Serotonin Transporter Gene (SLC6A4), Long Term Orientation, and the Environment

Abstract

The relationship between cultural traits and genes within a population is of increasing interest for cross-cultural psychologists. Using nations as our unit of analysis, we present evidence showing that a gene-culture co-evolution was moderated by the environment. More specifically, we identified a significant and strong correlation between the distribution of the allele version of the SLC6A4 serotonin transporter gene and the cultural dimension of Long Term Orientation. However, such a relationship existed only within populations that co-evolved in environments in which at least one major environmental threat (disease prevalence or natural catastrophes) was present. In environments without such threats, the relationship vanished, suggesting that SLC6A4 and Long Term Orientation tandem were actually undergoing a random drift without such threats. We also find evidence for two evolutionary equilibria in demanding environments, either nations evolved to be extremely short-term oriented and mainly having the long allele version of the SLC6A4 gene or being long-term oriented and having the short version of the gene, with intermediate values for the gene-culture tandem being the exception.

Keywords: gene-culture co-evolution, demanding environment, SLC6A4, serotonin transporter gene, long term orientation, disease prevalence, natural catastrophes, genetic drift

Gene – Culture – Environment Interaction: The Relation between Serotonin Transporter Gene (SLC6A4) and Cultural Long Term Orientation in Safe and Demanding Environments

Introduction

During our evolution as the human species, our genes, the environments in which we had to survive, and the cultures we were born into interacted continuously, bringing forth the variety of cultures we see nowadays. According to Lumsden and Wilson (2000; 2005), the ability of humans to develop culture, as a tool to solve problems in their environment, led to a unique evolutionary trajectory. During this process, the forces of selection fine-tuned cultures and genes to certain characteristics of the environment (e.g., climate or topography). Supporting this theory of a gene-culture-environment interaction, many empirical studies have found similarities between cultures that evolved under similar environmental conditions, e.g., the selection of spicy food in areas of high bacterial infestations (Billing & Sherman, 1998), an increase of type 2 diabetes (a more thrifty metabolism system) in tribes who experienced harsh long open-ocean voyages (Myles et al., 2007), and language vocalizations (more vocals vs. consonants in the language) following environmental conditions (savannah vs. colder climate) (Maddieson & Coupé, 2015).

Despite the many aspects of cultures studied, few have managed to explain the origin or the process through which psychological constructs co-evolved with genes and the environment. As an exception, Fischer, Lee, and Verzijden (2018) found a relationship between extraversion and the dopamine genotype, but only in demanding environments. In the societal level, Fincher, Thornhill, Murray, and Schaller (2008) found that individualism and collectivism varied with the prevalence of diseases in a region. Chiao and Blizinsky (2010) stipulate that the relationship between individualism/collectivism and disease prevalence is mediated by the distribution of a serotonin transporter gene (SLC6A4) in the population. In this paper, going beyond stipulation, we directly look at the effect of the environment on the relation between genes and cultural dimensions. As such, we examine the environmental boundary conditions under which a certain phenotype is realized in combination with cultural adaptation.

The central gene taken into account in this paper is SLC6A4 which regulates serotonergic neurotransmission (5-HTT) (Canli & Lesch, 2007). This gene contains a polymorphic region known as 5-HTTLPR comprising a short (S) allele and a long (L) allele version (Lesch et al., 1996). The S and L allele refer to a variable tandem repeat (VNTR) with either 14 or 16 repeats (Murdoch, Speed, Pakstis, Heffelfinger, & Kidd, 2013). These two common allele sizes result in differential 5-HTT expressions and functions (Hariri, 2009). Individuals with the S-allele version produce significantly less 5-HTT mRNA

and protein, resulting in a relatively higher concentration of serotonin in the synaptic cleft (Lesch et al., 1996). Behaviorally, S allele carriers have been shown to experience increased negative emotions and heightened anxiety (Munafò, Clark, & Flint, 2005), increased harm avoidance (Munafò et al., 2005) and are more susceptible to fear conditioning (Lonsdorf et al., 2009). However, S-allele carriers also experience enhancement of a wide range of cognitive functions, such as stochastic abilities and less temporal discounting (Holmberg & Lesch, 2011). Furthermore, they have better visual memory and shorter reaction times when dealing with complex tasks (Enge, Fleischhauer, Lesch, Reif, & Strobel, 2011). It seems that the S-allele promotes a "hypervigilance" state with heightened anxiety, leads to a close monitoring of the environment, and hence an enhanced ability to integrate and profit from feedback (Holmberg & Lesch, 2011).

The two versions of the allele are not only interesting due to the differentiation they exhibit but also due to their distribution across populations. In certain nations, most (80%) of the population is of the S-allele type (China, Japan, and Taiwan) while in other nations, most (80%) of the population is of the L-allele type (Zambia, Zimbabwe, and Uganda). The relationship between S/L-allele distribution and cultural dimensions has recently drawn the attention of cross-cultural psychologists. Chiao and Blizinsky (2010) linked the S/L-allele distribution with Collectivism/Individualism, with short allele being adaptive for the collectivist culture and the long allele being adaptive for the individualist culture. Chiao and Blizinksy (2010) based their analysis on data from 29 countries. Minkov, Blagoev, and Bond (2015), using a broader set of 59 countries, found no correlation between the distribution of S/L allele and Collectivism/Individualism. Instead Minkov, et al. (2015) found strong relation between S/L-allele distribution and long term orientation, with the short allele linked to long term orientation and the long allele to short term orientation. To get a better understanding of this relationship, this paper will reexamine the relationship between short/long term orientation (LTO) and S/L allele distribution by taking features of the environment into account.

We propose a model where the demandingness of an environment has a moderating role in the relationship between LTO and S/L allele distribution. Demandingness of the environment has long been thought to exert an impact in many domains of the society. Culture, as an adaptive mechanism to the environment is no exception (Pagel, 2012). We thus assume that demandingness of the environment will also exert an impact on the genotype dealing with emotional regulation such as the S/L allele of the

SLC6A4 gene, as well as on adaptive mechanism such as cultural short/long term orientation. A tendency to be anxious (which is associated with the S allele) and thus acting with more caution is beneficial in demanding environments. Similarly, responding to environmental threats will be more successful if the society adopts a long term perspective. When the environment is safe, these considerations matter less. Thus, we hypothesize that the relationship between allele types and long term orientation is stronger in demanding environment in comparison to safe environment.

We will now give a short description of the short/long term orientation followed by conceptualizations of the environmental threats, followed by illustration of our model. Succeeding a long history of Chinese philosophy, short/long-term orientation was conceptualized by M. Bond as a cultural value (Chinese Culture Connection, 1987). This value labeled Confucian Dynamism was then adopted by Hofstede as a cultural dimension. Hofstede defined long-term orientation as "the fostering of virtues oriented towards future rewards, in particular, perseverance and thrift. Its opposite pole, short-term Orientation, stands for the fostering of virtues related to the past and the present," (Hofstede, 2001, p. 359).

Environmental threat comes in multiple ways. A common proxy of environmental threat is the prevalence of diseases (Murray & Schaller, 2010). Thus, we will include disease prevalence as a measure in our model. Disease prevalence has a very high correlation (~.65) in the data available to us with climate based indices, and as such, we do not include climate based indices in this paper. A different independent operationalization of environmental threat is the propensity to natural catastrophes (r ~ .13 with disease prevalence). Hence, we will include natural catastrophe as our measure. Although both measures capture aspects of what makes environments demanding, disease prevalence and natural catastrophe have different effects on the society. Disease prevalence seems to induce compliance (Schaller & Murray, 2008) because contamination is crucial to prevent the spread of disease. In case of diseases, infrastructure and the elites are more likely to survive, thus a centralized organized power is likely to emerge, forcing subservience. Natural catastrophe, on the other hand, tends to favor innovation (Bates et al., 1963; Cavallo, Galian, Noy, & Pantano, 2013) because disasters like earthquakes or hurricanes often eradicate existing structure and as such, allows new ones to emerge. We refrain from using Gross Domestic Products (GDP) or poverty indices because these variables only started to manifest relatively recently on an evolutionary time scale.

In order to test the relationship between LTO, S/L allele, and environmental threat, we will use both types of threats. We expect that both threats moderate the relationship between LTO and S/L allele. In high threat situation, we expect that short allele dominant population will adopt long term orientation and long allele dominant population will adopt short term orientation because short allele (anxious tendency) in combination with long term orientation will successfully manage threat situation, whereas long allele (mental resistance) in combination with short term orientation will successfully handle the consequences of threat situation. We expect that the relation between S/L allele and LTO weakens in non-demanding environment because of a less selective environment and thus genetic drift (Masel, 2011).

We propose a model linking LTO and S/L allele with the environment playing a moderating role as shown in Figure 1. The relation between genotype and culture works both ways. On the one hand, the existence of certain percentage of S or L allele in the population leads to either short or long term orientation on a societal level, particularly in demanding environment where the selective pressure on the allele is high. On the other hand, for societies that already adopted either a short or long term orientation, this cultural environment in combination with demanding environments, work as a selective force on the S/L allele.
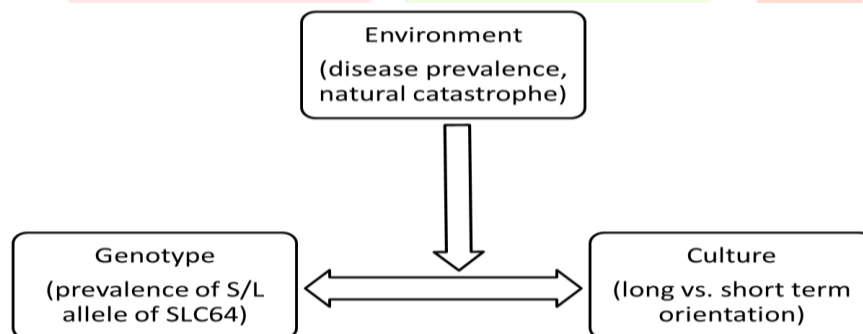

Figure 1. Moderation hypothesis of environment on the relationship between genotype and culture

Methods

Measures

S/L allele index: Distribution of S/L allele (SLC6A4) across 60 countries was taken from Minkov, Blagoev, and Bond (2015).

Individualism/Collectivism index: Distribution of Individualism/Collectivism across 52 countries was taken from Hofstede (2001).

Short/Long Term Orientation (LTO) index: Distribution of short/long term orientation (LTO) across 62 countries was taken from Hofstede (2001).

Disease Prevalence index: Distribution of disease prevalence across countries was taken from Murray and Schaller (2010). Prevalence of either nine or seven infectious diseases was recorded in 230 geopolitical regions worldwide. The diseases were leishmanias, schistosomes, trypanosomes, leprosy, malaria, typhus, filariae, dengue, and tuberculosis.

Risk of Natural Catastrophe index: Distribution of risk of natural catastrophe was taken from the World Risk Report (2016). The World Risk index calculated risk for 171 countries on the basis of exposure to natural hazards (earthquakes, cyclones, floods, droughts, and sea-level rise), infrastructure vulnerability, coping and adapting capacities of the government. We realized that coping and adapting capacities of the government are themselves a product of culture. The World Risk Index (WRI) is however, the most comprehensive index on natural catastrophe to date.

Number of Observations: For 37 countries we had data for all above mentioned variables and for 52 countries data was incomplete for not more than one variable.

Statistical Analyses

First, we start by testing for correlations between LTO or the allele type and environmental demands (natural catastrophe and disease prevalence). Second, we test in separate regression models to which extent the relationship between LTO and the allele type interacts with environmental demands. Third, we construct a new variable which is aggregating the different environmental demands and test the relationship between LTO and the allele types separately in countries with high, medium and low environmental demands. The result section ends with additional analyses in which we replace LTO with risk-taking index or math performance as well as replacing S/L allele serotonin percentages with dopamine percentages.

Results

Long Term Orientation (LTO)

Table 1 shows a curious pattern between LTO and the allele type on the one hand and the two types of risks by which an environment can be characterized. In summary, although we see a close link between LTO and allele type, each one individually seems to be linked to different types of threats in the

environment. While allele type appears to be linked to threats such as natural catastrophes, LTO appears to be linked to threats such as disease prevalence. Note, that both types of threats are also independent.

Table 1: Correlations of main variables used in our analyses

	S/L Allele Distribution	Long Term Orientation	Natural Catastrophe
Disease Prevalence	.07	.27*	.13
Natural Catastrophe	.32**	.11	-
Long Term Orientation	.44**	-	-

Note. $* = p < .05, ** = p < .01$

To test this complex relationship in more comprehensive models, we estimated regression models with either the allele distribution or LTO as the dependent variable and the other respectively LTO or the allele distribution as the independent variable. Furthermore, all models include controls for the environment and their interaction with LTO or the allele distribution. We also tested a model in which we used an aggregate of the two environmental variables as a control (both variables were demeaned and then added). Table 2 gives an overview of the models and their estimates.

Table 2: OLS estimates for three different models

	Standardized Estimates		
	Model 1	Model 2	Model 3
% S-allele	dependent variable	dependent variable	-0.13
LTO	0.38***	0.46*	dependent variable
Disease Prevalence		-0.82**	-0.69
Natural Catastrophe		0.21	-0.93*
Environment Aggregate	-0.54**		
LTO * Disease Prevalence		1.10***	
LTO * Natural Catastrophe		-0.03	
% S-allele * Disease Prevalence			0.35
% S-allele * Natural Catastrophe			1.20**
LTO * Environment Aggregate	0.93***		
R-squared	.42	.50	.34
df	47	45	45

Note. $* = p < .10, ** = p < .05, *** = p < .001$

The estimates of model 1 are in line with our moderation hypothesis of environment on the association between LTO and the allele type. The significant interaction term implies that the association is stronger in environments that are demanding.

Putting models 2 and 3 into context, we again see the association between the allele type and the disease prevalence on the one hand and LTO and the risk of natural catastrophes. The significant interactions in model 2 and 3 show that the relationship between LTO and the allele type is stronger in environments that are characterized by high risk with regard to the relevant environmental variables.

Figure 2 shows the relationship between the allele type and LTO separately in (1) countries where the risk of both, natural catastrophes and diseases, are below the median of all countries (henceforth safe countries), (2) countries where values for either (but not both) threats are below the median (henceforth relatively demanding), and (3) countries where both risks are above the median of all countries (henceforth very demanding). While there seems to be a strong relationship between LTO and allele type in both relatively demanding (r =.58, $F(1,13) = 6.61$, $p = .02$), and very demanding countries (r =.67, $F(1,15) = 12.15$, $p = .003$), we even found a negative relationship between the two in countries/environments categorized as safe ($r = -0.48$, $F(1,17) = 5.22$, $p = .03$). However, looking at the slope of the linear model for safe countries in Figure 2, the relevance of this negative correlation seems to be minor. Furthermore, slope analysis indicates no difference between the slope of very demanding and relative demanding countries ($t(45) = 0.92$, $p = .63$), whereas safe countries are significantly different to very demanding and relatively demanding countries ($t(45) = 2.52$, $p = .04$ and $t(45) = 3.82$, $p = .001$).
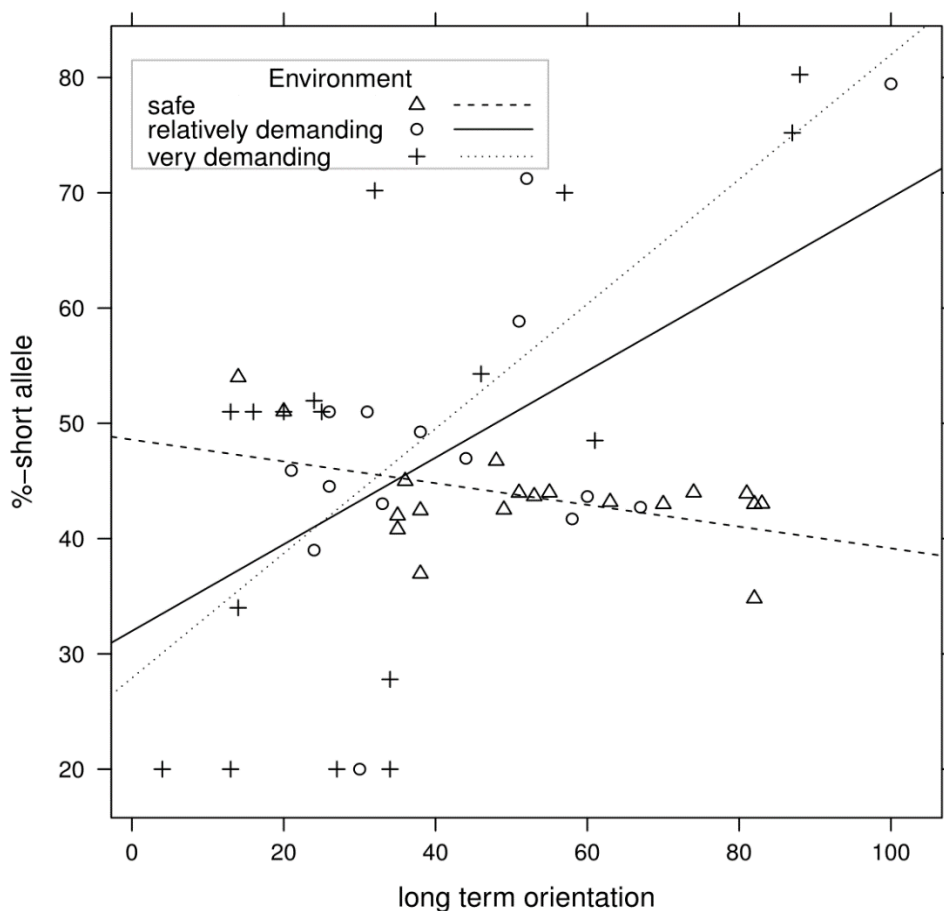

Figure 2. Relationship between LTO and the frequency of short allele across countries. Lines show separate linear predictions for safe and relatively demanding and very demanding countries.

Individualism/Collectivism

Following the work of Chiao and Blizinsky (2010), we reiterated our analyses with individualism/collectivism instead of LTO as dependent variable. We did not find any meaningful pattern. However, there were fewer data available (40 countries with data for both S/L-allele distribution and individualism/collectivism) so the data available might have been too few to identify effects.

Additional Analyses

To understand which aspect of LTO is linked to S/L allele percentages and external threats, we reiterated our moderation (interaction) analyses with persistence and risk-taking indicators instead of LTO as dependent variable. As persistence indicator, we used 2015 PISA scores in Mathematics (OECD, 2015). LTO and math scores have been found to be highly correlated (Hofstede & Minkov, 2010). As risk-taking indicator, we used answers to the World Values Survey Wave 6, variable 76, "Adventure and taking risks are important to this person; to have an exciting life" (WVS, 2015). Summarized, we found a similar though weaker moderation pattern with regard to Math scores instead of LTO and no such pattern when using risk-taking indicators.

Lastly, we are aware that no single gene is solely responsible for any behavioural or cultural manifestation (Chabris, Lee, Cesarini, Benjamin, & Laibson, 2015). As such we encourage researchers to reiterate our analyses with other genes within the serotonergic system once the data becomes available. As a first step, using data taken from Fischer, Lee, and Verzijden (2018), we reiterated our moderation analysis using an index of dopamine functioning instead of percentage of S/L allele (SLC6A4 gene). In predicting LTO, we found no interaction effect between the dopamine index and the external threats.

Discussion

We looked at the relationship between the short and long allele version of the SLC6A4 gene (henceforth, S/L allele) and cultural dimensions. Contrary to previous work, we controlled for the environment in which genes and cultures co-evolved. Indeed, we found evidence that the relationship between the version of the allele and long-term orientation of cultures is moderated by the environment in which they evolved. While we found only a weak association between the allele type and long-term orientation in environments which can be characterized as "safe" (low probability of natural catastrophes

or dangerous diseases), we found very clear and strong relationships in environments that were more demanding. Thus, it seems that the version of the S/L allele only affects cultures in demanding environments, while this allele seems to undergo random genetic drift (Masel, 2011) in safe environments.

Furthermore, we found that the variance with regard to the allele type is low in safe countries (35-55% having the short version), while the variance is much higher in demanding countries (20-80% having the short version). For safe countries, we interpret this as evidence for either of the two: there was no or a low selection pressure in safe countries on the allele and therefore we observe both versions of the allele equally often, or, a relatively even mix between carriers of the long and short allele works best on a population level in safe countries. Either way, the dynamics seem to be very different in countries with demanding environments. Here, the selection pressure seems to have been higher, leading to populations with unequal proportions of the allele. In a demanding environment, there seem to be two strategies/evolutionary equilibria to which the population can adopt: 1) take as much as the environment allows before it collapses (e.g., due to pandemic or natural catastrophe) or 2) taking precautions against the catastrophe. Both strategies seem to be stable solutions since we observed countries at both ends of the distributions of the allele type.

Summarized, the results show that much is to be gained by analyzing the relationships between genes and culture while controlling for the environment in which they co-evolved. Our analysis presents evidence that in particular the relationship between SLC6A4 gene and cultural variables such as long-term orientation is much more nuanced then previous studies suggested and that such a relationship may only exist in demanding environments.

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