Rice Cultivation, Cooperativeness, and Evidence for Gene (Dopamine D4 Receptor) – Culture Coevolution

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Abstract
We investigate how culture induced by rice cultivation influences people's cooperative behavior with 1,213 Chinese university students in Beijing indexed by the proportion of rice farming in their birth province. First, we found that cooperativeness proxied by the level of contribution in an incentivized public goods game (PGG) varies positively with the proportion of rice cultivation. Second, we extended our laboratory-based results by using survey data relating to cooperativeness from the China Family Panel Studies (CFPS). Third, we showed that the dopamine receptor D4 (*DRD4*) exon III coding region repeat polymorphism 2R genotype is associated with increased cooperativeness in the PGG. We further observed a positive correlation between frequency of the 2R genotype and province-level history of the introduction of rice farming, suggestive of gene-culture coevolution on a time scale across 10,000 years.

Keywords: Public Goods Game, Cooperation, Dopamine D4 Receptor (*DRD4*), Rice cultivation, Gene-culture Coevolution

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Introduction

Rice and wheat are among the most important food crops worldwide[1]. In China, rice has a long history of cultivation originating about 10,000 years ago at the dawn of the world agricultural revolution[2] and rice farming has become a prominent feature of Chinese culture especially in its southern regions. The long history of rice cultivation and paddy farming has been widely investigated and amply documented suggesting the notion that rice farming is likely to have influenced the psychology, cognition, and cultural attitudes of the Chinese people, extending across generations[3].

The development of large-scale cooperation for the collective good among genetically unrelated people[4] has been a longstanding puzzle and the subject of research since Darwin's *Descent of Man* in which he presents his ideas on human cultural evolution[5,6]. As noted by Alexander[7] in his highly influential article, "we have still not clarified all those circumstances in which the structures or functions of one individual may have been formed for the exclusive good of other individuals within its own species." It seems reasonable to posit a relationship between cooperativeness at the societal level and rice paddy farming at the village level since rice cultivation requires much more labor and coordination in comparison with wheat and other crops. For instance, Fei[8] observes that the irrigation system in the Yangtze River requires the cooperation of all families in a village to operate manually the paddle-driven water-lifting wheels. In this regard, the emergence of a rice culture is conducive to the development of large-scale cooperation and helps insulate peoples in the rice-suitable regions from the tragedy of the commons arising from the use of water as a common pool resource[9]. Our hypothesis is compatible with the finding in Talhelm *et al.*[10] linking interdependent-independent and analytic-holistic thinking types to the rice and wheat farming regions in China. They offered convincing evidence of the persistence of culture having a lasting effect on behavior into the modern era, independent of the individual's experience with actual farming practices. This persistence further points to a possible underlying mechanism of gene-culture coevolution as hypothesized in a number of papers[4,11-13]. Indeed, gene-culture coevolution theory, complementary to purely cultural evolution, offers one possible explanation of how culture becomes embedded in the genome thereby contributing to the persistence of culture on human behavior. In this regard, the culture of rice paddy farming in China with its large Han Chinese population and long, well-studied history as well as prehistory, provides a unique window into the proximate psychological and molecular genetic underpinnings of the evolution of human cooperation.

In the current study, using experimental economics games, we find that cooperativeness in a region is related to whether it is rice or wheat growing. This finding is corroborated by our analysis of data from the nationally representative China Family Panel Studies (CFPS)[14] using questions that relate to cooperativeness. These findings are further augmented by molecular genetics analysis which reveals their likely basis in terms of gene-culture coevolution. With a large group of 1,213 university students in Beijing, we make use of a standard game in experimental economics, the Public Goods Game (PGG), to elicit cooperative behavior that reflects real-world willingness to cooperate for a public good when the opportunity to 'free ride' is present. The PGG arguably resonates with the cooperative behavior characterizing community-level paddy rice farming. Our hypothesis is that rice culture predicts greater contributions to the public pool. Towards a deeper understanding of the choice behavior elicited in the PGG, we use the trust game (TG), the modified dictator game (MDG), the jealous game (JG), and the sequential prisoner's dilemma game (SPDG) and show that rice culture overall encourages efficiency enhancing behavior which underpins cooperativeness. In parallel, we perform data analysis based on the 2010 wave of the CFPS which

includes questions on getting help and giving help - relating to cooperativeness and find support for our hypothesis that rice farming regions are characterized by a greater disposition towards cooperativeness.

The dopamine D4 receptor (*DRD4*) gene has a notable evolutionary history with some evidence for recent selection in the past 50,000 years possibly related to propensity to migrate[15-18]. Given that polymorphic variants of this gene appear to have evolved at the same time as the emergence of modern humans, it serves as a particularly attractive candidate for the study of gene-culture coevolution[16-18]. This gene-culture coevolution hypothesis is also consistent with the suggestion in Kitayama *et al.*[19] of *DRD4* as a norm-congruous behavioral gene[19-21], and a plasticity gene that confers behavioral sensitivity to the social environment[22-26]. We are led to examine the relationship between the dopamine D4 (*DRD4*) exon III coding region polymorphisms and individual contributions in the PGG along with rice versus wheat farming across China. This leads us to hypothesize that some *DRD4* exon III genotypes will enhance cooperativeness and will be more prevalent in the rice farming areas in the extreme long run over the millennia since the invention of rice cultivation in China.

Results

To investigate the relationship between the rice farming ratio and people's cooperative behavior, we use both ordinary least square (OLS) regression and instrumental variable (IV) regression. The following equation is our baseline regression model:

$$Y_{i,p} = \alpha + \beta Rice_p + \lambda X_{i,p} + \eta W_p + e_{i,p} \qquad (1)$$

where $Y_{i,p}$ refers to cooperative behavior elicited using experimental games or survey data for individual i in province p, $Rice_p$ is the proportion of rice farming in province p, $X_{i,p}$ refer to individual control variables including gender, family income, and whether parents are farmers etc., W_p refer to province level control variables such as provincial GDP per capita in 1996, the proportion of agriculture sector in the whole economy in 1996, and population density in 1996, and the last item $e_{i,p}$ is a random error term.

The IV regression is used to address potential measurement errors arising from the earlier date of the 1996 rice farming data and possible reverse causality between rice farming and cooperative behavior[27]. The United Nations Food and Agriculture Organizations Global Agro-ecological Zones database offers several indices on the environmental suitability for growing rice and other crops, which are computed using multiple dimensions of geographic information from temperature, humidity, evaporation, soil quality, and slope. These suitability indices have been used in previous studies[28,29] as instruments to address possible endogeneity problems relating to agricultural production using IV regression. Following Talhelm *et al.*[10], we also adopt the rice suitability index $RiceIndex_p$ as instrument to assess the percentage of rice farming and arrive at an additional equation for the first-stage regression for IV:

$$Rice_p = \mu + \delta RiceIndex_p + \kappa X_{i,p} + \varphi W_p + \nu_{i,p} \qquad (2)$$

where $\nu_{i,p}$ is a random error term. In addition, we cluster the standard error at the province level to handle the possible correlations inside the same province due to culture or other factors.

The Public Goods Game (PGG)

In the two-person public goods game, each subject is endowed with 80 yuan and decides on the amount to contribute to the group anonymously. The amount contributed will be multiplied by 1.6 and the total will be divided equally between the two subjects. The PGG is one-shot hence

participants only make the decision once. The descriptive statistics for the main variables, sample distribution, and average contributions across provinces are in *SI* Table S1 – S4. The average contribution is 49.338 yuan pointing to the rejection of the assumption of pure selfishness. Table 1 shows the ordinary least squares regression (OLS) and instrumental variable (IV) regression results of the public goods game. As predicted, in OLS regressions (Model 1), the contribution amount in the public goods game is positively related to the proportion of paddy rice farming area relative to the total planted area in the province, with control variables of gender, family income, whether parents are farmers, provincial GDP per capita in 1996, the proportion of agriculture sector in the whole economy in 1996, and population density in 1996 etc. The coefficient of rice farming proportion is 9.117 ($p = 0.019$) suggesting that a subject born in a province with 100% paddy rice farming will contribute 9.117 yuan more in the PGG than an individual born in a province with no paddy rice farming, which indicates that an increase of one standard deviation in the proportion of rice farming leads to an increase of 0.06 standard deviation of contribution in the PGG. Our hypothesis is further strengthened from the results of the IV regression (Model 2), showing that the coefficient of rice farming proportion increases to 12.525 ($p = 0.007$) indicating a greater effect of rice farming on contribution amount. The coefficients for both family income and province level GDP per capita in 1996 are negative suggesting that in our student sample, higher income level is associated with smaller contribution (See Table S5 in *SI* which displays the full results relating to Table 1). In addition, if one of the participant's parents is a farmer, he or she contributes more. We also find a sizable gender effect, viz. females tend to contribute less than males by about 2.8 yuan. The first-stage and the reduced form regression results of the IV regressions, are shown in *SI* Table S6. Complementarily, in *SI* Table S7 we investigate the effect of wheat farming on cooperativeness, and observe a negative relation replicating the corresponding finding in Talhelm *et al*.[10].

Additional Experimental Economics Tasks

Towards a more penetrating understanding of the motivations underlying how rice culture encourages increased cooperativeness in the PGG, we examine behavior in several related experimental economics games, namely the trust game (TG), the modified dictator game (MDG), the ultimatum game (UG), the jealous game (JG), and the sequential prisoner's dilemma game (SPDG) (see *SI Experimental Instructions* for detailed descriptions). In the TG, the trustor (Player 1) is endowed with 80 yuan. She decides on the amount of money, which reflects a level of *trust*, to be sent to the trustee (Player 2) who receives thrice this amount and has the option to send any portion of the amount received back to the trustor. We use the TG to further examine whether the behavioral motivation driving cooperation associated with rice farming proportion is associated with increasing the size of the social pie. The overall results from the TG (see *SI* Table S9) are consistent with the efficiency motive notion that is observed in the PGG. In the OLS regression, the rice farming proportion is positively correlated with trust proxied by the amount sent by the trustor ($P = 0.002$); in the IV regression, the results between rice farming and trust are similar ($P = 0.003$). Interestingly, we do not observe significant effects of rice farming proportion on the reciprocal behavior of the trustee. This suggests that rice culture mainly influences peoples trusting behavior in potentially delivering a bigger social pie than trustworthiness, which is more attuned to their sense of reciprocity.

We next examine whether the effect of rice cultivation on cooperative behavior is influenced by social efficiency concerns using a modified dictator game (MDG) as suggested by Andreoni and Miller[30]. In the MDG, each subject is endowed with different amounts of money and decides to

send parts of the endowed amounts to the other player at a specific factor R of 1/3, 1/2, 1, 2, and 3. The subject keeps the unsent balance. Giving is efficient when R = 2 and 3, i.e., the social pie increases. By contrast, giving is inefficient when R = 1/3 and 1/2. In *SI Results* Table S10, when giving is inefficient, the coefficients of rice farming ratio are negative and significant in IV regressions. Subjects from more rice farming regions give less in the MDG when the social pie is diminished. In the case of inefficient giving, the coefficients of rice farming ratio are not significant, albeit positive. When R = 1, the coefficients of rice farming ratio are positive but not significant.

We provide additional evidence that the effect of rice cultivation on cooperative behavior is driven by social efficiency concerns using a jealous game (JG). In the JG, there are two players: Person A and Person B. Person A decides how much of a $30 endowment Person B receives. Person A always receives $0 regardless of his or her decision. Person B makes no decision and solely receives the amount decided by Person A. In this context, the amount Person A decides to send to Person B is a measure of social efficiency, since Person A receives no benefit from sending less money. In *SI Results* Table S11, the coefficients of rice farming ratio are positive and significant in both OLS and IV regressions. If Person A is from a region with a higher percentage of land suitable for rice farming Person A sends more money to Person B. These results provide further support of our core hypothesis that social efficiency motivation is the main driving force underpinning the relationship between rice cultivation and cooperative behavior.

We further examine the role of rice farming on cooperative behavior using the sequential prisoner's dilemma game (SPDG). For Player 1, while moving Left is efficiency enhancing in increasing the social pie, she exposes herself to the risk of a much lower payoff should Player 2 move Right which pays higher. On the other hand, moving Right would guarantee a moderate payoff should Player 2 also move Right while retaining the possibility of a much higher payoff should Player 2 move Left. For Player 2, moving left is always efficiency enhancing. Here, we differentiate between unconditionally cooperative (i.e. moving left regardless Player 1 has moved Left or Right) and conditionally cooperative (i.e., moving left when Player 1 has moved Left and moving Right when Player has moved Right). *SI Results* Table S13 shows the results for the linear probability regression on the Player 2 choosing cooperative behavior with two measures: a dummy variable of unconditional cooperation and a variable for the strength of the cooperative behavior. These results are in line with participant's behavior in the PGG, in the TG, in the MDG, and in the JG. In other words, people from higher rice farming proportion areas tend to prefer an efficiency-enhancing option and reciprocate positively by moving Left when the first player moves Left and refrain from reciprocating negatively and move Left even if the first player moves Right.

In summary, results from analyzing additional economic games including the TG, MDG, JG, and SPDG suggest that the impact of rice culture on cooperative behavior first observed in the PGG remains robust and supported by the results showing efficiency-enhancing behavior in additional games eliciting social preference.

China Family Panel Studies Data (CFPS)

Given that subjects who participated in the PGG and other economic games are university students, they may not be representative of the Chinese population. This leads us to test the generalizability of our finding to the national level. The China Family Panel Studies (CFPS), a large nationally representative panel survey, includes two questions concerning one's experience in seeking help and giving help which provide additional information to test for the robustness of our findings

from economics experiments in the laboratory (for details see *SI Methods, China Family Panel Studies*). We find that the relation between rice culture and cooperativeness elicited from experimental economic tasks is replicated with the CFPS data. Our focus variable is Giving help and take it as a measure of cooperativeness. Column (1) and Column (2) in Table 2 are OLS and IV estimation results for Giving help, and the coefficients of rice farming proportion are positive and significant for IV. In Column (3) to Column (4) of Table 2, the coefficients of paddy rice ratio are 0.081 in OLS ($P < 0.1$) and 0.095 in IV ($p < 0.01$) for Giving help after additional control for Getting help: when the rice farming proportion increases by 10 percent, the probability of Giving help will increase by around 1 percent. These results demonstrating a positive and significant relationship between rice farming proportion and cooperativeness with data from the CFPS are consistent with and support the preceding laboratory-based results underscoring the notion that experimental economics paradigms can inform observed behavior in the real world.

Norm Sensitivity, Rice Culture and DRD4

We analyze gene data to explore whether *DRD4* 2R genotypes will enhance cooperativeness in addition to rice culture. Table S4 in *SI Results* displays the distribution of the variable number of tandem repeats (VNTR) of *DRD4* among the 1,180 subjects who have genotyping information. In line with the literature[20,31], we adopt the notation of 2R and 7R referring to both homozygous and heterozygous genotypes involving a 2-repeat or a 7-repeat respectively with 4R referring to homozygous and heterozygous genotypes involving a 4-repeat without overlapping with 2R or 7R. This results in 390 subjects (33.1%) being classified as 2R, three subjects classified as 7R (0.3%), and 784 subjects (66.4%) classified as 4R. Two other subjects (0.2%) are homozygous with a 5-repeat. We hence focus our analysis on the comparison between the 2R and 4R subjects numbering 1175 and constituting 99.4% of the total sample. We show in *SI* Table S18 and Table S19 that our analysis is robust towards inclusion of four 4/7 subjects within 2R as well as inclusion of two 5/5 subjects within 4R.

As shown in Table 1 we find a significant main effect of *DRD4* on contributions in the PGG. As predicted, Model 3 (OLS) and Model 4 (IV) reveal that 2R genotypes are associated with greater contributions in the PGG. In both Model 5 (OLS) and Model 6 (IV regression with both the rice suitability index and the product of rice suitability index and *DRD4* dummy serving as instruments), the main effect of rice culture remains significant after adding the Rice farming $\times$ *DRD4* interaction term, while we observe a negative interaction between *DRD4* and rice culture (significant in IV with $P < 0.1$). To better understand the interaction between *DRD4* and rice culture, we stratify subjects by genotype: 2R versus 4R. The regressions in Table S17 examine the effect of rice farming proportion in these two groups – Model (1) and (2) include solely 4R subjects while models (3) and (4) include only 2R subjects – and find that rice farming proportion is a significant predictor of PGG contributions for 4R subjects but not for 2R subjects.

To investigate further how rice farming generates the cultural framework for the persistence of more cooperative life style as suggested in Talhelm *et al.*[10], we employ the data from Peng *et al.*[32] to arrive at Figure 1 which relates the proportion of *DRD4* 2R genotypes at the province level and the temporal incidence of rice domestication over 10,000 years in 14 provinces of China whose data is available. The regression coefficients in Table S20 for the proportion of 2R genotype is 0.021 ($p = 0.07$) indicating an increase of 2R genotypes at 2.1% per millennium in the presence of rice farming lends support to the hypothesis of the coevolution of *DRD4* 2R genotypes and rice culture. This is consistent with suggestions in the literature[16-18] on the positive selection of *DRD4* exon III 2-repeat and 7-repeat alleles. In *SI* Figure S2 and Table S21, we consider an alternative definition of rice age data from Gong *et al.*[33], and the results remain robust.

Discussion

The relatively homogeneous student sample and the transparent and incentivized measures of cooperativeness elicited through the PGG support a rigorous internal validity for our results. Our results based on the nationally representative CFPS data add external validity to our laboratory findings in delivering an additional measure of cooperativeness involving the general populace. Besides rice theory, we test the two alternative hypotheses discussed in Talhelm *et al.*[10] – the modernization hypothesis and the pathogen prevalence theory – and arrive at a similar view that they are not consonant with our overall observations that it is rice culture coupled with the gradual change in *DRD4* exon III genotype frequency that drives cooperativeness over the long haul (see Table S15 and Table S16 in *SI*).

The overall evidence presented in the current study suggests that the gradual adoption of rice paddy farming in China over the past 10,000 years has been the driving cultural force of enhanced cooperation observed using both experimental economics paradigms involving university students and in the general population using data from the CFPS. Intriguingly, we find that the enhanced cooperation is explained partially by changes in *DRD4* exon III genotypes frequency, viz. students from provinces that first adopted rice cultivation are characterized by higher frequency of 2R genotypes. We suggest the notion that 2R genotypes underpin the cognitive mechanisms enabling large-scale cooperation crucial for paddy farming, leading 2R to be associated with increased contribution in the PGG. In addition, we also use additional genetic data to verify that our participants indeed come from different parts of China, and the migration is not a confounding factor (See Figure S1 in *SI*).

Like complex behavioral traits in general, social decision-making traits may be determined by both genes and environment including the cultural milieu. Cultural evolution, e.g. adoption of rice paddy farming – a form of niche exploitation, can mold the social environment for selection of specific genotypes. Genetic polymorphisms that enable their carriers to easily recognize relevant community norms such as cooperation at the village level for irrigation needed for rice fields, and adherence to such norms will enable such individuals to enjoy the social benefits of norm-compliance, viz. more rice in the pot and at the same time avoid community-level sanctions for non-compliance. Whereas a few studies have identified specific cultural elements and gene interactions: oxytocin, distress and culture[34], independent versus interdependent cultures, social learning and *DRD4*[19,20], a clear link to gene-culture coevolution has been lacking. Leveraging well documented historical knowledge regarding the introduction of paddy rice farming by province in China (see Figure 1) with a determination of allele frequency of the *DRD4* exon III repeat region, we 'make a case' that changes in the relative prevalence of the 2R genotypes coevolve with rice paddy farming, and that rice culture provides the environment for increased frequency of the 2-repeat taking place as paddy farming spreads across southern China. Moreover, we suggest that our measurement of paddy rice farming such as rice farming proportion in 1996 and the more recent rice suitability index are reasonable proxies for the extent of rice culture in the recent several decades. In this regard, the results from Table 1 and Table S15 suggest that rice culture has a more salient effect in inducing cooperative behavior for 4R carriers compared to 2R carriers. If as Kitayama *et* al[19] suggest that the 7/2R allele is a norm-congruous gene, then in China a Confucian society[35] emphasizing harmony and cooperation that are the sine qua non of successful social interactions, possessing the 2R allele from birth nudges individuals through the subtle influences at the family, school and village-levels towards adopting a maximally collectivist norm-sensitive style. Only carriers of the 4R repeat, who are less norm-sensitive than 2R individuals, are responsive to the rice culture way of life and can be further nudged along the spectrum towards a

more collectivist living style. 2R variant carriers do not need the prodding of rice culture to be more cooperative since the collectivist framework is sufficient to maximize their *DRD4* genetic potential for cooperativeness, viz. they are possessive of a genetic 2R 'nudge' factor. Conversely, 4R carriers need the extra nudge of rice farming culture to contribute more in the PGG, viz. they need an additional 'cultural' nudge factor provided by rice farming. Along the lines of 'nudge theory', we suggest the notion that just as gentle nudges by society can enhance socially-sensitive decision making, genetic variants also serve as subtle influences on decision making.

Our finding supports the hypothesis of gene-culture coevolution of *DRD4* arising from the suggestion in Kitayama *et al*.[19] of *DRD4* as a norm-congruous behavioral gene[19-21], and a plasticity gene that confers behavioral sensitivity to the social environment[22-26], specifically, its 2R genotypes being able to explain partially the social cognitive underpinnings of human cooperation in relatively large populations as part of a norm psychology which can be generationally transmitted by culture, viz. memes[36], and reinforced by evidence of the heritability from twin studies of prosocial traits such as trust[37], empathy[38], and fairness[39]. An underlying mechanism may be due to the Baldwin effect[40] about behavior (in our case adoption of paddy farming) serving as the initial and more transient driver of the end-point of evolutionary change (e.g. shifts in changes in *DRD4* exon III genotype frequency). The idea underlying the Baldwin effect underscores the part played by behavioral plasticity in allowing colonizers of new niches, e.g. paddy farming, to endure through phenotypic modification *before* adaptive evolution (change in genotype frequency) commences and eventually fixes behavior in hard-wiring of brain neural networks. A gene such as *DRD4*, associated with norm-congruous behaviors (viz. cooperation in irrigating) and sensitivity to the social environment, makes good biological sense as a likely candidate with multiple attributes that enable gene-culture coevolution.

Conclusions

The overall evidence presented in this paper reveals a relationship between paddy rice farming and cooperativeness elicited in the laboratory and measured using survey data, augmented with its association with the *DRD4* gene. This suggests that rice culture has generated the environmental milieu for gene-culture coevolution of human social behavior – large-scale cooperation based on changes in the population frequency of a coding region polymorphism. This notion is buttressed by the evolutionary history of this gene, including human[17,18,41] and animal studies[42-46] and the unique properties of this gene that confer sensitivity to social environment[25] and enhance norm adherence[19,20]. Altogether, the paper supports the gene-culture coevolution hypothesis that changes in *DRD4* exon III amino-acid coding genotype frequency in Chinese provinces practicing paddy rice farming. There are few if any other such examples of culture providing the environment conducive to evolutionary changes in a specific gene contributing to human social behavior, viz. large-scale human cooperation, in the past 10,000 years.

To our knowledge, our paper is the first to show that rice culture increases cooperativeness using experimental economics tasks[47]. In contrast to Ruan *et al*.[48], this study supports the original findings of Talhelm *et al*.[10] with new data from observed choice behavior when performing experimental economics tasks. This relation is further corroborated by the result of analysis of data from the CFPS containing questions relating to cooperativeness. As the first study to explore the relationship between gene, culture of rice farming, and cooperativeness, we arrive at a finding of a gene-culture coevolution driven in part by the *DRD4* gene. We further emphasize that the first finding in our paper is reinforced by the result in a parallel study by Zhou[49] that rice culture enhances participants' contribution in the standard PGG as well as PGG with punishment. While

Zhou's data is based on 524 subjects from four Chinese provinces, our study has a larger sample of 1,213 of participants from 28 provinces. Together with Zhou's paper, the overall evidence points to the positive impact of rice farming culture on people's cooperative behavior.

The wellsprings of dissimilarities in prosociality especially cooperativeness in diverse human communities and culture has been and remains a focus of intense interest in the social sciences. In a recent review[50] the paradoxes of cooperativeness are posed, viz. "Why do people cooperate in situations in which they could benefit more through selfishness?" Towards addressing the overarching problem of human cooperativeness and prosociality, studies implementing diverse perspectives and settings from behavioral and experimental economics to transcultural field studies are commonly employed. Differences in agricultural practices within and between cultures have provided a fruitful arena of investigation in understanding the origins of cooperative behavior – an enigma that has intrigued philosophers, scientists, economists including some of humanity's most sagacious thinkers.

The current study examines the cultivation of rice and wheat as the world's most important crops and whose origins go back to the dawn of civilization at the nexus of the shift from hunter gatherer societies to settled communities in the Middle East and East Asia. Rice farming, in particular, poses a challenge to early Chinese societies – how to exploit a common pool resource such as rivers to irrigate rice paddies while ensuring equitable and effective access to water for the farming community. In this context, rice theory offers a framework to link people's living and working environment to their cultures and actual behaviors. It also offers a novel perspective to explore how culture intertwined with agricultural practices and mediated by gene-culture coevolution may have enduring influence on how people make decisions over the long haul.

Methods

In 2010 and 2012 we recruited 1,213 Han Chinese university students in Beijing. They took part in a decision making experiment and contributed 20 ml blood for extracting DNA. Subjects were paid around RMB 320 on average for their participation. The Institutional Review Board of National University of Singapore approved this study, and subjects signed the information consent form before the experiment.

In the experiment, subjects make decisions in a series of pen-and-paper tasks involving two-person groups which were assigned randomly without repetition: the public goods game (PGG), the trust game (TG), the modified dictator game (MDG), the ultimatum game (UG), the randomized ultimatum game (RUG), the jealous game (JG), and the sequential prisoner's dilemma game (SPDG). The experimental tasks were incentivized using the random incentive mechanism. Each subject was compensated based on her decision in a randomly chosen task. Subjects were seated in the same classroom, and each subject does not know exactly whom he or she is interacting with, hence the decisions by the two players were anonymous with respect to each other. The working language of the experiment is Chinese. The detailed descriptions and instructions to these tasks are provided in *SI* under *Method* and *Experimental Instructions*.

The genotyping information for *DRD4* is in *SI Method Genotyping*. All statistical analyses are performed using STATA Version 14.

Code availability. All computer code used to generate the results can be accessed.

Data availability. The data sets will be available from the corresponding author on request.

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References

1 Seck, P. A., Diagne, A., Mohanty, S. & Wopereis, M. C. Crops that feed the world 7: Rice. *Food Security* **4**, 7-24 (2012).

2 Huang, X. *et al.* A map of rice genome variation reveals the origin of cultivated rice. *Nature* **490**, 497-501 (2012).

3 Nisbett, R. *The Geography of Thought: How Asians and Westerners Think Differently... and Why*. (Simon and Schuster, 2010).

4 Richerson, P. J. & Boyd, R. *Not by Genes Alone: How Culture Transformed the Evolutionary Process*. (Chicago: University of Chicago Press, 2005).

5 Axelrod, R. & Hamilton, W. D. The evolution of cooperation. *Science (New York, N.Y* **211**, 1390-1396 (1981).

6 Nowak, M. A. Five rules for the evolution of cooperation. *Science (New York, N.Y* **314**, 1560-1563 (2006).

7 Alexander, R. D. The evolution of social behavior. *Annual Review of Ecology and Systematics* **5**, 325-383 (1974).

8 Fei, H.-T. *Peasant Life in China: A Field Study of Country Life in the Yangtze Valley*. (Routledge & Kegan Paul, 1962).

9 Ostrom, E. E. *et al. The Drama of the Commons*. (National Academy Press, 2002).

10 Talhelm, T. *et al.* Large-scale psychological differences within China explained by rice versus wheat agriculture. *Science (New York, N.Y* **344**, 603-608 (2014).

11 Richerson, P. J., Boyd, R. & Henrich, J. Gene-culture coevolution in the age of genomics. *Proceedings of the National Academy of Sciences* **107**, 8985-8992 (2010).

12 Ebstein, R. P., Israel, S., Chew, S. H., Zhong, S. & Knafo, A. Genetics of human social behavior. *Neuron* **65**, 831-844 (2010).

13 Sasaki, J. Y. Promise and challenges surrounding culture-gene coevolution and gene-culture Interactions. *Psychological Inquiry* **24**, 64-70 (2013).

14 Xie, Y. & Hu, J. An introduction to the China family panel studies (CFPS). *Chinese Sociological Review* **47**, 3-29 (2014).

15 Chen, C., Burton, M., Greenberger, E. & Dmitrieva, J. Population migration and the variation of dopamine D4 receptor (DRD4) allele frequencies around the globe. *Evolution and Human Behavior* **20**, 309-324 (1999).

16 Matthews, L. J. & Butler, P. M. Novelty‐seeking DRD4 polymorphisms are associated with human migration distance out‐of‐Africa after controlling for neutral population gene structure. *American Journal of Physical Anthropology* **145**, 382-389 (2011).

17 Wang, E. *et al.* The genetic architecture of selection at the human dopamine receptor D4 (DRD4) gene locus. *The American Journal of Human Genetics* **74**, 931-944 (2004).

18 Ding, Y.-C. *et al.* Evidence of positive selection acting at the human dopamine receptor D4 gene locus. *Proceedings of the National Academy of Sciences* **99**, 309-314 (2002).

19 Kitayama, S., King, A., Hsu, M., Liberzon, I. & Yoon, C. Dopamine-system genes and cultural acquisition: the norm sensitivity hypothesis. *Current Opinion in Psychology* **8**, 167-174 (2016).

20 Kitayama, S. *et al.* The dopamine D4 receptor gene (DRD4) moderates cultural difference in independent versus interdependent social orientation. *Psychological Science* **25**, 1169-1177 (2014).

21 Jiang, Y., Bachner-Melman, R., Chew, S. H. & Ebstein, R. P. Dopamine D4 Receptor Gene and Religious Affiliation Correlate with Dictator Game Altruism in Males and not

Females: Evidence for Gender-sensitive Gene x Culture Interaction. *Frontiers in Neuroscience* **9** (2015).
22 Pappa, I., Mileva-Seitz, V. R., Bakermans-Kranenburg, M. J., Tiemeier, H. & van Ijzendoorn, M. H. The magnificent seven: A quantitative review of dopamine receptor d4 and its association with child behavior. *Neuroscience & Biobehavioral Reviews* **57**, 175-186 (2015).
23 Knafo, A., Israel, S. & Ebstein, R. P. Heritability of children's prosocial behavior and differential susceptibility to parenting by variation in the dopamine receptor D4 gene. *Development and Psychopathology* **23**, 53-67 (2011).
24 Belsky, J. *et al.* Vulnerability genes or plasticity genes? *Mol Psychiatry* **14**, 746-754 (2009).
25 Pluess, M. Individual differences in environmental sensitivity. *Child Development Perspectives* **9**, 138-143 (2015).
26 Sheese, B. E., Voelker, P. M., Rothbart, M. K. & Posner, M. I. Parenting quality interacts with genetic variation in dopamine receptor D4 to influence temperament in early childhood. *Development and Psychopathology* **19**, 1039-1046 (2007).
27 Wooldridge, J. M. *Econometric Analysis of Cross Section and Panel Data*. (MIT press, 2010).
28 Dube, O., García-Ponce, O. & Thom, K. From maize to haze: Agricultural shocks and the growth of the mexican drug sector. *Journal of the European Economic Association* **14**, 1181-1224 (2016).
29 Alesina, A., Nunn, N. & Giuliano, P. On the origins of gender roles: women and the plough. *Quarterly Journal of Economics* **128** (2013).
30 Andreoni, J. & Miller, J. Giving according to GARP: An experimental test of the consistency of preferences for altruism. *Econometrica* **70**, 737-753 (2002).
31 Reist, C. *et al.* Novelty seeking and the dopamine D4 receptor gene (DRD4) revisited in Asians: Haplotype characterization and relevance of the 2‐repeat allele. *American Journal of Medical Genetics Part B: Neuropsychiatric Genetics* **144**, 453-457 (2007).
32 Peng, Y. *et al.* The ADH1B Arg47His polymorphism in East Asian populations and expansion of rice domestication in history. *BMC Evolutionary Biology* **10**, 1 (2010).
33 Gong, Z. *et al.* The temporal and spatial distribution of ancient rice in China and its implications. *Chinese Science Bulletin* **52**, 1071-1079 (2007).
34 Kim, H. S. *et al.* Culture, distress, and oxytocin receptor polymorphism (OXTR) interact to influence emotional support seeking. *Proc Natl Acad Sci U S A* **107**, 15717-15721 (2010).
35 Triandis, H. C., Bontempo, R., Villareal, M. J., Asai, M. & Lucca, N. Individualism and collectivism: Cross-cultural perspectives on self-ingroup relationships. *Journal of personality and Social Psychology* **54**, 323 (1988).
36 Chudek, M. & Henrich, J. Culture–gene coevolution, norm-psychology and the emergence of human prosociality. *Trends in cognitive sciences* **15**, 218-226 (2011).
37 Cesarini, D. *et al.* Heritability of cooperative behavior in the trust game. *Proceedings of the National Academy of sciences* **105**, 3721-3726 (2008).
38 Melchers, M., Montag, C., Reuter, M., Spinath, F. M. & Hahn, E. How heritable is empathy? Differential effects of measurement and subcomponents. *Motivation and Emotion* **40**, 720-730 (2016).

39 Wallace, B., Cesarini, D., Lichtenstein, P. & Johannesson, M. Heritability of ultimatum game responder behavior. *Proc Natl Acad Sci U S A* **104**, 15631-15634 (2007).
40 Simpson, G. G. The Baldwin effect. *Evolution* **7**, 110-117, doi:10.2307/2405746 (1953).
41 Thagaard, M. S., Faraone, S. V., Sonuga-Barke, E. J. & Østergaard, S. D. Empirical tests of natural selection-based evolutionary accounts of ADHD: a systematic review. *Acta Neuropsychiatrica*, 1-8 (2016).
42 Mueller, J. C. *et al.* Behaviour-related DRD4 polymorphisms in invasive bird populations. *Molecular Ecology* **23**, 2876-2885 (2014).
43 Verhulst, E. C. *et al.* Evidence from pyrosequencing indicates that natural variation in animal personality is associated with DRD4 DNA methylation. *Molecular Ecology* **25**, 1801-1811 (2016).
44 Garamszegi, L. Z. *et al.* The relationship between DRD4 polymorphisms and phenotypic correlations of behaviors in the collared flycatcher. *Ecology and Evolution* **4**, 1466-1479 (2014).
45 Seaman, M. I., Chang, F. M., Deinard, A. S., Quiñones, A. T. & Kidd, K. K. Evolution of exon 1 of the dopamine D4 receptor (DRD4) gene in primates. *Journal of Experimental Zoology* **288**, 32-38 (2000).
46 Inoue-Murayama, M., Niimi, Y., Takenaka, O. & Murayama, Y. Allelic variation of the dopamine receptor D4 gene polymorphic region in gibbons. *Primates* **41**, 383-392 (2000).
47 Lu, Y. *Essays on Risk and Social Preferences: Evidence from Genes, Culture, and Strategic Interactions* PhD thesis, National University of Singapore, (2015).
48 Ruan, J., Xie, Z. & Zhang, X. Does rice farming shape individualism and innovation? *Food Policy* **56**, 51-58 (2015).
49 Zhou, X. Rice Farming and the Emergence of Cooperative Behavior. *Working paper, Royal Holloway University of London* (2017).
50 Simpson, B. & Willer, R. Beyond altruism: Sociological foundations of cooperation and prosocial behavior. *Annual Review of Sociology* **41**, 43-63 (2015).

Table 1. Contribution in the Public Goods Game

	(1)	(2)	(3)	(4)	(5)	(6)
	OLS	IV	OLS	IV	OLS	IV
Variable	Contribution	Contribution	Contribution	Contribution	Contribution	Contribution
Rice	9.117**	12.525***	8.711**	11.820**	10.677**	15.522***
	(3.666)	(4.638)	(4.023)	(5.185)	(4.703)	(5.926)
DRD4			3.497**	3.391**	5.322***	7.288***
			(1.493)	(1.426)	(1.702)	(1.935)
Rice×DRD4					-5.356	-11.389*
					(4.873)	(5.814)
Controls	Yes	Yes	Yes	Yes	Yes	Yes
Session effect	Yes	Yes	Yes	Yes	Yes	Yes
Observations	1,098	1,098	1,065	1,065	1,065	1,065

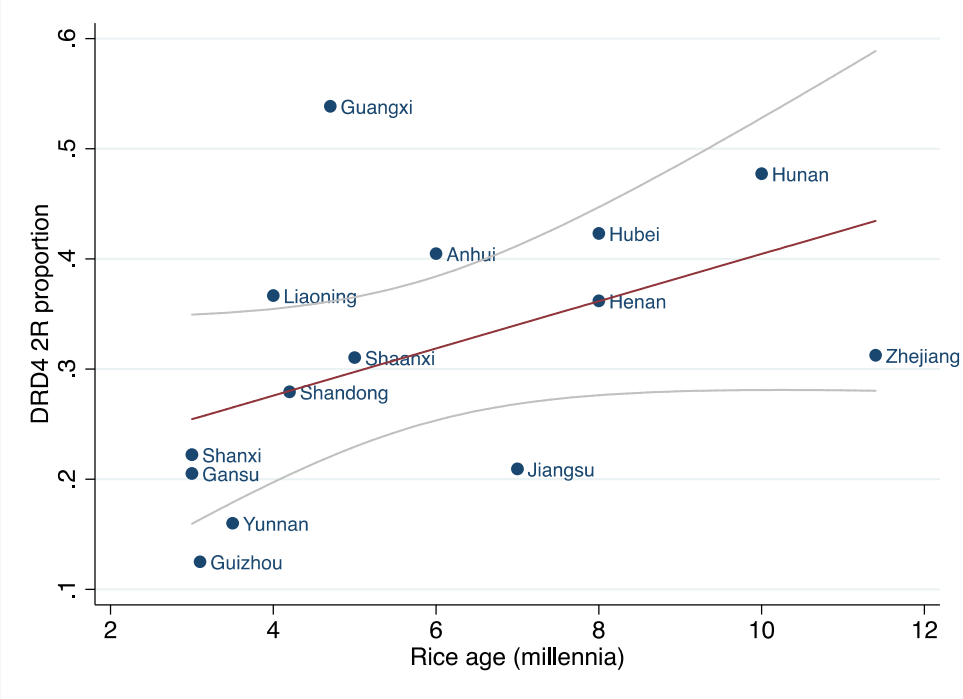
Notes: Standard errors in parentheses clustered at the province level. * significant at 10%; ** significant at 5%; *** significant at 1%. Rice is the proportion of paddy rice farming relative to the total planted area in the province. DRD4 is a dummy in which 1 refers to 2R genotypes and 0 refers to 4R genotypes. Rice×DRD4 is the interaction term between Rice and DRD4. The controls include sex, family income, parents are farmers, provincial GDP per capita in 1996, the proportion of agriculture sector in the whole economy in 1996, and population density in 1996. The session effects are a set of dummy variables for 21 experimental sessions. The full regression results are provided in *SI Results* Table S5.

Table 2. Get and Give Help in CFPS

	(1)	(2)	(3)	(4)
	OLS	IV	OLS	IV
Variable	Give help	Give help	Give help	Give help
Rice	0.097	0.132**	0.081*	0.095**
	(0.066)	(0.057)	(0.047)	(0.041)
Get help			0.349***	0.349***
			(0.015)	(0.015)
Controls	Yes	Yes	Yes	Yes
Observations	28,563	28,563	28,096	28,096

Notes: Standard errors in parentheses clustered at the province level. * significant at 10%; ** significant at 5%; *** significant at 1%. Rice is the proportion of paddy rice farming relative to the total planted area in the province. The controls include sex, family income, rural Hukou dummy, provincial GDP per capita in 1996, the proportion of agriculture sector in the whole economy in 1996, and population density in 1996. The full regression results are provided in *SI Results* Table S14.

Figure 1. *DRD4* VNTR Distribution Correlates with Rice Cultivation Age



Notes: *DRD4* 2R proportion is the proportion of 2R genotypes in each province, and Rice age is the earliest year (in unit of 1000 years) from now the rice cultivation began. This information comes from Peng *et al.*[32], and the Rice age data are only available for 14 provinces[32].