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Variants of the Monoamine Oxidase A Gene (MAOA) Predict Free-riding Behavior in Women in a Strategic Public Goods Experiment

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Variants of the *monoamine oxidase A gene* (*MAOA)* predict free-riding behavior in women in a strategic public goods experiment

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Abstract Laboratory experiments have documented substantial heterogeneity in social preferences, but little is known about the origins of such behavior. Previous research on public goods experiments suggests that individual-level demographic and psychological variables correlate with player types. However, the key question about biological sources of variation in these preferences remains open. The aim of this study is to uncover genetic variations that influence differences in cooperative behavior. For this reason, we identify types of players within a strategic public goods experiment. We explicitly test for an association between individual variance in strategy choice and the functional promoter-region repeat of the *monoamine oxidase A gene* (*MAOA*). Our experimental findings suggest a link between *MAOA* and the occurrence of free-riding in females. Females with *MAOA-L* are less likely to behave like weak free-riders than *MAOA-H* carriers, whereas among males, our results did not support a significant relation between genotype and player type. Furthermore, *MAOA-L* female carriers contribute more than *MAOA-H* subjects to the public good if they know that others contribute nothing, and they showed slightly lower scores on the Machiavellianism scale. This is the first piece of evidence that genotype might predict player type within a public goods setting. It contributes to our understanding of biological drivers of economic decision-making and points to the need for further exploration.

Keywords *gene; player type; public good; conditional cooperation; experimental economics*

JEL Classification *H41; D87; C91; C72*

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1 Introduction

A puzzle of great interest to biologists, economists or psychologists is the often observed large-scale cooperation with genetic strangers. Indeed, robust experimental findings in the lab and in the field point to a strong willingness of the average individual to contribute sizeable shares of an endowment, although free-riding on others' contributions is the rational, payoff-maximizing strategy. Furthermore, recent studies suggest that most people follow the social norm of "conditional cooperation" (Chaudhuri, 2011; Fehr & Fischbacher, 2004; Fischbacher & Gächter, 2010): contributions to public goods depend directly on how other group members behave. At the same time, individuals with multiple behavioral types exist, each of them involving a distinctive behavioral pattern (Brosig, 2002; Burlando & Guala, 2005; Fischbacher et al., 2001; Kurzban & Houser, 2005; Ostrom, 2000). What we still do not know is whether there are biological sources of variation in these preferences for cooperation. This study considers the possibility that genotype predicts player type (e.g., conditional cooperators, free-riders) within a strategic public goods experiment. By means of an incentivized controlled laboratory experiment, we rigorously test the impact of a particular gene on individuals' preferences towards cooperation.

Many factors, including gender, culture, and age, have been considered explanatory variables for cooperative behavior. Gender alone fails to predict cooperation. By referring to a multitude of studies on behavior in public goods games, Croson and Gneezy (2009) concluded that there are inconsistent results regarding gender-dependent cooperation, with women being more or less cooperative than men in various studies. Cross-cultural studies comparing the distribution of player types and individual preferences across different countries confirm that cultural background influences one's attitude towards cooperation (see e.g., Anderson et al., 2011; Burlando & Hey, 1997). Herrmann and Thöni (2009), for example, showed that the cultural background, rather than the socio-economic environment within a society, has an effect on people's preferences towards cooperation. Kocher et al. (2008) found that conditional cooperation was prevalent in subject pools from three different continents. The distribution of player types (e.g., conditional cooperators, free-riders) as well as the extent of conditional cooperation, however, differs across countries. Andersen et al. (2008) provided evidence that a society's structure is critically linked to its provision of public goods. They find that matrilineal societies not only have fewer strong free-riders, but also the highest level of public goods provision.

These results provide support for the argument that human groups largely differ in their social norms, but the key question as to whether these norms are learned or have a more fundamental basis remains open. By conducting experiments with young children, Fehr et al. (2008) gained insight into the developmental origins of social preferences. Their results showed that at the ages of 3–4, the majority of children behave selfishly, while with increasing age, children follow the social norm of inequality aversion.

Although all of these findings are important in understanding and modeling behavior in social dilemma situations, they do not *explain* the observed differences. In search of the ultimate forces behind individual differences in preferences towards cooperation, economists started to take the idea seriously that "nature" matters as well. A steadily increasing number of studies have examined the link between economic preferences and hormones (e.g., Apicella et al., 2011; Buser, in press), or genetic markers (e.g., Beauchamp et al., 2011). Hormones such as testosterone and cortisol mediate behavior by either increasing or decreasing the probability that an individual will express a certain behavior by acting on the neuronal mechanisms underlying the behavior (Soares et al., 2010). Recently, women treated with testosterone were found to experience a disruption in cooperative behavior together with an increase in self-oriented and more egocentric behavior (Wright et al., 2012). Besides hormones' rapid effects on the functional level due to changes in the neural circuit, hormones and neurotransmitters can have long-lasting effects by changing an individual´s phenotype during prenatal and early childhood developmental stages (Soares et al., 2010). Those behavioral traits are likely to determine one's social behavior and can also be influenced by genetic and epigenetic differences (Liu et al., 1997; Meaney, 2001). Empirical findings from a field called "*genoeconomics*" (Benjamin et al., 2007; Beauchamp et al., 2011; Navarro, 2009) suggest that this holds true for economic behavior as well. One strand of research focuses on twin studies, investigating the impact of genetic factors on economically relevant behavior in monozygotic (identical) and dizygotic (fraternal) twin pairs raised in identical environments. Researchers have identified a significant degree of genetic influence on variables such as income (Taubman 1976), education (Behrman & Taubman, 1989), political attitudes (Alford et al., 2005), cooperativeness in trust games (Cesarini et al., 2008), bargaining behavior (Wallace et al., 2007), the tendency to be self-employed (Nicolaou & Shane, 2010), risk preferences (Zhong et al., 2009b), and preferences for giving and taking risks (Cesarini et al., 2009a). These studies have found that economic preferences have a genetic component, with heritability[4] estimates ranging from 18 to 42 %.[5] However, in public goods games the

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[4] Genetics uses the concept of "heritability" to describe the proportion of the variability on a trait that is contributed by genes. Cesarini et al. (2008), for example, reported a heritability estimate of 20 % in a trust game with Swedish twins. Heritability of 20 % does not mean that trusting behavior is 20 % determined by genes.

underlying biological sources for variation and the impact of genetics on economic behavior are still largely unknown.

Another strand of literature builds upon recent improvements in individual gene identification, which have allowed us to study particular genetic factors that influence a given *trait*, i.e., a single quantifiable measurement of an organism, such as an individual's attitude towards economic risk taking (Zhong et al., 2009a). *Genetic association studies* attempt to identify the occurrence—more often than expected by chance—of a trait together with a given genetic variant (i.e., a given version of a gene, known as an *allele*) in a population. *Targeted studies* focus on "candidate genes," which have been identified based on previously reported associations.

When studying the association between genetic variants and economic traits, researchers are increasingly relying upon experimental games. Several recent targeted studies have followed this approach and have provided evidence of an association between economic preferences and particular genes. Knafo et al. (2008) showed that fund allocation in the dictator game was, in part, determined by length of the arginine vasopressin 1a gene (*AVPR1a*) RS3 promoter-region repeat. Kuhnen and Chiao (2009) found that variants of two genes (*5-HTTLPR* and *DRD4* repeat) that regulate dopamine and serotonin neurotransmission and which were previously linked to emotional behavior, anxiety and addiction, were significant determinants of risk-taking behavior in investment decisions. Dreber et al. (2009) also found this association between DRD4 and risk preferences, but Dreber et al. (2011) reported this association only among men and not women, and Frydman et al. (2010) failed to replicate this association. De Neve et al. (2012) found a correlation between *5-HTTLPR* and subjective well-being in their initial study and mixed results in their replication study. Israel et al. (2009) demonstrated that genetic polymorphisms for the oxytocin receptor (OXTR) were associated with pro-social fund allocation in the dictator game. However, Apicella et al. (2010) could not replicate these findings albeit their larger sample size. Zhong et al. (2009a) found that carriers of the low variant of the *monoamine oxidase A gene* (*MAOA-L*) are more likely to exhibit risky behavior. This finding has been substantiated by Frydman et al. (2011), who showed that these individuals only engage in more risky behavior when it is advantageous to do so. The authors concluded that their results provide a cautionary tale on

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Rather, it means that if all subjects were raised in the exactly the same environment, we would see 20 % of the variability we see now.

[5] Navarro (2009) noted that heritability measures of socio-economic variables are of similar magnitude to those of physical occurrence of common diseases.

the interpretation of previous behavioral results related to the *monoamine oxidase A gene* (*MAOA)*.

Three important insights follow from these prior findings and have inspired the present study. First, targeted studies generally appear to be quite valuable and promising in identifying particular genes that might be associated with economic decision-making. Indeed, as much of the behavioral neuroscience literature points to the serotonergic, dopaminergic, and noradrenergic systems' important role in decision-making, it seems justified to focus initially on one of the genes involved in the transport, binding, or degradation of these neurotransmitters. Second, we need to be aware that the replication of candidate gene studies might be difficult due to the polygenetic architecture of those traits and the small effects of individual genes on that given trait (discussed in Benjamin et al., 2012). Third, subjects with similar preferences might still make quite different choices, depending on the behavioral specificity of their defined phenotype (Frydman, 2011). Thus, using simple but accurate preference elicitation procedures, which eliminate difficulties resulting from complex decision environments such as repeated play or strategic interaction, may allow for an improved interpretation of previous results. In this study, we shed further light on the previously reported association between voluntary contributions towards a public good and *MAOA* (Mertins et al. 2011) by allowing the same subjects to make additional choices using a different procedure. These findings may help to get a clearer picture of the link between cooperation preferences and this particular gene.

MAOA encodes the enzyme monoamine oxidase A that degrades neurotransmitters such as serotonin, dopamine and epinephrine (Hariri et al., 2005). Different variants of it regulate transcription, metabolism, and signal transfer between neurons, all of which have an effect on social interactions (Craig, 2007; Spitzer et al., 2007). In particular, a variable number of tandem repeats (VNTR) in the promoter-region of *MAOA* leads to high and low activity variants. Alleles with 3.5 and four copies are transcribed more efficiently than those with three or five copies. The less transcriptionally efficient alleles are called *MAOA-L,* and the more efficient are called *MAOA-H* (Sabol et al., 1998). *MAOA-L* has been found to be associated with various kinds of antisocial behavior, including violence and aggression, both in the field (Caspi et al., 2002) and in the lab (Gallardo-Pujol et al., forthcoming). McDermott et al. (2009), for example, show an association between *MAOA-L* in males and behavioral aggression following provocation (i.e., high take rates by proposers in the power-to-take game). Aggression and cooperation may represent two sides of the same coin in child development and are two critical features in children's social domain. In combination with maltreatment in children, lower *MAOA* expression predicts aggression (Kim-Cohen et al., 2006), whereas it might be associated with normal behavior in children that were in good hands. On the other hand, a less active promoter might result in higher neurotransmitter levels in the brain, which might lead to more cooperative behavior. In a murine knockout model (Cases et al., 1995), mice completely lacking *MAOA* were found to be highly aggressive. However, mice with normal *MAOA* levels (independent on the VNTR) displayed the whole range of species-specific behavior with respect to social relationships, and they displayed intense social investigation, which are usually highly cooperative among clan members. Additionally, brain imaging studies have shown an activation of similar brain areas in aggression (Nelson & Trainor, 2007) and cooperation (Decety et al., 2004) suggesting similar underlying neuronal mechanisms that are determined by genetic and environmental factors. Furthermore, brain functions during cognition, emotional arousal, personality test-takings, and working memory activation (Meyer-Lindenberg et al., 2006; Rommelse et al., 2008; Ziermann et al., 2012) as well as the function and anatomy of specific brain regions in the limbic system (reviewed in Nordquist & Oreland, 2010) were affected by the *MAOA* VNTR.

Recently, we showed a genetic association between *MAOA* and individuals' behavior in a repeated public goods game (Mertins et al., 2011). As we aimed to study decision-making in conditions of uncertainty, the setting was a dynamic one that offered subjects increasing information about group members' cooperativeness over the course of the game. We found that *MAOA-L* male subjects held more pessimistic beliefs about others' cooperativeness than *MAOA-H* male carriers, resulting in fewer contributions to the provision of the public good. With decreasing uncertainty about others' behavior, however, the genetic effect diminished. For females, an opposite pattern was observed: there was no genetic influence in the early rounds, but a strong genetic influence in late rounds of the game. Furthermore, *MAOA-L* female carriers held more optimistic beliefs about others' willingness to cooperate, and accordingly, contributed more than *MAOA-H* females. In line with these findings, recently, the *MAOA-L* was related to higher levels of happiness in women but not in men suggesting that *MAOA-L* women may be more sensitive to positive aspects of the environment and less susceptible to stressors (Chen et al., 2012).

Our present study using the same subjects as in the previous paper differs from the former one in terms of the decision procedure. By using the strategy method (Selten, 1967), participants stated contingent responses for each information set, i.e., they were asked to indicate their complete strategy: each player decided how much to contribute to the public good for all feasible group contributions. Therefore, we focused on players' strategic behavior and excluded any confounding factors resulting from variations in expectations. To this end, we replicated Fischbacher et al.'s (2001) one-shot experiment with anonymous interaction partners, which enabled us to measure subjects' preferences unaffected by potential confounds. There is an ongoing debate by experimentalists as to whether the strategy method and direct elicitation procedures produce different results. The use of the strategy method may force participants to think about each set of information in a different way than if they could primarily concentrate on each set as it arises throughout the course of the game (Roth, 1995). For instance, highly emotional responses may be suppressed: it is plausible that people will have stronger emotional reactions to actual observed actions than to hypothetical actions that might be taken ("hot" versus "cold" environment). Laboratory findings have been mixed. Brandts and Charness (2000) found no behavioral difference between hot and cold settings, whereas Brosig et al. (2003) and Güth et al. (2001) do. Thus, it seems warranted to explore the relationship between cooperative player types and *MAOA* in a cold environment to either corroborate our prior research in the hot setting or to identify differences between both environmental settings.

Our study provides new insights in several respects. This is the first study on the association of a particular candidate gene and cooperativeness in a strategic public goods experiment. Linking the assessed genotype with the observed player type may allow us to derive evidence of a potential genetic basis for different behavioral patterns. Whereas most of the recent *MAOA* association studies have focused on phenotypes with negative connotations such as antisocial or aggressive behavior, our design permits the study of a complete range of feasible actions (including positive behaviors) that are directly dependent on others' behavior. Little research so far has considered the association between molecular genetics and voluntary cooperation. Furthermore, the vast majority of association studies have used self-reported questionnaires only. We are among the first to combine methods and techniques of experimental economics and behavioral genetics and to use data from questionnaires to confirm our findings. Last, our subject pool consists of both genders, whereas most *MAOA* studies have used males only (see e.g., Garllado-Pujol, forthcoming; McDermott et al., 2009). However, it is necessary to consider males and females separately, as recent findings have suggested that the pattern of associations between genotypes of *MAOA* in females differ from males.[6] In particular, our previous findings (Mertins et al., 2011) suggested significant gender

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[6] For example, female subjects carrying the *MAOA-H* showed a higher risk of being high alcohol consumers, whereas among men, *MAOA-L* was related to higher alcohol consumption (Nilsson et al., 2010). Among girls with psychosocial risk, *MAOA-H* confers an increased risk for criminal behavior, whereas among men, the low activity variant and social risk interacts to predict criminal activity (Sjöberg et al., 2007).

differences in the association between *MAOA* and cooperativeness. Those differences might be due to hormones such as testosterone and estrogen and their receptors, which act on gene regulation and subsequent brain development in a gender-specific manner (Hines, 2011; Kuo et al., 2010). Additionally, *MAOA* has an androgen response element in its promoter region, which can be occupied by testosterone bound androgen receptors (Ou et al., 2006). A significant interaction effect of high testosterone levels and *MAOA* on antisocial behavior has been shown only in male *MAOA-L* carriers (Sjoberg et al., 2008). Therefore, higher testosterone levels in men could compensate the *MAOA-L* effect seen in women leading to an increased likelihood of negative *MAOA-L* effects in men. In women, those effects will not be compensated due to the much lower levels of testosterone. Third, estrogens play an important role as a neuromodulative reagent and influences the dopaminergic neurons in the brain (Riecher-Rössler & de Geyter, 2007), which may have an additional positive effect in *MAOA-L* females.

In the present study, we found some experimental support for the notion that *MAOA* is weakly associated with cooperation and the occurrence of free-riding in females: Females with *MAOA-H* are less cooperative than *MAOA-L* carriers and show a significantly higher risk of being weak free-riders. Furthermore, there are several suggestive patterns in the questionnaire data, which merit further exploration in the link between *MAOA-L* and cooperativeness in females. In males, we did not find evidence to suggest an association between genotype and player type. This is the first study to link player types derived from contributions to the public goods in an incentivized strategic game to a specific gene. It complements recent findings on the impact of genetics on economic preferences and provides starting points for further investigations of biological modulators of economic behavior.

2 Experimental Design and Procedures

To elicit subjects' preferences within a public goods game, we replicated Fischbacher et al.'s (2001) experiment[7]. In this game, the strategy method (Selten, 1967) was used in which subjects indicated, in an incentive-compatible way, their willingness to contribute to the public good, depending on the other group members' average contributions. In this one-shot linear public goods experiment, subjects were endowed with 20 tokens and were randomly divided into groups of four. Each subject decided how much of the endowment to keep and

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[7] As we used exactly the same protocol, we refer the reader for any details of the design to the original source and to the appendix. The design has recently been used, e.g., by Fischbacher and Gächter (2010) and Herrmann and Thöni (2009). Subjects played the strategic game (reported here), and the repeated game afterwards (reported in Mertins et al., 2011). Since the game under consideration was played first, no behaviorally relevant interferences need to be accounted for.

how much to contribute to a "project," the public good. The payoff function was given by the following equation:

$$\pi_i = 20 - g_i + 0.4\sum_{j=1}^{4} g_j$$

with $g_i \in \{0, 1, \dots 20\}$ being individual i's contribution to the public good. The sum of all group members' contributions was multiplied by the factor 1.6 and the outcome equally shared among all group members, independent of individual contributions. As the private marginal return of any token contributed to the public good was 0.4, rational selfish players were expected to contribute nothing.

Subjects were first asked to fill out a contribution table, that is, to decide on their own contribution to the public good dependent on the other group members' average contributions (21 choices, as the other group members' average contributions were rounded to integers). This setting allows individual levels of cooperativeness to be measured in the presence of other group members who, on average, completely free ride, contribute a small, medium, or large share of their endowment, or even contribute their full endowment. The contribution table yields complete strategy profiles for each subject and thus allows players to be classified according to type. In addition, subjects chose one unconditional contribution and indicated what they thought the others would contribute. At the end of the experiment, a random device chose one group member who was paid according to the contribution table. The remaining three subjects were paid following their unconditional contribution and therewith defining the payoff for the randomly chosen group member.

The comparative advantage of this experimental design is that we measured individuals' complete preferences over the whole strategy space in the absence of uncertainty regarding others' behavior. That is, we obtained data on any contingent state of the world: for each individual, we observe his/her reactions to other group members' average decisions, but expectations about others' behavior did not play a role in subjects' decisions. Besides, averages might mask considerable heterogeneity among individuals. An approach which addresses this concern is given by player type classification. Following Fischbacher et al. (2001), we considered four distinct player types: *free-riders* (who contributed nothing), *conditional cooperators* (who raised contributions if the average contributions of the other members increased); *hump-shaped* or *triangle cooperators* (who had a hump-shaped contribution pattern as a function of others' average contributions) and *erratic* (who had very irregular contribution patterns).These types have been proven to occur in robust shares (Fischbacher & Gächter, 2010) and are stable over time[8] (Fischbacher et al., 2001).

As a second measure of cooperative player types, we elicited the individual levels of Machiavellianism (Christi & Geis, 1970) using the German version (see Shajek, 2007) of a 20-item questionnaire. Machiavellianism has been considered a combination of selfishness and opportunism (Spitzer et al., 2007). Subjects indicated their degree of agreement with statements such as "Never tell anyone the real reason you did something unless it is useful to do so," and, "Most people are basically good and kind." Following Kurzban and Houser (2001) and Gunnthorsdottir et al. (2002), people with low levels of Machiavellianism (low Machs) are more likely to conform to social norms to pursue their self-interest. High Machs, on the other hand, are individuals who tend to be opportunistic and rational, and thus are expected to free-ride. In short, low Machs are expected to be more cooperative than high Machs.

As said before, we had to consider male and female subjects separately because significant gender x genotype interaction effects have been observed in previous studies. Based upon our previous results using the same subject pool (Mertins et al. 2011), we might expect that female carriers of *MAOA-L* would be more cooperative than *MAOA-H* subjects (as observed in late rounds in our repeated public goods game). Accordingly, *MAOA-L* female subjects should be less susceptible to play the free-riding strategy in the actual game. For male subjects, our previous results suggest no association between *MAOA* and player type. Although we had found a highly significant association between *MAOA-H* and contributions in early rounds of the repeated public goods experiment, no link was observable in late rounds when uncertainty about others' behavior diminished. An environment with low uncertainty most closely resembles our strategic setting, thus we should not expect to observe an association between *MAOA* and cooperativeness for male subjects. To test whether after all such a link either for males or females exists, we applied two-sided tests throughout the paper.

As previously reported (Reif et al., 2008), both men and women were assigned to two groups: male carriers of 4 repeats were assigned to *MAOA-H*, carriers of 3 repeats to *MAOA-L* (see Appendix for *MAOA* genotyping). The *MAOA* is located on the X chromosome; therefore in men the 3/4 genotype does not exist. The high activity group of female subjects consists of 3/4 and 4/4 genotypes, the low activity group of 3/3 genotype. Within our subject pool of 33 males and 63 females, this assignment resulted in 33 % of *MAOA-L* men (which is equivalent

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[8] To test for stability, Fischbacher et al. (2001) asked their subjects in a post-experimental questionnaire again to fill out a hypothetical "contribution table." The results were almost identical to the schedules submitted in the actual experiment; therefore type classification has test-retest reliability.

to the average proportion found in Western subject pools) and 19 % of *MAOA-L* women (five subjects were excluded from the analysis due to genotyping problems). All participants were non-related, randomly chosen Caucasians derived mainly from the ethnically homogenous Frankonian population of Rhineland-Palatia, Germany. All alleles tested were found to be in the Hardy-Weinberg equilibrium. Thus, we can exclude population stratification as a putative bias.

As control variables, we gained self-reported data on a wide range of individual characteristics[9] such as subjects' risk attitudes, patience, and impulsivity on an 11-point scale, with zero indicating the lowest possible levels of their willingness to take risks, patience, and impulsivity. We used the same wording of the questions as in the 2004 wave of the German Socio-Economic Panel Study. Also, subjects completed a 15-item (German-language) version of the well-established NEO-FFI developed by Costa and McCrae (1989) (see Gerlitz & Schupp, 2005 on the implementation and reliability of this short version of the personality test), a personality questionnaire indicating individuals' five main personality dimensions (the so-called "Big Five": conscientiousness, neuroticism, openness to experience, agreeableness, and extroversion). In addition, we collected survey measures on individuals' reciprocal inclinations from the 2005 wave of the German Socio-Economic Panel (see Dohmen et al., 2009 for details). Furthermore, we used the German version of a questionnaire (Graf, 2004) to measure self-monitoring (Snyder 1974). In addition, we gathered additional socio-demographic data including participants' age, gender, and major in university.

The experiment was conducted at Trier University. Subjects were recruited with ORSEE (Greiner, 2004). Ninety-six subjects took part in the experiment, which consisted of four sessions with 24 subjects each. All participants were students from various fields. Instructions were read aloud, and then subjects had to solve several control questions before the experiment started. The experiment was computerized using z-tree (Fischbacher, 2007). Individuals were separated from the rest of the participants by sitting in cubicles. As this experiment was the first in a sequence of experiments, there were no interference effects from previous subjects' decision-making. Subjects first completed the experimental tasks and the post-experimental questionnaire. Thereafter, people were genotyped using buccal swabs and Listerine mouth wash. Participants gave informed written consent prior to participating. The study was approved by the university's ethics committee. The experiment (including genotyping) lasted about 40 minutes and subjects earned an average of € 8.91 (including a show-up fee of € 5).

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[9] The questionnaires are available from the corresponding author upon request.

3 Results

3.1 Overview

Figure 1 shows the average contributions, according to the contribution table, for female (Fig. 1A) and male subjects (Fig. 1B) who were classified as *MAOA-L* or *MAOA-H* carriers. For females, MAOA-L carriers nearly fit the 45-degree line of perfect conditional cooperation up to an average group contribution of 50% (i.e., 10 tokens), whereas *MAOA-H* carriers contributed less. On a descriptive level, we see that *MAOA-L* female carriers contributed more, especially in a highly uncooperative environment. However, there were no statistically significant differences ($p \geq 0.059$) between *MAOA-L* and *MAOA-H* for any group contribution level using a two-sided Mann-Whitney test (M-W test). Classifying others' contributions into three rough categories (low contributions: 0–6, medium contributions: 7–14, high contributions: 15–20) also yielded no significant differences between *MAOA-L* and *MAOA-H* ($p \geq 0.056$). The same was true for the contribution levels of *MAOA-H* (mean = 7.085) and *MAOA-L* (mean = 8.130) females averaged over all feasible contributions of others (p = 0.321, M-W test).

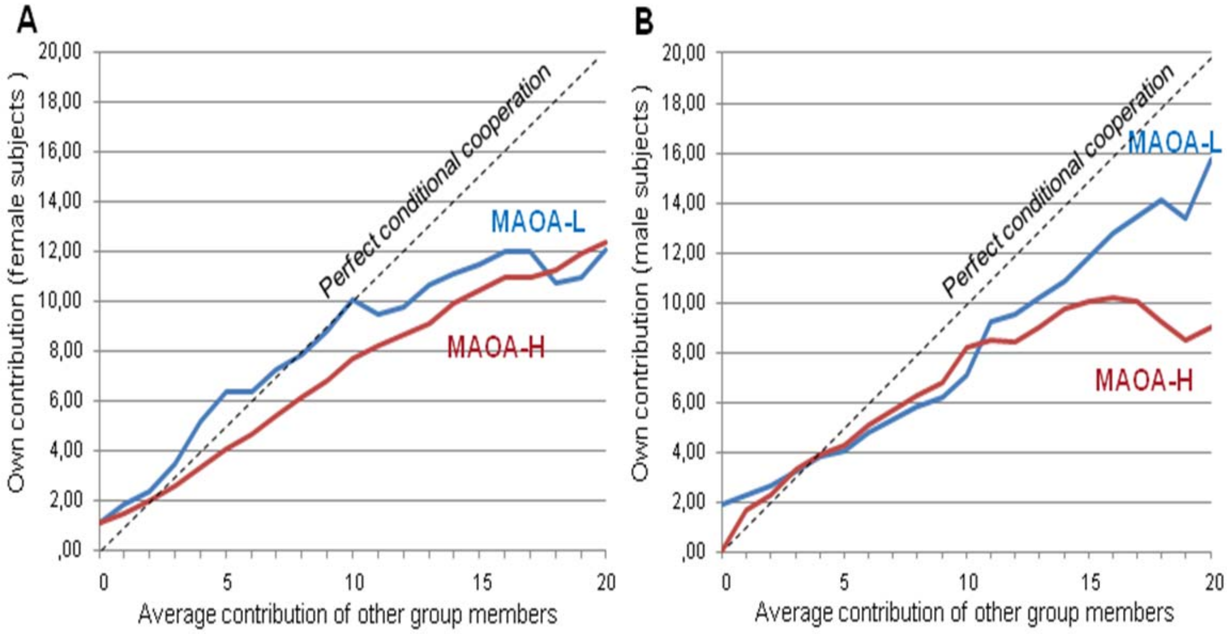

Figure 1. Subjects' average contributions dependent on other group members' average contributions

For males, Figure 1B shows that the average contributions of *MAOA-L* and *MAOA-H* subjects are strikingly identical up to an average cooperation level of others of about 75 %. Beyond that, *MAOA-L* and *MAOA-H* carriers developed in opposite directions: whereas *MAOA-L* subjects still followed an increasing path (parallel to the ideal line of perfect conditional cooperation), *MAOA-H* subjects held their contributions constant for several given contributions of others and ultimately decreased them. For high group contributions, *MAOA-L* male carriers seemed to be more cooperative than *MAOA-H* carriers, but there was no significant difference according to the Mann-Whitney test. For example, in cases where subjects were facing a maximum mean contribution of 20 from other group members, *MAOA-H* subjects contributed 9.05 tokens on average, whereas *MAOA-L* carriers contributed 15.73 tokens.[10] This difference was, however, not significant (p = 0.057, two-sided). The same was true for the contribution levels of *MAOA-H* (mean = 6.693) and *MAOA-L* (mean = 8.022) males averaged over all feasible contributions of others (p = 0.192).

A feasible approach, considering the heterogeneity in contribution preferences, is to compare the slopes and intercepts of linear regressions. To this end, we computed them for all subjects. For male subjects, we did not find a significant difference between the slopes for *MAOA-L* (mean = 0.705) and *MAOA-H* (mean = 0.460, p = 0.205) subjects. The same was true for the female subjects carrying *MAOA-L* (mean = 0.543) and *MAOA-H* (mean = 0.591, p = 0.820). Similarly, no significant difference was detected in intercepts for males (*MAOA-L* mean = 0.971; *MAOA-H* mean = 2.097, p = 0.203). For female subjects, however, genotype made a slight difference. Whereas the average individual intercept of linear regression was as high as 2.700 for *MAOA-L* genotypes, the mean was 1.178 for *MAOA-H* females. The difference was significant with p = 0.04, pointing to stronger cooperativeness of *MAOA-L* genotypes in cases where others did not contribute.

3.2 Distribution of Player Types

Next, we turn to the analysis of the complete individual contribution schedules. Table 1 shows the distribution of male player types according to Fischbacher et al.'s (2001) classification, Table 2 the respective data for females. First, we tested whether *MAOA* impacts the frequency of player types. We found that the distribution of types did not differ significantly between *MAOA-L* and *MAOA-H*, neither for the male (p = 0.135) nor the female subjects (p = 0.213) using the conservative Fisher's exact test.

We now turn to a detailed analysis of male player types. As can be seen in Table 1, the share of *free-riders* among *MAOA-H* (4.5 percent) and *MAOA-L* (18.2 percent) did not differ significantly across genetic predispositions when using the Fisher's exact test (p = *0.252)*. Similarly, unconditional contributions and beliefs did not differ (p > *0.221*, M-W test).

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[10] Note that differences in the corner of a distribution should generally not be over-interpreted, as players might attach only a small probability to the notion that these states of nature are decisive.

Table 1: *Distribution of Male Player Types Separated by Genotype*

	Male subjects					
	MAOA-L			***MAOA-H***		
n	11			22		
	distrib.	average uncond. contrib.	average belief	distrib.	average uncond. contrib.	average belief
Free-riders	18.2%	4.00	8.00	4.5%	0	19.00
Conditional cooperators	72.7%	13.88	10.13	50.0%	9.45	9.27
Triangle contributors	0.0%	n/a	n/a	22.7%	7.80	7.40
Others	9.1%	10.00	10.0	22.7%	9.20	10.20

The difference in the proportion of *conditional cooperators* (72.7 % for *MAOA-L* and 50 % for *MAOA-H*) was also insignificant ($p = 0.278$, Fisher's exact test). Within this behavioral type, we found that the average unconditional contribution of *MAOA-L* carriers (*mean* = 13.88) was higher than that of *MAOA-H* genotypes (*mean* = 9.45), but again, the difference was not statistically significant ($p = 0.066$, M-W test). The same was true for the average belief about others' contributions ($p = 0.867$, M-W test). The share of *triangle cooperators* varied not significantly ($p = 0.143$, Fisher's exact test) across genetic predisposition, although no *MAOA-L* carrier belonged to the type of *triangle cooperators*, whereas 22.7 % of *MAOA-H* subjects did. The same was true for the difference between shares of *others* ($p = 0.637$, Fisher's exact test).

To test whether the distribution of player types among female subjects differed between genotypes, we compared respective shares. We did not find a significant difference for *free-riders* ($p = 1.00$), *conditional cooperators* ($p = 0.475$), or *triangle contributors* ($p = 0.580$, Fisher's exact test). *MAOA-L* female carriers belonged more often to the group *others,* which was characterized by very different behavioral patterns (such as a decreasing path or constant positive contributions), indicating a higher degree of heterogeneity among this genotype. The share, however, did not vary significantly across genetic predisposition ($p = 0.056$, Fisher's exact test). Furthermore, average unconditional contributions and beliefs did not differ significantly within player types and across genotypes.

Table 2: *Distribution of Female Player Types Separated by Genotype*

	Female subjects					
	MAOA-L			***MAOA-H***		
n	11			47		
	distrib.	average uncond. contrib.	average belief	distrib.	average uncond. contrib.	average belief
Free-riders	0.0%	n/a	n/a	6.4%	0.00	3.67
Conditional cooperators	63.6%	9.57	9.71	74.5%	10.40	9.60
Triangle contributors	0.0%	n/a	n/a	8.5%	7.50	6.50
Others	36.4%	12.00	11.25	10.6%	10.80	7.40

Previous studies, however, have suggested different classification schemes. In order to capture different player types' general tendencies, Kurzban and Houser (2001) suggested assigning to each subject the type that was consistent with their greatest number of moves. This procedure allows for some heterogeneity in each type's play and accommodates the fact that *free-riders* (in a wider sense) occasionally contribute some part of their endowment, while *conditional cooperators* occasionally contribute less than the "ideal" level. Whereas the classification of *conditional cooperators* proposed by Fischbacher et al. (2001) is able to capture some degree of heterogeneity due to the application of the Spearman rank correlation coefficient, this is not the case for *free-riders*. Therefore, we applied an alternative classification for this type. We used Kurzban and Houser's (2001) scheme to determine a contribution as being consistent with the *free-rider* type if it is less than 20 % of the endowment (i.e., less than four) independent of the average group contribution. We then simply counted the number of decisions consistent with the free-rider rule. If the majority of all decisions were consistent with it, we assigned the type *weak free-rider* to the subject.

Table 3: *Shares of Weak Free Riders Separated by Genotype*

		Male subjects		**Female subjects**		
		MAOA-L	***MAOA-H***	***MAOA-L***	***MAOA-H***	SUM
Weak free-rider	Yes	18.2% (2)	22.7% (5)	0% (0)	31.9% (15)	24.2% (22)
	No	81.8% (9)	77.3% (17)	100% (11)	68.1% (32)	75.8% (69)
SUM		100% (11)	100% (22)	100% (11)	100% (47)	100% (91)

As can be seen in Table 3, this assignment resulted in about 24 % belonging to the group of *weak free-riders*. For male subjects, the share of *weak free-riders* varied only slightly across genetic predisposition (18.2 vs. 22.7 %). Not surprisingly, the difference was insignificant ($p = 1.00$, Fisher's exact test). For female subjects, however, a clear–cut picture emerged: whereas no *MAOA-L* carriers behaved like *weak free-riders*, 31.9 % of *MAOA-H* subjects belonged to this group. The difference in the share across genetic predisposition is weakly significant ($p = 0.05$, Fisher's exact test). Therefore, we can state that the genotype has some predictive power in explaining the player type: female subjects carrying *MAOA-L* are less likely to behave like weak free-riders than *MAOA-H* subjects.

As seen before, by applying the strict *free-rider* definition of zero contribution, we did not detect a significant difference between female genotypes. Results for the wider definition (very low contributions), however, were somewhat different and pointed to a link between genotype and behavioral type. This brings up the question of whether this finding is a technical artifact of this particular classification scheme. This is of particular importance, as there seems to be agreement that players use strategies that differ in systematical and discernible ways, but no consensus on the correct classification scheme (Kurzban & Houser, 2001). Thus, all schemes are, to some extent, arbitrary. Therefore, as a robustness check, we varied how *weak free-rider* was categorized in that we considered the subjects' average contribution within the contribution table (mean of 21 decisions). We tested whether the share of weak *free-riders* varied across genetic predispositions when we applied a threshold of 20 % (four tokens). We found that the difference was significant only at a 10 % level ($p = 0.097$, Fisher's exact test). A similar statistical difference occurred when we assumed a threshold of 15 % or three tokens ($p = 0.097$, Fisher's exact test). Decreasing the threshold further yielded no difference, as already detected by applying a threshold of zero. Therefore, we can conclude that our data suggest a moderate association between weak free-riding and *MAOA* for female subjects. This link can be found by applying various player type classifications. However, there is neither a correlation between strong free-riding (i.e., zero or very little mean contributions) and *MAOA* for females, nor any link between *MAOA* and the occurrence of free-riding among males. Further research with larger samples is needed to establish a clearer picture of this potential link.

3.3 Questionnaire Data

We administered an extensive ex-post questionnaire for two different reasons. First, we intended to study our variable of interest, cooperation, in a different way to determine the robustness of our experimental results. Second, we intended to exclude the possibility that behavioral differences between genotypes are due to (exogenous) socio-economic background variables or (endogenous) personality variables. To verify the latter, we administered a questionnaire on background characteristics (e.g., age, field of study (economics yes/no) and number of friends) within an experimental session, as well as various personality measures. As all of these variables have previously been shown to affect individuals' level of cooperation, we tested whether the groups of *MAOA-L* and *MAOA-H* were comparable in terms of their background characteristics. We verified that behavioral differences between genotypes could not be attributed to differences in exogenous and endogenous background characteristics, as they did not differ at a 5 %-level between *MAOA-H* and *MAOA-L* for male and female subjects (see Table 4).

Table 4: *Background Characteristics Across Genotypes*

	Male			**Female**		
	MAOA-L	***MAOA-H***	***p*-value**	***MAOA-L***	***MAOA-H***	***p*-value**
Age	25.45	24.82	0.381	24.91	24.53	0.825
Friends	0.27	0.50	0.635	0.55	0.26	0.455
Economics (1=yes)	0.27	0.41	0.703	0.18	0.28	0.710
Risk aversion (0 to 10)	4.36	5.50	0.272	5.55	5.00	0.414
Patience (0 to 10)	5.82	5.18	0.460	4.45	4.81	0.734
Impulsivity (0 to 10)	4.91	3.91	0.272	5.00	4.72	0.747
Self-monitoring (0 to 18)	10.73	9.14	0.191	8.64	8.06	0.506
Conscientiousness (1 to 7)	4.45	4.83	0.767	5.21	5.18	0.894
Neuroticism (1 to 7)	4.39	3.65	0.149	4.42	4.58	0.691
Openness (1 to 7)	5.15	4.98	0.727	4.58	4.99	0.525
Agreeableness (1 to 7)	5.18	5.08	0.873	4.79	4.98	0.506
Extroversion (1 to 7)	4.36	4.76	0.399	5.00	4.70	0.626
Positive reciprocity (1 to 7)	6.15	6.11	0.583	6.33	6.16	0.393
Negative reciprocity (1 to 7)	3.70	3.71	0.962	3.39	3.19	0.518
Machiavellianism (1 to 7)	**2.96**	**2.59**	**0.503**	**2.42**	**2.73**	**0.068**

With regard to the first aim (i.e., illuminating the link between genotype and player type in a non-experimental way), we measured individuals' willingness to cooperate by making use of a standardized, psychologically validated 20-item questionnaire on Machiavellianism (Christie & Geis, 1970). The questionnaire data showed that female *MAOA-L* carriers, who have already been shown to be less likely to free-ride, had lower scores on the Machiavellianism scale than *MAOA-H* individuals at a significance level of 6.8 % (M-W test, two-sided). Thus, we found that—consistent with our experimental findings—*MAOA-L* female carriers had lower scores on the Machiavellianism scale than *MAOA-H* individuals, indicating that the former are more likely to conform to a social norm of cooperation rather than to pursue their self-interest. As we found only Machiavellianism, but not other psychological and socio-demographic factors we measured, to be associated with *MAOA*, this finding reinforces the notion that the predictive power of genotype is not spurious. In addition, it provides further support for *MAOA* as a genetic predictor of cooperative behavior.

For males, however, we did not observe such a relationship ($p = 0.503$, M-W test, two-sided) which is in line with the findings from the strategic public goods experiment. To conclude, the association between the low activity allele of *MAOA* within females and Machiavellianism suggests an additional pathway between genes and cooperation.

4 Discussion

In 2000, Ben-Ner and Putterman realized that biologists' distinction between genotypes and phenotypes would be especially useful for the study of human preferences, but it took about a decade until the first efforts to make such a distinction were visible. At the same time, it is important to reconsider that it has long been routine to predict outcomes conditional on personal characteristics such as gender, health, and race that are themselves partially determined by genes (Manski 2011). Hence, Manski (2011) argued that one may now similarly predict outcomes conditional on gene measurements. With our study, we address an increasing demand for a deeper understanding of genetic—in addition to environmental—factors that shape human behavior. In particular, we are not aware of any other attempt to link genotype and player type.

Recent findings in genoeconomics using both twin studies (e.g. Cesarini et al., 2009b) and genetic association designs (e.g., Knafo et al., 2008) have shown a genetic component to the other-regarding behavior revealed in economic games. From this point of view, searching for a genetic basis for the observed variation in individual preferences seems to be a promising avenue of research. We complement the literature on the (outside economics) widely-studied *MAOA* testing for an association of this candidate gene and behavior in a strategic public goods game. We offer initial evidence that the free-riding strategy is associated with *MAOA* gene variants in females. Our findings suggest a moderate effect of genetics on individuals' preferences towards cooperation: in females, genotype can, to some extent, predict player type. Female subjects carrying *MAOA-L* are significantly less likely to be weak free-riders than *MAOA-H* subjects. This finding is true for various classification schemes of the weak free-rider type. Furthermore, the association between genotypes of *MAOA* in females and preferences towards cooperation seems to be independent of the elicitation procedure. Indeed, we not only found a link between a particular genetic variant and females' behavior in an incentivized public goods experiment, but also between this gene and responses in a non-incentivized personality questionnaire testing Machiavellianism. This reinforces our finding that *MAOA-L* female carriers are more cooperative than *MAOA-H* carriers. Furthermore, *MAOA-L* female subjects are significantly more cooperative than carriers of the highly efficient alleles in the presence of others who contribute little or nothing. Taken together, these results corroborate our previous findings (Mertins et al., 2011) using different elicitation procedures. In particular, by investigating behavior in a setting where there is no uncertainty, we ensure that behavioral differences do not stem from differences in expectations.

Recently, Chen and colleagues reported *MAOA-L*'s predictive effort on happiness in female carriers and argued that *MAOA-L* women may be more sensitive to positive aspects of their environment (Chen et al., 2012). This rather positive motivation of *MAOA-L* women together with higher levels of serotonin in the brain of *MAOA-L* carriers corroborate our finding of higher cooperativeness in *MAOA-L* females. However, more work needs to be done before we can tentatively report a true association.

With respect to male subjects, we found no statistically significant difference between both genotypes. We observed, however, a potentially interesting pattern in the data. If the other group members are willing to contribute large shares, *MAOA-L* and *MAOA-H* carriers develop in opposite directions: while *MAOA-L* males still increase their contributions as others increase their average contributions, *MAOA-H* subjects remain constant at a lower level. The difference is at its greatest when all group members contribute their full endowment. Further research is needed to clarify the non-significant results. Is there indeed no association for males, or do the null results stem from the relatively small number of subjects? A replication study using a somewhat larger sample size might render the results from just under the significance level to above. Although the observed tendency should not be over-interpreted, it points to a suggestive pattern in the data: *MAOA-L* male subjects are more cooperative than *MAOA-H* subjects in a highly cooperative environment. Instead, we expected *MAOA-L* carriers to be susceptible to free-riding rather than cooperation. An association to pro-social behavior is surprising at first glance, as it has been repeatedly been shown that *MAOA-L* male carriers are susceptible to a variety of antisocial behaviors, including physical violence and criminal behavior. These findings recently motivated Beaver et al. (2010) to examine the association between *MAOA* and gang membership. They found that the low *MAOA* activity alleles conferred an increased risk of joining a gang for males, but not for females. Indeed, an important aspect of gang membership is the gang members' tendency for violence. Another aspect, however, is their feeling of solidarity and their willingness to be there for each other. In this regard, an exceptionally high level of cooperation in a group of highly pro-social others is not contradictory at all. Rather, our findings might contribute to a comprehensive picture that requires further exploration.

Our genoeconomic approach enlightens our understanding of individuals' heterogeneity. Identifying causes, genetic and/or environmental, is crucial because it may help to explain differences and similarities between individuals and/or groups. Fergusson and colleagues demonstrate that the combination of a range of adverse environmental and personal factors together with the *MAOA-L* variant, but not genotype alone, triggers anti-social behavior (Fergusson et al., 2012). Brain imaging studies clearly show that functional genetic variants of *MAOA* a) have an effect on the brain development; b) are modulators of environmental factors in terms of gene-environment interactions, which often display sex differences; and c) result in developmental alterations to specific neuronal circuits, causing different responses to external stimuli (Nordquist & Oreland, 2010). However, the fact that one single variant in a given gene is (moderately) associated with variability in a given trait should not be over-interpreted. Genoeconomics is a nascent field and a frontier area. Many more studies are needed to understand the neural underpinnings of pro-social behavior. Genoeconomics, together with neuroscience, may help to identify causes, either genetic, environmental, or both (Navarro, 2009). We are convinced that a better understanding of all determinants of cooperative behavior and their interactions will benefit economic modeling and will inform policy analysis. In this regard, our study is the first step towards establishing a link between genes and cooperation preferences. Further research is needed to clarify the exact role of *MAOA* and other genes in transmitting social preferences and their interactions with each other and with the environment in males and females.

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Appendix

Genotyping

DNA was obtained from buccal cells followed by a mouthwash with Listerine (Qiagen Gentra Puregene Buccal Cell Kit, Hilden, Germany). PCR was performed in 50 µl reactions with a total DNA concentration of 100 ng, 1.5 mM MgCl2, 10 pmol of each primer, 0.2 mM dNTPs and 1.25 U Hot Star *Taq* Polymerase (Qiagen). *MAOA* primer sequences were previously described (Sabol et al. 1998): *MAOA* Fwd (5'-ACAGCCTGACCGTGGA-GAAG-3') and *MAOA* Rev (5'GAACGGACGCTCCATTCGGA- 3'). Thermal cycling was carried out using the following conditions: pre-step 15 min at 95°C, 5 min denaturing step at 94°C, 40 cycles at 94°C for 30 sec, 63°C for 40 sec, 72°C for 30 sec and a final extension phase at 72°C for 7 min. PCR products were separated on a 2 % agarose gel and visualised with ethidium bromide under UV light. The PCR products resulted in fragments of 291 bp, 321 bp, 336 bp, 351 bp and 381 bp corresponding to the 2-, 3-, 3.5-, 4- and 5-repeat alleles, respectively. Group definition for *MAOA-L* (low activity) and *MAOA-H* (high activity) were previously described (Reif et al. 2008).

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