

Monoamine oxidase A gene (MAOA) predicts behavioral aggression following provocation

Rose McDermott^{a,1}, Dustin Tingley^{b,1}, Jonathan Cowden^c, Giovanni Frazzetto^d, and Dominic D. P. Johnson^{e,2}

^aDepartment of Political Science, Brown University, 36 Prospect Street, Providence, RI 02912; ^bDepartment of Politics, Princeton University, Princeton, NJ 08544; ^cDepartment of Political Science, University of California, Santa Barbara, CA 943106; ^dResearch Centre for the Study of Bioscience, Biomedicine, Biotechnology, and Society, London School of Economics, Houghton Street, London WC2A 2AE, United Kingdom and European Molecular Biology Laboratory, I-00015 Monterotondo (Rome), Italy; and ^ePolitics and International Relations, University of Edinburgh, 15a George Square, Edinburgh EH8 9LD, Scotland

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Monoamine oxidase A gene (MAOA) has earned the nickname “warrior gene” because it has been linked to aggression in observational and survey-based studies. However, no controlled experimental studies have tested whether the warrior gene actually drives behavioral manifestations of these tendencies. We report an experiment, synthesizing work in psychology and behavioral economics, which demonstrates that aggression occurs with greater intensity and frequency as provocation is experimentally manipulated upwards, especially among low activity MAOA (MAOA-L) subjects. In this study, subjects paid to punish those they believed had taken money from them by administering varying amounts of unpleasantly hot (spicy) sauce to their opponent. There is some evidence of a main effect for genotype and some evidence for a gene by environment interaction, such that MAOA is less associated with the occurrence of aggression in a low provocation condition, but significantly predicts such behavior in a high provocation situation. This new evidence for genetic influences on aggression and punishment behavior complicates characterizations of humans as “altruistic” punishers and supports theories of cooperation that propose mixed strategies in the population. It also suggests important implications for the role of individual variance in genetic factors contributing to everyday behaviors and decisions.

warrior gene | genetics | punishment | power-to-take game | hot sauce paradigm

One of the common assumptions of rational choice theory is that individuals are purely self-interested utility maximizers. However, research in economics and other social sciences has found that individual preferences can also include other-regarding factors, such as altruism, status, and fairness. In addition, individuals are often willing to incur nontrivial costs to influence others' behavior, even when such behavior can confer no direct or strategic personal benefit. In particular, humans readily try to harm others who have hurt them or their group, despite the fact that such behavior may not generate any future individual benefit (1). Because in many cases those who punish do not end up better off overall, it remains a puzzle as to why such behavior survives if it does not improve prospects for cooperation (2, 3). An additional puzzle arises in the face of cross-cultural data suggesting that individuals in some societies do not engage in costly punishment as much as those in Western industrialized societies (4, 5).

Although it varies somewhat across societies, real life cooperation and punishment behavior does not always follow the predictions of rational choice theory (4, 6). Various models have tried to address the reasons for this discrepancy (7–11). Here, we suggest a possible genetic source of individual variation in this behavior. This is the first study to investigate a genetic basis for punishment and the first to provide some evidence for a gene-environment interaction in the context of a behavioral economics experiment. Our results support previous work using financial incentives, which indicates that the experimental punishment literature may in fact reflect a broad based tendency to punish.

In this study, we examine conditions under which individuals pay money to cause physical pain to others who have taken money from them in a previous interaction. This study not only replicates previous experimental work demonstrating a willingness to engage in costly punishment, but also tests the influence of the monoamine oxidase A (MAOA) gene, which has been linked to aggression.

We draw on two separate but overlapping literatures: One from behavioral genetics, examining the effect of a genetic polymorphism on propensity for aggression; and a second from economics, addressing an individual's willingness to pay to punish others. In so doing, we combine a behavioral measure of aggression from psychology with a clear and simple economic game to investigate the conditions under which people will aggress against others despite incurring a financial cost to themselves. Previous literature suggests that one of those conditions may be individual variability in genetic alleles, such that individuals with a low activity form of the gene that encodes monoamine oxidase A (MAOA-L) will be more likely to react with aggression to challenge (12). Recent work in behavioral genetics has stressed the importance of interactions between genetic predispositions and environmental contingencies (13).

We build on an emerging literature examining genetic influences within experimental economics, including twin studies demonstrating the influence of heritability in trust game (14) and ultimatum game play (15) among a sample of both American and Swedish subjects. Although there is mounting evidence that behavior in experimental economic games has a heritable component, implying an influence from some unidentified part of the whole genome, there have been few studies explicitly testing for a relationship between economic behavior and a single gene. One recent experimental study suggests a link between a common human polymorphism in vasopressin (AVPR1a RS3) and monetary allocations in a Dictator Game (16), but there have not been any studies of genes related to aggression in such games, and none of this previous work has looked for a link between genetic and environmental interactions. Ours is the first study to look at any gene explicitly in two-player interactions, and the first to examine genetic correlates of behavioral punishment. We conduct this test examining the role of MAOA in aggressive behavior toward others in the context of an economic power-to-take game.

The MAOA gene codes for the enzyme monoamine oxidase A that plays a key role in the catabolism of neurotransmitters,

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¹R.M. and D.T. contributed equally to this work.

²To whom correspondence should be addressed. E-mail: dominic.johnson@ed.ac.uk.

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including dopamine, norepinephrine, and serotonin (12, 17). Earlier studies found that mice with MAOA knockouts were more aggressive than their normal counterparts or mice with MAOB knockouts (which regulates different neurotransmitters) (17). A Dutch family with a repeated incidence of violent criminal behavior among males across several generations was also found to have an abnormality in MAOA (a missense mutation of a single nucleotide of the gene) (18). Recent imaging work in a large sample demonstrates that during emotional arousal, MAOA-L men show greater reactivity in the amygdala and lower activity in the regulatory prefrontal areas. Such work suggests the emotional and cognitive channels that link MAOA-L to impulsive forms of aggression (12, 19).

Among humans, a functional polymorphism in the MAOA gene can mediate the impact of traumatic early life events on the propensity to engage in violence as an adult. Specifically, children who had suffered abuse and who had the low activity form of MAOA were much more likely to develop antisocial problems as adults (20, 21). Later studies replicated the risk of low activity MAOA, in combination with traumatic early life events, for both psychiatric patients and healthy adults' predispositions toward physical aggression (22). A major gap in the literature remains, however, in that it is unclear whether self-report measures of aggression actually reflect behavioral aggression (i.e., actions rather than words).

We combine this work with a second literature drawn from economics. Our experiment also taps into the growing literature on punishment behavior, in which subjects voluntarily incur costs to punish others. A key result from experimental economics is that even where individuals are not the beneficiary of any postpunishment change in behavior (because partners are anonymous and never meet again in subsequent rounds), they often pay to punish those who violate social norms such as cooperation or reciprocity (23–27). However, the link between punishment and aggression is not always clear. Fehr and Gächter's famous experiment included post game self-reports, which suggested that punishers were motivated by anger at free-riders (1). Later replication demonstrated this same association between anger and punishment where free-riding was not allowed. This link was exacerbated with the increasing presence of monetary inequality. These findings indicate that the motivation to punish others may not derive simply from the desire to punish free-riders but also (or instead) from egalitarian motives (26). This literature in economics has not, however, examined whether individuals would be willing to harm someone *physically* in response to economic harm. Therefore, it seems important to examine the underlying causes of aggression and punishment—in themselves—given that they appear to be linked even in widely different social scenarios. Our experiment aims to do this, by examining a genetic proclivity for engaging in costly aggressive behavior in the context of environmental provocation. In short, we deploy hypotheses from behavioral genetics, by using a psychological paradigm, to address an economic puzzle. In this way, we seek to test the extent to which these differences relate to variance in MAOA allele expression.

Methods Primer. In 2008 we collected genetic samples from 78 male subjects, who were assigned to 2 groups: those carrying the high activity (MAOA-H) or low activity (MAOA-L) allele (*SI Text* Section S1 and *Table S1*). Women were excluded because of the difficulty of assigning levels of MAOA enzymatic activity in heterozygous females and to minimize potential confounding factors.

We used the “hot sauce” paradigm (28) from the psychological literature, in which subjects have the opportunity to administer unpleasantly hot (spicy) sauce to an opponent who is known to not like its taste. How much hot sauce the subject administers constitutes the behavioral measure of their aggression (*SI Text* Section S2). The punishment elicitation experiment comprised 4 rounds and had a structure similar to a “power-to-take” game (29, 30) (*SI Text* Section S3). In each round, subjects had an experimentally

manipulated portion of their earnings from a vocabulary task stripped by an anonymous — and unknown to them, fictional — person. Subjects then were given the opportunity to punish this player through the forced administration of hot sauce.

The exact procedure was repeated for 3 subsequent rounds with a (purportedly) new partner each time. Subjects were told that in each round they would have a new supply of hot sauce that they could either administer to their partner or trade in for money. After the experiment, subjects were fully debriefed.

We focus on an individual's willingness to pay to harm someone who had just taken money from them (money that they had worked to earn). The experiment manipulated the amount taken at two levels: 80% and 20%. We label the 80% decision a “high take” outcome and the 20% decision “low take”. We hypothesized that subjects who had 80% taken from them would be more likely to administer hot sauce, and administer more of it, than those who had only 20% taken.

Further, if MAOA has an effect on behavior, we predict that it will depend on the nature of the stimulus. From previous brain imaging work demonstrating greater sensitivity to social rejection among MAOA-L types (31), we hypothesized that MAOA-L subjects should behave no differently than other subjects with low takes, because this represents little provocation to the individual irrespective of genotype. Conversely, MAOA-L subjects are predicted to respond more aggressively than MAOA-H subjects when 80% is taken. Thus, subjects with MAOA-L were hypothesized to behave more aggressively, but only when significantly provoked (i.e., a gene by environment interaction).

Results

Our analysis drops 8 subjects that in a postexperiment survey expressed disbelief in whether they were actually forcing other subjects to eat hot sauce [although our results change little whether we include these subjects or not (*SI Text* Section S5 and *Table S2*)]. We find clear support for our initial hypothesis that high take subjects behave in an aggressive manner toward their opponent more frequently, and with greater intensity, than low take ones. Because our design randomized the amount taken in each round, approximately half the people in each round had 80% of their earnings taken whereas the other half had 20% taken. Because of the nonnormal distributions of our data we use Wilcoxon rank-sum tests. We also report one-tailed test statistics in keeping with our directional hypotheses. Pooling across all 4 rounds of the experiment, subjects demonstrated higher levels of behavioral aggression when 80% was taken than when 20% was taken ($n = 292$, $Z = -6.16$, $P < 0.001$, Fig. 1). A test of proportions also revealed that subjects were more likely to try to harm their adversary by some amount (rather than nothing) when 80% was taken than 20% (66% versus 39%, $n = 292$, $Z = -4.70$, $P < 0.001$). We also observed highly significant differences in the same direction when analyzing each of the rounds separately and when we include observations only of the *first* time someone experienced 20% or 80% taken from them (*SI Text* Section S6).

Furthermore, a battery of emotional surveys administered after the first round showed that those having 80% taken were more likely to report being ‘mad’ and ‘angry’ than those who had 20% taken (*SI Text* Section S7).

For our subsequent hypotheses we divide subjects by MAOA genotype. Fig. 2 pools observations across rounds and shows a significant difference between MAOA types when 80% was taken ($n = 139$, $Z = 2.33$, $P < 0.01$) but no difference when 20% was taken ($n = 141$, $Z = .87$, $P = 0.19$). The proportion of observations in which subjects meted out any aggression (rather than none) when 80% was taken was also higher among MAOA-L types (75%) versus MAOA-H types (62%) ($n = 139$, $Z = 1.40$, $P = 0.08$). When 20% was taken there was no difference between MAOA types (40% versus 34%, $n = 141$, $Z = .71$, $P = 0.24$). Ignoring the amount taken, MAOA-L types had higher levels of aggression ($n = 280$,

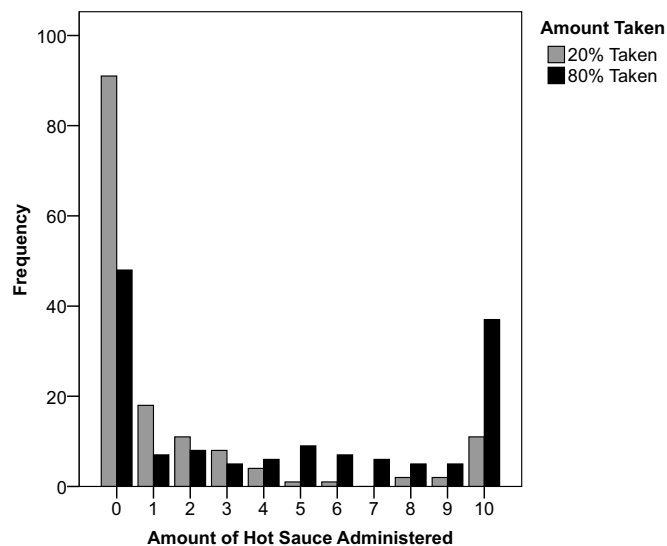


Fig. 1. Amount of hot sauce subjects chose to administer (our measure of aggression) after having 20% (gray bars) or 80% (black bars) of their winnings taken by their (supposed) interaction partner. Wilcoxon ranksum test: $n = 292$, $Z = -6.16$, $P < 0.001$.

$Z < 1.98, P < 0.05$). This suggests that the influence of genetic differences may be moderated by the environmental stimulus, in this case the amount taken.

Because our subjects participated in the task several times, in the next part of the analysis we (a) check for interference across rounds (e.g., did those who received the 80% treatment in round 1 behave differently in round 2 from those who received the 20% treatment?), and (b) analyze each round separately. First, although we did not observe any significant interference between rounds (*SI Text* Section S8), we also compare behavior across MAOA types for the *first* time someone had 80% taken and the *first* time someone had 20% taken (to eliminate any confound or noise arising from past experience). MAOA-L subjects were slightly more likely to be aggressive the first time 20% was taken ($n = 67$, $Z = 1.39$, $P = 0.08$), but we see a larger, and significant, difference across MAOA types when 80% was taken ($n = 66$, $Z = 1.85$, $P = 0.032$; see Fig. 3). This suggests a main effect influence of MAOA but that this effect is

moderated by the environmental stimulus (take amount). Furthermore, if we ignore the amount taken, but directly incorporate the repeated measure nature of our design (using a repeated measure ANOVA), we find a main effect for MAOA (*SI Text* Section S9 and [Fig. S1](#)).

Second, we considered each round separately (Fig. 4). In round 1 there was a significant difference between high and low MAOA types among those who had 80% taken ($n = 33$, $Z = 3.09$, $P < 0.001$), whereas there was no discernible difference in genetic types between those who had 20% taken ($n = 37$, $Z = .58$, $P = 0.28$). Rounds 2 and 3 show no statistical difference and round 4 shows a slight difference (see Fig. 4 legend for full statistics).

In our experiment we bounded the amount of hot sauce that someone could use to try to hurt their partner. In reality, subjects may have wished to give up more points and behave even more aggressively toward their partner with a larger amount of hot sauce. Thus, our data are artificially censored from above by our experimental design.

To address this we compare the proportion of observations that administered the *maximal* amount by MAOA and experimental treatment (i.e., subjects that used all possible \$3 to punish). When 80% was taken, 44% of observations from MAOA-L administered the maximal amount of hot sauce, whereas only 19% of observations from MAOA-H types did ($n = 139$, $Z = 2.95$, $P < 0.01$). When subjects had 20% taken from them, 12% of observations from MAOA-L types and 6% from MAOA-H types administered the maximal amount ($n = 141$, $Z = 1.31$, $P = 0.1$). We obtain similar results if we look at the first time someone had 80% or 20% taken. We also obtain similar results if we examine rates of aggression depending on whether more or less than half the amount of hot sauce was assigned. The message from this exercise is that comparing those who administered the highest amount of hot sauce to those who administered less than this amount reveals the same patterns as our other analyses above.

Finally, Table 1 reports results from a tobit regression model to account for this censoring. Our dependent variable is the amount of behavioral aggression. We include a dummy variable for whether 80% was taken (*80%Take*), a variable equal to one if the subject had the low activity form of the gene (*MAOA-L*), and an interaction between these variables (*MAOA-L* $\times$ *80%Take*). In the results that follow, we estimate models for each round separately, and when pooling all observations. In the first round the interaction term is positive and highly significant ($t = 3.51, P < 0.001$). For the second round the interaction term is negative ($t = -1.39, P = 0.085$).

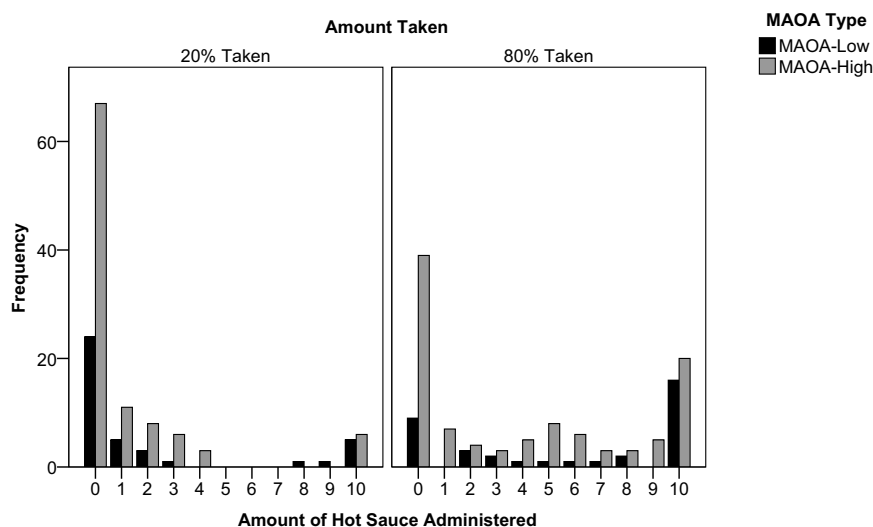
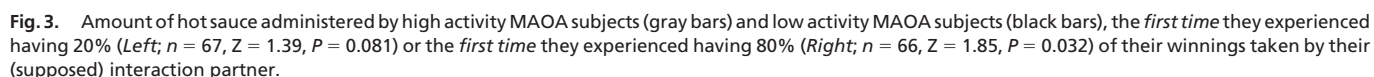


Fig. 2. Amount of hot sauce administered by high activity MAOA subjects (gray bars) and low activity MAOA subjects (black bars), after having 20% (*Left*; $n = 141$, $Z = .865$, $P = 0.19$) or 80% (*Right*; $n = 139$, $Z = 2.33$, $P < 0.01$) of their winnings taken by their (supposed) interaction partner.



Although our results suggest MAOA plays a role in aggression, a major question remains as to how and why individual genetic differences cause different behavioral outcomes. In other words, what might be the underlying *psychological* phenomena at work? In a previous study, Eisenberger *et al.* showed how MAOA related to a negative socio-emotional experience (31). Although MAOA-L individuals are more aggressive, the psychological mechanisms by which this occurs have been unclear. They may be more aggressive because they are *hyposensitive*, and care less about harming others, or because they are *hypersensitive* and overreact. Eisenberger *et al.*'s research examined the relationship between MAOA and trait forms of both aggression and interpersonal hypersensitivity, and neural responses in brain areas associated with rejection-related distress. They found that individuals with MAOA-L demonstrated higher trait aggression and higher trait interpersonal hypersensitivity than those with MAOA-H. In addition, such MAOA-L individuals showed greater activity in the dorsal anterior cingulate cortex (dACC), an area that has been associated with distress related to rejection or status challenges. Because the relationship between MAOA and aggression was mediated by the dACC activity, the authors suggest that MAOA might produce aggression

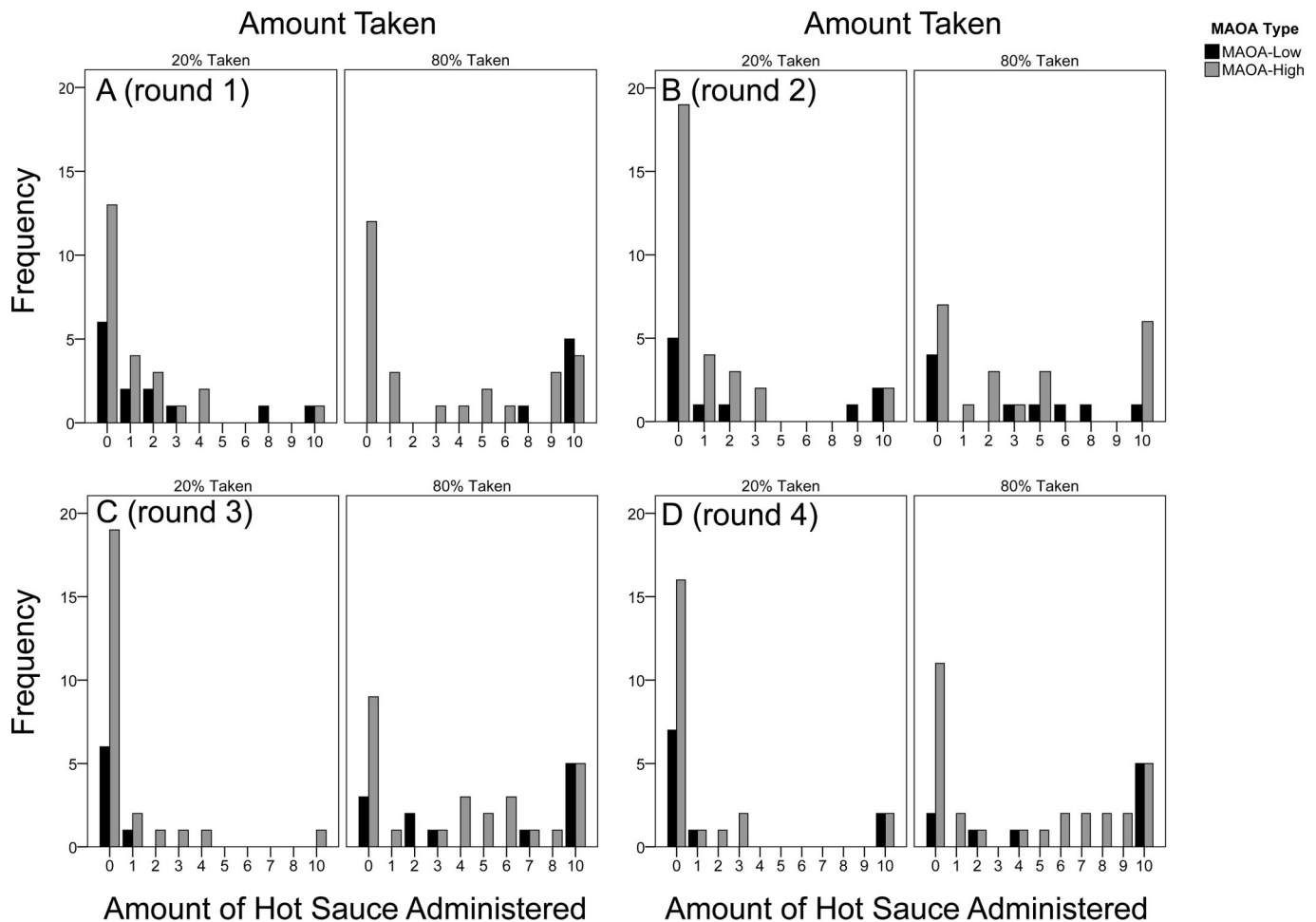


Fig. 4. Amount of hot sauce administered by high activity MAOA subjects (gray bars) and low activity MAOA subjects (black bars) for each of the 4 rounds of the experiment (A–D). Each round had subjects who faced the 20% take treatment (Left), or faced the 80% take (Right). Wilcoxon tests of aggression by MAOA type: Round 1: 20% ($n = 37$, $Z = .58$, $P = 0.28$), 80% ($n = 33$, $Z = 3.09$, $P < 0.001$); Round 2: 20% ($n = 40$, $Z = 1.03$, $P = 0.153$), 80% ($n = 30$, $Z = -.35$, $P = 0.637$); Round 3: 20% ($n = 32$, $Z = -.66$, $P = 0.746$), 80% ($n = 38$, $Z = .81$, $P = 0.2$); Round 4: 20% ($n = 32$, $Z = .23$, $P = 0.41$) 80% ($n = 38$, $Z = 1.45$, $P = 0.073$).

through heightened, rather than reduced, sensitivity to social rejection.

Our findings confirm a role for MAOA genotype in response to provocation, and in particular extend this link to aggressive behavior in response to financial loss. The demonstration of a gene-environment interaction also helps establish the importance of examining genetic variance within particular ecologically valid contexts. Replication across additional populations and within diverse environmental contexts now appears warranted.

A final remaining question involves the *evolutionary* implications of these results. Subjects proved willing to incur private financial cost to punish others in an actual physical way, even

when such actions did not provide any return on their investment. This suggests that a primary puzzle of human economic behavior is “spite” (behavior that is costly to self and others), not “altruistic punishment” (costly to self but beneficial to others) (33). Indeed, recent behavioral games suggest that, since spite is costly, winners do not punish (2). Although spite has been the “neglected ugly sister of altruism” (34), there is good reason to expect it may have played a significant role in the evolution of social behavior.

The influence of genotypic variation among individuals also complicates the notion that humans are “altruistic” punishers because it raises questions about whether one behavioral strat-

Table 1. Effect of MAOA-L and take interaction

	Rnd1	Rnd2	Rnd3	Rnd4	AllRnds
80%Take	2.315 [1.005]	3.291 [1.177]	3.620 [1.050]	3.151 [1.312]	3.101 [0.583]
MAOA-L	0.833 [1.231]	2.249 [1.503]	−0.746 [1.589]	1.004 [1.773]	0.978 [0.775]
MAOA-L × 80%Take	8.922 [2.544]	−3.086 [2.227]	2.372 [2.081]	2.250 [2.585]	1.567 [1.140]
Constant	1.341 [0.729]	1.297 [0.745]	0.889 [0.745]	1.481 [0.985]	1.247 [0.412]
Sigma constant	3.563 [0.340]	4.067 [0.395]	3.716 [0.360]	4.594 [0.462]	4.124 [0.202]
Observations	70	70	70	70	280

Tobit regression for each round of the experiment and pooling across all rounds. Dependent variable: punishment amount (censoring at 10). SE in brackets.

egy is really common to a majority of people. Models of the evolution of cooperation might usefully be revisited with this in mind, especially because recent game theoretic treatments find that punishment may evolve in some subsections of the population but not others (raising the possibility of frequency dependence or mixed strategies) (8). Our study suggests that there may be genetic bases for such a hypothesis. Indeed, our results beg the question of why the MAOA-L allele has been maintained in the population [typically 1/3 in western populations, although approaching 2/3 are reported in Maori populations (32)] if it promotes aggressive behavior. There is some evidence of an underlying positive selection sweep in human population structures in some areas (32). One possibility for why MAOA-L has not become universal lies in frequency dependent selection; if everyone were MAOA-L, its advantages would disappear. If everyone were MAOA-H, there may be a niche for more aggressive individuals to exploit (8). Another possibility is that genetic variation is preserved because it is linked to other genes or has a mix of positive and negative characteristics. Finally, genetic differences in aggression may be an example of the adaptive logic of “moralistic aggression” in promoting effective reciprocal bargaining or cooperative relationships (35, 36). All of these hypotheses are ripe for investigation.

Methods

Genotype frequencies among our group of college subjects (27% MAOA-L) did not significantly deviate from those reported from other western populations (20, 22) (SI Text Section S1). Basic demographic breakdowns are given in SI Text Section S10.

We asked subjects whether they wanted to first try the hot sauce themselves. We inquired as to whether subjects tasted and liked the hot sauce. There was no significant difference in behavior based on those who liked and did not like hot sauce (SI Text Section S11).

In each round, subjects were told they were being paired up with an anonymous person in a separate laboratory located across campus but connected through the internet. Then subjects took a quiz where they completed five multiple choice vocabulary questions. Subjects were told that each vocabulary question they answered correctly was worth 20 points, with an

exchange rate of 10 points to 1 US dollar. After submitting their answers they were told how many points they had earned (\$10 maximum). In reality, we fixed the number of points earned in each round (to either 100 or 80) to allow across subject control in subsequent rounds. Such control is desirable both because different earnings might have translated into substantial differences in the amount of money taken, and because people may make their decisions in response to the amount taken, or the percentages taken. Thus, within any given round, subjects earned the same amount, but we varied this amount across rounds to ensure realism. Subjects were then forced to wait a small, randomly determined period during which their partner “decided” whether they would take 0%, 20%, or 80% of the money earned by the subject. In reality, each subject was paired up with a computer that randomly chose to take either 20% or 80%. Although deception is forbidden in many economic laboratories, it remains a common and effective (often essential) methodology in experimental psychology (37). In this case, we had to deceive subjects because ethical considerations ruled out inflicting potential pain on subjects by making them actually ingest hot sauce. Because we knew from previous work that subjects respond differently to people than to computers, we needed to deceive them about the true nature of their opponent (27). Our subjects were told that their partners had also completed a similar vocabulary task for money. Subjects then were shown a screen telling them the percentage taken by the other player and given the opportunity to behave aggressively toward the other person who had just taken their earnings.

Subjects were told that they had been given a fixed endowment of 10 1/8 teaspoon doses of hot sauce. They could choose to force the other person to drink an amount of the hot sauce, or trade the hot sauce in for money, at a rate of 3 points per dose and 10 points to a dollar (i.e., they could keep a total of \$3 or use some or all of it to hurt their partner; they could not use their prior earnings to buy or administer extra hot sauce). They were told that the other person would have to drink the hot sauce to keep the money they took. Otherwise, the stolen points were returned to the experimenters. In either case, the subject would lose the points taken by their partner. We told subjects their partner's supposed rating of how much they liked the hot sauce. This value was fixed for all subjects within a round to a low level (either 1, 2, or 3 of 10) of enjoyment (varied for realism). We found no difference in behavior as a function of partner rating across rounds (SI Text Section S4).

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Supporting Information

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SI Text

S1: Description of MAO-A Typing. DNA was obtained from buccal swabs (Oragene, DNA Genotek, Inc.). PCR was carried out using the following conditions: initial 5-min denaturing step at 95.0 °C, followed by 35 cycles at 94.0 °C for 1 min, 53.8 °C for 1 min and 72.0 °C for 1 min 30 s, and a final extension phase at 72.0 °C for 10 min. Primer sequences were those described by (1): MAO-F (5'-ACAGCCTGACCGTGGA-GAAG-3') and MAO-R (5'-GAACGGACGCTCCATTCGGA-3'). Reactions were performed in 25 µl of total volume with 50 ng of genomic DNA, 1.5 mM MgCl₂, 10 pmol of each primer, 0.33 mM dNTPs, and 1.5 U of native Taq (Promega). PCR products were assayed on a 3% agarose gel. The primers used yielded 290-, 320-, 335-, and 380-bp fragments corresponding to the 2-, 3-, 3.5, 4-, and 5-repeat alleles, respectively.

S2: Description of Hot Sauce Paradigm. This paradigm has been used in several notable studies of aggression in psychology. In one study, which tested terror management theory, McGregor and colleagues (2) conducted 4 separate experiments, which demonstrated that threatening a person's world view increased their motivation for aggression against the threatening target. A second study that used the hot sauce paradigm tested an evolutionary model of self-esteem and aggression. Kirkpatrick *et al.* (3) found that self-perceived superiority increased aggression toward a target, whereas social inclusion decreased such aggression. In a third study, Meier and Hinsz used the hot sauce paradigm to examine the difference between individual and intergroup aggression (4).

S3: Experimental Interface and Script Read During Experimental Session. Experiment was programmed using the Multistage software package (<http://multistage.ssel.caltech.edu/>). All subjects made all choices through the computer interface.

Script read aloud: During the experiment you will be paired with people in another computer lab. You will not see the people you play against but you will be linked to them through the web. Everything will be anonymous, and you will never be paired with the same person twice. In this experiment you will earn points that will be converted to real money using a 10 points to every 1 dollar conversion rate. Please click on the icon that says "PP" and enter in your 5 digit number and click submit.

[To confederate: "Could you please go tell the other lab that we are ready to begin."]

In this part of the experiment, we ask you to answer some vocabulary questions. For each correct answer, you will earn 20 points. After you finish the questions, you will be randomly paired with someone in the other lab that has also completed a similar task for money. They will be allowed to take some of the points you have earned answering questions. They can take nothing, 20%, or 80% of what you have earned. After you see their decision, you will have a chance to force them to eat an amount of hot sauce. You will be able to choose the amount, and they must eat it to keep the points they took. If they do not eat the hot sauce, then the points they took go back to the experimenters. Any hot sauce you do not force the other person to eat can be exchanged for points for yourself. You will play this game several times, each time you will be paired up with a new person. Each round of play will have a set amount of hot sauce, and hot sauce is not transferred between rounds. In each round, you must decide how much hot sauce to use and how much to exchange for points.

Subjects then completed 4 rounds of the experiment. In each round a subject first answered 5 vocabulary questions. Next, they saw a screen telling them they had earned either 100 or 80 points. They were then shown a screen that had them wait a small, random, amount of time during which they were paired with another person. Next they were shown a screen indicating the (randomly determined) identification number of their partner and again waited a small (randomly determined) amount of time while their partner "decided" how much money to take. Finally, they were shown a screen indicating how much hot sauce was taken. Subjects then selected on a slider how much hot sauce they would administer.

S4: Punishment by Partner's Enjoyment Rating of the Hot Sauce.

Within a round, the hot sauce rating of subject partners was fixed to 1, 2, or 3 of 10. We conducted Wilcoxon tests to see whether punishment rates differed by partner ratings. We compared those paired with a subject with a 1 rating to those with a 3 rating. For those who had 80% taken there was no difference ($n = 76$, $Z = -.075$, $P < 0.47$). For those who had 20% taken there was also no difference ($n = 70$, $Z = -.75$, $P < 0.23$). Tests for differences between 1 versus 2 ratings and 2 versus 3 ratings also did not reveal significant differences.

S5: Disbelievers. The analyses reported in the body of the article excluded 10 subjects, of which we also had genetic typing on 8 subjects. It is standard practice to exclude subjects who are suspicious of the experimental manipulation (5). Nevertheless, we replicate all of the statistical tests from figures in the article without excluding these subjects. All statistical tests are those used in the main article (Wilcoxon ranksum tests). We report statistical tests for each figure from the main text below, and report results from Table 2 in Table S2. Figure 1: Amount of hot sauce subjects chose to administer (our measure of aggression) after having 20% or 80% of their winnings taken by their (supposed) interaction partner. Wilcoxon ranksum test: $N = 332$, $Z = -5.59$, $P < 0.001$. Figure 2: Amount of hot sauce administered by high activity MAOA subjects and low activity MAOA subjects, after having 20% ($N = 151$, $Z = 0.325$, $P = 0.37$) or 80% ($N = 161$, $Z = 2.27$, $P = 0.01$) of their winnings taken by their (supposed) interaction partner. Figure 3: Amount of hot sauce administered by high activity MAOA subjects and low activity MAOA subjects, the *first time* they experienced having 20% ($N = 72$, $Z = 1.08$, $P = 0.14$) or the *first time* they experienced having 80% ($N = 74$, $Z = 1.51$, $P = 0.065$) of their winnings taken by their (supposed) interaction partner. Figure 4: Amount of hot sauce administered by high activity MAOA subjects and low activity MAOA subjects for each of the 4 rounds of the experiment. Each round had subjects who faced the 20% take treatment, or all faced the 80% take. Wilcoxon tests of aggression by MAOA type: Round 1: 20% ($N = 38$, $Z = 0.38$, $P = 0.35$), 80% ($N = 40$, $Z = 2.62$, $P = 0.004$); Round 2: 20% ($N = 44$, $Z = 0.54$, $P = 0.29$), 80% ($N = 34$, $Z = -0.04$, $P = 0.52$); Round 3: 20% ($N = 33$, $Z = -0.79$, $P = 0.786$), 80% ($N = 45$, $Z = 0.92$, $P = 0.179$); Round 4: 20% ($N = 36$, $Z = 0.01$, $P = 0.5$) 80% ($N = 42$, $Z = 1.21$, $P = 0.113$).

S6: Hot Sauce Amount by Amount Taken and Round. For each round the frequency of punishment is contrasted by treatment type. Sample sizes, test statistics for Wilcoxon rank sum tests, and p values given for each round. Round 1: $n = 73$, $z = -2.69$, $P =$

0.004; Round 2: $n = 73$, $z = -2.52$, $P = 0.006$; Round 3: $n = 73$, $z = -4.08$, $P < 0.001$; Round 4: $n = 73$, $z = -2.9$, $P = 0.002$

S7: Emotional Manipulation Check. After the first round, all subjects were asked to indicate their levels of particular emotions. Subjects who had 80% taken had higher levels of mad and angry emotions than those who had 20% taken (“Angry”: $z = -2.24$, $P = 0.013$; “Mad”: $z = -2.48$, $P = 0.007$). Furthermore, among those who had 80% taken, those with MAOA-L reported nearly double the levels of anger as those with MAOA-H ($n = 33$, $Z = 1.50$, $P = 0.065$). There was no significant difference across genotype among those having 20% taken ($n = 37$, $Z = .88$, $P = 0.19$).

S8: Interference. Subjects repeated 4 rounds of the experiment. It is possible that subject behavior could depend on how much was taken in an earlier period. We do not find evidence for interference. For round 2, we consider whether the difference in treatment (80% versus 20% take) still had a differential effect on the amount of punishment when 1) subjects had 20% taken in round 1 ($n = 38$, $Z = -2.2$, $P = 0.014$) and 2) subjects had 80% taken in round 1 ($n = 35$, $Z = -1.386$, $P = 0.083$). In each case we still find a difference in round 2 according to the treatment type when we separate cases out by the round 1 treatment. We also compare punishment rates within round 2 treatments by whether or not subjects faced the 20% treatment in round 1 or the 80% treatment. For those subjects facing round 2 treatment of 80%, there was no difference by their round 1 treatment status ($n = 32$, $Z = .27$, $P = 0.39$). For those subjects facing round 2 treatment of 20%, there was no difference by their round 1 treatment status ($n = 41$, $Z = -.07$, $P = 0.47$).

S9: Repeated Measures ANOVA. Our results support a role of MAOA in punishment whether looking at all data, round 1 only, other rounds separately, or the first time a subject experienced a given take amount. Here, we test whether the result holds when all rounds of the experiment are taken into account in a single “repeated measures” test. To deal with the repeated measures of punishment across all four rounds of the experiment, a 2×3 “one-between, one-within” ANOVA on punishment amount was conducted with MAOA genotype as the between-subjects

factor and round (round 1, 2, 3, 4) as the within-subjects factor. Fig. S1 shows that marginal means for punishment were higher for MAOA-L subjects than MAOA-H subjects in every round of the experiment.

Note that this repeated measures analysis does not control for take amount (i.e., whether 20% or 80% was taken before each punishment decision), for 3 reasons. First, take amount cannot be included as an additional repeated measure, because it would need to be a continuous variable (take amount is a binary variable: either 80% or low 20%). Also, take amount is not a subject response, but a treatment factor. Second, take amount cannot be included as a covariate in the model, because it is not a single variable—there are 4 separate take amount variables (one for each round). Finally, we cannot conduct 2 separate repeated measures tests of all data for 20% takes, and then all data for 80% takes, because splitting up the data this way results in many cells (given the 2 MAOA types $\times$ 4 Rounds $\times$ 2 Take amounts) with little or no data.

The results of each of our tests must be considered in combination. MAOA type plays a consistent role in punishment across a wide range of alternative tests. This is again supported by the repeated measures test reported here.

S10: Demographic Breakdowns. Ethnicity: 61% Caucasian, 14% Asian, 10% Hispanic, 4% African-American, and 11% other.

Age: mean 22, SD 4.7

Student status: 11% Graduate Student, 37% Senior, 19% Junior, 33% Sophomore.

S11: Punishment and Own Hot Sauce Preferences. We investigate whether punishment amount varied by whether or not someone liked the hot sauce they sampled. For those selecting to try the hot sauce we had them rate how much they liked the hot sauce on a 0–10 scale. We coded all those indicating a 5 or above as liking the hot sauce, and coded all other subjects as not liking the hot sauce. We then compared punishment rates by hot sauce preference by using Wilcoxon-Mann-Whitney tests for the first time someone had 80% taken ($z = -1.06$) and the first time someone had 20% taken ($z = -1.43$). In each case those that liked hot sauce were slightly more likely to punish, but this difference was not statistically significant.

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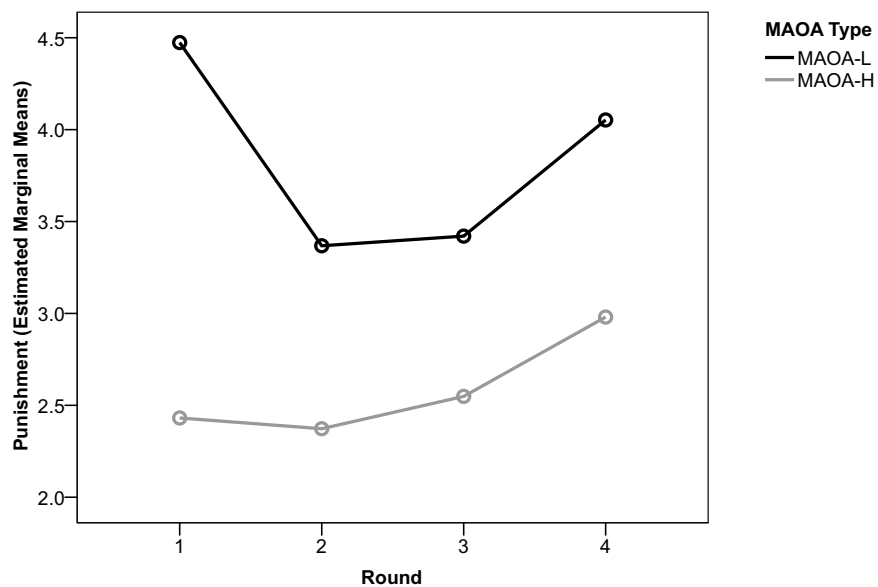


Fig. S1. Marginal mean punishment amounts for each round by MAOA genotype.

Table S1. Allele frequencies for subjects in experiment

MAO-A Typing	Frequency	Percentage	Cum
Low (MAOA-L)	19	27.14	27.14
High (MAOA-H)	51	72.86	100
Total	70	100	

Table S2. Effect of MAO-L and take interaction, tobit regression

	Rnd1	Rnd2	Rnd3	Rnd4	All Rnds
model					
80%Take	2.071 [1.030]	2.737 [1.063]	2.976 [0.989]	2.536 [1.251]	2.587 [0.549]
MAO-L	0.681 [1.288]	1.654 [1.342]	−0.763 [1.496]	0.476 [1.697]	0.658 [0.734]
MAO-Lx80%Take	6.536 [2.255]	−1.923 [2.047]	2.515 [1.948]	2.205 [2.458]	1.743 [1.074]
Constant	1.347 [0.781]	1.273 [0.697]	0.888 [0.738]	1.783 [0.936]	1.315 [0.400]
Sigma constant	3.818 [0.347]	3.931 [0.357]	3.681 [0.334]	4.639 [0.439]	4.102 [0.188]
Observations	78	78	78	78	312

Including subjects that indicated doubt about their actually administering hot sauce change our results very little. The statistical significance of differences across take treatment decreases slightly. The statistical significance of differences across MAOA type decreases slightly. The significance of the interaction term in table 1 increases slightly.