjects do not always act to maximize profit. Subjects are willing to cut down on their profit to punish unfair acts done to them or even to share some of their profits with other. Behavioral economics is also oriented towards more realistic assumptions about human behavior by making use of advances in neuroscience and psychology (Camerer 2003a). Experiments, mostly economic games, are conducted to estimate the predictive value of models in explaining and anticipating behavior. These games investigate fairness, cooperation, altruism, punishment and selfishness on a more or less proximate level. These experiments are designed to reveal behavioral tendencies. But, certain individual-based biological traits have been shown to affect behavior in economic games. So, it can be predicted that these traits affect cooperative and punitive behavior in natural settings. By investigating these biological traits, an optimal explanation could help explain these behaviors.

Since economic models assume humans to be rational in their economic decision-making, they expect experimental results to be highly similar, i.e. human behavior to be uniform.

However, empirical data suggest that there are many factors affecting economic choice in game playing. Among these factors are individual-level biological traits, some of which have already been shown and others still yet to be. More recently, experimental economic games show that subjects' behavior is influenced by many factors, e.g. their notions of fairness (Page & Nowak 2000), previous and potential future interaction with opponent players (Roth 1995), true or manipulated information about the other player's resources (Camerer & Thaler 1995; Boles et al. 2000; Croson et al. 2003), sex (Solnick 2001; Eckel & Grossman 2001) and attractiveness of the player they are interacting with (Solnick & Schweitzer 1999).

This chapter will review recent research using economic games to study human cooperative behavior with emphasis on the ultimatum game, and public goods game. The ultimatum game and public goods game were both used in my research in both Jamaica and Lebanon. I also review briefly the dictator game because it has interesting and close connections to the ultimatum game. The rest of chapter is divided into four sections. The second, third and fourth sections will review research on the ultimatum game, the dictator game and the public goods game respectively. Finally, the last section briefly discusses some of the neurological and physiological mechanisms involved in game playing.

II. The ultimatum game: An opportunity of cooperation for two

The ultimatum game is frequently used as an experimental tool for studying cooperative and punitive behavior between two individuals. It is simple, grants real monetary

rewards, and can be applied in a variety of contexts. The game fits the model of non-repeated game theory, which is about situations with strangers without a history or a future of interaction. It involves two players who share an amount of money. According to classical economic theory, it is expected that individuals will play the game in order to maximize and pursue self-interest.

Overview

The ultimatum game in its basic form has minimal rules and is typically a one-shot interactioin. A proposer, player one, is given an amount of money (usually $10 with college students). Player one is asked to make an offer from the allocated money to player two, the responder. If player two accepts the offer, both players split the money accordingly. If player two rejects the offer, nobody receive anything. Both players are aware of all the rules of the game and the responder is also informed of the proposer's initial allocation. Rejecting the offer is viewed a costly act of punishment and reflects the responder's dissatisfaction with the offer. The game typically ends with the responder's response and there are no counterproposals, hence the name 'ultimatum'. The two players are fully informed about all the rules of the game. The game is played anonymously to control for situations where previous interaction could affect players' decisions to future repercussions.

i. The self-interest model

According to economists a “rational model” or a “self-interest model” of economic thinking assumes both players behave to maximize profit. Thus, player one is predicted to offer the smallest nonzero offer (i.e. smallest divisible monetary amount) and player two to accept a nonzero offer. Guth et al. (1982) conducted the first ultimatum game study. Subjects played for 10 deutsch-marks. Behavior in the study was not support the claim that people should act to maximize profit. First subjects rejected some offers; 20% of offers were rejected. Second, subjects made offers that were higher than just over zero, In fact, mean value of all offers was 30% of the amount allocated per game and the modal offer was 50%. More than twenty four years of research show that the mean offer in ultimatum games ranges from 40% to 50% (Oosterbeek et al. 2004), and offers less than 20% are likely to be rejected (Page & Nowak 2000; Camerer 2003b). On average 16% of offers are rejected (Oosterbeek et al. 2004). In fact, when responders are told that they would receive money independent of how they respond to offers (‘outside options’), rejection rates increase (~50% in Knez & Camerer 1995). Having already earned some money, responders can turn around and punish proposers for low offers. Furthermore, rejection rates are significantly higher under a tight (10 s) than under a very weak time (100s) constraint (Sutter 2003). Perhaps humans are selected to decline from cooperating under time constraints, i.e. when they do not have enough time to assess the costs and benefits involved. Declining from cooperation in these situations probably is the safest way to reduce cost to self, given the lack of necessary information. If pressured by time, an individual might not be able to assessing the costs of an act and the perceived benefits. So, comparing between investing in an undetermined outcome and declining from investing or bearing the cost altogether, the latter option appears less costly.

Since rejections are more frequent than predicted by classical economic theory, this implies that players disregard the optimal economic model perhaps for other considerations. Punishing proposers who make lower offers is perhaps an act of "moralistic aggression", a mechanism that would protect the individual from disadvantageous situations of reciprocity (Trivers 1971). One explanation is that perhaps individuals have previously established preferences on the basis that interaction with the other player is recurrent (Tullberg 1999). In effect, when the game is repeated, offers move closer to 50-50 split (Ruth 1995). Individuals may assume, in recurrent interaction with the other player, that their game partners are innately prone to cooperative behavior, and seek to establish "lifetime" reputations in this regard (McCabe et al. 1996). Güth et al. (2001) alternatively argue that responders tend to reject low offers because they do not want the proposer to get a large share as if this would give an advantage to a rival or competitor. A third explanation is that economic game playing is primarily predetermined by existing cultural norms, which may vary across cultures (Henrich 2000). I believe that subjects behave in this game similarly to how they would behave in an everyday situation, although the conditions sustaining the game are sometimes far from being similar to real life. In one-shot trials, the element of learning is rarely present in these games and players act almost spontaneously, in an immediate response to the situation at hand. Interestingly enough when student of economics play the game, the element of learning assumed to be present in fact seems to be absent (Carter & Irons 1991; Frank et al. 1993; Tullberg 1999). Students of economics are somehow different from other

college students; they behave more in accordance with a self-interest model, i.e. offer less and accept less (Carter & Irons 1991).

ii. Evolutionary theory and fairness

According to evolutionary game theory, animals behave so as to maximize a utility function: fitness (Page et al. 2000). This would lead individuals to adopt a "fair" strategy. Fair, in this sense, corresponds a system of resources distribution, and this could vary across societies. If players are interested in pursing fairness, it is not for fairness sake (Page et al. 2000). Achieving fairness means that all parties involved gain some benefit at least equal to or more than the costs bestowed on them. When more than one strategy is adopted simultaneously in a society, it would be difficult for responders to figure out which strategy to use in an ultimatum game, especially in an anonymous interaction. In effect, they are likely to make an offer with they themselves count as fair. Thus, they usually make the 50-50 split offer (Page & Nowak 2000). Fairness, in this sense, would be selected for when individuals live within close proximity (Page et al. 2000) and when information about previous interaction is available (Nowak et al. 2000). It would be context specific and not absolute. When players are given some information about player two, e.g. sex or attractiveness. Variables, whether of proposers or responders that could affect the outcome of the game will be reviewed in greater detail later on.

iii. Two common variants and a subvariant

The ultimatum game could be played in two ways: the game method and the strategy method. In the game method – the version described earlier – the proposer makes an actual offer which a responder accepts or rejects. In the strategy method, both players make decisions simultaneously and separately. The responder reports a minimum acceptable offer (MAO), i.e. the minimum he/she would accept from a particular amount, rather than responding on an actual offer. After than, proposers make the offer as usual. While the game method presents responders with an actual offer, the strategy method requires them to make a hypothetical decision. One advantage about the MAO or the strategy method is that it can measure likely reactions regardless of actual offers which might be interesting in the absence of variability in offers made (especially when it comes to very low offers) (Camerer 2003b). It can generate data to study rejections when they are rare in some studies.

Some researchers used a modified version of the ultimatum game in both models. Proposers are given a limited set of options from which they can decide to split the allocated amount of money. For example, they can choose from 50%-50%, 80%-20%, 20% - 80% and 100% - 0% with the former number going to proposers and the latter to responders (Falk et al. 2003). This is thought to be a better experimental design to study rejection rates and variability since offers in both the method and strategy models tend to be quite identical. Another study includes subtle options. For example out of 20 the options are: 17-3, 11-9, 10-10, and 9-11 (Guth et al. 2001).

Multiple vs. one-shot games

There has been some controversy in experimental economics as to whether one-trial experiments are reliable in producing generalizable conclusions. In the ultimatum game, some research showed that a simple second trial could induce slight (usually insignificant) change in the predicted results (Binmore et al. 1985; Knez & Camerer 1995; Slonim & Roth 1998; List & Cherry 2000). With multiple trials, offers are expected to increase and rejections to decrease as offers get closer to 50-50 splits.. However, other studies show no effect for multiple trials (Bolton & Zwick 1995; Roth 1995). Harrison and McCabe (1996) show that providing information about offers and the mean accepted offers of all other subjects in the study lowered accepted offers to almost 15%. In a study of an eight-trial ultimatum game, there were two treatments, one where responders' responses were hidden from proposers (till the end of all trials) and in another open to proposers (after every trial) (Abbink et al. 2004). Overall rejection rates were higher in the open trials, but by the end of the eighth trial rejection rates are the same for both treatments, ~22%.

Sometimes increased experience in a multiple trial game decreases the ability to maintain offers as if subjects "unlearn" their game-playing skills (Binmore et al. 1991). Basically, experience with rejected offers is expected to affect some future behavior (Roth 1995). Still, in order to account for the consequences of the proposer's actions and the fairness of their intentions, a multiple trial game might be needed (Falk et al. 2003). Although repeated games can be useful, preference over one-shot games depends only on the research question sought (Henrich 2001). Henrich lists three main reasons to support the

preference for one-shot games. First, real life includes numerous one-shot games where individuals are required to make one-time decisions without prior encounter. For example, people get married once. Second, in some experiments the results are not affected by multiple trials. Third, repeating the game may introduce new variables since what is measured is then not only what people bring with them to the experiments, but the experiences they have just learned from them. Furthermore, as argued by Henrich, because players bring with them to the experiments the assumption of multiple interaction, whether this is regulated by innate domain-specific mechanisms of reciprocity strategies or socially acquired norms, single trials are likely to yield results similar to repeated games. Experiments investigating how certain biological characteristics affect cooperative behavior (to be reviewed later) can help determine the extent to which such behavior is influenced by pure socially transmitted norms.

One interesting aspect of multiple shot games is that they allow the study of possible deceptive and retributive behavior of players. Self-interested bargainers (proposers) may be motivated to engage in deception to increase benefit to self and thus undermine concerns for cooperation or fairness. This might lead responders to be retributive by repeatedly rejecting the offers proposed to them. In Boles et al. (2000), proposers interact with the same respondent for four successive rounds, where they split $27, $47, $25 and $13 respectively. Responders are given a small “outside option” of $2, $3, $5 and $1 for the four rounds respectively. In some of the trials all subjects know that the money allocated for games ranges from $10 to $50 and outside options from $1 to $8, without having information about the exact amount. In other trials, no such information is

provided. Responders are asked to send proposers any message they wish before the offer is made. This allows responders to make threats, to state the amount of money they would like to be offered, or to reveal information about their outside option. When the money allocated is the largest, proposers exploit responders' lack of knowledge on the amount allocated for the game. Results show that proposers offer significantly less to responders who do not know the amount allocated for that game than they do to responders who do know. Moreover, proposers offer less when they know the responders' outside option than when they do not. Responders who discover that proposers are being deceptive are significantly more likely to reject subsequent offers than those who are deceived and are not aware of it.

Cross-cultural research

The simplicity of the ultimatum game has proven effective in cross-cultural anthropological research. The application of one-shot ultimatum game in cross-cultural research shows some behavioral variability in economic play and departure from the mean offer value of most research studies (40-50%). The first cross-cultural comparative research was conducted by Roth et al. (1991) in USA, Israel, Japan and Yugoslavia. Ten rounds were played, each with a different partner, and by the tenth round, offer values range from 40-50%. In the first round, the offer mode for all countries was 50%, and in the last round, for US and Slovenia 50%, for Japan 40% and 45%, and for Israel 40%. Offers in the US and Slovenia are more similar and higher by 10% than those in Japan

and Israel. In the Israeli sample offers are quite small, and respondents are more willing to accept small offers.

Cross cultural research, and particularly in non-western societies, has been growing more recently (see table 3.1). Here I review some of it. In a study done in a rural Nigerian village, the mean offer for the ultimatum game came out to be 43% (Gowdy et al. 2003). Another study on two sympatric Tanzanian ethnic groups (Sukuma and Pimbwe) reveals that close groups can vary on average; Sukuma's offers are higher than those of Pimbwe. The Sukuma are particularly generous similar to the Lamalera of Indonesia (Alvard 2005).

Gurven (2004) also used the ultimatum game, in addition to other economic games, to study cooperation among the Tsimane, a group of forager-horticulturalists living in the Bolivian Amazon. The mean offer was 37%, which is slightly less than the mean for westernized socities. Offers ranged from 12-77%, and none of the offers were rejected.

More recently, the game was also played among illiterate adults gypsies in Valeecas, Madrid, Spain (Bra˜nas-Garza & Cobo-Reyes 2006). Using the strategy method, 25% of people said they would accept a zero offer, and their most common argument was, "if he really needs it." Interestingly enough, in reality, 97% of the subjects proposed the equal split.

One major study recruited subjects from 15 small-scale societies exhibiting a variety of economic and cultural backgrounds to play the ultimatum game (in addition to the public goods game and the dictator game) (Henrich et al. 2001). Twelve researchers worked in 12 countries on four continents and played the game with 15 small-scale societies. The societies consist of four foraging/horticulture groups (the Hadza of East Africa, the Ache, the Au and Gnau of Papua New Guinea, and the Lamalera of Indonesia), four horticulturalists (Machiguenga (Henrich 2000), Quichua, and Achuar of South America and the Tsimané), four pastoral groups (the Turguud, Kazakhs of Central Asia, the Sangu of East Africa and the Orma), two sedentary, small scale agricultural societies (the Mapuche of South America and Shona of the Niger-Congo) and one foraging and trading group (the Lamalera). The mean ultimatum game offers for the 15 societies range from 26% to 58%, and the mode ranges from 15% to 50%. While the responders from Achuar, Ache and Tsimané accept all offers made, offers among the Au and Gnau are frequently rejected although they are frequently more than half in value. The variability in offer average and acceptance rates, as researchers argue, is due to group-level differences in economic organization and the degree of market integration. The higher the degree of market integration and the higher the payoffs to cooperation, the greater the level of cooperation in experimental games. The rationale for market integration is that the more frequently people experience market transactions, the more they will also experience abstract sharing principles concerning behaviors toward strangers of which the UG is an example. Moreover, the authors believe individual economic and demographic variables do not explain behavior either within or across groups. Authors believe that the nature

and degree of cooperation and punishment in the experiments appear to be consistent with daily economic patterns in these societies.

What is sometimes lacking in such cross-cultural research is an explanation that goes beyond interpreting behavior in the ultimatum game merely in terms of local social norms and the choice of abiding or violating them (i.e. making an offer according what is considered fair or not) (Henrich et al. 2001; Henrich & Boyd 2001). Such an explanation is incomplete. The fact that people play the ultimatum game differently in different societies is hardly surprising. Using market integration explains some aspect of these differences. Other cultural particularities and individual biological traits could build up a much more interesting picture. These traits include among testosterone levels, age and attractiveness, all of which will be reviewed shortly.

Furthermore, supporters of strong reciprocity use results from cross-cultural ultimatum games to argue that one-shot anonymous interactions are frequent in our everyday life (Gintis et al. 2003). In other words people make non-zero offers and reject non-zero offers in the ultimatum game because we have been selected to act in ways that benefit our groups and have no direct bearing to our own self-interest. I believe people make non-zero offers in the ultimatum game not out of altruism or for the benefit of the group, they do so in order to maximize the chance of their offer being accepted, thus generating returned benefit. They do so because it this could be the first costly step in a series of reciprocal exchanges. Because fifty-fifty splits are the most guaranteed, they make up the modal offer in the ultimatum game in strictly double-blind ultimatum games. But, once

you introduce some information about, the responder, for example, a shared degree of relatedness, proposers adjust their offers as I will show in the next chapter. Offer rejections in the UG, I believe, also do not count as acts of altruism or acts that are done to benefit the group. Responders feel betrayed by low offers and thus would want to inflict some cost back or prevent proposers from gaining benefit. Discussion of my research findings will highlight these claims throughout my dissertation.

High versus low stakes games

A classical criticism of the original work by Guth et al. (1982) is that the amount of money played for is relatively small to matter, i.e. to make people care enough to accept or reject. This resulted in a line of research that tested whether players behave differently when playing for a bigger amount of money. Researchers conduct their project nowadays keeping in mind that the amount of money allocated should be sufficient to make both players interested in playing. In other words, it is not usually a random number. Researchers usually double or triple a day's wage for the local population. Raising the stakes in the ultimatum game has shown no effect in one-shot games (Roth et al. 1991; Forsythe et al. 1994; Camerer & Thaler 1995; Hoffman et al. 1996, Slonim & Roth 1998; Carpenter et al. 2005). Hoffman et al. (1996) played the ultimatum game with 50 pairs of subjects for $100. The results were compared to previous results where players played for $10. No significant difference was found between the two in terms of offer value and rejection rates. As for research in a non-western society, in Indonesia, Cameron (1999) raised the stakes to three times the monthly expenditures of the average participants.

Proposer behavior is largely indifferent to stake changes. Responders do exhibit increased willingness to accept a given percentage offer in higher stakes games; however, this can be due to the fact that offers with high stakes got slightly more generous (although this rise in offer size was not significant).

Finally, one study (List & Cherry 2000) found an effect for stake size but only with multiple trial games. Rejection rates neared zero when people got closer to 50-50 splits playing for high stakes whereas they found no effect for high stakes or in single trial games on rejections.

While raising the stakes did not affect proposers' offers, they affected responder's decisions in a study that uses the strategy method (Munier & Zaharia 2002). For responders, the lowest acceptable offers were proportionally lower in the high-stake condition than in the low-stake condition. But, then again, subjects have been shown to change their minds after deciding on a MAO and then playing on a real offer (Armantier 2006). Responders also are less willing to accept an offer when the strategy method is employed (Oosterbeek et al. 2004), which means those playing the low stakes could change their minds and still accept the offer. It is therefore difficult to take results from Munier and Zaharia as conclusive.

Biological characteristics

Here I review research showing that some individual-based biological traits affect behavior in the ultimatum game. Many of the studies will be reviewed again later in separate chapters where they set up the ground to my research.

i. Sex

Sex of players has been shown to influence behavior in an ultimatum game. While males and females make on average similar offers, women reject less often (Rapoport & Sundali 1996; Eckel & Grossman 2001). Solnick (2001) also shows that males and females made similar offers, and both sexes offer more to males than they offer females. Moreover, both sexes as responders choose a higher minimum acceptable offer (MAO) when playing with female proposers (Solnick & Schweitzer 1999). In other words, less is demanded from men. In a non-western context, a study in rural Nigerian village shows no significant difference between offers made by men and women (Gowdy et al. 2003). Thus, while sex of proposer has no effect on offer size, sex of the responder does affect amount offered by proposer.

ii. Attractiveness

The effect of attractiveness on economic and cooperative behavior has also been studied. In a study 70 undergraduate proposers played as proposers and as responders for a strategy ultimatum game. They were then photographed and rated by 20 judges on the basis of attractiveness (Solnick & Schweitzer 1999). The most and the least attractive 6

pictures for males and females were shown to another group of 108 subjects. The 108 subjects also played as proposers and responders by stating their MAO. The study does not reveal significant differences in what attractive people offer or demand. Nevertheless, attractive people are offered more – especially in this case if they were men – and more is demanded of them. Joergensen and Hancock (2001; cited from Hancock & DeBruine 2003) reported an ultimatum game where proposers saw a picture of the responder. Offers were higher to faces rated as attractive, but the effect was stronger for attractive women. However, the effect of attractiveness disappeared in a second round of the game following information about who had refused low offers. More recently, Takahashi et al. (2006) have shown that male defectors are judged (from photos) to be physically more attractive than male cooperators, while no such effect is found in females.

iii. Age

Ultimatum game experiments were conducted with same-age as well as mixed-age groups of Asian (including Malaysian, Indian and Chinese) adolescents and adults (Hoffmann & Tee 2006). Subjects were either adults or adolescents, and they were asked to make two offers, one to a responder of their age group and another to one of the other age group. Compared with adults, adolescents made significantly larger offers to adult responders and were less likely to reject offers from adults. Adults made the same offer whether to an adult or to an adolescent. These results, though, are better explained as an effect of the responder's age. An adolescent made a more generous offer to an adult than

to his peer perhaps because he thought adults were going to be less tolerant about lower offers. When the mean offer was just below 50%, it was above 50% when adolescents offered adults.

iv. 2D:4D and testosterone

Males with lower 2:4 digit ratio, a trait related to prenatal exposure to androgens, state higher minimum accepted offer (MAO) (Van den Bergh & Dewitte 2006). This is consistent with the finding that males with lower finger ratios have a preference for the fair split (Millet & Dewitte 2006). This result is also consistent with the finding that males with higher testosterone levels are more likely to reject higher offers in a $40 ultimatum game (Burnham, manuscript). In Burnham's study, offers were constrained to either $5 or $25. Subjects who rejected lower offers had 52% higher testosterone levels, assayed from saliva, than those who accepted these offers. But those with higher testosterone were more generous. Interestingly, this direction does not hold when sex cues are introduced prior to playing the game (Van den Bergh & Dewitte 2006). After rating 15 photos of females in swimsuits or underwear, heterosexual males with lower 2:4 digit stated lower MAO.

v. Degree of relatedness

Does the degree of relatedness between players affect the value of the offer and the game outcome? This question will be addressed in the following chapter.

III. Dictator game: An opportunity for altruism?

The dictator game provides an opportunity for altruism where proposers have no strategic motive to be generous. It is similar to the ultimatum game, except player two has no say. In other words, player one dictates a certain amount of money on player two –sometimes called a 'recipient', who knows what player one's allocation is. First played by Kahneman et al. (1986), out of 161 dictators, 122 split $20 equally. However, only 8 of the dictators were actually paid –thus rendering results quite inconclusive. Forsythe et al. (1994) played the game for $5 and $10, and 64% of dictators in the $5 game and 79% of dictators for the $10 game gave at least $1. The mean offer is 20%. Similar to the ultimatum game, these results do not change if stakes are much higher (Diekmann 2004; Carpenter et al. 2005).

The dictator game is usually played alongside the ultimatum game by economists to compare how subjects behave in the absence and presence of potential punishment (player two's rejection).When it might seem implausible that any individual would want to give away money for no returned benefit, some results show that it actually does occur. The majority of research where the dictator game is played in its simplest form with undergraduate students in the US shows that the mode is 50% with another secondary mode of 0%. Nevertheless, mean offer for the dictator game is almost always less than that for the ultimatum game in the same sample. Subjects can be motivated to give more when told that their recipients are poor (47% gave full amount) or when they are asked to make donations towards medicines for their sick recipients (72% game full amount)

(Branas-Garza 2006). Similar to the UG, subjects gave less in a dictator game that was played with a face-to-face interaction than they would in an anonymous interaction (Rankin 2006).

As for sex differences, males are more likely to be either perfectly selfish or perfectly selfless while females are likely to be 'egalitarians" and share evenly (Andreoni & Vesterlund 2001). In a dictator game, women on average gave twice as much as men to their anonymous partner (Eckel & Grossman 1998). In a group of three dictator game, groups were more generous when women were the majority, but the most generous groups were those with two men and one woman (Dufwenberg & Muren 2006). However, one study showed somehow disparate results when women and men split $10 with a completely unknown person or a person of known gender (Ben-Ner et al. 2004). Results revealed that sex information significantly affected giving only in the case of women, who gave systematically less to women than to men and persons of unknown gender. Women also gave less than men on average, although the difference was not statistically significant. Saad and Gill (2001) also found an effect of the recipient's sex on offers made. While male and female gave similar amounts on average, males offered significantly more to females than to males, that being conditional to whether they gave anything at all to start with.

When the game is played back and forth by the same players, it becomes a typical case of reciprocity (Ben-Ner et al. 2004, Diekmann 2004). When the two players are matched another time and roles are switched, the amount sent back is strongly correlated with the

amount received despite the fact that the game is played anonymously. When anonymity is eliminated, dictators become more generous (Burnham 2003). Proposers and responders view photos of their partner players in a usual dictator game. The modal offer for this study is 50% in the photograph treatment versus 20% in the control (i.e. when no photos are shown). Not only did seeing recipients' faces affect outcome, but so did recipients' level of attractiveness. Hancock and Ross (2002) showed that the correlation between dictator offers made to photos independently rated for attractiveness was high (R=0.91).

The game has also been used in cross-cultural research reviewed here very briefly. Consistent with most research, the mean offer for the dictator was slightly lower than that of the ultimatum game in the rural Nigerian village study (Gowdy et al. 2003). While that of the ultimatum game was 43%, it was 42% for the dictator game. While women offered less than men in the dictator game, the difference was not significant. For the Orma of northeastern Kenya, the mean offers for the ultimatum and the dictator game were 44% and 31% respectively (Ensminger 2000). Similarly for the Amazonian Tsimane, the mean offer for the dictator game (32%) was lower than that of the ultimatum game (37%) although the two games were played in different villages.

So, is it that proposers in the dictator game are concerned about fairness in what they offer to receivers? Forsythe et al. (1994) pursued this issue. They tested whether fairness alone could explain proposer's generous offers in the dictator and ultimatum game. Both games were played with two conditions, with and without monetary payment. The

distributions of offers in the dictator and ultimatum games with the real pay condition were significantly different. Offers in the ultimatum are more generous than in the dictator game. The distribution for the dictator was bimodal with peaks of 0% and 50%, consistent with other research. While 36% of proposers in the dictator game offered 0%, none of the proposers in the ultimatum game offered 0%. As for the games without real pay, the distributions of offers in both kinds of games were quite similar. This dismisses fairness as the only reason for explaining the 40-50% offers that people made rather than giving the very minimal. If players made generous offers to be fair, results from the pay and no-pay games should be quite similar, which was not the case. Without pay, the dictator and the ultimatum games became the same, since punishment or real cost was no longer an option. Players had nothing to lose or gain, and thus they played in accordance with their wishes. Proposers were not concerned with responders' rejections and so acted as if they were playing a dictator game. When real pay was introduced, players had to worry about rejections/punishments. That was perhaps why offer value increased to avoid rejections.

The dictator game has also been tried out with children (6 – 12 year-old) to see whether the so-called altruistic behavior in children was similar to that of adults (Harbaugh & Krause 2000). Children gave 29% of their allocated tokens. These children also played the public goods game (details later to come).

IV. The public goods game: An opportunity for cooperation among many

The public goods game (PGG) is an opportunity for cooperation that could involve more than two people. It is used to test whether subjects will act according to the self-interest model. Similar to the ultimatum and dictator game, subjects exhibit a higher rate of cooperation than would have been expected on the basis of the self-interest model. In the PGG, players are allocated an amount of money from which they can contribute to a public account, which will return some benefit to them, or they may keep it to themselves. This section examines the game in detail.

The contribution stage only

The public goods game has many versions, but it is mostly played anonymously (except for Andreoni & Petrie 2004). All group members have access to a public account or good even those who do not contribute to it, and thus each member could have the opportunity to free ride on the contributions of others (Fehr & Fischbacher 2004a). A common version of the game consists of only one stage, the contribution stage (Ledyard 1995; Gintis 2000a; Bowles & Gintis 2002; Fehr & Fischbacher 2004a). In a group of subjects (ranging from 2 to 10), each is given a monetary endowment E to be deposited in their private account as a reward for participating in each of the ten rounds of the experiment. For every 1 MU that a subject moves from its private to the public account, the experimenter multiplies it by a certain number (b/ $b \geq 0.5$) and deposits it in the public account which is divided equally among the players at the end of the game. Subjects also take whatever is in their private accounts. Consider this example, E= $1 and B= 0.5. If all players put $1, by the end of the first round there will be $15 in the public account, and

by the end of the tenth there will be $150. Each player walks out with $15. If one subject, X, keeps his $1 in each round and others pitch in their $1 for every round, X walks out with $23.5 and the others with $13.5 each. If no one pitches in for all ten rounds, each subject walks out with $10. If one player deposits $1 for each of the ten rounds, he gets $1.5 and each of the other players gets $11.5. The public goods game resembles a prisoner's dilemma; whatever the other subjects do on a round, a player's highest payoff results from not contributing anything to the public account. If everyone cooperates, it is best for oneself to defect; if everyone refrains from cooperating, it is also best for oneself to defect. It is better when everyone cooperates than when everyone defects. Subjects are sometimes willing to increase their contribution to the public account when others contribute more (Fischbacher et al. 2001). Results show that in round one, some subjects usually have optimistic expectations about other's behavior and thus tend to make higher (40 - 60%) contributions (higher than those made later), but with each round cooperation deteriorates to low levels (Andreoni 1995; Gintis 2000a; Fehr & Fischbacher 2003a, 2004) and sometimes to virtually nothing at all (Ledyard 1995). This led researchers to introduce the option of punishing non-cooperators or cheaters in public goods games to study whether this option affects the outcome of the overall interaction, which will be discussed shortly.

The version described above is also referred to as the VC format (voluntary contributions). Another format for the PGG is the CPR (common pool resources). The payoff distribution of the CPR format is identical, except that instead of receiving an

endowment, players can make limited withdrawals from the common account. Whatever is left after everyone has withdrawn is increased by 50%, or doubled, and distributed equally among all group members. All studies reviewed here use the VC format, except in one case where it will be clearly indicated.

The contribution and the punishment stages

Field experiment results showed that captive rhesus monkeys made food calls when discovering food 45% of the time (Hauser 1992). Individuals who failed to call and were detected with food by other group members received significantly more aggression than those who called. Aggression could be interpreted as a form of punishment that group members use to deal with non-cooperators or cheaters although data on whether this aggression reduces cheating is not available for rhesus monkeys. Data showing that punishment can reduce cheating is, however, available for humans (Fehr & Fischbacher 2004b).

Moralistic aggression, social control or punishment is when an individual bears a cost to inflict cost on another as a result of being cheated out of some interaction (Enquist & Leimar 1993), and this acts to help deter defectors (Trivers 1971, Axelrod & Hamilton 1981; Alexander 1987). Punishment are willing to bear a cost to inflict costs on others. When punishment of free-riders is an option, cooperation could be sustained (Yamagishi 1986, 1988; Ostrom et al. 1992; Fehr & Gächter 2000; Fehr & Gächter 2002; Boyd et al. 2003). Researchers introduced a punishment stage following the contribution stage to the

PGG to test this prediction. In the punishment stage, the contributions of each subject are made public and each player is given the opportunity to reduce the pay-offs of another subject at a cost to the punisher. Interactions among players are still anonymous and there are three partner matching treatments. In the 'partner treatment' subjects do not change group membership whereas in the 'stranger treatment' subjects change groups after each round. In the 'perfect stranger' treatment, no two subjects interact more than once (Bowles & Gintis 2002). In all these treatments, cooperation was sustained by the punishment condition to a higher degree than without it (Fehr & Gächter 2000). Here I review Fehr and Gächter (2002) where the 'perfect stranger treatment' was used.

Undergraduate students in groups of four (N=240; 31% females) played the PGG with two treatment conditions punishment and no-punishment. In five sessions, subjects first played the punishment treatment and then the no-punishment treatment, and in the other five sessions, the sequence was reversed. Each player received 20 monetary units (MUs) and could contribute from 0 to 20 to the public account. Subjects kept the money that they did not contribute to the public account. For each 1 MU a subject contributed every member of the group gets .4 MU, i.e. total of 1.6 MU. In effect, it is in the self-interest of any subject to keep all MUs privately - irrespective of how much the other three players contributed. If all contributed all their MUs, each would get 32 MUs instead of 20. In the punishment condition, subjects could punish after finding out what the others have done (0-10). Each point used to punish cost the punished 3 MU, which were deducted from his/her account. Results showed that 74.2% of the punishment acts targeted those who contribute below average, and the more a subject's investment fell short of the average,

the more the subject was punished. Moreover, punishment acts substantially increased the amount that subjects invested in the public good. When a subject was punished before period 6, this subject raised investment in the next period on average by 1.62 MUs. When the punishment condition was the first treatment, the average contributions was much higher in the punishment periods. (See Figure 2.1 from Fehr and Gächter (2002).)

Figure 2.1: Comparing treatments in the PGG where punishment trials coming first with punishment trials coming second (from Fehr and Gächter (2002)

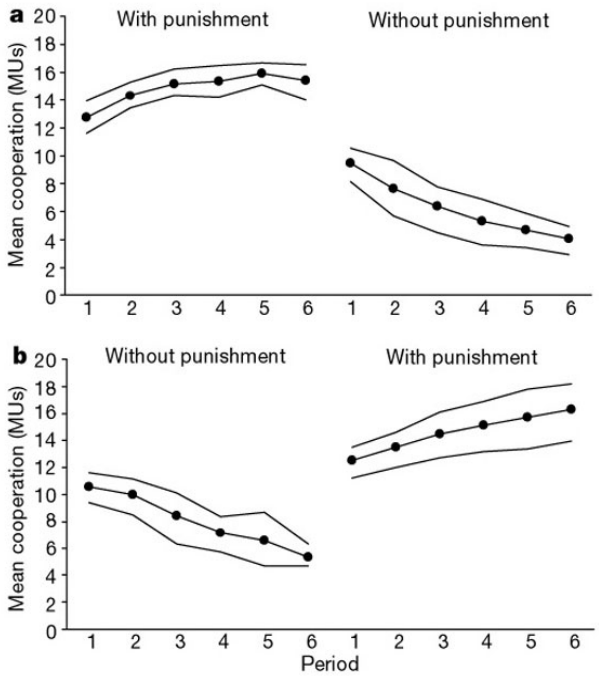


Figure 2.1: Time trend of mean cooperation together with the 95% confidence interval. **a**, During the first six periods, subjects have the opportunity to punish the other group

members. Afterwards, the punishment opportunity is removed. **b**, During the first six periods, punishment of other group members is ruled out. Afterwards, punishment is possible (from Fehr and Gächter (2002).

Once again advocates of strong reciprocity use results from the PGG to argue that people are predisposed to act altruistically, specifically here to those that violate group norms. In my view, subjects' self-interest is hardly irrelevant to their decision to punish in a PGG. Subjects' return benefit is directly affected by what other players pitch in the common account, and in that highly motivated by self-interest if they chose to punish. I will refer to this in the discussion section of my PGG results in chapter five.

Anonymity, group identity and sex

This section reviews some experiments that investigate whether some treatments could affect the outcome of the PGG. Andreoni and Petrie (2004) designed an interesting public goods game that unmasked subjects in a systematic and controlled way. The experiment was run on a computer and had three treatments: (1) the information treatment, where subjects knew exactly what each group member contributed to the public account, (2) the photos or identity treatment, where subjects saw photos of other group members without access to information on contributions; and (3) the information-and-photo treatment, where subjects saw pictures and have information on other members' contributions. Interestingly, knowing the distribution of contributions and not the identity of other players had no discernible effect whereas knowing only the identity without the

contribution distribution slightly increased a subject's contribution. When subjects had access to other players' identity and contributions, this significantly increased contributions. Even more interestingly, when subjects were given the choice to reveal their identity, they contributed more. Another recent study obtained similar results (Rege & Telle (2004). When subjects' identity and contribution were revealed, contributions significantly increased. These results imply that these games reflect certain real life situations of cooperation, in which humans care about whom they are interacting with. This further entails that there is more to these games, than just one-shot trials. The fact that subjects increase contributions upon seeing photos suggests that they might be hoping to pursue or perhaps prevent some interactions with their group members.

Solow and Kirkwood (2002) tested the effect of group identity and sex in the public good game. For the former, they recruited members of a marching band and compared results with a random sample. Members of the marching band significantly contributed more than members of the random sample. Males contributed more than females in every round and this was highly significant. Furthermore, males in the marching band contributed more than males in the random sample, and the same applied to females when testing for group identity. Another study found similar results when players in a group were family members, i.e. parents and their children (Peters et al. 2004). Parents and children contribute significantly more to a PGG when in groups with other family members than when in groups with strangers. Nevertheless, parents gave an average of 78% whereas children gave an average of 53% when playing with family members. Parents also gave more than children when playing with strangers.

The previously reviewed study investigating economic behavior in children (6 – 12 year-old) had them also play the public goods game (Harbaugh & Krause 2000). Instead of money, children were given five white poker chips (value of each is 10 cents), and were told that by the end of the experiment they could buy a number of items with whatever they earned. Each group had 6 children and played ten trials. Children at the earlier trials behaved like adults, but then repetition had a difference effect. As discussed earlier, in later trials adults reduced their contributions. Younger children, on the other hand, increased their contributions in later trials of the experiment.

One study investigated the effect of 2:4 digit ratio on behavior in a hypothetical public goods game (Millet & Dewitte 2006). Subjects were not playing for real money, and the game was organized in a way that when a particular provision unit has been reached (e.g. 100, 160), the public account is distributed over all four group members. Subjects of both sexes with lower 2:4 digit ratio were more likely to make their provision, but less likely to go under and or above. These results on 2D:4D and others from the ultimatum game will be discussed in much detail in the chapter on PGG and 2D:4D in Jamaica.

In a parallel growing line of research, a study by Ferraro et al. (2003) examined whether humans play differently when playing with a computer than when playing with other fellow humans. Ferraro et al. introduced “virtual players”, i.e. replacing all but one human player by programmed computer software, in the public goods game. In comparison to an all- human subjects game, the mean contribution of one total game

decreased from $6.09 to $4.6 out of $12 originally allocated per round. It appears that people cared about sharing or returned benefit only with humans, i.e. when it mattered, and acted in a more self-interested way when playing with computers.

Cross-cultural research

The public goods game has also been played in different cultures although not as much as the ultimatum game has because it is more complex and involves multiple rounds. Ensminger (2000) also ran the game with the Orma, northeastern Kenya. The Orma contributions were pretty high (58%), and so were they for the Amazonian Tsimane (54%) (Gurven 2004).

Henrich et al. (2004) review some of the PGG played in the 15 small scale societies described earlier with the ultimatum game results. This table (2.1) summarizes the variations they found.

Table: 2.1: Variations in contributions in a public goods game in 7 small scale societies (from Henrich et al. 2004)

Group	Format[1]	Group Size	MPCR[2]	Sample Size	Stake[3]	Mean	Mode[4]	Full Cooperation	Full Defection (%)
Michigan[5]	CPR	4	0.375	64	0.58	0.43	0 (33%)	26	33
Machiguenga[5]	CPR	4	0.375	21	0.58	0.22	0 (38%)	0	38
Tsimane	VC	4	0.50	134	0.75	0.54	0.67 (17%)	1.5	5
Mapuche[6]	VC	5	0.40	12	0.33	0.34	0.1 (42%)	0	0
Huinca[6]	VC	5	0.40	12	0.33	0.58	0.5 (25%)	17	0
Aché	VC	5	0.40	64	1	0.65	0.40 (30%)	3.1	1.6
Orma	VC	4	0.50	24	0.5	0.58	0.40 (37%)	25	0

[1]CPR is the common-pool resources format; VC is the voluntary contributions format.
[2]Marginal per capita return.
[3]Stakes sizes are standardized to a one-day wage in the local market, so this column is the endowment received by each player divided by one-day's wage.
[4]The percentage in parentheses is the total proportion of the sample at the mode.
[5]Both the experimenters and protocols were identical between Michigan and the Machiguenga (Henrich & Smith 2004). Comparing the distributions yields a p-value of $p = 0.05$ using the Epps-Singleton test.
[6]Both the experimenters and protocols were identical between the Mapuche and Huinca (Henrich & Smith 2004). An Epps-Singleton test for a difference between the distributions yields $p = 0.09$. Huinca are non-Mapuche Chileans, described in section 7.

V. Emotional and neurophysiological mechanisms in game playing:

A study by de Waal (1997) shows that the exchange of favors between male chimpanzees was partner-specific. The tendency of chimp A to share food with B was higher if B had recently groomed A rather than not. De Waal also presented well-documented evidence to support the thesis that the exchange of social services among chimps was based on cognitive abilities, which allow current behavior to be dependent on a history of interaction (de Waal 2003). Similarly for human, certain cognitive and emotional mechanisms are expected to operate in decisions related to cooperation and also in economic games.

If reciprocal altruism is an evolved system of cooperation, it is expected that natural selection would favor psychological and emotional mechanisms that regulate it. These

mechanisms were originally discussed by Trivers (1971). When initiating cooperation, an individual bears a certain cost which puts it in a position vulnerable to cheaters. Natural selection thus would select for mechanisms to reduce cost and increase potential benefit.

Fessler and Haley (2003) discussed thirteen different emotions affecting cooperative behavior. Some emotions lead actors to resist the temptation for short-term defection (love, gratitude, shame, pride, admiration, elevation, and mirth), others lead to reciprocating harm or benefit received (anger, envy, contempt, righteousness, moral outrage, and corporate emotions), and others encourage repairing damaged relationships (guilt). These categories are not exclusive; some emotions could affect cooperative behaviour in different ways. These emotions fall in two broad categories: emotions that operate primarily in dyadic relationships, and those that operate in collective contexts. These mental states act as motivators and moderators of cooperative behaviour (Stevens & Hauser 2004).

It would be interesting to understand the positive and negative feelings players would have when participating in a certain experiment. Haselhuhn and Mellers (2005) investigated which payoffs gave players the greatest pleasure and whether the pleasure they felt about payoffs predicted their decisions to cooperate. They asked players to consider a fixed set of offers and report their preferences over all offers. Players also reported the pleasure they imagine feeling from each possible payoff. Results showed that players differed in the extent to which they derived pleasure from fairness or greediness. Players whose pleasure primarily depended on larger payoffs made fair offers

in the ultimatum game and selfish offers in the dictator game. Players who derived greater pleasure from fairness tend to act fairly in both games.

The study of the neural basis of economic decision-making has been flourishing recently. Here I review a study using fMRI while responders made their decisions on the ultimatum game (Sanfey et al. 2003). In the study, subjects responded to offers made by either a human being or by a computer, a treatment they knew about, and were brain scanned by fMRI at the time the decision was made. All subjects received the same offers regardless of whether the offer was made by a human or a computer. Consistent with other studies, subjects accepted all 50-50 splits, and 10-20% offers were rejected with that being significant when offers are made by humans versus by the computer. (See Figure 2.2, from Sanfey et al. 2003.). This suggests that there could be a greater emotional response to unfair offers when made by humans versus by a computer. This was also validated when it came to neural or brain responses. There was significantly greater brain activation when an unfair offer was made by a human than when it was made by a computer. Brain areas activated in response to unfair offers were also activated in response to disgusting tastes and odors, again suggestive of an emotional response. In sum, unfair offers elicited activity in brain areas associated with emotion and cognition. The intensity of the brain activation predicted whether the offer would be rejected or not on that trial. Other research has also documented certain neurological pathways involved in making decisions in other economic games again with stronger activation in response to human rather than computer offers (McCabe et al. 2001; Rilling et al. 2001, 2002, 2004).

Figure 2.2: Difference in acceptance rates when offers made by computer vs. human (from Sanfey et al. 2003)

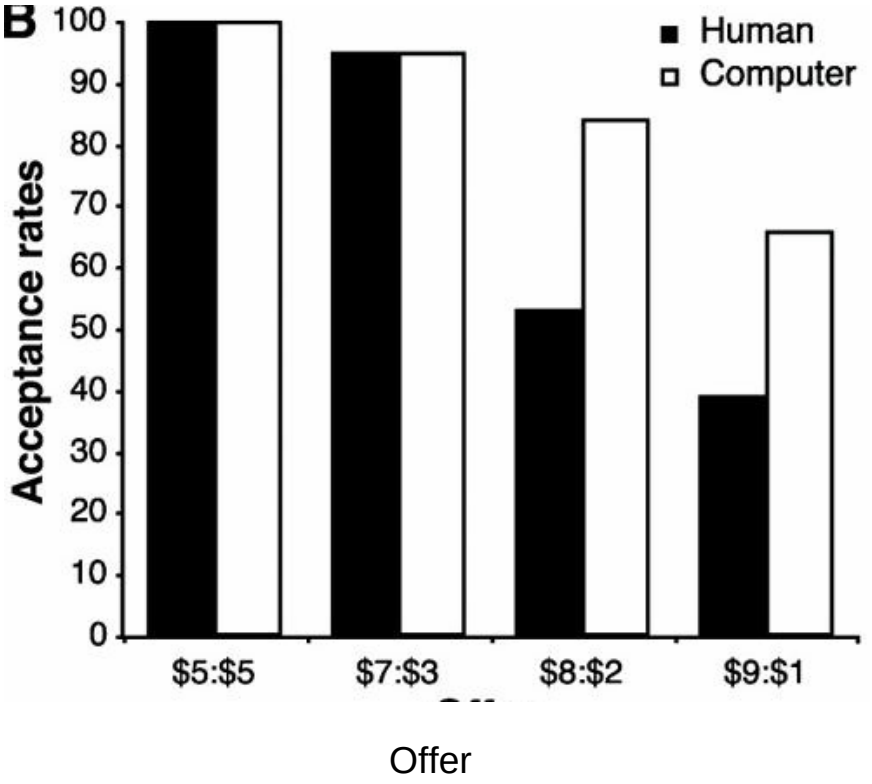


Figure 2.2: Behavioral results from the Ultimatum Game. These are the offer acceptance rates averaged over all trials. Each of 19 participants saw five $5: $5 offers, one $7: $3 offer, two $8: $2 offers, and two $9: $1 offers from both human and computer partners (20 offers in total) (from Sanfey et al. 2003).

More recently, a group of subjects played the ultimatum game while their skin conductance responses were measured as an autonomic index of affective state (van't Wout et al. 2006). Results showed that skin conductance activity was higher for unfair offers and was associated with the rejection of unfair offers (30% and below). These

results were only observed in response to offers made by humans rather than by computers.

VI. Conclusion

Behavioral game theory has a wide range of applications in the study of human cooperation in dyads (ultimatum and dictator games) and in groups (public goods games). An economically rational model by itself is not sufficient to explain economic behavior in light of the new findings. But, the question is: are we to interpret human economic behavior in terms of social rules and market access, or in reference to some individual biological characteristics, or a combination of both? The two approaches are not mutually exclusive. Perhaps the default setting that players operate on in a simple ultimatum game knowing nothing about their game partner is to play according to what they think would be fair in their society. This perhaps explains why there are no generalizable results when it comes to sex difference and behavior in economic games. However, studies show that once proposers have some sort of information on their partners (e.g. attractiveness, sex, age), they adjust their offers. This also highlights the interaction of one's own traits with their partners, e.g. both males and females give more to males than they do to females, and females give more still to males (Solnick & Schweitzer 1999). My research set out to investigate the effect some of these biological traits could have on behavior in the ultimatum and PGG game in two populations Jamaica and Lebanon, whether those traits are important in themselves and/or in interaction with partner's traits.

Chapter three: Clans and ultimatum game decisions in Lebanon

I. Introduction

In this chapter I explore whether an existing degree of relatedness between two people could affect their cooperative interactions. An ideal natural setting for such research is Lebanon where kinship ties are crucial and where segmentary descent groups are strong and organization within these groups could be taken a proxy for degree of relatedness.

Cooperation in evolutionary theory revisited

Hamilton (1964) transformed the way evolutionary biologists think of altruism among kin when he introduced the concept of "inclusive fitness". Individuals contribute genetically to future generations both directly, by personally reproducing, and indirectly, by helping other relatives reproduce. By helping a relative, one increases the relative chances of passing on its genes (many of which are the same as one's own) to the next generation. Individuals are therefore expected to be more altruistic to relatives than non-relatives, and cooperation is likely to increase as a function of relatedness. This has been widely documented in nature in cases where individuals help raise their relatives' offspring. For example, in cooperatively breeding birds, helping in the form of provisioning is often directed towards close genetic relatives (Emlen et al. 1991, Emlen 1995). The frequency of care allocated to immatures is positively correlated with the degree of relatedness between them and a helper. In humans, data collected on

alloparental care among the Ye'kwana of Venezuela reveal positive relationship between degrees of relatedness and care giving (Hames 1989). Similar results are found in western societies. Women from Los Angeles reported an increased willingness to help (e.g. financially) as genetic relatedness among them increased (Essock-Vitale and McGuire 1985).

Reciprocal altruism provides resolves the puzzle of altruistic behavior among non-relatives (Trivers 1971). It is the trading of favors between individuals in which the benefit to other is larger than the cost to self so that over time both parties enjoy a net benefit. Reciprocity may be selected for when interaction is frequent and when individuals render roughly equivalent benefits to each other at roughly equivalent costs. An individual would be willing to bear a certain cost and initiate interaction for the purpose of returned benefit. In effect, this allows cheaters to take advantage of the other party by accepting the benefit given and then by failing to reciprocate. Nevertheless, with frequent interaction, cheating decreases because cheaters can be punished by being deprived of future help when they need it.

This paper studies cooperation among segmentary descent group members in the Beq'aa Valley of Lebanon. It examines the degree to which cooperation among kin differs from cooperation among non-kin and how variation in cooperation among kin is associated with variation in genetic relatedness. It combines ethnographic variables with an experimental economic game, the ultimatum game. The game helps tease out the

different levels of cooperation within descent groups compared to other members of the same community who do not belong to any clan.

Segementary descent groups

Kinship generally constitutes all of an individual's relatives while descent specifically constitutes only a subset of it (Cronk and Gerkey 2006). Descent can be organized by tracing back individuals through the male or female line. When kin groups are segmented according to the descent rule, they are segmentary descent groups (Schneider 1965, Holy 1976). Segmentary descent groups became a central topic of anthropological research because of the important role such groups played in the lives of the peoples studied by anthropologists (e.g., Radcliffe-Brown and Forde 1950, Sahlins 1961, 1972, Lévi-Strauss 1969, Schusky 1973, 1974, Keesing 1975). Recent work on descent groups has focused on the role they play in overcoming collective action problems such as the provision of public goods. It is thought that the principle of descent is commonly used to structure cooperation in large groups because it makes group membership unambiguous (van den Berghe 1979, Acheson 1989, Brown 1991, Jones 2000, Alvard 2003a). The bigger the group gets, the more ambiguous group membership becomes. Thus, groups involved in collective action would benefit greatly if membership is made obvious by a form of social organization. Recent literature includes several examples in which kinship and descent are used to overcome collective action dilemmas and provide public goods. Alvard (2003b) focused on whaling as a collective action dilemma in the community of Lamalera, Indonesia. In Lamalera, sibships (sibling groups) are not large enough to run

whaling operations, and descent facilitates the formation of larger corporate groups that are capable of conducting whale hunting while also policing free riders. By contrast, Northern Alaskan societies also depend on whaling for subsistence but use kinship networks rather than descent as the central organizing principle of whale hunts (Sheehan 1985). In Maine, information on lobster location is crucial for obtaining resources for lobstermen. Intense competition and territoriality is widespread among different groups, and groups that keep information secret and accurate are the most successful ones. In fact, information flows according to a network of descent organization which maintains secrecy and accuracy on lobster location (Palmer 1991). In theory, supressing intragroup conflict and competition makes such groups more successful at times of conflict with other groups or with the state itself (Scheffler 2001).

II. Ethnographic description: The Beq'aa Valley of Lebanon

Descent in Lebanon

"I and my brother against my paternal cousin, and I and my paternal cousin against a stranger." This is a very vivid and widely used saying across various groups in Lebanon, where kinship relations (*nasab*), the collectivity of all of one's relatives, have been central to all spheres of social activity (Joseph 1982, 1997). Descent in Lebanon is patrilineal although maternal relatedness is acknowledged and interaction with maternal relatives is encouraged (Joseph 1999). In rural areas or 'villages', males tend to marry from within their community (Farsoun and Farsoun 1974), and it is typically a patrilocal

system, where males do not tend to disperse from their natal area after marriage, although this is not without exceptions. However, women do not lose connections with their kin; in fact, female's kinship relationships to maternal relatives are typically strong. The extended kin social order is reinforced by marriage practices favoring lineage endogamy (cousin marriage) (Khuri 1970, McCabe 1983), mostly for the purpose of preserving inherited property or family business. Males tend not to subdivide property inherited from fathers/grandfathers, and they often invest with each other in businesseses (Joseph 2000).

Hermel, the Beq'aa Valley

The Beq'aa Valley borders Syria and hosts a large Palestinian refugee camp. This narrow 75-mile-long open-field corridor between two mountain ranges stretching north-south and is a major agricultural area in the country. Hermel, the second major city in the Beq'aa Valley of Lebanon, is a typical Beq'aa city in demographics, social organization and socio-economic status. Although a city, Hermel is highly rural and has a population of approximately 109,000, mostly Muslim Shiites, with a minority of Sunni Muslims and Christians. The average household size in Hermel is 5.77 (UNDP report).

Descent groups and clans in the Beq'aa Valley

Despite the weakness of the Lebanese state in development programs and providing social welfare, social stability is maintained in the Beq'aa, at least in part, by the strength

of descent groups. A theme in Lebanese society and culture is the value of depending upon kin as the anchor of one's security and the center of one's social life (Joseph 1997). Nepotism in general was prevalent during the civil war among most Lebanese (1975-1990), but segmentary descent groups specifically seemed to gain many benefits because of strong ties, lobbying and exchange of resources and political dominance. It has been shown recently and particularly in Iraq that at times of physical insecurity, xenophobia increases and so does in-group solidarity (Inglehart et al. 2006). In Lebanon, sixteen years after the civil war and with the government's attempts at reestablishing power, nepotism is decreasing on some levels very slowly, but in the Beq'aa, descent groups persist and provide their members with a sense of security, order and a system of various benefits. Descent group members support one another at times of crisis and monitor one another to prevent corruption and defection.

The prominent level of segmentary descent group organization in the Beq'aa Valley is the clan,*'asheera*, (pl.*'asha'er*). A clan is a large patrilineal descent group, i.e. it identifies descent through the father's lineage, and may be as large as 20,000 people. The clan is named after the original ancestor's last name, e.g. the clan of *al* Shammas or Shreif. In the Beq'aa all clans are Shiite muslims, in fact, most clans in Lebanon are Shiites, except for very few Sunni ones in the north. Clans are further divided into lineages, *ajbab* (*joub* for singular), in addition to extended and nuclear families. A *joub* can hold up to three generational descendants, and so on average there is a higher degree of relatedness within a *joub* than across *joubs*, i.e. within the clan. In everyday interactions, a clan member's surname, which is the clan's name, is dropped and replaced by a grandfather's or the third generational ancestor's first name in order to indicate what

joub the person come's from. So, instead of saying Hussein Shammas, he would be referred to as Hussein Abbas, Abbas being his grandfather's name. But this name is not official but only locally used. It is also common in Lebanon and more so for clans to name the first son after his paternal grandfather. This helps maintain the *joub*'s name further in future generation. It is also a common practice among *joub* members to call one another a first paternal cousin even what they are actually second cousins or more. Many clan members from different *joubs* can identify relatedness to one another, but actual relatedness is usually complicated and is not as easily identified as among *joub* members. As for kin endogamy (in-marrying), it is a common practice within the clan but even more so in a *joub*. The most common form in Lebanon and for clans as well is patrilineal parallel cousin marriage (i.e. marriage of paternal first cousins from fathers) (Joseph 1999). Therefore, since endogamy is more frequent within *joubs* – where members already share a higher degree of relatedness to one another rather than to other members of their clan – than across *joubs*, the degree of relatedness is made even higher on average within a *joub* than it is across *joubs*, i.e. in the clan overall.

The clan provides services to its members that can range from physical security to job opportunities. Complying with codes of duty and obligation toward the group is associated with honor and good reputation, and failure to comply is condemned by members of descent group. Clans facilitate cooperative behavior on a large scale by reducing ambiguities in group membership despite the fact that clan members may be residentially dispersed among people who are members of other clans (or of no clan at all). Clans are recognized as an organizational entity by other community members. They

blend with their communities while still maintaining their distinctiveness. Clan members are highly cooperative among themselves and with other members of their community as well, and thus loyalties to the clan or the community are diffused occasionally. However, loyalty to the clan takes primacy and is made unambiguous when it matters: times of conflict and times of great need for help that would not be provided by community members who do not belong to their clan. In fact, affiliation with the clan is expressed by giving or receiving what I call “positive” and “negative” actions. Positive actions refer to bearing a cost in order to help out; these include offering a clan member assistance or services, free medical care, financial loans, a job and so on. Negative actions refer to bearing a cost in order to punish; these include avenging a cost to a clan member by punishing or inflicting a cost on a community member. Negative acts often include vandalism, physical clashes, or even gunfire attacks. If a member of a certain clan is involved in some conflict, the victim or the victim’s family or clan redirects aggression against the aggressor or any other member of the aggressor’s clan (Humphrey 1998). Such counter-aggression can be very severe and is facilitated by the ability to identify clan or family members partly due to communities’ small size and frequent interaction and partly on the basis of recognizable resemblance features.

Clan hierarchy and socioeconomic status

Cooperation and hierarchical organization among clan members are fundamental aspects of social life. Membership to a clan is not a matter of choice; it is automatically by descent. There are costs and benefits to belonging to a clan. These could vary according

to where an individual falls in the social hierarchy of the clan. Individuals on the upper end tend to bear the least cost unlike individuals on the lower end. Those on the upper end typically have higher socio-economic status. They are better off financially (merchants and businessmen), many with professional degrees (medical doctors, lawyers, university professors) and some in government positions of relative power. Most have many contacts outside the clan and outside the area as well. This allows them to offer a wider range of services for members of their clan although they rarely participate in any negative action on behalf of clan members. Thus, the costs involved in belonging to the clan are relatively low. These members do not benefit much from belonging to the clan. Most of the benefits they get from helping a clan member are directed towards establishing or maintaining outside contacts and social status within the community and the clan, for example by pleasing an external contact with a right man from the clan to do some job. Occasionally they might need someone from their clan to obtain some official legal document from the more distant government offices. They also monitor within clan politics by resolving intragroup conflict and muting it, especially during times of intergroup conflict.

Individuals on the lower end of the clan hierarchy are of lower social and financial status and subsist on minimal resources. They benefit greatly from opportunities provided by higher status members for short-term and part-time jobs, such as chauffeuring, moving, and other part-time assignments. They are also the most likely to participate in potentially risky negative action. The services they get are crucial for subsistence, which increases their sense of loyalty to the clan, which, in turn, increases their readiness to bear the costs

involved, especially in negative actions, since there is little that they can do in offering positive action.

The costs and benefits of belonging to the clan therefore vary with members' socioeconomic status. For example, a clan member, a medical doctor, who is in the upper end of the hierarchy, can offer free medical examinations and sample medications to a member on the lower end. This is of little cost to the doctor whereas it is enormous benefit to the receiver. In this sense, higher status members are more likely to offer low cost benefits to other members and are less likely to participate in high cost actions especially negative actions, even if it were their son they would be avenging for. A clan member, on the lower end of the hierarchy is more likely to take on such a task.

Solidarity among community members

Descent is not the only organizing principle of social life in the Beq'aa Valley. Moral codes motivating cooperation among community members who are not part of any clan are also very important. The moral obligation to aid members of one's community (town) regardless of clan membership, class or religious background is encoded in the term *awneh* – mutual assistance. Individuals in need of assistance with physical labor, e.g. building an annex to the house, can call for assistance from community members by invoking the principle of *awneh*. Once someone is called upon by this term, there is a moral obligation to respond with help. For example, the owner of the café where subjects participating in an experimental part of this project were offered lunch used the principle

of *awneh* to call on young community members to help cater for around 150 people without pay. The principle of *awneh*, however, is not usually applied to clan members; they are expected to help out without formal request. While the range of help sought from community members is mostly concerned with immediate physical labor, help sought from clan members is diverse and includes harvesting crops, offering temporary residence, arranging employment, and offering financial loans and gifts.

III. Hypotheses

Inclusive fitness considerations influence the types and contexts of social interactions expected among family members (Hamilton 1964).The degree of helping tends to positively correlate with the degree of relatedness among kin (recall birds; Emlen 1995). Reciprocal altruism influences social interactions among non-kin. But, cooperation among kin cannot all be interpreted in terms of the increase in an individual's inclusive fitness. For example, although they are closely related, Maine lobstermen's system of information sharing can only be explained with reference to a bigger and complicated web of reciprocally altruistic relationships among the lobstermen and their families and friends (Palmer 1990). Furthermore, relatedness alone cannot structure cooperation in groups much bigger than nuclear families because of ambiguous group membership sas group size increases (Alvard 2002). Ambiguity increases when the degree of relatedness is low. It has been shown that hunters of Lamalera, Indonesia, affiliate during cooperative hunts more strongly to lineage membership than they affiliate according to genetic kinship. In this sense, individuals behave cooperatively because it is in their own direct

self-interest and benefits obtained through kin are a by-product. It is also argued that natural selection is expected to favor organisms who could define and redefine degrees and kinds of kin relationships according to changing circumstances (Fox 1971).

The prediction from inclusive fitness considerations, then, is that one expects a lower demand for reciprocity from kin than from non-kin. The direct advantage to the close kin is what usually makes the behavior selectively advantageous and not its chance of being reciprocated. It was shown for the Meriam, a population of Melanesian gardeners, fishers, and hunters in Australia's Torres Strait, that in some situations involving close relatives the cost of not sharing from one's hunt could outweigh the benefits of keeping more for oneself (Bird and Bird 1997). Hunting is seasonal and when resources are scarce only good hunters can obtain any food. So, if individuals do not share, they do not receive reciprocated benefit at times when they need it.

This project set out to test whether cooperative behavior varies within a *joub* and across *joubs*. When it comes to being a *joub* member, the degree of relatedness one has to another member is higher on average than one has towards a clan member. When interacting with *joub* members, individuals are expected to be more cooperative and more tolerant of cheating with other *joub* members than they would be with more distant relatives, i.e. members of their clan (but not their *joub*), and members of the community who do not belong to their clan. Interactions based on kin selection are limited to close relatives. When interacting with other clan members, individuals are expected to be more interested with exchanged favors and reciprocated benefits and thus less giving than they

would be towards their *joub* members. In fact, because relatedness is low among clan members and because interaction with non-clan community members is frequent, little difference is expected between levels of cooperation among clan members and community members. On another hand, because clan members share some degree of relatedness, as low as it is, and because of the dutiful loyalty to their clan, clan members are expected to be more tolerant of cheating by their clan members than community members would be.

The ultimatum game: An opportunity for cooperation

The ultimatum game is an opportunity for cooperation between two individuals, a proposer and a responder. The proposer is given an amount of money to split with the responder. If the responder accepts the split, the two share the money accordingly. If the responder rejects it, neither player receives any money. Rejecting the offer is perceived an act of punishment to an unjust offer.

Although this game is one-shot and is played anonymously, it is believed to reflect an individual's sense of fairness and cooperative tendencies, evolved for a world of frequent interaction (Hagen & Hammerstein 2005). In other words, individuals know from their everyday interactions what counts as fair, i.e. what responders would agree to, and "what counts as fair" could vary according to the degree of relatedness they share with their game partner.

Cross-cultural ultimatum games show some behavioral variability and depart from the average offer in most western studies (40-50%) (Camerer 2003). It has been argued that group-level differences in economic organization and the degree of market integration help explain this variability (Henrich et al. 2001, 2005). The higher the degree of market integration and the higher the payoffs to cooperation, the greater is the level of cooperation in experimental games. However, this does not explain variation of behavior within groups or within and across descent groups. One study using experimental economic games showed that parents and children contribute significantly more to a public goods account when playing with family members than when with strangers (Peters et al. 2004). Here I compare behavior of related versus unrelated individuals, however, this chapter goes on to explore behavior on three levels: the *joub*, the clan and the community (with the *joub* representing highest degree of relatedness).

Experimental design and predictions

The ultimatum game was played with three groups in the city of Hermel, Lebanon. Two groups were composed by using descent as a proxy for genetic relatedness (*r*), and the third group was the control, non-descent group. Group 1 consisted of members of the Shamas clan (the lower *r*). Group 2 included members of a particular *joub* (the higher *r*). Group 3 included a random sample from the local population (negligible *r*). All players were males to control for sex difference and because males are more likely to participate in such research. The game was played anonymously to control for previous interaction and avoid future repercussions. All that subjects knew about the person they were playing

with was that he was a member of their clan (group 1), a member of their *joub* (group 2), or a member of their community (group 3). Subjects were asked to arrive at the place of study with the knowledge that they would be playing a game where they could earn some money and they would be offered lunch. The amount allocated per game was 30,000 Lebanese pounds ($20) which corresponds to two day's minimum wage. Subjects played either as proposers or as responders. They made real offers with no pre-set restrictions (smallest unit of vision is 50 lebanese pounds (¢3.3) and responders responded to actual offers and then filled out a questionnaire on socio-economic background. Based on ethnographic information and the cooperative systems discussed above, the following results were expected:

- Prediction one: *Clan (lower r) and community offers (negligible r) are expected to be more similar to each other than are joub (higher r) and community offers.* The kin ties are expected to influence the *joub* games but not the clan games.

- Prediction two: *Offer in the joub games (higher r) is expected to be higher than both clan and community games (lower r).* Because the degree of relatedness is high in the *joub* games, proposers are expected be more generous than in the clan and community games.

- Prediction three: *Offers within the community games (negligible r) are expected to be mostly 50-50 splits.* Offers below that will be rare because when relatedness is very low, players are expected to act equitably to avoid rejection.

- Prediction four: *Acceptance rate for low offers in the joub games (higher r) is expected to be higher than in the clan (lower r) and community games (negligible r).* Once again, because of the high level of relatedness, *joub* members are expected to be more tolerant of low offers consistent with their general attitude of altruism and generosity towards fellow members.

IV. Results

Subjects were all males (n=98), age range 18 – 70. One-shot 49 games were played: clan game (n=19), the *joub* game (n=15), and the community game (n=15) (table 3.1). The mean offer for all games was 56% (s.d.=16). Offers ranged from 33% - 100% (fig. 1) and the mode was 50%. Subjects could offer any amount that they wanted. Rejection rate was only 10% (n=5). Because rejections were very few, statistical analysis was difficult. There was no significant correlation between the proposer's income as reported in the questionnaire and the offer he made (Kendall's tau b=.184; *p*=.151; Spearman's rho=.208; *p*=.152). There was also no correlation between the responder's income and whether or not he decided to accept the offer (Kendall's tau b=.202; *p*=.124; Spearman's rho=.222; *p*=.125). Unexpectedly, married subjects gave more than single ones (Levene's test for equality of variances shows that equal variances cannot be assumed; mean difference between being single and married is 11% and significant at p = .01 on a two tailed t-test) (fig. 2).

Table 3.1: *UG offers by group*

		Offer		
Group	Number of games	Mean	Mode	S.D.
1: Clan (lower *r*)	19	54 %	50 %	16.82
2: *joub* (higher *r*)	15	64 %	50 %	18.83
3: community (negligible *r*)	15	51%	50 %	4.3

Figure 3.1: Offer frequencies distributed by group game

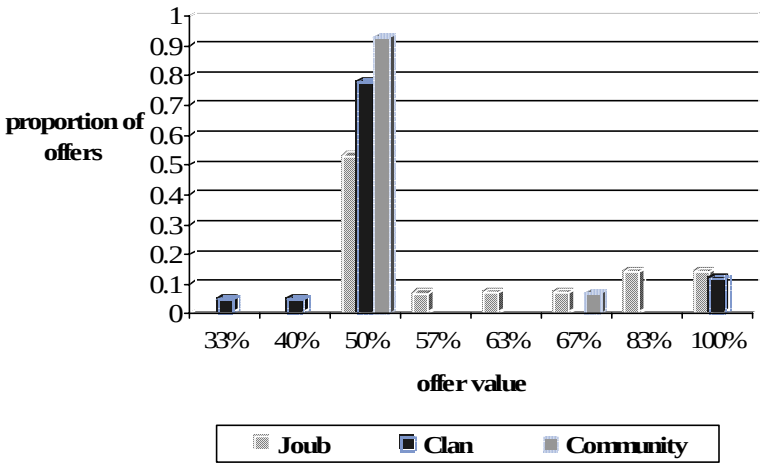


Figure 3.2: Offers according to marital status

In preliminary analyses, a 1-way ANOVA was performed to compare offers across the three different groups. The effect was insignificant but showed a trend at p = 0.065. Nevertheless, it was close enough to continue the analysis and compare two groups at a time. This was also motivated by the hypotheses predicting that the major difference in offers was going to be between *joub* and community. Further statistical analyses related to the above predictions yielded the following results.

Prediction one

Were clan and community offers more similar to each other than were *joub* and community offers? Recall mean offers: clan (54%), *joub* (64%) and community (51%). No significant difference was found between offers made by clan and community (t= .684, *p*= 0.5). However, *joub* offers were significantly different than those made by the community (t= 2.495, *p*= 0.02) (table 3.2).

Table 3.2: Comparing means between groups

Samples compared	Mean offer	t-test (2-tailed)	p-value
Joub vs.	.64	t= 2.495	p= .02
community	.51		
Clan vs.	.54	t= 0.684	p= .50
community	.51		
Joub vs.	.64	t= 1.583	p= .123
clan	.54		

Prediction two

Did *joub* members make offers higher than those made by both clan and community members? Since no significant difference in offers was found between clan and community games, they were pooled together. On average, *joub* members offered 64% of what was given to them whereas clan and community members combined offered 53%. The difference was significant (t= -2.04, *p*= 0.05).

Prediction three

Were community offers mostly 50-50 splits? In the community games, 93% of proposers made 50% offers (figure 3.1.) As mentioned before, 50% was the modal offer for all games. It constituted 53% of offers in the *joub* games and 79% of the clan games.

Prediction four

Were *joub* members more likely to accept lower offers than clan and community members? This prediction could not be tested because no offers below 50% were made in the *joub* games or in the community games. Interestingly enough the only two offers lower than 50% (33.3% and 40%) were made in the clan games, and they were both accepted.

V. Discussion

Based on ethnographic knowledge of the Beq'aa Valley and ontheoretical models of ckin-selection, various predictions were made about behavior in the ultimatum game. All predictions were verified except for one (prediction four) where the data were insufficient to allow for testing. The ultimatum game is valuable in testing how individuals act in situations that call for an internal sense of fairness. While still played anonymously, it was sufficient to give a kinship term to subjects in order for them to adjust their game play accordingly. When playing with a close relative (*joub* member) subjects offered significantly more than what subjects offered in games with more distant relatives and in games where subjects shared nearly no relatedness. As expected, subjects in the community games mostly made 50-50 splits. This is typically the modal offer (Camerer 2003) and least to be rejected. But, there is no significant difference between what was offered on average between the community and the clan games. Although there was no difference on average on how clan games and community games were played, there was more variability in clan games. While it appeared as if community members did not take any risks to have their offers rejected (i.e. low offers) and mostly acted according to what counts as fair in this interaction, clan members made two low offers. The two lower offers made were accepted. This perhaps indicates that clan members might tolerate some cheaters within the clan. This is also consistent with a saying widely used in Lebanon and emphasizes relatedness, "Blood can never turn into water." Clan members also made 100% offers which are typically rare. The offers made by the most closely related group (*joub*) had the highest standard deviation, but none of them were below 50%. These results suggest that humans might be driven by inclusive fitness benefits and would be

more generous when it comes to a close relative, consistent with research from nature (Emlen et al. 1991), in non-western societies (Hames 1988) and in modern western societies (Essock-Vitale and McGuire 1985) and in economic behavior (Peters et al. 2004). The likelihood of interaction for all members of the Hermel community is high whether they belong to the same clan or not or no clan at all, and whether they are members of the same *joub* or not. But, interactions among *joub* members are more important in the kind of benefit they bring on. So, the generosity seen in the *joub* game is less likely to be interpreted in terms of distinct frequent interaction and delayed reciprocity but more in terms of the higher coefficient of relatedness dictating distinct norms for interacting with close versus distinct relatives or non-relatives.

Nevertheless, this perhaps does not exclude the possibility that the difference in offers could be due to some system of exchange of favors and public goods among segmentary descent groups that supercedes existing blood ties. Descent groups have typically played a role in overcoming collective action problems such as the provision of public goods (Olson 1965), they provide one-on-one solutions to everyday important problems among members of a descent group. The two, social organization and genetic relatedness, could be very much woven together. Nevertheless, this research is a step in the direction of better understanding cooperative behavior of segmentary descent group members by emphasizing genetic relatedness.

Implications for strong reciprocity

The mean offer of all Hermel games (56%) falls among the highest in comparison to research done on 15 small-scale societies (see table 3.3 for Henrich et al. research summary table). In fact, the mean offer from the clan games would fall second to the current highest (57%) and from the *joub* games would be the highest (64%). Results from these societies have been used by some to provide support for strong reciprocity (Henrich et al. 2005). None of the research done in the 15 small-scale societies investigated any kinship effect on offer values. Therefore, it was a matter of importance to test find out whether high offers correlated with genetic relatedness, i.e. in which the possibility that a subject would be playing with a relative is meaningful.

Table: 3.3 Ultimatum game experiments in 15 small-scale societies (from Henrich et al. 2005)

Group	Sample size	Stake	Mean	Mode (% sample)[a]	Rejections	Low rejections[b]
Lamalera[c]	19	10	0.57	0.50 (63)	4/20 (sham)[d]	3/8 (sham)
Ache	51	1	0.48	0.40 (22)	0/51	0/2
Shona (resettled)	86	1	0.45	0.50 (69)	6/86	4/7
Shona (all)	117	1	0.44	0.50 (65)	9/118	6/13
Orma	56	1	0.44	0.50 (54)	2/56	0/0
Au	30	1.4	0.43	0.3 (33)	8/30	1/1
Achuar	14	1	0.43	0.50 (36)	2/15[e]	1/3
Sangu (herders)	20	1	0.42	0.50 (40)	1/20	1/1
Sangu (farmers)	20	1	0.41	0.50 (35)	5/20	1/1
Sangu	40	1	0.41	0.50 (38)	6/40	2/2
Shona (unresettled)	31	1	0.41	0.50 (55)	3/31	2/6
Hadza (big camp)	26	3	0.40	0.50 (35)	5/26	4/5
Gnau	25	1.4	0.38	0.4 (32)	10/25	3/6
Tsimane	70	1.2	0.37	0.5/0.3 (44)	0/70	0/5
Kazakh	10	8	0.36	0.38 (50)	0/10	0/1
Torguud	10	8	0.35	0.25 (30)	1/10	0/0
Mapuche	31	1	0.34	0.50/0.33 (42)	2/31	2/12
Hadza (all camps)	55	3	0.33	0.20/0.50 (47)	13/55	9/21
Hadza (small camps)	29	3	0.27	0.20 (38)	8/29	5/16
Quichua	15	1	0.25	0.25 (47)	0/14[f]	0/3
Machiguenga	21	2.3	0.26	0.15/0.25 (72)	1	1/10

Let us consider the highest ranking in terms of mean offer (57%), the Lamalera whale hunters of Indonesia, briefly discussed earlier in this chapter (Alvard 2005). The Lamalera village population is approximately 1,200 and is divided into 21-major clans that are based on patrilineal descent, the largest of which are further divided into named lineages or segments. Whaling operations are typically organized within these lineages or clan segments, and primary distribution of meat is divided among the crewmembers who tend to be clansmen. The later step of distribution is when meat might go to a non clansman. Alvard did not discuss the high mean offer result in light of kinship or genetic relatedness, but rather in light of market integration (as reviewed in the previous chapter). The author also explained the generosity of offers as the hunters' way to coordinate and cooperate for efficient whaling. But, Alvard failed to note whether subjects belonged to the same clan, lineage or the degree of genetic relatedness they might have shared. Given the small population size of the village and given that subjects were hunters and hunting is mostly operated by clan segments or lineages, it is likely that those hunters were related and that perhaps one reason behind the high offers are patrilineal descent of clansmen and the underlying genetic relatedness. (is clan membership based on underlying patrilineal descent).

Let us take the other extreme, the lowest mean offers made by the Quichua men (~25%). The explanation provided in Patton (2005) for the low offers is that the Quicha males do not have strong coalitions or ethnic identity, on top of a high level of exposure to outsiders and outside institutions (in other words market integration). But, the author

ignores in his explanation the fact that the Quicha are matrilocal and so males are rarely related to other men in the community. Males marry in from other communities. This could be one aspect explaining the unusually low offers (as well as weak alliances and lack of ethnic identity.)

These are just two examples that suggest the value of analyzing the anthropological setting more precisely and of looking at economic theory as explaining only some aspects of the situation. I do not claim that relatedness is the sole driving force in these interactions. Rather, that relatedness and dispersal do contribute to the social organization of group members and perhaps influence cooperative behaviors. Many of the explanations behind low versus high offers made in the ultimatum game proposed by proponents of strong reciprocity appear to be selective and provide an incomplete story.

Chapter four: Fluctuating asymmetry and behavior in the ultimatum game in Jamaica

I. Introduction

The ultimatum game revisited briefly

The ultimatum game is an experimental tool for measuring cooperation between two individuals (Guth & Schmittberger 1982, Camerer, 2003). It is simple, grants real monetary rewards and can be applied cross culturally. 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. He (or she) proposes a split and if the responder accepts the offer, the two split the money accordingly. If player two rejects it, neither player receives any money. There is no further interaction between the two individuals. On face value, 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%, 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 the game is played anonymously, a useful device for excluding effects of previous and subsequent interactions. As reviewed in chapter three, some researchers use results employing this device to claim that individuals have been selected to act appropriately in one-shot, anonymous interactions, without any other benefit to inclusive

fitness, including later return effects (Fehr & Henrich 2003; Gintis et al. 2003). I shall tackle this view again later. The ultimatum game is a good measure of 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 non-experimental 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, the 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 interesting to know whether individual variables are associated with variation in behavior in such games, and here I look at whether an important measure of biological quality—an individual's degree of fluctuating asymmetry (FA)—had any effect on individual behavior in the ultimatum game. That is, what are the correlations between a proposer's FA and the size of offers made, and also between responders' FA and the offer values that are rejected?

Fluctuating asymmetry

Fluctuating asymmetry (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 & Swaddle 1997; Polak 2004; Møller 2006). The more symmetrical an individual is (low FA), the better is the rest of his or her 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 the individual may be able to functionally adapt to its own degree of FA. Negative correlations between FA and physical abilities suggest that physically strong and independent individuals may be less willing initiate cooperation might than individuals who are less physically capable. I test these hypotheses using the ultimatum game on a population of 13 to 20 year old Jamaicans well characterized for the degree of bodily FA in both 1996 and 2002 (Trivers et al. 1999).

I 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 and/or desire to maintain dominance), especially if physical aggression is involved. Put another way, I 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). This assumes that people act in the ultimatum game as if they were embedded in a world of repeated interactions (Trivers, 2004, 2006; Hagen & Hammerstein 2006; Burnham & Johnson, 2005).

Symmetrical men (but not women) have been found to be more likely to participate in fights, to start them and to have a high opinion of their ability to win fights (self-reports: Furlow et al. 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, 1996). Aggression may permit a male to seize resources from another without offering any cooperative benefit in return. In general, insofar as aggression and cooperation are inversely related, I expect low FA men but not women to be less cooperative (offer less on the first move and be more reluctant to accept unfair offers).

More recently, Takahashi et al. (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 (Gangestad et al. 1994; Thornhill & Gangestad, 1999; Hughes et al. 2002; Brown et al. 2005), their argument gives predictions congruent to my own.

It is unclear if 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 were made. Finally, I viewed these possibilities as being provisional and pursued the work in an exploratory spirit, with an eye out for unexpected associations that require explanation.

II. Method

Participants

One hundred and fifty-three Jamaican young adults (84 males and 69 females; mean age 15.93 years, SD = 1.67, mode 15, age range 13 – 20) from Southfield district of St. Elizabeth parish participated in the ultimatum game study in March, 2004. The sample comprised part of the Jamaican Symmetry Project, which is a long-term study of fluctuating asymmetry in rural Jamaican Children (Trivers et al. 1999).

Morphometric measurement

Morphometric measurements were collected in 1996 and 2002 (wrists, ankles, elbows, 3rd digit, 4th digit, 5th digit, and feet) with vernier calipers (0.01mm accuracy). Digits were

measured via photocopies 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 averaged (Trivers et al. 1999). Bilateral trait measurements were found to be reliable indicators of between-subject differences and reflect true FA rather than biologically significant directional asymmetry. Relative composite fluctuating asymmetry 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) and summed the absolute values across all traits. FA in 1996 was positively correlated with FA in 2002 ($p < 0.0001$, $r^2 = 0.16$).

There were 112 children missing at the second measurement stage in the current study (39 percent). Ignoring missing values can yield biased estimates and inferences (Laird, 1988; Jones, 1996; Engels & Diehr 2003). Missing values for 2002 were replaced by the average of two missing value replacement methodologies - Last Observation Carried Forward (LOCF) and the Expectation-Maximization (EM). These methods are accepted for missing value replacement in longitudinal studies when random data are missing (EM preferred – Enders, 2001) or when non-random date are missing LOCF preferred Engels and Diehr (2003). It appears that data in the Jamaican Symmetry Project are missing at random. Specifically no variable was associated with absence at time two. Importantly, FA in 1996 was not related to whether or not an individual had missing FA data in 2002, $r = -0.04$, $p = 0.50$. Since non-random missing values cannot be ruled out due to unmeasured factors, both EM and LOCF methods were used in the current study. After missing values was replaced the sum for all trait averages were 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 averaged across 1996 and 2002 for inclusion as a covariate in the models as body size is correlated with FA (Manning, 1995; Trivers et al. 1999). BMI was square root transformed due to a slight positive skew in the distribution.

Friendliness was measured in 2000. Peer-ratings of friendliness were collected. All subjects rated photographs of their peers for degree of "friendliness" on a Likert scale ranging from 1 (Very unfriendly) to 5 (Very friendly). Sociability was included in this study to determine if individual differences in this variable are positively related to ultimatum game offers. Also I wanted to assess the independent association between FA and offers when sociability was held constant.

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 responders were matched with offers randomly. Subjects were told that they could be matched with any of their peers, whether a male or a female. The players were asked to split $1,000 Jamaican dollars (16 US dollars), equivalent to about two days of wages at the low end of the socio-economic 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 unless their offers got rejected.

Data analyses

Data were analyzed using SPSS version 13. The primary hypothesis was tested using a 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) and composite relative fluctuating asymmetry (FA). This analytic method was used to test whether or not fluctuating asymmetry was correlated with ultimatum game offers independent of the background variables included in the model. To test whether the effects of FA were equivalent across the sexes, a sex x FA interaction term was added to the model. Sex was dummy coded so that "0" represented males and "1" represented females (Aiken & West, 1991; Jaccard & Turrisi, 2003).

III. Results

Descriptive statistics

In this sample the mean offer was 341.91 Jamaican Dollars (out of 1,000; 34.2%) (SD = 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 dollars. Friendliness differed between the sexes whereby females were friendlier than males, t (108) = 4.62, $p < 0.001$. Due to this baseline sex difference, friendliness was included as a covariate. No other sex differences were found among the study variables.

Fluctuating asymmetry and ultimatum game offers

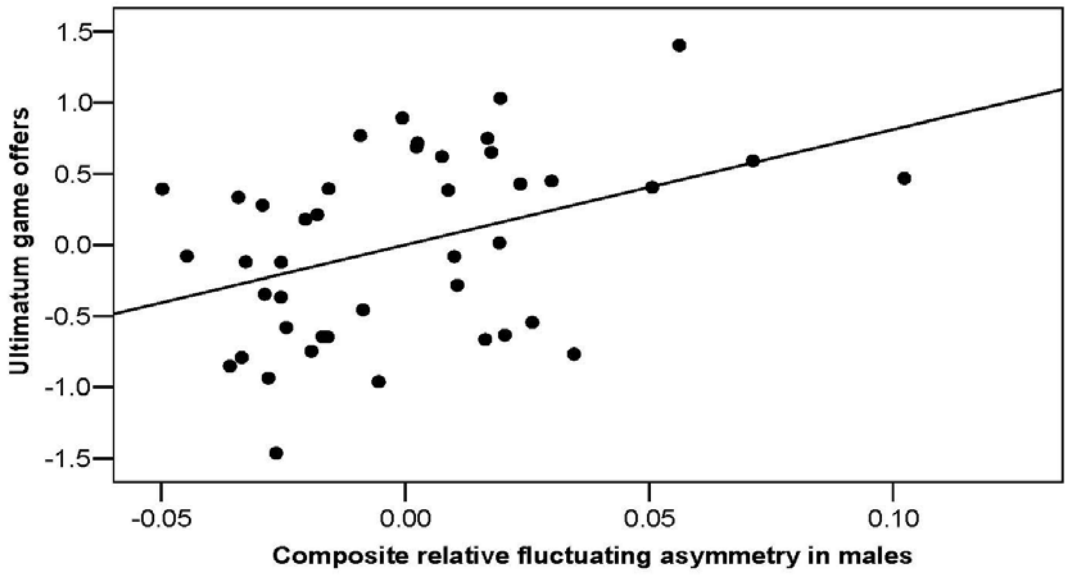
The squared multiple correlation for the entire model was .31, which was statistically significant (F (7,77) = 4.40, $p < 0.01$; Table 1). The standardized regression coefficient for male FA, 0.59, was the association between male FA and offers. FA had a significant positive effect on size of offer in males (t = 4.76, $p < 0.001$). The squared semi-partial 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. Females BMI was negatively correlated with ultimatum game offers, standardized regression coefficient = -0.26, t = -2.12, $p < 0.05$ accounting for 6 percent of offers in the ultimatum game (Table 1). However, male BMI was not related to offers, semi-partial $r^2 = 0.00$, p = 0.59. In other words, women larger for their height made lower offers. Neither female FA nor any other variable were related to offers, all t's < 1.61 and all p's > 0.07 (Table 1).

Fluctuating asymmetry and ultimatum game rejections

Very few individuals rejected offers (n = 15; i.e. < 10%), and so a parametric statistical model cannot be conducted to test whether FA is correlated with amount rejected. Spearman rank correlations were used, but FA was not significantly related to amount rejected (Spearman r = -0.07, n/s).

Figure 4.1: Correlation between male FA and offer size



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

Table 4.1: Standard regression for offer size for males vs. females based on age, BMI, FA

Raw, standardized coefficients, t-values, and partial r squared values from a standard regression in which ultimatum game offer was regressed on age, BMI, FA of player, sex interaction terms for FA and BMI of player for male versus female main effect models.

	Ultimatum Game Offer (Female Offer Model)					Ultimatum Game Offer (Male Offer Model)				
	B	*SE B*	*b*	*T*	*part r²*	*B*	*SE B*	*b*	*t*	*part r²*
Age	.09	.07	-.26	1.22	.02	-	-	-	-	-
Sex	-1.77	1.11	-1.35	-1.60	.04	-	-	-	-	-
BMI[a]	-.06	.03	-.26	-2.12*	.06	-.02	.04	-.09	-.49	.00
BMI*Sex	.04	.05	.55	.78	.01	-	-	-	-	-
FA[b]	.69	3.14	.04	.22	.00	9.31	1.95	.59	4.76**	.25
FA*Sex	8.62	3.66	1.03	2.35*	.07	-	-	-	-	-
Friendliness	.11	.11	.12	1.04	.02	-	-	-	-	-
Constant	2.70	1.02	-	2.65*	-	-	-	-	-	-

Note. [a] Body Mass Index; [b] Fluctuating Asymmetry; "Female Offer Model" sex was dummy coded such that 0 = Female, 1 = Male; "Male Offer Model"
sex was dummy coded such that 0 = Male, 1 = Female;*$p < .05$, ** $p < .01$: (Both Models $R^2 = .31$, $p < .001$). *F (7,77)* – 4.40**.

IV. 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). I join previous research in showing that individual characteristics can bias behavior in economic games. Among traits that have been shown to affect behavior in the ultimatum game are age (Murnighan and Saxon 1998; Hoffmann and Tee 2006), race (Eckel & Grossman, 2001), 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).

My results are the first to find a significant difference between the sexes in the ultimatum game, not as independent variables themselves, but in 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 (Solnick, 2001; Eckel & Grossman, 2001). As I predicted, males with low FA made 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 especially from cooperative relationships with both sexes.

The two sexes appear to develop different strategies in response to an important biological trait (FA). I suggest that this 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 there is a tendency towards "strong reciprocity" varying with FA, where the former 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, 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 FA of their partner is revealed? Likewise, it would be interesting to see how FA affects behavior in other economic games, such as the public goods game. Experiments designed to address these kinds of questions are now underway in Lebanon and Jamaica. Finally, it would be useful to have simultaneous measures of physical attractiveness, aggression and FA for the same sample in the ultimatum game, so as to differentiate alternative hypotheses for the effects observed.

Chapter five: Digit ratio and behavior in a public goods game in Jamaica

I. Introduction

After using the ultimatum game to explore cooperative behavior in dyadic interactions, I wanted to explore cooperative and punitive behavior in groups. I was curious whether individuals would adopt cooperative strategies – different than those in the UG – in an interaction involving three other people and whether they would be more willing to punish group members ithat defect from cooperating than they have in the UG. To explore these issues, I ran a public goods game (PGG) involving both a contribution and punishment stage with Jamaican youngsters in March 2005.

Second to fourth digit ratio

Research suggests that second (index finger) to fourth (ring finger) digit length ratio reflects the degree to which humans are exposed to prenatal androgens during development (Manning 2002). The higher the level of testosterone exposure, the lower the digit ratio (2D:4D) (Lutchmaya et al. 2004; Manning et al. 1998), and the right hand has consistently shown a stronger correlation (Williams et al. 2000; Manning 2002). On average, males have a lower 2D:4D than females and this is seen in children as young as two years old (Manning et al. 1998). In British males, for example, the 4^{th} digit tends to be longer in males, while in females the 2^{nd} and 4^{th} digits in females are equal in length. But, why would finger length be affected by prenatal androgens? The same *Hox* genes

(*Hoxd* and *Hoxa*) are related to both the development and differentiation of the unriogential system and the appendicular skeleton in vertebrates, i.e. gonads and digits (Kondo et al. 1997; Manning et al. 1998). Since genital masculinization is controlled by androgens (Becker et al. 2002), and since digits and genitals develop over similar timeframes (Anders et al. 2006), it is likely that finger length is affected by androgens during development. So, exposure to high prenatal androgens, low prenatal estrogens, or both could result in lower or more masculine digit ratios (Manning 2002; Lutchmaya et al. 2004; Cattrall et al. 2005; van Anders et al. 2006). Studies provide evidence that sex differences in 2D:4D arise from in utero concentrations of sex steroids (Manning 2002; Lutchmaya et al. 2004). For adult males, lower ratios are also correlated with greater sperm count and circulating testosterone concentrations, and for adult females higher 2D:4D with greater estrogen, luteinizing hormone and prolactin concentrations (Manning et al. 1998; Manning et al. 2003). Since hormones show correlations with various behaviors (e.g. Mazur & Booth 1998), 2D:4D is expected to correlate with such behaviors.

In fact, lower 2D:4D is correlated with a number of behaviors and physical traits: greater number of sexual partners in males (Hönekopp et al. 2006a), greater number of children fathered (in males) (Manning et al. 2000), higher levels of courtship behavior in males (Roney & Maestripieri 2004), aggression in wargames (McIntyre et al. 2007), masculine gender identity in females (Csatho et al. 2003), sexual orientation in females (self-identified "butch" lesbianism; Brown et al. 2002) superior ability in males in music (Sluming & Manning 2000) and competitive sports (Manning & Taylor 2001), higher

exercise frequency in males (Hönekopp et al. 2006b), and aggression in males (Bailey & Hurd 2005) and in females (Benerlioglu & Nelson 2004). Lower 2D:4D is also correlated with some other physical traits: good health in males (Manning 2002), higher physical attractiveness in males (Roney & Maestripieri 2004), and physical fitness in both males and females (Hönekopp et al. 2006b). Low 2D:4D is also correlated with lower levels of pro-social behavior in pre-school girls (Williams et al. 2003), and to physical aggression in school boys (Manning 2002).

2D:4D, testosterone and economic games

Because of the negative correlations reported between 2D:4D and testosterone, aggression and pro-social behavior, researchers consistently predicted that low 2D:4D would correlate with low cooperative and high punitive behavior. Results from two economic games are reviewed here. When playing a $40 ultimatum game, males with higher testosterone levels are more likely to reject higher offers (Burnham, manuscript). Offers were constrained to either $5 or $25. Subjects who rejected lower offers had 52% higher testosterone levels, assayed from saliva, than those who accepted these offers. This is consistent with the finding that males with lower 2D:4D state higher minimum accepted offer (MAO) in UG ($p < 0.01$) (Van den Bergh & Dewitte 2006). In this version of the UG, responders do not decide on a real offer; rather, they state the minimum that they would accept and everything else stays the same. Interestingly, this result does not hold when sex cues are introduced prior to playing the game. In one study, after rating 15 photos of females in swimsuits or underwear, heterosexual males with lower 2:4 digit

stated lower MAO compared to those who saw nonsexual photos (Van den Bergh & Dewitte 2006).

One study investigated the effect of 2D:4D ratio on behavior in a hypothetical public goods game (PGG) with multiple rounds (Millet & Dewitte 2006). Subjects received an endowment of 40 points and had to decide each round whether to keep it or contribute to the public account. When contributions reach 100 points, 160 points are distributed among all four group members. Subjects from both sexes with lower 2:4 digit ratio were more likely to contribute their share in order to reach the provision point, but less likely to go under or above what was needed to reach the provision point.

Predictions on 2D:4D and behavior in the PGG in Jamaica

Based on the correlations between 2D:4D and aggression (Manning & Wood, Manning 2002; Benerlioglu & Nelson 2004; Bailey & Hurd 2005) and between testosterone and rejection rates in the UG (Burnham, manuscript), I predicted that both sexes with lower 2D:4D would be less cooperative and more punitive in a public goods game in Jamaica. This was also inspired my data from an UG in 2004 on the same Jamaican population. Digit ratio had no effect on amount offered by both males and females, but showed some significant effect on rejections, where those who punished had lower 2D:4D particularly in the case of females. There were only 14 rejections, two of which were females. Participants with lower 2D:4D ratios rejected higher offers, Spearman $r = -0.73$, $p = .007$.

Since rejections were few, these results were inconclusive. The effect was also primarily due to the only two females who rejected, who also had low 2D:4D.

II. Methods

Participants

One hundred and sixty seven Jamaican young adults (95 males and 72 females; mean age 18.14 years, SD = 1.67, range 15 – 22) from Southfield, of St. Elizabeth parish participated in the public goods game study in March, 2005. Subjects were once again members of the Jamaican Symmetry Project, a long-term study of fluctuating asymmetry in rural Jamaican children (Trivers et al. 1999).

Measurements

Digits were measured from photocopies of subjects' ventral surface of both their right and left hands. Second and fourth digit lengths were measured from the ventral crease to the tip of the finger (see Manning, 2002 for reliability of measurements associated with this procedure) using calipers accurate to 0.01mm. If a finger had multiple creases, the measurement was made from the crease proximal to the palm. All fingers were measured twice to test for reliability. First and second measure correlations were between .995 and .998 (both p's < .001), therefore length measurements were averaged for each digit. Repeated measures ANOVA analyses have shown that between-individual differences in

digit lengths were greater than error differences in the Jamaican sample (Manning et al. 2006).

Friendliness had been measured based on peer ratings. All participants in the Jamaican Symmetry Project rated photographs of all their peers on whether they thought the person looks like could be a friend or an enemy. These ratings were averaged for each subject. So, ratings for every subject included subjects who played the public good game and others who did not.

Public goods game

In each session, two groups of four were gathered at the same time in a relatively big classroom to play a one-round public goods game, each person on a separate desk. Identities of their group members were not revealed to subjects. They knew their group members were going to be three out of the other seven people in the same room at the time. Rules of the game were explained and demonstrated on a chalkboard, and subjects were instructed to make their decisions on paper. Each subject was endowed with 300 Jamaican dollars (equivalent to ~4.8 U.S. dollars) that they could keep to themselves or make a full or partial contribution to their group's public account. Whatever goes in the public account is doubled and then divided among all four members. After subjects made their decisions, papers were collected and filled with information on all three group members' decisions and earnings at the end of the contribution stage. Papers were then returned to subjects in order to complete the punishment stage of the game. Subjects

could see how much money they and how much other group members had contributed and made so far. Subjects now played the punishment stage where they had the opportunity to punish one of their group members by any amount they wish that is no more than 100 Jamaican dollars and writing down the number of the player they wish to punish. Any amount paid to punish was then be doubled and subtracted from the funds made by punished subject. Subjects then filled out a questionnaire on socioeconomic status, why they punished if they did, whether they had any kin in the room and whether they worked or not. Participants received subject payments independent of the outcome of their game.

III. Results

General descriptive results

By the end of the contribution stage, 88.6% of subjects contributed to their groups' public account. Contributions ranged from 20 to 300 Jamaican dollars, mean = 111.07 and SD = 79.16 Jamaican dollars (i.e. 37.02% with 26.39% SD). There were no sex difference whatsoever in contribution and punishment rates and values between males and females. Although males and females did not differ in their contributions, males contributed slightly more than females and more females made contributions than males (table 5.1). For the punishment stage, 47.9% of subjects punished and the mean punishment was 59.5 Jamaican dollars (ranging from 10 to 100 and SD = 23.9). Women punished more often than males but males paid more towards punishment than females (table 5.1).

Table 5.1: PGG contribution and punishment distributions

	Contributed		Contribution			
	Yes	No	N	Mean	SD	Range
Total	88.6%	11.4%	148	41.77%	24.21	6.67 – 100
Males	85.3%	14.7%	81	44.79%	25.63	6.67 – 100
Females	93.1%	6.9%	67	38.13%	20.02	6.67 – 100
P-value				0.091		

	Punished		Punishment (≤100 J.D.)			
	Yes	No	N	Mean	SD	Range
Total	47.9%	52.1%	78	59.49 JD	23.90	10 – 100
Males	41.1%	58.9%	38	64.74 JD	25.12	10 – 100
Females	56.9%	43.1%	40	54.50 JD	21.83	20 – 100
P-value				0.058		

2D:4D and contributions

With data pooled for both sexes, there was no relation between whether subjects decided to make a contribution or not to their group's public account and their 2D:4D. Nor was there a relation between the amount of contribution (when they did contribute) and

subjects' 2D:4D (table 5.3). But, split by sex, males who tended to make contributions had higher 2D:4D ratios (p=0.025; see table 5.2). The correlation did not hold for females.

Table: 5.2: Male contribution and average 2D:4D

Males average 2D:4D

Contributed	N	Mean	SD	SE Mean	(F)	p-value
Yes	68	0.943	0.032	0.004	5.236	0.025
No	10	0.930	0.047	0.015		

Table: 5.3: Contribution size and average 2D:4D

Average 2D:4D	Statistic label	Statistic
Males & females	R-value	0.038
	Sig. (2-tailed)	0.658
	N	138
Males	R-value	0.150
	Sig. (2-tailed)	0.190
	N	78
Females	R-value	-0.160
	Sig. (2-tailed)	0.222
	N	60

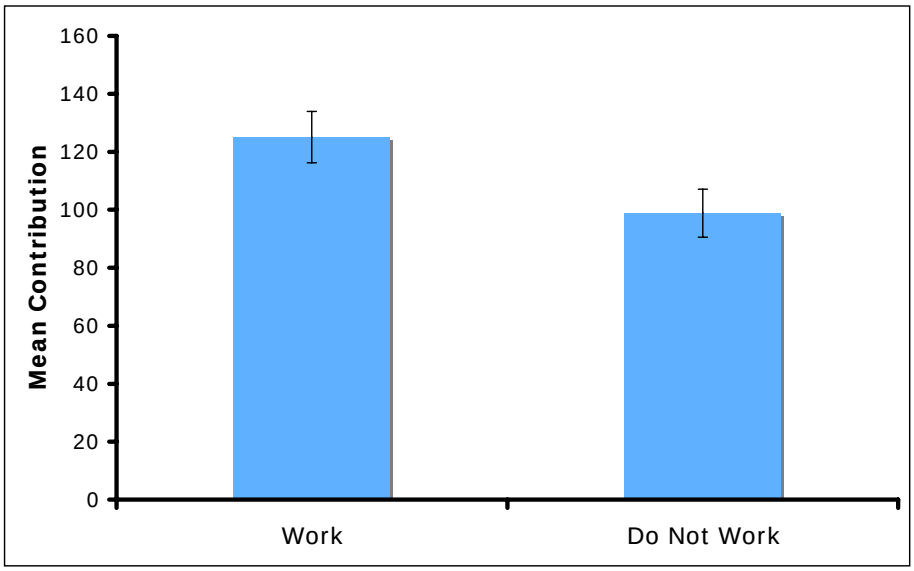
Friend and contribution size

Interestingly, there was a negative relationship between peer friend ratings and contribution size. For both sexes combined, there was a negative correlation between the average friend rating and contribution amount: $R(75)=-0.275$, $p=0.017$. A Kolmogorov-Smirnov test for normality determined that "contribution amount" is not normally distributed. Grubbs test identified that this was not due to outliers (all $p>0.05$). A Spearman's Rho correlation (rank order correlation), which does not assume normality, showed that the correlation is robust ($Rs(75)= -0.254$, $p=0.028$).

Work and contribution size

There was no relation between whether subjects worked and whether they contributed or not, but those that worked contributed more and that was highly significant [$F(1,165)=8.209$, $p=0.005$] (fig. 5.1).

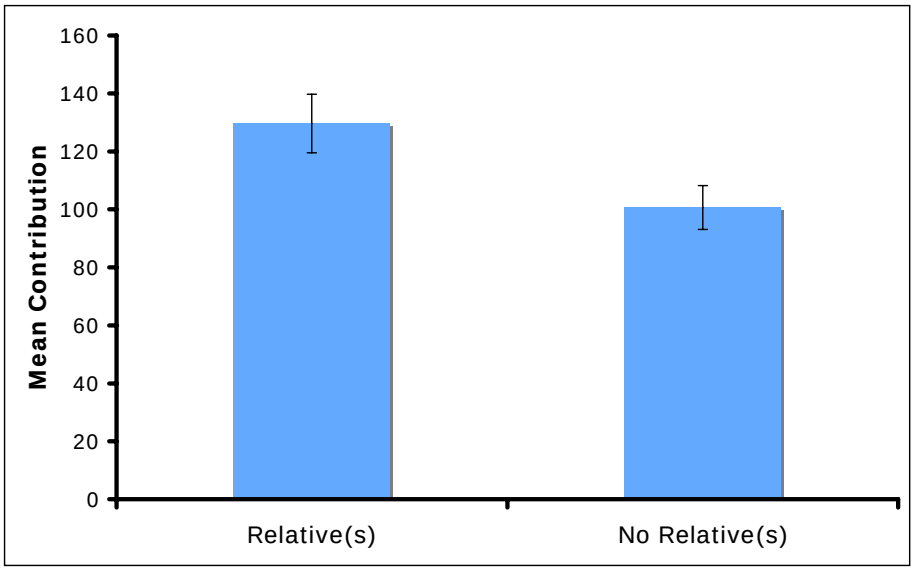
Figure 5.1: Contribution size and work status (F(1,165)=8.209, p=0.005)



Relatedness and contribution size

Subjects who reported that there were relatives of theirs in the same room with them at the time of playing the game, i.e. at least one person out of the seven remaining subjects for the same session was a relative, contributed more than those who did not, and the result was significant [F(1,165)= 5.286, p=0.023] (fig 5.2).

Figure 5.2: Contribution size and presence of relatives (F(1,165)=5.286, p=0.023)



Contribution, rank and punishment

There was a negative correlation between those who punished and their rank, i.e. where they are with respect to the rest of their group in terms of amount of money made after the contribution stage (with 1 ranking highest and 4 lowest) R(37)=-0.308, p=0.064. In other words, those who punished were more likely to be those who earned less money in comparison to other group members.

Consistently with the above, there was a significant negative correlation between the rank of the player who was punished and the amount of money this player contributed

(R(58)=-0.315, p=0.016)). This means that of those punished, higher earners had contributed less.

The strong but not significant result suggesting low rankers were more likely to punish seems to be driven by the fact that those ranking second were the most likely to punish, and the ones most to be punished were those who ranked first (table 5.4). This was similar for the both sexes and so the two sexes are reported together.

Table 5.4: Frequency of punishers and punished distributed by rank (1= earned highest in group, and 4=lowest)

	Punisher		Punished	
Rank	N	Percentage	N	Percentage
1	25	33.8	33	57.9
2	29	39.1	14	24.6
3	11	14.9	7	12.3
4	9	12.2	3	5.3

Digit ratio and punishment

Among females, those with low 2D:4D punished more often (right 2D:4D R(60)=0.386, p=0.002; average 2D:4D: p=0.052). There was no effect for males. Interestingly, for

females, there was a positive correlation between 2D:4D ratios and the amount females put to punish (average 2D:4D R(60)=0.352 p=0.002 (fig. 5.3), and right 2D:4D r(60)=0.386, p=0.002). There was also a positive correlation between 2D:4D and the amount females paid to punish as a percentage of what they had earned average 2D:4D (R(60)=0.260 p=0.045 (fig. 5.4), and right 2D4D R(60)=0.313, p=0.015). No such effects were revealed for males.

Figure 5.3: Female average 2D4D and punishment value (R(60)=0.352 p=0.002)

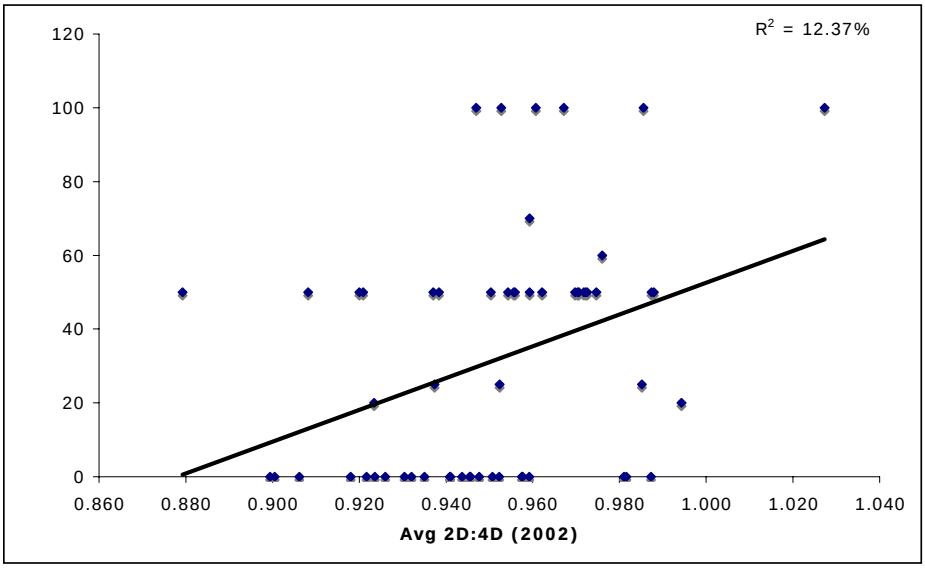
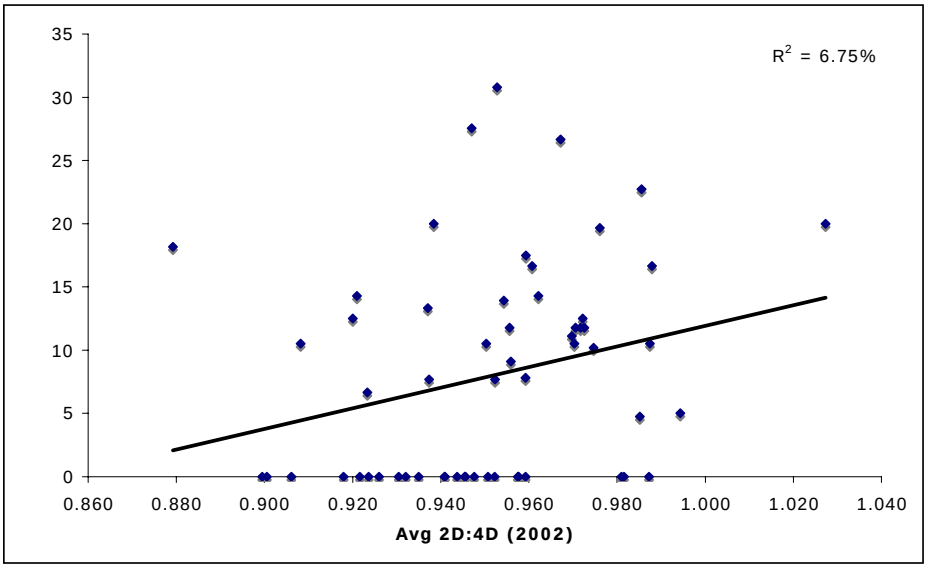


Figure 5.4: Female average 2D4D and percentage of punishment from money earned (R(60)=0.260 p=0.045)



IV. Discussion

The majority of subjects contributed to their groups' public account and a bit less than 50% of them punished others. While there was no effect of digit ratio of whether both sexes contributed or not, digit ratio positively correlated with males' contribution size. Recall that there is a negative relation between 2D:4D and aggressive behavior and also with physical abilities. Results for FA have the same pattern. Recall also that there was a positive correlation for males between FA and offer size in the UG (2004 in Jamaica, chapter four). It was proposed that because of their greater ability in obtaining resources, low FA males do not have to be as cooperative as higher FA males. Consistently, the

same logic applies here. Higher 2D:4D males are expected to benefit more from a series of cooperative interactions with others, and thus would benefit more from making higher contributions to the group account.

As for punishment, females with lower 2D:4D were more likely to punish, but interestingly, those with higher 2D:4D ratios invested more in their punishment. The negative relation between 2D:4D and aggression in females might explain females' tendency to bear some cost to inflict some on others. Higher 2D:4D being positively correlated with levels of estrogen, likelihood of being married and greater reproductive success suggests that it correlates with good quality and mate choice. In effect, high 2D:4D females are likely to be receivers of gifts and resources, for example, as part of courtship or parental investment. Resources being more accessible to them might lead them to invest more in punishment.

There were no correlations between males' 2D:4D and whether they punished or not, or with the amount they paid to punish (when they did). Recall results given from Van den Bergh and Dewitte (2006); there was a negative correlation between MAO and 2D:4D, i.e. those who had lower digit ratios stated higher MAO. The correlations disappeared showed up after subjects were presented with a sexual stimulus. When subjects in my study played the PGG, other people of both sexes were around. So, perhaps the presence of females had the effect of sexual stimulus leading males to refrain from punishment. Males seeking a mating opportunity would surely not benefit by punishing females, and would benefit more by refraining from punishing males. Not punishing other males

would entice a sense of coalition among males, and this would be helpful in decreasing competition for females.

Final words on punishment and strong reciprocity

For proponents of strong reciprocity, people punish norm violators for the sake of the group's benefit, and this is supported by results from the PGG. My view is that in a PGG, subjects' self-interest is hardly irrelevant to their decision to punish. They are affected directly by what other players contribute to the common account. But, if the goal of punishing is to deter norm violators in a group, then it would be expected that punishers would be the most generous contributors and it would not be expected to find punishers among the least generous contributors. As Gintis and colleagues put it (2003), "The strong reciprocity interpretation suggests that high contributors will be high punishers, and punishees will be below-average contributors." My results disprove these expectations.

In addition to punishing players who contributed less than they did (n=41), Jamaican participants in the PGG also punished players who contributed the same amount as they did (n=12) and those who contributed even more than they did (n=21). These results are hard to explain on the basis of group benefit. Why would an individual punish someone for the contributing same amount or more than he/she did? In my view, these behaviors are driven by competition and self-interest enhancement. Since players knew how much each player contributed and also earned, it makes sense to look at the rank of both the

punisher and the punished and understand punishment as possibly motivated by cutting down on others' payoffs. Some participants asked me in private during the punishment stage to help them do their calculations. They ranked second highest in terms of amount earned after contributions had been made and wanted to know the minimum amount they need to pay to exchange ranks with the first ranking. When asked why they wanted to punish, some said, "I want them to lose money," and "I didn't want them to make a lot of money." Individuals appear willing to bear some cost so as to prevent others from gaining access to a bigger resource or from obtaining some resource equivalent to what they have received. This is supported when looking at frequencies of punishment with respect to ranks. The most frequent case of punishment was second ranking punishing first ranking (n=23), followed by first ranking punishing the player who ranked first alongside with him/her (n=12), followed by first ranking punishing second ranking (n=8), followed by fourth punishing first (n=7) and third punishing first (n=7), and others (n=11). Same rank punishment could be viewed as a tendency to eliminate competition, and lower rank punishment as a tendency to increase loss for others and enhance own status by widening the gap between self and other. Punishing higher ranking is probably driven by spite as a response to others' failure to cooperate.

Chapter six: Ultimatum game in Lebanon

I. Introduction

In chapter four, I found a negative correlation relation between Jamaican males' bodily FA and offer size in Jamaica. As discussed earlier, FA is an important biological measure that reflects degree of environmental stability in a wide range of organisms, including humans. It negatively correlates in humans with dancing ability, attractiveness and physical ability, among others (Brown et al. 2005; Møller & Swaddle 1997; Polak 2004; Møller 2006). Being an important biological trait, it was expected that individuals adjust their cooperative strategies according to their degree of bodily FA. Since low FA males are stronger and have better access to resources, it was predicted that they would bear less cost to initiate a system of benefit exchange. Higher FA males would benefit more from a system of trading of favors and those would be more motivated to pursue such a system.

Being an important biological measure, FA is expected to be important in other human populations. So I set out to investigate whether symmetrical males in Saida, Lebanon, would adopt cooperative strategies similar to what Jamaican males, as associated with their degree of bodily symmetry. In, particular, would low FA Lebanese males make lower offers like Jamaican males did? One difference is that this time instead of using bodily symmetry, I explored facial symmetry. Bodily symmetry has been shown to correlate with facial symmetry for males in Jamaica. And so I expected the same trend to occur for males in Lebanon using facial symmetry.

Furthermore, Takahashi et al. (2006) have shown that in four other economic games, male defectors are rated 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 (Gangestad et al. 1994; Thornhill & Gangestad, 1999; Hughes et al. 2002; Brown et al. 2005), low facial FA males – being capable of obtaining resources on their own rather than being more dependent on a series of reciprocated exchanged from others – are likely to offer less than high facial FA males.

For females, I expected the opposite effect. More symmetrical females are going to offer more than asymmetrical ones. While resources are probably more abundant to symmetrical females having higher reproductive value, they would not be so for asymmetrical ones. So, symmetrical females could afford to be more generous unlike asymmetrical ones who are predicted to hold on to as much they could as possible. However, since no effect was found in Jamaican females, it was likely that none would be found either in Lebanon.

Femininity and Masculinity of faces

In addition to looking at facial symmetry, I also looked at facial masculinity and femininity. An average male's face is a shape based on combining and averaging 600 faces into a template, which is later used to measure how much other faces deviate from it. The same applies for an average females face. Studies have shown that femininity in females and masculinity in males to be attractive (Perrett et al. 1998). It is thought that femininity/ masculinity may be cues to heritable fitness benefits and so related to attractiveness. Femininity of the face shape is also associated with youth (Perrett et al. 1998), and, therefore, male preferences possibly reflect attention to youth, an indicator of fertility and fecundity (Buss and Barnes 1986). Males also prefer feminine female faces (Cunningham 1986; Jones and Hill 1993; Grammer and Thornhill 1994).

If femininity of female faces act as cues about youth and fertility and are thus attractive, then females sending these cues have higher reproductive value and so likely to receive gifts and resources from males as courtship. So, these females are expected to act more generous due to availability of such resources or as a way of sending off another cue indicating higher quality. If females can afford to spend some resources, then this is an honest signal of their quality in terms of the abundance of their resources.

I also tested whether 2D:4D and WHR showed any correlations with offer size in the UG. Since low 2D:4D has been shown to correlate with more aggressive behavior (Manning 2002) and better physical abilities (Hönekopp et al. 2006b), individuals with lower digit

ratios were expected to offer less and reject more often (assuming enough rejections were generated). For females, low WHR is another signal of good quality, the same logic behind symmetrical females being generous applies here. Low WHR females were expected to be more generous. However, which did not have an effect on offer size and rejection rates in Jamaica would be important in another population. Finally, I also explored whether subjects birth order had any effect on behavior in an UG.

II. Participants and methods

One hundred and sixty six young adults from the Quala' Secondary School in Saida, Lebanon played the ultimatum game in January of 2006 (76 females; age range 15-18 years old, mean=16.26 years and SD=0.85 and 90 males; age range 14-18 years old, mean=16.19 years, and SD=0.93). To prevent subjects from exchanging information on the game, all subjects played the game on the same day and within the same three hours. Subjects were brought in as groups to a big hall to play the ultimatum game. As soon as the group finished the game, subjects were sent back to their classrooms to resume their school day, and so they never got the chance to interact with someone who had not played the game yet. Each subject was seated individually on a desk with significant distance from other subjects. Subjects were not permitted to talk or share any information with any other person. Offer and response sheets were distributed. The game was explained and subjects were asked to indicate the offer they would like to make. Papers were then collected, shuffled and redistributed back to subjects. Subjects had no means to

trace back identity of proposers. Papers were then collected again at which point body measurements were taken.

Subjects' both left and right hands were scanned on a CanoScan LiDE. Scans were later measured for 2D:4D using computer software, autometric 2.2. Tape measure was used to measure waists and hips for males and females. Face front photos were also taken for subjects. Facial symmetry and masculinity/femininity trends were measured using computer software psychomorph 8.4.7.0 (copyright of University of St. Andrews). Template for symmetry, masculinity and femininity are each separately compiled from 600 faces (femininity, all females; masculinity all males; and symmetry, both sexes) These photos were used in a later project in Jamaica (March 2006). Data regarding age and birth order were also collected.

III. Results

Offer size

One hundred and sixty six subjects played the ultimatum game. Mean offer for all subjects was 45%, 46.4% for females and 43.8% for males. The difference was not significant ($t_{164} = 0.92$, $p = 0.358$) (see table 6.1).

Table 6.1: Distribution of offers made in the UG

	Mean (%)	n	mode	range	SD	SE
All	45.00	166	50	0 – 100	17.75	1.38
Female	46.38	76	50	0 – 100	13.82	1.59
Male	43.83	90	50	0 – 100	20.50	2.16

No sex difference ($t_{164} = 0.92$, $p = 0.358$)

Proposers' traits and offer size

A multiple regression model shows no significant effects for any of these four variables: 2D:4D, WHR, age, and the sum of vertical and horizontal facial symmetry (see table 6.2). For females age would have been significantly negatively correlated with offers ($p=0.0034$) if the overall model had been significant. But this effect seems to be driven mainly by two 15 year-olds who offered 100% while no other females offered so much. However, looking closer at females, both FA ($p=0.0495$) and age ($p=0.0037$) are significantly negatively correlated with offer value. No pattern whatsoever was found for males for any of the variables.

Table 6.2: Multiple regression for 2D:4D, WHR, age and sum of vertical and horizontal facial symmetry, and then with sex as an added variable.

	F	R^2	P
Total	$F_{4, 158} = 1.75$	0.042	0.14
Females	$F_{4, 71} = 2.7$	0.13	0.037
Males	$F_{4, 82} = 0.33$	0.016	0.86
Sex as a variable	$F_{5, 157} = 1.42$	0.043	0.22

Femininity and masculinity of faces and offer size

The index of masculinity that is based on facial measurement Z-scores separates males (mean = 1.36, SE = 0.23) and females (-1.61 +/-.31) ($t_{164} = 7.52$, $p < 0.0001$). Masculinity was added in as a variable in the multiple regressions with offers made. Other variables were mean 2D:4D, WHR, age, sum of horizontal and vertical facial FA (table 6.3)).

Table 6.3: Multiple regression for 2D:4D, WHR, age, sum of vertical and horizontal facial symmetry and masculinity, and then with sex as an added variable.

	F	R^2	P
Total	$F_{5, 157} = 1.41$	0.043	0.22
Females	$F_{5, 70} = 2.20$	0.14	0.064
Males	$F_{5, 81} = 0.28$	0.017	0.92
Sex as a variable	$F_{6, 156} = 1.21$	0.045	0.30

So, this led to a stepwise regression. For all the variables so far (age, sex, WHR, mean 2D:4D, summed facial symmetry, masculinity), the best model included only age, but it explained little variation in offers: $F_{1, 161} = 4.08$, $p = 0.045$, $R^2 = 0.025$. Once again for females the best model included both age and symmetry. Both age and FA negatively correlated with offers ($F_{2, 73} = 5.34$, $p = 0.0068$, $R^2 = 0.13$). For males, no model was significant.

Rejections and acceptance and sex

There were 30 rejections (18%), 14 by females and 16 by males (see table 6.4), and there was a sex difference trend ($p = 0.072$). There was no difference between males and females in the number of offers rejected. Females rejected 14 out of 76 (18.4%) and males 16 out of 90 (17.8%), and for both approximately 18%. With the contingency correction for a 2x2 table, Chi square (df=1) = 0, p>.999. There was also no sex difference in the value of offers accepted between males and females (see table 6.4).

Table 6.4: Distribution of offers rejected

	Mean (%)	n	range	SD	SE
All	25.67	30	0 – 60	18.22	3.33
Female	19.29	14	0 – 50	16.85	4.50
Male	31.25	16	2.5 – 60	18.01	4.50

Weak sex difference ($t_{28} = 1.87$, $p = 0.072$)

Most offers were accepted (82%), and there was no sex difference in what males and females accepted (table 6.5).

Table 6.5: Distribution of offers accepted

	Mean (%)	n	range	SD	SE
All	49.27	136	10 – 100	14.58	1.25
Female	50.48	62	10 – 100	13.84	1.76
Male	48.24	74	20 – 100	15.18	1.77

No sex difference ($t_{134} = 0.89$, $p = 0.374$)

Birth order and offer size

I also tested whether the order at which subjects were born had any effect of their offer size. They were divided in three categories, first born, middle born and last born. Birth order had no effect on size of offers: mean offer size for first born = 45.63 +/-2.25 (n=68), middle = 45.69 +/-2.49 (n=58), last = 44.03 +/-2.30 (n=36); ANOVA $F(2,159)=0.12$, $p=0.89$. There was no effect on offer size also when split by sex (for females, $F(2,71)=1.08$, $p=0.35$ and for males, $F(2,85)=0.49$, $p=0.61$).

IV. Discussion

Consistent with results from the Jamaican simple UG (2004, chapter four), 2D:4D did not have an effect on offer size or rejection results. The same applies for WHR. This again

could be due to the low rejection frequency. Little analysis could be done with few rejections.

The only interesting finding was the negative correlation between female's age and facial FA (both vertical and horizontal) with offer size. In other words, younger and more symmetrical females offered more. Lower FA females have been rated as more attractive. Having higher reproductive value, symmetrical and younger females are expected to be recipients of gifts and courtship. In one sense, they can afford to be generous, in which case the cost they bear is small in comparison to the benefit the receiver gets. On the other hand, being generous may also count as an honest signal of quality. The fact that these females can afford to squander some resources may signal their true good quality.

The negative correlation between symmetry and offer size found in Jamaican males (chapter four) was not repeated here. Recall that the Jamaican finding was based on bodily asymmetry while in the Lebanese study, I used facial symmetry. Recall also that in Jamaica a positive correlation was found for facial and bodily symmetry. Bodily symmetry may be a better measure of physical ability, and so a better measure of the individual's ability to access resources. Given that males who would benefit more from reciprocal exchanges would be inclined to initiate cooperation more often, bodily symmetry for males could have a stronger effect on cooperative strategies than facial symmetry would. It would be interesting to go back and measure subjects for bodily symmetry and see if results from Jamaica would then be repeated. One difference that might explain the non-repeatability of results is that it could be that in Jamaica physical

ability is more directly related to obtaining resources. Many of the subjects earn their living from farming and construction. In Lebanon, subjects are full-time students and almost no one works, even part time. Their resources are directly obtained from parents.

Chapter seven: Player two's quality and the ultimatum game in Jamaica

I. Introduction

Having shown that a male's bodily symmetry affects the amount he offers as player 1 (or proposer) in an ultimatum game, I set out to investigate whether offers by player 1 are influenced by player 2's (or responder's) facial symmetry and attractiveness – if the game is still played anonymously. I also tried to induce rejections by making subjects imaginary low offers, i.e. by presenting offers to subjects claiming that offers were offered by real people.

Previous relevant research

There has been some research revealing an effect of attractiveness on behavior in the UG. After playing a strategy ultimatum game, university students in one study were photographed and rated on attractiveness by 20 judges from another university (Solnick & Schweitzer 1999). The most and the least attractive 6 pictures for males and females were shown to another group of 108 subjects. The 108 subjects played as proposers and responders by stating their offer and their MAO (minimum accepted offer). The study did not reveal significant differences in what attractive people offer or report as the minimum they would accept. Nevertheless, attractive people *were* offered more and the MAO expected from them was higher. Joergensen and Hancock (2001; cited in Hancock & DeBruine 2003) reported an ultimatum game where proposers saw a picture of the

responder. Offers made to faces rated as attractive were higher made by both sexes, and the effect was stronger for attractive women than for attractive men.

More recently, Takahashi et al. (2006) have shown that in four other economic games, male defectors (those who decide to take from another allocation rather than give from their own) are judged (from photos) to be physically more attractive than male cooperators, while no such effect is found in females. The authors suggested 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.

General predictions

Given that people typically offer more to people rated attractive (by others), and given that low FA individuals (of both sexes) are consistently rated as more attractive than high FA individuals (Gangestad et al. 1994; Thornhill & Gangestad 1999; Hughes et al. 2002; Brown et al. 2005), I predicted that player 2's degree of symmetry is likely to affect player 1's offer. The more symmetrical player 2 is, the higher the amount would be offered to him/her. Moreover, I also investigated whether player 2's symmetry correlated with his or her attractiveness ratings, and whether player 2's attractiveness ratings, independent from symmetry, had any effect on player 1's offer.

II. Methods

Participants

One hundred and seventy two young adult (96 males and 76 females) (mean age 18.17 ± 1.73) Jamaicans from Southfield district of St. Elizabeth parish played three ultimatum games in March of 2006. The sample comprised part of the Jamaican Symmetry Project, a long-term study of fluctuating asymmetry in rural Jamaican children (Trivers et al. 1999). Some subjects who played in 2006 had already participated in the 2004 study of FA and ultimatum game (n=130).

The ultimatum game

Subjects were brought individually into a room to play the games. They were told that they were going to play the ultimatum game three times and each time with a different person. Recall that in an ultimatum game, a proposer (player 1) is given an amount of money to split with a responder (player 2). The proposer suggests 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. In the first two games, subjects were shown photos of opposite sexed individuals. Photos were taken from 166 young adults from Lebanon who played the ultimatum game in January 2006 see chapter six). Photos were taken with face front and were expressionless. I had already measured these photos for facial symmetry

and selected the five most symmetrical and the five least symmetrical individuals. Jamaicans played two UGs with one photo from each set, i.e. one with a highly symmetrical individual and the other with a highly asymmetrical one, always the opposite sex of the proposer. Subjects were first presented with one photo, asked to make an offer to this person and then presented with the second photo to make another offer. Individuals in the photo had neutral expressions. For each game, they were allocated 1,000 Jamaican dollars, equivalent to 16 US dollars to make their offers from. They were told that individuals in the photos came from a different country, and they had already decided on how much they would accept. Offers below 30% were rejected and offers of exactly 30% were rejected with a probability of 1/3. The latter strategy was chosen to confuse subjects before they came to play in case subjects were sharing information on what they offered and how much money they made. In the third UG, they were presented with an offer of 100, 200 or 300 Jamaican dollars to respond to. They were told that a third individual from another country has made them the offer to respond to.

After playing all three games, subjects rated the two photos on a scale of 1 to 5 on attractiveness (with 1 being very unattractive, 5 very attractive, and 3 neither or neutral) and reported whether they thought the person in the photo looks like “could be a nice person” or “not too nice”. If they made different offers to the two photos, they were asked why they gave more to one than the other. The niceness ratings and the question on why they gave more were not in the original design of the project. I was interested in whether there were any correlations between symmetry and niceness ratings, in addition to attractiveness and niceness ratings. I was also curious whether rating somebody as nice

was related to making this person a higher offers. So, this part of the project was run in a more relaxed yet systematic way, and in a conversational manner.

I went back in March 2007 and played 16 more games. Results reported in the following two sections *Photos' degree of FA and offer value* and *Order of photo presentation and offer value*. The remaining results will not include data from these 16 extra games.

III. Results

Throughout the result and discussion sections (and for the sake of brevity), I will use the term symmetrical photos, to refer to stimulus photos of Lebanese subjects acting as responders that were the 5 most symmetrical (low FA), and the term asymmetrical for the 5 least symmetrical (high FA).

Correlations with the UG in 2004

Before reporting any results on subjects' behavior in this ultimatum game, I investigated the correlation between subject's behavior in the UG in March 2004 and March 2006. Furthermore, a directional bias might also indicate that there was some learning involved from the previous game which again might confound the variables of interest. Results show that there was no pattern between the two games, with total amount offered to both pictures $p = 0.94$, r-squared < 0.001; with size of first offer only $p = 0.61$, r-squared =

0.001. An individual's behavior in the ultimatum game of March 2004 does not predict his or her behavior in response to photos in 2006.

Photos' degree of FA and offer value

When all 188 subjects were pooled together, there was significant tendency (p=0.032) for subjects to give more to symmetrical than asymmetrical photos. (See table 7.1.)

Table: 7.1 Distribution of offers with respect to photos' degree of symmetry

	More to symmetrical % (N)	Offer to symmetrical Mean ± SE	More to asymmetrical % (N)	Offer to asymmetrical Mean ± SE	Equal to both %(N)	P
Total	47.3 (89)	385.75 ± 12.83	29.3 (55)	365.77 ± 13.21	23.4 (44)	0.032
Males	44.3 (47)	394.53 ± 17.06	31.1 (33)	377.03 ± 17.23	24.5 (26)	0.19
Females	51.2 (42)	374.39 ± 19.52	26.8 (22)	351.22 ± 20.53	22 (18)	0.072

When offer sizes are split by sex of player, there is no significant effect of sex (with total amount offered, unpaired $t_{186} = 0.94$, $p = 0.35$. Results are also not significant if compared just within symmetrical or asymmetrical, as symmetrical – asymmetrical, or if analyzed in repeated measures ANOVA).

Order of photo presentation and offer value

Recall that for some trials the more symmetrical face was presented first followed by the less symmetrical face. The order was reversed for other trials. I tested whether the order in which the photos were presented had an effect on offer size. There is no significant effect of the order in which photos were presented (see table 7.2). If symmetrical offered first (n = 126), mean symmetrical -asymmetrical was 28.25 ± 11.56. If asymmetrical offered first (n = 61), mean symmetrical - asymmetrical was 0.74 ± 15.31 (t185 = 1.39, p = 0.17).

In 2-way ANOVA with order and sex (dependent variable = symmetrical –asymmetrical), neither is significant (order p=0.20, sex p=0.81), nor is interaction (p=0.70). For males, if symmetrical offered first mean = 29.56, if asymmetrical = -4.08; for females means are 26.72 and 8.70.

If symmetrical photo were presented first (n = 126), mean offer to symmetrical was 383.49 ± 15.51 and to asymmetrical was 355.24 ± 15.66. If asymmetrical photo was presented first (n = 61), mean offer to symmetrical was 390.98 ± 23.36, and to asymmetrical was 390.25 ± 24.47. In repeated measures ANOVA order, symmetrical /asymmetrical interactions are not significant.

There was also no significant effect order on total offer size. When symmetrical photo was presented first, the total was 738.73 ± 28.95. When asymmetrical first, the total was 781.23 ± 45.33 (t185 = 0.81, p = 0.42).

Table: 7.2: Photo order effect on offer size

	Symmetrical first	Asymmetrical first	P
N	126	61	
Mean offer ± SE Symmetrical Asymmetrical	 383.49 ± 15.51 355.24 ± 15.66	 390.98 ± 23.36 390.25 ± 24.47	0.42
Mean (sym – asym) ± SE	28.25 ± 11.56		0.17
Mean (asym – sym) ± SE		0.74 ± 15.31	

Photos' attractiveness ratings and offer size

Subjects offered more to photos they thought were attractive. A comparison of amount offered to photo judged to be more attractive vs. photo judged to be less attractive shows: paired t_113 = 2.94, p = 0.004, mean difference = 36.62. The highly significant difference was mostly due to males: (paired t_61 = 2.58; p=0.012; mean difference = 47.18) as effect in females was not significant (paired t_51 = 1.46; p = 0.15; mean difference = 24.04) (table 7.3). There is no difference in this distribution between males and females (Chi-square=0.60, df=2, p=0.74).

Table: 7.3: Comparison of amount offered to photos judged to be more attractive versus photos judged to be less attractive

	How many offered more to the more attractive photo % (N)	Mean offer to the more attractive photo ± SE	How many offered more to the less attractive photo % (N)	Mean offer to the less attractive photo ± SE	Equal to both %(N)	P=
Total	46% (66)	370.79 ± 15.06	19% (27)	334.17 ± 16.51	15% (21)	0.004
Males	56% (35)	393.87 ± 20.46	23% (14)	346.69 ± 22.57	21% (13)	0.012
Females	60% (31)	343.37 ± 21.84	25 % (13)	319.23 ± 24.30	15% (8)	0.15
Total: Paired $t_{113} = 2.94$, p = 0.004, mean difference = 36.62 Males: Paired $t_{61} = 2.58$, p = 0.012, mean difference =47.18 Females: Paired $t_{51} = 1.46$, p = 0.15, mean difference = 24.04						

I also tested the relation between photo attractiveness ratings by the proposer and the amount offered. I used the difference in attractiveness rating between the 2 photos, and ran a correlation with the difference in the size of the offers. The difference in attractiveness rating versus the difference in offer size was almost significant (F(1,164)=3.18, p=0.08, R-squared=0.019), and this was due primarily to the effect in males (F(1,92)=2.40, p=0.12, R-squared=0.025); for females (F(1,70)=0.71,p=0.40, R-squared=0.01).

If the symmetrical photo was rated more attractive, there was a tendency to give

more to symmetrical photos (mean difference in offer size=37.99 +/-12.77, n=102). If rated less attractive, subjects tend to give more to asymmetrical photos (30.77+/-45.48, n=13). And if rated the same, subjects tend to give close to the same amount (2.55 +/-13.10, n=51); ANOVA with 3 categories (symmetrical is more attractive, less attractive, same): F(2,163)=2.73, p=0.069).

I also tested whether subjects who rated both photos equally attractive gave them the same offer. The modal difference in offers was zero (17 of 51) and 37 of 51 were within $100. 18 offered more to the symmetrical photo, 16 to asymmetrical. For males, 10 of 32 gave the same amount to photos rated equally attractive (10 gave more to symmetrical, 12 to asymmetrical), 24 of 32 within $100. For females, 7 of 19 gave the same amount to those rated equally attractive (8 gave more to symmetrical, 4 more to asymmetrical), 13 of 19 within $100.

Degree of symmetry of photos and their attractiveness ratings

Symmetrical opposite sex photos were judged to be more attractive than asymmetrical ones by both sexes (on a scale of 1 to 5, with 5 being very attractive). The mean attractiveness rating for symmetrical photos was 4.04 ± SE=0.077 while it was = 3.21 ± SE= 0.088 for asymmetrical photos. (Paired t165 = 7.97, p <0.0001, mean difference = 0.83 (N = 166).)

This was also highly significant when split by sex of raters: for males alone, t93 = 5.41, p

<0.0001, mean difference = 0.78; symmetrical photos ratings = 4.10 ± 0.11, asymmetrical photos ratings = 3.32 ± 0.12; for females alone, t71 = 5.98, p < 0.0001, mean difference = 0.89; symmetrical photos ratings = 3.96 ± 0.11, asymmetrical photos ratings = 3.07 ± 0.13.

Because symmetrical photos tended to be rated more attractive, I also considered how offers varied with the symmetrical and asymmetrical photos along with attractiveness ratings. Among symmetrical photos, there was no correlation between attractiveness rating and offers made: F(1,164) = 0.68, p=0.41, R-squared=0.004 (females only: F(1,70) = 0.020, p=0.89, R-squared=0.0003; males only: F(1,92) = 0.72, p=0.40, R-squared=0.008)

But for asymmetrical photos the correlation is nearly significant (F(1,164) = 3.67, p=0.057, R-squared=0.016). This effect is mostly due to females (F(1,70) = 3.04, p=0.086, R-squared=0.028); for males there was no effect (F(1,92) = 0.78, p=0.38, R-squared=0.008).

Degree of symmetry of photos and their niceness ratings

Subjects were more likely to rate both symmetrical and asymmetrical photos as nice than as not nice. However, there was a tendency for symmetrical photos to be rated as nice (83.6% nice) more often than were asymmetrical photos (72.4% nice). This difference is almost significant (p = 0.057).

For symmetrical photos, there was no significant difference in attractiveness ratings of photos judged to be nice (mean attractiveness nice = 3.99 ± 0.10) vs. not nice (not too nice = 3.74 ± 0.23 (t_114 = 1.01, p = 0.32)). For asymmetrical photos this difference was significant. For those judged to be nice, mean attractiveness was 3.28 ± 0.10 while for those rated not nice it was 2.63 ± 0.30 (t_114 = 2.40, p = 0.018) (independent groups t – test)). In other words, when an individual is asymmetrical and is labeled nice he or she is more likely to also be viewed as also attractive; if labeled not nice, he or she is less likely to be seen as attractive.

Photos' niceness rating and offer value

Subjects who rated both photos as equally nice tended to offer them the same. The modal difference in offers was zero (21 of 75) and 57 of 75 were within $100; 30 offered more to the symmetrical photo, 24 to asymmetrical.

For males, 11 of 44 gave the same amount (15 gave more to symmetrical, 18 to asymmetrical), 32 of 44 within $100. For females, 10 of 31 gave the same amount (15 more to symmetrical, 6 more to asymmetrical), 25 of 31 within $100.

Why give more? Offer variation and reported justification

When asked why they gave more to one photo versus the other, subjects gave a variety of reasons (table 7.5). These revealed interesting patterns although numbers were too small to analyze by sex. For example, 30 gave more to a photo because they thought it was more attractive or cute; 24 of these picked the symmetrical photo. Nine gave more to the one they said needed it more, and all of these picked the asymmetrical photo. These effects were all significant (table 7.4). Indeed the difference between the tendency of those giving on grounds of attractiveness to favor the symmetrical while those giving on grounds of need to favor asymmetrical is highly significant ($p < 0.0001$).

Table: 7.4: Distribution of reasons for giving a photo more split by degree of symmetry of photo

Gave more to	symmetrical	asymmetrical
More attractive/cute	24	6
Looks to be nicer	8	4
Need it more	0	9
Looks like wanted more	1	1
Sick/sad	2	4

Table 7.5: Comparison between reasons for giving more to a photo (need vs. attractiveness) split by photo symmetry

	Reason for giving more to a photo	
	need	attractiveness
Symmetrical	0	24
Asymmetrical	9	6

P-value (chi square)	<0.01	<0.001
2 X 2 contingency chi square with continuity correction for 0 and 9 versus 24 and 6: X^2 =16.717, p<0.0001 (df=1).		

Other reasons given were sick/sad, looks like wanted more, looks nicer, like him/her more. If we combine all reasons into two consistent categories: positive (cute/attractive, like him or her more, looks nicer) and negative (needed it more, wanted more, sick/sad), the difference is also highly significant (p=0.0002) (table 7.6).

Table: 7.6: Comparison between reasons for giving more to a photo (combined into positive and negative categories) split by photo symmetry

	Reasons for giving more to a photo	
	Negative	Positive
Symmetrical	12	14
Asymmetrical	33	3
P-value (chi square)	<0.01	<0.01
2 X 2 contingency chi square with continuity correction for 33 and 12 vs. 3 and 14: X^2 = 13.510, p=0.0002 (df=1).		

Reported justification as a function of subject's own FA

A cutoff was used to divide symmetrical and asymmetrical individuals (composite FA (from 1996 and 2002) of less than 0.12 for symmetrical (n=72) and greater than 0.15 for asymmetrical (n=75) (121 individuals are in between .12 and .15). For symmetrical individuals who said they gave more to a picture because they said it was more attractive

or cute, 10 of 10 gave more to the symmetrical photo. For asymmetrical individuals who said they gave more to a photo because it was more attractive/cute, only 2 of 6 gave more to the symmetrical photo (Fisher's Exact Test p=0.0082). No sex differences were apparent.

Subjects' FA and their ratings of photos on attractiveness

There was no correlation between subjects' own symmetry and ratings of the attractiveness of photos as function of photo symmetry. For symmetrical photo F(1,161)=0.56, p =0.46, R-squared=0.003; for asymmetrical photo F(1,161)=0.15, p=0.70, R-squared=0.001. Males only: symmetrical photo F(1,89)=0.00002, p=0.997, R-squared~0; asymmetrical photo F(1,89)=0.43, p =0.52, R-squared =0.005. Females only: symmetrical photo F(1,70)=1.56, p=0.22, R-squared=0.022; asymmetrical photo F(1,70)=1.91, p =0.17, R-squared =0.027.

Subjects' friendliness and their ratings of photos on attractiveness

Results revealed a correlation between subjects' scores on friendliness ratings and their ratings of the attractiveness of photos (as function of photo symmetry). For symmetrical photos F(1,65)=0.001, p =0.98, R-squared~0; for asymmetrical photos F(1,65)=-4.94, p=0.030, R-squared=0.07. This means there is a negative correlation between an individual's (i.e. subjects themselves') friendliness and the attractiveness ratings he/she gives to asymmetrical photos. But this is partly caused by one outlier (individual with by

far the lowest friendliness rating gave the highest possible attractiveness score to both photos); with this individual removed the negative trend is still apparent but the correlation is no longer significant: F(1,64)=-2.84, p=0.097, R-squared=0.043.

The above correlation for the asymmetrical photos is mostly due to males [F(1,35)=-3.32, p=0.077, R-squared=0.087; females only (F(1,28)= -1.58, p=0.22, R-squared=0.053)].

Offer rejections

In the third and last UG, subjects got a fictional offer ranging randomly from 100-300 Jamaican dollars, which supposedly came from someone in a different country. They were given the chance to accept or reject the offer. For offers accepted, the mean offer size was 189.33 ± 6.21, n = 150; for those rejected, the mean offer size was 171.43 ± 15.65, n = 21. The mean difference is not significant (p = 0.31, r-squared = 0.01 in logistic regression). Furthermore, FA was not correlated with rejecting (spearman r = -0.10, p = 0.65 (n = 21). “Friendliness”, on the other hand, did correlate positively with accepting offers. For those who accepted, mean friendly rating was 3.56 ± 0.08, n = 55, and for those rejecting offers it was 3.11 ± 0.21, n = 13; logistic regression, p = 0.029, r-squared = 0.08.

There was no significant difference between the amount subjects as proposers offered to photos in the first two games and whether subject accepted/rejected offers themselves as responders. For those who accepted, the total offer size was 734.17 ± 26.39, n = 150, and

for those who rejected total offer size was 750.47 ± 71.50, n = 21 (t(169) = 0.22, p=0.83). (Similar results are obtained when using size of first offer or size of offer to symmetrical instead of total.)

I investigated any correlations between rejections in March 2004 and rejections in March 2006. In March 2004, subjects responded to real offers that ranged from 0 to 1000 Jamaican dollars; there were a total of 15 rejections, with the mean offer size 117.00 +/- 22.65; in 2006 there were 21 rejections with a mean of 171.43 +/- 15.65. Since the games were played differently, no comparison was made here. There was also no relationship between those who rejected in March 2004 and those who did here in 2006. There were 14 rejections in 2004, and 12 of them accepted in 2006 and only 2 rejected. The 2 individuals who rejected offers in both games were offered $100 each in 2004 and 100 and 200 in 2006. For individuals who rejected in 2004 and then accepted in 2006 (n=12), the amounts they were offered differed significantly (paired t = 2.674, df=11, p=0.0216); first game mean = 121.25 +/-28.42, second game mean = 191.67, +/- 22.89. Again, this is because the game was run differently in both years. While subjects in 2004 responded to real offers ranging from 0 to 1000 J.D., in 2006 they responded to fake offers ranging only from 100 to 300 J.D.

I also looked at whether individuals who accepted in 2004 then rejected in 2006 (n=17). So, the mean amount they were offered (and accepted) in 2004 is 335.29+/-37.32, and the mean they were offered (and rejected) in 2006 is 176.47+/-18.25. The difference is

significant with a paired t-test (t=3.561, df=16, p=0.0026).

Subjects' own traits and offer values

I used a multiple regression with total offer value (i.e. both photos) as the dependent variable and the following independent variables: FA (the composite FA used in chapter five, 2D4D, WHR, BMI, friendliness, sex, age. The basic regression model was not significant = [F (7,50) = 0.46, p=0.86], nor where any of the individual variables significant (for FA p=0.37, the lowest p-value is for friendly at 0.13). R-squared values in all the analyses shown here are essentially zero when adjusted for multiple variables. Taking out friendliness greatly increases the sample, as there were a lot of missing values for friendliness, but doesn't change the outcome: F(6,121)=0.57, p=0.75.

Accepting offers and friendliness

Friendliness of subjects was correlated with accepting offers. For those who accepted offers, mean friendly rating was 3.56 ± 0.08, n = 55. For those who rejected offers, the mean friendliness was 3.11 ± 0.21, n = 13; logistic regression p = 0.029, r-squared = 0.08).

Subjects' FA and offers

There was no difference between symmetrical and asymmetrical individuals in their tendency to give more to either symmetrical or asymmetrical photos (table 7.7).

Table 7.7: Subjects' FA and offer as an effect of symmetry of photo

Gave more to	symmetrical	asymmetrical	same amount
Symmetrical individuals	25	11	7
Asymmetrical individuals	25	16	9

Chi-Square = 0.65, p= 0.72, df=2

IV. Discussion

Data from 2004 showed that Jamaican males with low FA made lower offers than males with high FA. Males appear to adopt different strategies depending on their phenotypic quality as measured by FA. Because of their potential superior ability in obtaining resources, low FA males do not have to be as cooperative as higher FA males. Alternatively, since less attractive, high FA males may be inclined toward long-term relationships with high paternal investment. And cooperative relationships with both sexes could be highly beneficial. Females did not show the same pattern. Both sexes appear to adopt a similar strategy when playing with individuals of the opposite sex varying in their degree of symmetry. These results need to take into account mating strategy.

Subjects adjusted their offers according to the symmetry of the person they played with. However, unlike in 2004, they did not adjust their offers according to their own degree of symmetry [for 2006, males with variables: FA, age, sqrt mean BMI, friendly: $F(4,27)=0.65$, $p=0.63$, R-squared=0.087; p for FA = 0.91]. Subjects in 2006 offered more to symmetrical photos than to asymmetrical ones. This effect was primarily due to females. The justifications they gave as to why they offered the symmetrical ones more all referred to a positive trait about the individual in the photo, e.g. for being cute, attractive or nice. This also correlated with their symmetry, i.e. when symmetrical individuals gave more to somebody they thought was attractive, that person also tended to be symmetrical.

Behavior in the UG, in my view, reflects tendencies selected in a world of frequent interactions. Subjects take these tendencies with them to the games, and so a higher offer may be a first act in a series of exchanges. Because individuals in the photos were in a different country and subjects were aware of this fact, it is hard to believe that making generous offers to these photos induces group benefit. On the contrary, by offering more to symmetrical photos, it seems as if subjects wish to reward someone for being of good quality or for having attractive physical traits, and this could be implied from their justifications. Because subjects were playing with the opposite sex, generous offers to symmetrical photos could be viewed as an act to initiate some relationship, perhaps a mating opportunity. Males acted generously to females who appeared to be of a good quality perhaps as a form of display of resources. As for women, in Jamaica men do not provide much parental investment, and women tend to be more selective about mate

quality (Brown et al. 2005). This is supported by the fact that females were mostly responsible for the effect of photo symmetry on offer size. By being generous, females could initiate a series of interactions perhaps leading to a mating opportunity with a good quality male. Or generous offers could also possibly be a female's way of telling the male she has resources of her own to sustain a relationship and she is interested in genetic quality.

This interpretation is supported by other findings. Subjects appeared to perceive possible long term benefits to their behavior in the games, and this was revealed by the justification they gave to why they gave more to a photo rather than another. When they thought the person was attractive and perhaps wanted to court with them, they offered more. When they thought the person looks in need, they offered more to help him/her out.

Subjects also rated the symmetrical photos as more attractive than the asymmetrical photos, and the effect was mostly due to males. Subjects also found symmetrical photos to be nicer than asymmetrical photos. Consistently, they also gave more to subjects they rated as more attractive than to those they rates less attractive.

Alternatively, perhaps males assume that good quality or symmetrical females would not accept low offers, and so males tend to make higher offers to maximize the chance for acceptance. Good quality females could be accustomed to receiving resources or gifts from courting males.

Unlike the data from March 2004, subjects' FA in 2006 did not correlate with behavior in the UG. But, an interaction effect of proposer FA and the responder FA on offer sizes could be expected. It could be expected that one's own FA would bias one's attractiveness ratings of others (or one's ratings of others' dancing ability, as in Brown et al. 2005). So, for example, a high FA male might not wish to pursue a very low FA women because he is unlikely to succeed. He would be better off transferring his resources and efforts to pursue another woman, who would be more likely to show interest in him. But, this was not found in these results. In fact, results show that both symmetrical and asymmetrical individuals of both sexes used the same strategy when playing with a symmetrical opposite-sexed photo, and that is to be more generous. This could be due to the fact that subjects were not playing for a lot of money and so they do not really have much to lose by trying their luck (at being generous).

Friendliness is an interesting factor in accepting offers. Subjects rated by their peers as friendly were more likely to accept offer than those who were not rated as friendly. As for rejections, once again the sample size was too small for any rigorous analysis (e.g. FA).

Although the project was set up to induce rejections (fake offers ranging from 100-300 Jamaican dollars), not many Jamaicans rejected offers (n=12; 12.2%). This might be due to a number of reasons that are not mutually exclusive. First, it could be due to the fact that after proposing two offers subjects still did not know how much money they made, if any at all. Rejections have been shown to increase when subjects at leastd get some pay

for playing the game over and above winnings(see review of Knez & Camerer 1995 in chapter two). Second, subjects might have felt detached from the proposers making them an offer. When they made the offers, they were looking at photos of Lebanese and they might have felt a human connection and perhaps behaved accordingly. The third game had no photo. Third, subjects knew that the proposer was not one of their peers.

Chapter eight: Conclusion

Anthropology has been recently invigorated by a new line of work – experimental economics – to study cooperation among people. This type of research started with European and US college student samples, but anthropologists took the games (mostly the ultimatum game (UG), the dictator game (DG), and the public goods game (PGG) outside the lab in cross-cultural research. Such research shows great promise because the games, simple as they are – especially the UG – can be played almost identically in different cultures. So far, the game has mostly been used to characterize gross differences in levels of cooperation among different societies and possible relevant functions such as: (1) degree of global market integration and (2) benefit to cooperation, i.e. local cultural practices (Henrich et al. 2005). My research extended this work into investigating *within* society variation. That is, what individual-level factors could affect behavior in these cooperation games? The traits I tested included fluctuating asymmetry (FA), degree of shared relatedness (*r*), second-to-fourth digit ratio (2D:4D), and waist-to-hip ratio (WHR) (see table 8.1). I also explored traits such as friendliness, marital status, and body mass index (BMI).

Waist-to-hip ratio (WHR) is an important biological trait for females. Lower WHR is correlated with survival, fecundity and attractiveness (Singh 1993a, 1993b, 1995). However, WHR did not show any correlations with behavior in either the ultimatum game (UG) or the public goods game (PGG). Interestingly, BMI in Jamaican females negatively correlated with offer size in UG – that is females with higher body mass index

offered less. Perhaps bigger females need more resources and so make lower offers, or perhaps they are inclined to seek out more resources because they are bigger, the result appears to make sense. There was no effect of BMI on male behavior in the UG and none for either sex on behavior in PGG. BMI was not tested in Lebanon.

The degree of relatedness shared between two players in an UG had an effect on offer size in Lebanon. When playing anonymously with another male who was a close relative on the father's side, and without knowledge of the exact degree of relatedness, males made higher offers compared to those who played with males that were more distantly related and with those whose relatedness was negligible. Relatedness also had an effect on behavior in PGG in Jamaica. Each session was made up of two groups of four. This was intended to make group member identity ambiguous. The presence of relatives in the room, without subjects knowing that their relatives were on their group, was sufficient to make subjects of both sexes make higher contributions to the common account of their group.

I investigated whether two variables related to friendliness had an effect on behavior in the UG and PGG in Jamaica. One variable was the average rating for each subject by peers based on photos on how friendly he or she looked. The other variable was the average rating for each subject by peers based on photos of whether he or she looked like a friend or an enemy. The average friendly rating, i.e. the former variable, positively correlated with offer acceptance. In other words, those rated more friendly were more likely to accept offers made to them anonymously. For the latter variable, i.e. the average

friend rating, those rated more likely to be a friend contributed less to the common account in the PGG.

Both bodily and facial fluctuating asymmetry (FA) are associated with behavior in the ultimatum game, while neither was associated with behavior in the PGG. Jamaican males with lower bodily FA offered less than those with higher FA. However, younger and lower facial FA Lebanese females offered more than those who were older and had higher FA.

Second-to-fourth digit ratio had important effects on behavior in the PGG in Jamaica, unlike the case with UG. The only finding for the UG was that Jamaican subjects with low 2D:4D were more likely to punish, but this result was driven by the only two females who happened to punish and have low 2D:4D. In the PGG, males and not females with higher 2D:4D made higher contributions to the public account. As for punishment, females and not males with low 2D:4D were more likely to punish, but females with high 2D:4D paid more to punish, i.e. bore higher cost on themselves to exert a bigger cost on others.

Two other traits were correlated with behavior in the UG and PGG. In Lebanon, males who were married made bigger offers than those who were reported being single. In Jamaica, subjects of both sexes who reported having a job tended to make greater contributions to the public account.

Table 8.1: Correlations between biological traits and behavior in economic games in Lebanon and Jamaica

	Males	Females	Both sexes
BMI (ch. 4)	none found	negative with offer size in UG	none found
r (shared between players) (ch. 3 and 5)	positive with offer size in UG	Not available for UG	positive with contribution in PGG*
Bodily FA (ch. 4)	positive with offer size in UG	none found	none found
Facial FA (ch. 6)	none found	negative (combined with age) with offer size in UG	none found
2D:4D contribution PGG (ch. 5)	positive with contribution in PGG	none found	none found
punishment PGG (ch. 5)	none found	negative with punishment frequency	none found
	none found	positive with punishment size	none found

Behavior in UG and PGG should be interpreted differently. The ultimatum game is an opportunity of cooperation for two while the public goods game involves more, four in the Jamaican study (chapter five). Punishment in the UG is in principle more costly; it is an all or nothing situation. If subjects reject an offer, they walk out with nothing from this interaction. Whereas in the PGG, subjects could punish and walk out with some of their

* Recall that subjects did not actually play with relatives, but I tested for an effect of the presence of relatives in the same room for the same game session, with 1/7 possibility that the relative is a group member in a PGG.

winnings still. Moreover, they might be motivated by the fact that they need only pay some amount for the punished person to lose twice this amount.

Since all the Jamaican games were played more or less with the same set of subjects, I compared behavior on all these games. No correlations were found between behavior in the ultimatum game in 2004 (simple anonymous game) and 2006 (offers made to photos), or between behavior in the ultimatum game (2004) and the public goods game (2006). The difference in behavior in the UG in the two years is probably due to the fact that each time the game measured something different. In 2004, subjects made offers to anonymous peers, and in 2006 subjects made offers to opposite sexed-photos of individuals who came from a different country.

One significant finding was the justification subjects gave as to why they offered one photo more than the other. When subjects offered the symmetrical photo more, they said that they did so because they thought this person is more cute/ attractive. However, when they gave the asymmetrical more, they said it is because this person looks like they need it. Subjects were very much aware of the fact that people in the photos came from a different country and they appear to have behaved as if this was a first act in a series of long-term interactions. Recall that subjects played with opposite sex photos. Being generous to someone they liked could initiate a likable relationship and perhaps a sexual opportunity. Being generous to someone in need could generate delayed benefit through reciprocation, a small cost to self and a bigger benefit to someone in great need – situations that may be reversed in future interactions. These results suggest that subjects

are oriented towards future individual benefits in these one-shot anonymous games, contrary to what supporters of strong reciprocity claim.

In this dissertation, I showed that a number biological traits correlate with an individual's cooperative and punitive behavior in two economic games, the ultimatum game and the public goods game. Furthermore, the quality of the interacting party had an effect on an individual's behavior in these games too. Some predictions were not fulfilled, e.g. WHR. This does not necessarily mean that this trait is unimportant. Perhaps with an improved experimental design, some of the effects could be revealed.

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Publications

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