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Improving Research in the Emerging Field of Cross-Cultural Sociogenetics: The Case of Serotonin

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Abstract

We offer a critical overview of studies associating genetic differences in the 5-HTTLPR VNTR in the serotonin-transporter gene with societal differences. We also highlight recent findings from individual-level research on 5-HTTLPR generating new hypotheses concerning the effect of genes on culture. We provide an expanded national index reflecting 5-HTTLPR S-allele prevalence as an improved tool for future research. Our preliminary tests of this tool suggest that national S-allele prevalence is not associated with individualism as has been claimed, but with national neuroticism, IQ and school achievement, Hofstede's fifth dimension of long-term orientation, and Minkov's societal hypometropia—a measure of risk acceptance and short-term vision in life history strategy. We encourage detailed research of these associations in future studies.

Keywords

genes, culture, serotonin-transporter gene, 5-HTTLPR polymorphisms, individualism, neuroticism, long-term orientation, IQ, cognition, societal hypometropia, life-history strategy

Traditionally, anthropologists viewed culture and biology as two completely separate fields (Brown, 1991). Yet, this notion began to erode at the end of the 20th century, as scholars from various fields proposed that genetic differences at the population level can account for societal differences in values, personality, cognitive abilities, and behaviors. The idea that some cultural traits may be associated with genetic patterns has recently become acceptable in the mainstream scientific literature. Laland, Odling-Smee, and Myles (2010) stated that researchers from diverse backgrounds are converging on the view that human evolution has been shaped by gene–culture interactions (see also Chasiotis, 2011). According to Chiao and Ambady (2007), genetic variation between cultures suggests that cultural variation may be a result of different interactions, including the gene–brain interplay.

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Way and Lieberman (2010) point out that the brain is a central hub where ecological, sociological, demographic, economic, psychological, and biological influences converge. Therefore, "genes affecting brain function are likely to influence the adoption and formation of cultural norms and, conversely, culture may also shape the expression and selection of genes" (p. 203). Chiao and Blizinsky state that culture–gene coevolution has recently emerged as an influential theory to explain human behavior as a product of genetic and cultural evolution. This theory suggests new directions for modern psychologists and anthropologists who are studying group-level differences in personality, behavior, and cognition. Genetic patterns can be used as independent variables in attempts to explain some of the variance in dependent variables related to culture, over and above the proportion of variance explained by other variables.

Schermer, Feather, Zhu, and Martin (2008) and Schermer, Vernon, Maio, and Jang (2011) found that individuals' values have a genetic component. Knafo and Spinath (2011) arrived at the same conclusion. Although we cannot assume isomorphism by default across levels of analysis, it is worthwhile investigating whether some values and some genes are correlated also at the societal level. If the outcome of this investigation is positive, and if the relationship withstands plausible controls, there may be important theoretical and practical consequences. The theoretical paradigm that views culture as something transmitted entirely through socialization and totally distinct from biology would be shattered. At the practical level, researchers would have new tools for analyses of group differences.

The idea that societal personality differences may result from differences in gene pools was launched a decade ago by Allik and McCrae (2004). Although there has never been much consensus among scholars on how exactly culture is to be conceptualized (for the most recent debates, see the January 2014 issue of the *Journal of Cross-Cultural Psychology*), it would hardly be controversial to view societal differences in aggregate personality traits as closely related to culture. Hofstede and McCrae (2004) showed that measures of personality traits aggregated to the national level are highly correlated with dimensions of national culture extracted from measures of values and beliefs. And, if personality is related to both genes and culture, these two entities must also be related.

One might object to the search for relationships between genetic and cultural measures, because genes and cultures evolve at very different speeds: Genes are very slow to change whereas at least some aspects of culture, such as degree of religiousness, can evolve fairly rapidly in some societies. We must not forget, however, that most cross-cultural comparisons in social science focus on relative differences or distances between societies, not on absolute positions. Many of the observed differences across cultural groups typically remain stable, despite changes in absolute levels. Besides, nobody claims that genes can explain all the variance in cultural differences. Even if they explain a small part of that variance, their effect would be worth considering.

The nascent field of cross-cultural sociogenetics (related to "cultural neuroscience" as described by Chiao, Cheon, Pornpattananangkul, Mrazek, & Blizinsky, 2014) has taken its first faltering steps and is likely to expand as population genetics develops and progress is made in the search for links between genes and individual behaviors, personality traits, or abilities. In this article, we focus on one particular field of cross-cultural sociogenetic research: national differences in a specific polymorphism in the serotonin-transporter gene and their cultural implications. In the first part of our article, we review the existing studies in this field and argue that their results are unconvincing. In the second part, we explain why this field of research is not a dead-end street despite its dubious start. We expand Chiao and Blizinsky's (2010) 5-HTTLPR S-allele prevalence database and show that it is a promising tool for future research. We then outline a number of broad directions for such research.

Essentially, we follow the lead of Murray and Schaller (2010) who composed and published an important and useful index: historical pathogen prevalence in 230 societies. That publication

also provided some correlations between the pathogen prevalence index and societal variables that might be associated with it. The goal of that article was not to test any of those associations against a null hypothesis. Nevertheless, Murray and Schaller's article proved useful, because it provided a new tool for investigating the origins of cultural differences. Later publications demonstrated that, when plausible control variables were taken into account, pathogen stress predicted societal differences in murder rates (Thornhill & Fincher, 2011), assortative sociality (Fincher & Thornhill, 2012), conformity (Murray, Trudeau, & Schaller, 2011), and cognitive ability (Eppig & Fincher, 2010), to name just a few associations. Other publications challenged some of these studies. For instance, Currie and Mace (2012) disputed the association between pathogen stress and sociality. In sum, pathogen stress theory and the pathogen prevalence index published by Murray and Schaller (2010) provoked a vigorous discussion and served as a starting point for a series of important studies.

Linking Cultural Traits to Prevalence of Genetic Polymorphisms

A number of studies in population genetics at the end of the 20th century and the beginning of the 21st show fairly clear distributions of genetic patterns, grouping human populations into five or six main clusters that correspond to major geographic regions (Bastos-Rodriguez, Pimenta, & Pena, 2006; Batzer et al., 1996; Rosenberg et al., 2002). Furthermore, a number of genes that regulate brain activity or brain size, such as the serotonin-transporter gene (SLC6A4), the dopamine-transporter gene (DRD4), microcephalin (MCPH1), and the androgen receptor gene (AR), have been found to be highly polymorphic and the worldwide distributions of the polymorphisms create clear geographic patterns. Likewise, all reliable dimensions of national culture reported so far define clearly distinguishable geo-economic patterns (Dobson & Gelade, 2012; Minkov, Blagoev, & Hofstede, 2013).

This confluence of results suggests that statistical associations between genotypes and cultural indices are very likely. In accordance with this logic, Wang et al. (2004) suggested that the DRD4 gene, whose polymorphisms are very differently distributed among East Asians and Amerindians, is a prime candidate for investigating gene and culture interactions. SLC6A4, MCPH1, AR, and other genes also seem to be promising candidates for such research.

The Serotonin-Transporter Gene and National Individualism

Chiao and Blizinsky (2010) proposed that national differences in individualism versus collectivism, as conceptualized and measured by Hofstede (2001), are associated with a polymorphism in the serotonin-transporter gene, SLC6A4. A variable number tandem repeat (VNTR) in this gene, known as 5-HTTLPR, has two common allele sizes—14 and 16-repeat—commonly known as short (S) and long (L) (Murdoch, Speed, Pakstis, Heffelfinger, & Kidd, 2013). According to Chiao and Blizinsky (2010), nations where the S allele is more common are more likely to have collectivist cultures (see also Way & Lieberman, 2010).

Why should high prevalence of the S allele in a cultural group promote collectivism? That allele is suspected to be implicated in a tendency toward anxiety and sensitivity to negative information at the individual level. Hence, Chiao and Blizinsky (2010) assert,

> S allele carriers may be more likely to demonstrate negative cognitive biases, such as engage in narrow thinking and cognitive focus, which facilitate maintenance to collectivistic cultural norms of social conformity and interdependence, whereas L allele carriers may exhibit positive cognitive biases, such as open, creative thinking and greater willingness to take risks, which promote individualistic cultural norms of self-expression and autonomy. (p. 535)

It is not clear what "narrow thinking" refers to, nor why it should facilitate interdependence. It is also not clear what risk taking has to do with individualism. Many types of risk taking, such as reckless driving (measured in terms of national road death tolls), adolescent pregnancy, or conscious discounting of the risk of HIV infection, are much more common in collectivist (economically poor) societies than in individualistic ones (Minkov, 2011, 2013). Claims about associations between behavioral variables and genes should start with an operationalization of the behavioral variable (how exactly risk taking was measured) and provide evidence of a statistical correlation at the individual level of analysis before moving to the national level of analysis.

However, the most serious problem with Chiao and Blizinsky's (2010) study is quite different: Eisenberg and Hayes (2011) pointed out that the nature of Chiao and Blizinsky's national samples does not allow a clear conclusion. This problem was highlighted even more clearly by the findings in a recent article by Murdoch et al. (2013), describing the distribution of the 5-HTTLPR alleles across the globe. The lowest prevalence of the S allele is found in sub-Saharan Africa. Apparently, this is a characteristic of the whole region. This finding clearly precludes any nation-level relationship between collectivism, as described by Hofstede (2001), and the S allele. If there were such a relationship, the African societies would have the most individualist cultures in the world. Instead, they have some of the most collectivist ones. The S allele also has a low prevalence among indigenous Amazonian populations and one Papua New Guinean ethnicity (Nasioi), which can hardly be suspected of *high societal individualism* in Hofstede's sense of the term. High individualism, in that sense of the term, can only describe the culture of a rich, modern nation. The statistical association between individualism and societal wealth is so strong that it rules out any possibility for a poor society's being individualistic.

The Serotonin-Transporter Gene and Societal Hierarchy

Fischer (2013) used Chiao and Blizinsky's 5-HTTLPR data to show that prevalence of the S allele is associated with endorsement of values (or more precisely, groups of values) that Schwartz (2008) calls "mastery" and "hierarchy." There are two concerns with Fischer's finding. First, these values are mostly about achieving material accumulation, social status, and power. It is not clear from individual-level studies, however, whether 5-HTTLPR polymorphisms are associated with such values. Second, Fischer apparently believes that stronger endorsement of these values by nations is associated with stronger social hierarchy across modern nations. Although this hypothesis is plausible, it has never been proven.

To the best of our knowledge, nobody has proposed a universally accepted operationalization of real social hierarchy for modern nations, for instance, one based on number of social layers associated with status, as in the Indian caste system. Arguably, the closest proxy for actual social hierarchy are Project GLOBE's measures of "power distance" (Carl, Gupta, & Javidan, 2004).[1] GLOBE measured this concept in two different ways: by asking middle managers in 61 countries to estimate how (un)evenly power is actually distributed in their own societies and to express their own ideologies concerning the ideal distribution of power that they would like to see in their own societies. This resulted in two negatively correlated measures, which GLOBE called power distance "as is" and power distance "should be." The first of these is correlated with S-allele prevalence as reported in Chiao and Blizinsky (2010; and subsequently in Fischer, 2013, where Korea's score is omitted) at .34 ($p = .08$, $n = 29$)—a weak and statistically insignificant correlation. The second GLOBE measure of power distance yields a correlation of .03 ($p = .87$, $n = 29$) and clearly rules out any association between the variables. The lack of a significant correlation between either of GLOBE's power distance measures and S-allele prevalence does not support Fischer's argument.

The Serotonin-Transporter Gene and National Differences in Corporate Corruption

In a recent study of corporate corruption, Kong (2014) reported an interactive effect of wealth and 5-HTTLPR polymorphisms on corporate corruption. The author starts from the finding that short 5-HTTLPR alleles stimulate fear and anxiety and assumes that this effect will be stronger in a poor economic environment. Because of their high fear and anxiety, corporate leaders in poor societies with a high prevalence of S alleles will avoid risky corruptive behavior. The main issue with Kong's (2014) theory is the same as in Chiao and Blizinsky (2010): The sample of nations contains only one African country (South Africa) and does not adequately represent the existing genetic variation across the globe.

The Serotonin-Transporter Gene and Gelfand's Tightness–Looseness

Unfortunately, Chiao and Blizinsky have ignored Eisenberg and Hayes's (2011) sound warning and have continued to use their unrepresentative genetic index to report associations between it and dimensions of national culture. The most recent example of this is the study by Mrazek, Chiao, Blizinsky, Lun, and Gelfand (2013). This study reports a significant association between Gelfand's "tightness versus looseness" dimension of national culture and 5-HTTLPR allele frequencies. This raises an intriguing question: How would the results change if tightness scores were available for four or five sub-Saharan African countries? If long 5-HTTLPR alleles really predict cultural looseness, the African countries should have the loosest cultures in the world. We would then observe a cultural contrast between Asia and Africa. Also, the reported correlation between Gelfand's dimension and 5-HTTLPR would rise. However, so would the correlation between tightness–looseness and Hofstede's long-term orientation (LTO), as it reveals the same statistical contrast between Asia and Africa. In that case, it would seem that Gelfand's dimension is nothing new but a variant of LTO, discovered by the Chinese Culture Connection (1987) nearly three decades ago. However, if the African nations do not have loose cultures, this finding would probably reduce the correlation between Gelfand's dimension and 5-HTTLPR to insignificance.

Optimism for Future Research at the Societal Level Using 5-HTTLPR S-Allele Frequencies

The problems and limitations of the existing studies that link 5-HTTLPR polymorphisms to cultural traits do not mean that cross-cultural sociogenetics is stillborn. The 5-HTTLPR alleles are still a prime candidate for meaningful associations with societal characteristics. Recent breakthroughs in individual-level studies of the effects of the 5-HTTLPR polymorphisms on cognition, emotions, and behaviors in humans and macaques are encouraging. Using data from macaques, Jedema et al. (2010) reported that 5-HTTLPR-associated behavioral effects reflect genotype-dependent biases in cortical development rather than static differences in serotonergic signaling mechanisms. In other words, the allelic variants of 5-HTTLPR are associated with differences in brain morphology. Hence, 5-HTTLPR studies could serve as a starting point toward the unraveling of many mysteries of the human brain that have social implications, far beyond those directly associated with the S and L alleles.

The reported findings in the literature on the serotonin-transporter gene suggest that the effects of the 5-HTTLPR polymorphisms are much broader than previously thought (Canli & Lesch, 2007). Based on literature reviews, two recent analyses (Dobson & Brent, 2013; Holmberg & Lesch, 2011) explicitly indicate that most previous studies focused on the negative effects of the

observed polymorphisms, such as the tendency of the S allele to promote anxiety and neuroticism. However, such polymorphisms would not have been maintained if their effects were entirely deleterious. In particular, the S allele could not be so extremely common in East Asians, if it did not bestow some benefits alongside its negative effects.

5-HTTLPR and Cognitive Ability

Holmberg and Lesch (2011) point out that the S allele is associated with enhancement of a wide range of cognitive functions, notably improved decision making through better probabilistic and temporal discounting. According to those authors, the reason for this association may be that, generally speaking, the S allele promotes "hypervigilance," associated with anxiety but also with close monitoring of the environment and an enhanced ability to integrate, and profit from, feedback. These effects of short 5-HTTLPR alleles have been witnessed in multiple studies in humans and in macaques, cited by Holmberg and Lesch (2011).

The literature reviews and analyses by Dobson and Brent (2013) and Holmberg and Lesch (2011) suggest that S-allele carriers outperform L-allele carriers on a variety of cognitive tasks, such as financial decision making, probably because of their hypervigilant decision-making style. Jedema et al. (2010) found that S-allele carriers make better probabilistic choices and perform better on a reversal learning task and on a pattern recognition memory test. Anderson, Bell, and Awh (2012) showed that S-allele carriers have better visual working memory. Enge, Fleischhauer, Lesch, Reif, and Strobel (2011) demonstrated that S-allele carriers have better visual memory and shorter reaction times when dealing with complex tasks. Verdejo-Garcia et al. (2013) found that in healthy controls, the S allele is associated with better performance and better learning on the Iowa Gambling Task (Figure 2, p. 1603). Borg et al. (2009) reported that the S allele predicts superior performance on the Wisconsin Card Sorting Test.

The serotonin-transporter gene is not an IQ gene, however. Holmberg and Lesch (2011) point out that S-allele carriers do not perform better on some typical IQ tasks, such as mental rotation. In a study of 572 Chinese college students, He et al. (2010) did not find a clear association between 5-HTTLPR alleles and performance on standard IQ tests, such as Raven's Advanced Progressive Matrices and a Chinese Version of Wechsler's Revised Adult Intelligence Scale.

5-HTTLPR and Risk Taking

Serotonin regulates attitudes toward risk taking in humans (Macoveanu et al., 2013) and in macaques (Long, Kuhn, & Platt, 2009). Holmberg and Lesch (2011) cite four individual-level studies that find associations between the S allele and risk aversion. Crisan et al. (2009) reached the same conclusion about this association. In another study, Stoltenberg, Lehman, Anderson, Nag, and Anagnopoulos (2011) found that the L allele predicts riskier decision making and that experience of childhood traumas is associated with poor decision making under risk, suggesting a gene–environment interaction.

5-HTTLPR and Religiousness

Dew and Koening (2014) analyzed data for 2,537 young Americans and found that carriers of the S allele had a lower average score than L-allele carriers on two behavioral measures of religiousness (religious attendance and frequency of prayer) and two subjective measures (importance of religion and religious experience). The negative relationship between the S allele and religiosity remained after controlling for race; therefore, it is not a mere statistical artifact produced by the fact that Blacks are more likely than Whites to be religious and L-allele carriers at the same time. Unfortunately, the authors of the study do not offer any explanation of this statistical relationship.

Hypotheses of the Present Study

Expected Significant Associations

The existing associations between 5-HTTLPR polymorphisms and personality or cognition at the individual level suggest that similar associations can be sought at the national level. We hypothesize that because the S allele is associated with anxiety, societies with a higher prevalence of that allele will be characterized by higher national neuroticism. Such societies may be more likely to seek ways to insure themselves against future adversity. Because of the superior probabilistic thinking of their numerous S-allele carriers, and their better ability to choose advantageous rewards, such societies are more likely to identify modern education as appropriate insurance. This will result in S-allele societies encouraging strong investment of effort in modern education. Better educated societies are more likely to have a higher average IQ and lower religiousness, or conservatism in a more general sense (Minkov, 2011, 2013).

Of course, educational performance is an extremely complex phenomenon and the role of environmental factors should not be overlooked. Some of these, such as malnutrition, can play a very serious role and explain a large part of the poor performance of children in economically disadvantaged societies, such as those in Africa. However, decades of efforts to explain why East Asian high school students perform better in mathematics than their West European peers, even when they are in the same social environment, have not produced a fully convincing result. Although differences in the serotonin-transporter gene may tell only a very small part of the story, this finding should not be dismissed out of hand simply because it sounds politically incorrect.

For these reasons, it is logical to hypothesize that national S-allele prevalence will be positively correlated with average national IQ and average national student performance in mathematics. It should also be associated with a dimension of national culture called Confucian work dynamism (Chinese Culture Connection, 1987) or LTO (Hofstede, 2001; Minkov & Hofstede, 2012). This is a dimension of national culture that distinguishes between two extremes: societies that strongly emphasize delay of immediate gratification (resulting in thrift) while encouraging persistence in future-related efforts, such as education, and societies that do not have these tendencies. (We note that this dimension may have nothing to do with other types of planning for the future, such as producing detailed business plans, etc.). A society with a higher prevalence of S-allele carriers is more likely to have a long-term orientation culture that encourages strong effort and mobilization of resources in modern education.

Because S-allele carriers are more risk-averse than L-allele carriers, we can expect that these allelic differences will be expressed at the societal level as differences in fast versus slow life-history strategy (LHS). LHS theory explains differences in risk acceptance and short-term orientation (including violence) in mating competition versus risk avoidance and a long-term orientation (Figueredo et al., 2005; Gladden, Figueredo, & Jacobs, 2008). Societies with a higher prevalence of the S allele should be characterized by slower LHS, that is, greater risk aversion and prudence, especially in mating effort.

Finally, because the S allele predicts lower religiousness, we can expect societies with a higher prevalence of that allele to be less religious.

Expected Insignificant Correlations

We have two reasons to expect insignificant correlations between S-allele prevalence and national individualism–collectivism. First, the data in Murdoch et al. (2013) show clearly that collectivist ethnic groups can be found at both extremes of the S-allele prevalence scale: high (Asians) and low (Africans). Second, we know that LTO is orthogonal to individualism (Hofstede, 2001;

Minkov & Hofstede, 2012). Therefore, if S-allele prevalence is closely related to LTO, it would probably be unrelated to individualism. For the same reason, it should be unrelated to power distance.

Method

As a first step, we expanded Chiao and Blizinsky's (2010) national S-allele prevalence database with data from studies that those authors did not consider. Then, we expanded the resulting database even further by making some highly plausible estimates. This was absolutely essential to avoid working with a skewed global sample of countries that omits important parts of the globe. Finally, we calculated correlations between our final national S-allele prevalence index and our variables of interest. We did not conduct detailed analyses of each association, controlling for all possible confounding variables, because the goal of our article is to outline directions for future studies that would do so; each association would warrant a study in its own right. However, in addition to the zero-order correlations, we also do report partial correlations, controlling for national wealth, which is the most common confounding variable in nation-level analyses.

5-HTTLPR S-Allele Prevalence Across Ethnic Groups

The publication by Murdoch et al. (2013) paints a fairly clear picture of the worldwide distribution of the 5-HTTLPR alleles at the ethnic level. It is helpful for future analyses although data for the Arab part of North Africa and for Southeast Asia (Malaysia, Indonesia, and the Philippines) are missing.

Murdoch et al.'s (2013) data reveal the following worldwide prevalence of the S allele at the ethnic level:

1. Highest in Asian populations (East Asian, Southeast Asian, Siberian), followed by Amerindian populations outside the Amazon and by Micronesian populations;
2. Intermediate in European, Middle Eastern (including Ethiopian) and Amazon populations;
3. Low in sub-Saharan Africans and in Papua New Guineans (Nasioi);
4. Lowest in Pigmy populations (Mbuti, Biaka).

As explained in Table 1, we used Murdoch et al.'s (2013) publication to expand Chiao and Blizinsky's (2010) database.

5-HTTLPR S-Allele Prevalence Across Modern Nations

We started from Chiao and Blizinsky's (2010) data, adding data for some additional countries, as explained in Table 1. Then, we made estimates for some countries for which there are no available studies. Our estimates were based on the well-known fact that many adjacent or nearby countries have populations that are very similar genetically in many respects, including 5-HTTLPR S-allele prevalence. For example, Chiao and Blizinsky's (2010) database indicates clearly that North European populations have an S-allele prevalence of 42% to 44%. Therefore, if we know the S-allele prevalence of a particular North European country, we can estimate that a neighboring country in the same region has the same, or very similar, prevalence. In other words, the score of Country A (prevalence of the S allele) can be assigned to Country B. Below, we provide more details concerning our estimation procedures.

Making estimates for Latin America is a fairly uncontroversial procedure. Although the data in Chiao and Blizinsky (2010) and in Murdoch et al. (2013) show that the worldwide variation of the

Table 1. S-Allele Prevalence Index for 59 Countries.

Country	Percentage carriers of the S allele	Source
Argentina	51.04	[a]
Australia	45.91	[a]
Austria	43.65	[a]
Azerbaijan	54.00	Estimate based on Turkey
Belgium	43.00	Estimate based on France, the Netherlands, and Germany
Botswana	20.00	[b]
Brazil	46.96	[a]
Burkina Faso	20.00	[b]
Canada	45.00	Estimate based on the Unite States
Chile	51.00	[c]
China	75.20	[a]
Colombia	51.00	[c], Escobar, Calderon, and Moreno (2011), Ospina-Duque et al. (2000)
Czech Republic	43.00	Estimate based on Germany, Austria, and Hungary
Denmark	40.80	[a]
El Salvador	51.00	[c]
Estonia	34.81	[a]
Ethiopia	44.00	Murdoch, Speed, Pakstis, Heffelfinger, and Kidd. (2013), data for Ethiopians
Finland	42.45	[a]
France	43.18	[a]
Germany	43.03	[a]
Ghana	20.00	[b]
Guatemala	51.00	[c]
Hungary	41.71	[a]
India	58.85	[a]
Iran	54.00	Estimate based on Turkey
Ireland	39.00	[a]
Israel	49.26	[a]
Italy	48.51	[a]
Japan	80.25	[a]
Korea	79.45	[a]
Mexico	51.96	[a]
Morocco	34.00	Nasserddine, Hamzi, Diakite, Serbati, and Nadifi (2012)
The Netherlands	42.72	[a]
New Zealand	43.03	[a]
Nigeria	20.00	[b]
Norway	42.00	Estimate based on Denmark and Sweden
Peru	51.00	[c]
Poland	36.96	[a]
Russia	43.91	[a]
Rwanda	20.00	[b]
South Africa	27.79	[a]
Singapore	71.24	[a]
Slovenia	42.52	[a]
Spain	46.75	[a]
Sweden	43.63	[a]

(continued)

Table 1. (continued)

Country	Percentage carriers of the S allele	Source
Switzerland	44.00	Estimate based on Germany, Austria, and France
Taiwan	70.57	[a]
Tanzania	20.00	[b]
Thailand	70.19	Tencomnao and Wongpiyabovorn (2010)
Turkey	54.29	[a]
Uganda	20.00	[b]
The United Kingdom	43.98	[a]
Ukraine	44.00	Estimate based on Russia
Uruguay	51.00	[c]
The United States	44.53	[a]
Venezuela	51.00	[c]
Vietnam	70.00	Estimate based on Thailand and data for Southeast Asian populations (Cambodians, Laotians) in Murdoch et al. (2013)
Yemen	44.00	Murdoch et al. (2013), data for Yemenites
Zambia	20.00	[b]
Zimbabwe	20.00	[b]

[a]From Chiao and Blizinski (2010).
[b]Estimate based on converging data for sub-Saharan ethnic groups (other than Pygmies) in Murdoch et al. (2013).
[c]Estimate based on Argentina, Mexico, and data for Europeans and Amerindians in Murdoch et al. (2013).

prevalence of the S allele is quite great—ranging from about 12% of all 5-HTTLPR allele occurrences among the African Mbuti to about 80% in some populations in East Asia—it is also clear that there is little variation among the Spanish-speaking Latin American nations—Argentina: 51.04%, Mexico: 51.96% (data from Chiao & Blizinsky, 2010). Clearly, the reason for this is the great genetic similarity in terms of S-allele prevalence between Europeans, and in particular, between Spanish (46.75%) and Italians (48.51%; data from Chiao & Blizinsky, 2010), as well as between most Amerindians, except some of those in the Amazon basin. Map A in Murdoch et al. (2013) suggests the following approximate prevalence of the main S allele for the available Amerindian ethnic groups outside the Amazon: Cheyenne—65%, Pima in Arizona—60%, Pima in Mexico—50%, Maya—65%, Quechua—65%. One can safely assume that the Spanish-speaking, Latin American countries that are well-represented in the World Values Survey and other large cross-cultural databases (Chile, Colombia, Guatemala, El Salvador, Peru, and Venezuela) have a prevalence of the S allele that is quite similar to that of Argentina and Mexico because the genetic mix of their populations is similar. The existing data for Colombia support this assumption.[2]

Likewise, according to Murdoch et al. (2013), the genotyped populations in sub-Saharan Africa fall into two categories with respect to their S-allele frequency: Pygmy ethnic groups (Mbuti and Biaka) among whom the prevalence of the S allele appears to be about 12.5%, and all the rest (Hausa, Ibo, Yoruba, Chagga, Maasai, Zaramo, and Sandawe), where the prevalence of the S allele is invariably about 20%. The latter value can be assigned to the African nations that are represented in the World Values Survey and other large cross-cultural databases of interest (Botswana, Burkina Faso, Ghana, Nigeria, Tanzania, Uganda, Zambia, Zimbabwe). Data for South Africa are already available from Chiao and Blizinsky (2010).

Although Europe is well-represented in Chao and Blizinsky's (2010) HTTLPR allele database, the number of European countries can be expanded by assuming that Belgium has an

S-allele prevalence of approximately 43% (based on France—43.18%, and the Netherlands—42.71%) and that Switzerland also has a prevalence of approximately 43% (based on Germany—43.03%, Austria—43.65%, and France—43.18%). Norway's prevalence can be estimated at approximately 42% (Denmark—40.8%, Sweden—43.63%).

In this way, we arrived at the S-allele prevalence index for 59 countries, presented in Table 1.

Table 1 suggests that the worldwide prevalence of the S allele at the national level is as follows:

1. Highest in East and Southeast Asian countries; followed by some other Asian countries (India, Turkey);
2. High-intermediate in Latin America and Southern Europe;
3. Low-intermediate in Northern Europe;
4. Lowest in sub-Saharan Africa.

Although the data in Table 1 seem plausible and sufficient to work with, we also tested some other hypothetical scenarios: Our S-allele prevalence estimates for the Latin American countries are based on Argentina, Mexico, and Colombia, but it is possible that some of the Northern Latin American countries, which have a high percentage of people from Amerindian descent, have a higher prevalence of the S allele than do Mexico and Argentina. After ascribing a prevalence of 55% to Colombia, Guatemala, Peru, and Venezuela, we recalculated all correlations with S-allele prevalence. They are reported in Column *r* (2) of Table 2.

We also attempted to expand our database further. We assumed that all Arab countries with missing S-allele prevalence data that are represented on at least one dependent variable of interest (Egypt, Jordan, Iraq, Malta, Syria, Tunisia, Saudi Arabia, UAE) have the same prevalence of the S allele as Yemen, Ethiopia, and some European countries, namely, 44%. We also assumed that Indonesia and the Philippines have an S-allele prevalence of 70%, similar to that of Thailand and the other Southeast Asian countries in Murdoch et al. (2013). In this scenario, S-allele prevalence in Latin America was as in our Table 1. The resulting correlations are shown in Column *r* (3) of Table 2.

We also tested the somewhat unlikely scenario that all Arab countries with missing values have the S-allele prevalence of Turkey (54%) rather than that of Yemen (44%), while retaining the values for Indonesia and Philippines from the previous test and using the values for Latin America as in Table 1. We report the results in Column *r* (4) of Table 2.

Finally, we considered what is probably the most unlikely scenario of all, in which the true S-allele prevalence values for the Northern Latin American countries and the Arab countries are the enhanced ones (55% and 54%, respectively), while holding the values for Indonesia and the Philippines at 70%. The results are shown in Column *r* (5) of Table 2.

Dependent Variables

For the expected significant correlations, we used the following composite nation-level variables: national neuroticism scores (Schmitt, Allik, McCrae, & Benet-Martinez, 2007); national IQ scores (Lynn & Vanhanen, 2002); national performance in mathematics in the eighth grade as measured by the nationally representative Trends in International Mathematics and Science Study (TIMSS) in 2003, 2007, and 2011 (Mullis, Martin, & Foy, 2005, 2007; Mullis, Martin, Foy, & Arora, 2012); and Confucian Work Dynamism/LTO (Chinese Culture Connection, 1987; Hofstede, 2001; Minkov & Hofstede, 2012). We also used national hypometropia scores from Minkov (2011), which represent the only published national LHS index (Minkov, 2014).

In addition, we used two simple items as measures of national religiousness: Items v187 and v9 in World Values Survey 2005-2008 (worldvaluessurvey.com). The first of these measures

Table 2. Nation-Level Correlations Between Prevalence of the S Allele and Relevant Variables.

Corr. no.	Variable	*r* (1)	*r* (2)	*r* (3)	*r* (4)	*r* (5)
Mostly significant correlations						
1	National neuroticism (Schmitt, Allik, McCrae, & Benet-Martinez, 2007)	.59** (*n* = 36)	.60** (*n* = 36)	.52** (*n* = 41)	.54** (*n* = 41)	.55** (*n* = 41)
2	National IQ (Lynn & Vanhanen, 2002, only study-based scores, excluding estimates)	.58** (*n* = 47)	.55** (*n* = 47)	.51** (*n* = 53)	.48** (*n* = 53)	.47** (*n* = 53
	Same, after controlling for gross domestic product (GDP) per person in 1999 (UN Statistics Division, 2009)	.62**	.61**	.57**	.53**	.53**
3	Average national school performance in mathematics in the 8th grade in 2003 (Mullis, Martin, & Foy, 2005)	.73** (*n* = 25)	.73** (*n* = 25)	.55** (*n* = 31)	.49** (*n* = 31)	.49** (*n* = 31)
	Same, after controlling for GDP per person in 1999 (UN Statistics Division, 2009)	.64**	.64**	.50**	.44*	.44*
4	Average national school performance in mathematics in the 8th grade in 2007 (Mullis, Martin, & Foy, 2007).	.64** (*n* = 24)	.61** (*n* = 24)	.56** (*n* = 24)	.51** (*n* = 24)	.49** (*n* = 24)
	Same, after controlling for GDP per person in 2005 (UN Statistics Division, 2009)	.63**	.60**	.56**	.55**	.52**
	Average national school performance in mathematics in the 8th grade in 2011 (Mullis, Martin, Foy, & Arora, 2012).	.69** (*n* = 22)	.69** (*n* = 22)	.58** (*n* = 30)	.48** (*n* = 30)	.47** (*n* = 30)
	Same, after controlling for GDP per person in 2005 (UN Statistics Division, 2009)	.70**	70**	.59**	.53**	.51**
5	Confucian work dynamism/Long-term orientation (Chinese Culture Connection, 1987)	.81** (*n* = 19)	.81** (*n* = 19)	.72** (*n* = 20)	.72** (*n* = 20)	.72** (*n* = 20)
6	Long-term orientation (Minkov & Hofstede, 2012)	.77** (*n* = 22)	.75** (*n* = 22)	.69** (*n* = 26)	.61** (*n* = 26)	.61** (*n* = 26)
7	Societal hypometropia (Minkov, 2011, 2013)	−.60** (*n* = 52)	−.57** (*n* = 52)	−.56** (*n* = 62)	−.58** (*n* = 62)	−.57** (*n* = 62)
	Same, after controlling for GDP per person in 2005 (UN Statistics Division, 2009)	−.62**	−.59**	−.58**	−.63**	−.62**

(continued)

Table 2. (continued)

Corr. no.	Variable	*r* (1)	*r* (2)	*r* (3)	*r* (4)	*r* (5)
8	Religiousness: national percentages describing self as "religious person" (Item v187 in World Values Survey 2005-2008; worldvaluessurvey.com)	−.65** (*n* = 42)	−.64** (*n* = 42)	−.59** (*n* = 46)	−.56** (*n* = 46)	−.55** (*n* = 46)
	Same, after controlling for GDP per person in 2005 (UN Statistics Division, 2009)	−.72**	−.71**	−.65**	−.64**	−.64**
9	Religiousness: national percentage indicating that "religion" is very important to self (Item v9 in World Values Survey 2005-2008)	−.41** (*n* = 42)	−.39** (*n* = 42)	−.30* (*n* = 46)	−.22 (*p* = .14, *n* = 46)	−.21 (*p* = .16, *n* = 46)
	Same, after controlling for GDP per person in 2005 (UN Statistics Division, 2009)	−.46** (*n* = 38)	−.45** (*n* = 38)	−.35* (*n* = 42)	−.27 (*p* = .07, *n* = 38)	−.27 (*p* = .08, *n* = 38)
Insignificant Correlations						
10	Individualism (Hofstede, 2001—only data from the IBM research, excluding unreliable subsequent replications)	−.15 (*p* = .32, *n* = 44)	−.19 (*p* = .21, *n* = 44)	−.18 (*p* = .17, *n* = 49)	−.21 (*p* = .15, *n* = 49)	−.24 (*p* = .10, *n* = 49)
11	In-group collectivism "as is" (Gelfand, Bhawuk, Nishii, & Bechtold, 2004)	.18 (*p* = .25, *n* = 42)	.20 (*p* = .22, *n* = 42)	.24 (*p* = .11, *n* = 45)	.25 (*p* = .09, *n* = 45)	.26 (*p* = .08, *n* = 45)
12	Exclusionism (Minkov, 2011, 2013)	−.16 (*p* = .25, *n* = 55)	−.14 (*p* = .31, *n* = 55)	−.11 (*p* = .38, *n* = 61)	−.08 (*p* = .58, *n* = 61)	−.07 (*p* = .59, *n* = 61)
13	Power distance (Hofstede, 2001—only data from the IBM research, excluding unreliable subsequent replications)	.09 (*p* = .57. *n* = 44)	.12 (*p* = .44, *n* = 44)	.16 (*p* = .28, *n* = 49)	.21 (*p* = .16, *n* = 49)	.23 (*p* = .16, *n* = 49)
14	Power distance "as is" (Carl et al., 2004)	.10 (*p* = .55, *n* = 42)	.12 (*p* = .47, *n* = 42)	.11 (*p* = .46, *n* = 45)	.10 (*p* = .50, *n* = 45)	.12 (*p* = .44, *n* = 45)
15	Power distance "should be" (Carl et al., 2004)	.04 (*p* = .80, *n* = 42)	.02 (*p* = .92, *n* = 42)	.03 (*p* = .84, *n* = 45)	.06 (*p* = .71, *n* = 45)	.04 (*p* = .79, *n* = 45)

Note. (1) Correlation with the data in Table 1; (2) correlation with the data in Table 1, but S-allele prevalence in Colombia, Guatemala, Peru, and Venezuela changed to 55%; (3) correlation with the data in Table 1, plus estimated S-allele prevalence for Egypt, Jordan, Iraq, Malta, Syria, Tunisia, Saudi Arabia, and UAE at 44%, for Indonesia and the Philippines at 70%; (4) correlation with the data in Table 1, plus estimated S-allele prevalence for Egypt, Jordan, Iraq, Syria, Tunisia, Saudi Arabia, and UAE at 54%, for Indonesia and the Philippines at 70%; (5) correlation with S-allele prevalence as in (2) plus (4).

*Correlation significant at the .01 level.

**Correlation significant at the .05 level.

national percentages describing self categorically as "religious person." The second item measures national percentages of those who say that religion is very important to them.

As a control variable—whenever it seemed relevant—we used national wealth, measured as gross domestic product (GDP) per person in 2005 (UN Statistics Division, 2009).

For the expected insignificant correlations, we used the following nation-level variables, the first three of which are variants of national individualism: individualism (Hofstede, 2001), in-group collectivism "as is" (Gelfand, Bhawuk, Nishii, & Bechtold, 2004), exclusionism (Minkov, 2011), and power distance (Carl et al., 2004; Hofstede, 2001).

Results

The results are presented in Table 2.

Discussion

Starting with the insignificant correlations in Table 2, we see that S-allele prevalence has nothing to do with Hofstede's individualism or other closely related variants of this dimension, such as GLOBE's in-group collectivism "as is" and Minkov's exclusionism. S-allele prevalence does not have anything to do with power distance or perceived power distance or desirable power distance either.

Although we have not tested the predictive properties of S-allele prevalence with respect to Schwartz's domains, it is unlikely that it is associated with any of them, including "mastery" and "hierarchy," as his cultural map of the world places East and Southeast Asia right next to sub-Saharan Africa (Schwartz, 2008), whereas S-allele prevalence places these regions at opposite extremes of a single continuum. Whether S-allele prevalence has anything to do with some other type of social hierarchy, whatever that may be, is a question that cannot be answered, as we lack the necessary data for validation purposes.

If hierarchy is conceived of as the existence of an autocratic and centralized state, Fischer (2013) may be right. Historically, ethnic groups with high S-allele prevalence tended to set up such states, although the Siberian, Micronesian, and North American populations on the territory of the United States for which data are available in Murdoch et al. (2013) violate this pattern. Vice versa, ethnic groups with low S-allele prevalence, such as those in Africa, the Amazon, and Papua New Guinea, did not have a historical tendency to set up centralized states and empires.

Concerning the significant associations that we have found, we believe that we have opened up a fruitful research field: the genetic underpinning of societal differences in LTO, LHS-hypometropia, and educational achievement. Ours is the first study ever that shows significant associations between a national genetic index and these variables across samples of countries that are broadly representative of global cultural variation.

Our results also bring up another interesting question: How do national neuroticism, LTO, LHS-hypometropia, and educational achievement relate to each other and interact, through the mediation of genes or without such mediation? For example, can we find support for the hypothesis that high S-allele prevalence stimulates national anxiety (a facet of neuroticism), which encourages thrift as insurance against an uncertain future? If demonstrated convincingly, this mediating effect of anxiety would be a plausible explanation of the relationship between 5-HTTLPR and LTO.

Limitations

Use of Estimated Scores

Admittedly, many of our S-allele frequencies are hypothetical. Yet, we considered a number of diverse scenarios and recalculated the correlations for each of them. We can safely assume that

the high and significant zero-order correlations that we found between S-allele prevalence and national neuroticism, cognitive performance, LTO, and hypometropia are unlikely to be successfully challenged by expansions or corrections of our S-allele prevalence with real data from 5-HTTLPR studies in countries with currently missing data. However, it is possible that some of the zero-order correlations will disappear in regression analyses with carefully selected independent variables meeting theoretical considerations.

Lack of Isomorphism Across Levels of Analysis

The high statistical correlations that we discovered seem to pose some problems. First, we know that at the individual level, the established or putative effects of single genes on behaviors, emotions, and cognition are small, although the cumulative effects of multiple genes may be much larger (Dobson & Brent, 2013). Yet, we find that a single polymorphism creates large effects at the national level, where societal factors can intuitively be expected to be much more important than genes. Part of the answer to this conundrum is that genes most likely do not produce societal effects single-handedly. Instead, they work synergistically with other genes. It is plausible that 5-HTTLPR prevalence correlates with the prevalence of other relevant genes that enhance each other's effect at the societal level. Future studies should also explore the mediating role of culture. It is possible that cultural traits reinforce genetic effects, epigenetically (Carey, 2012).

Simplistic Tests of 5-HTTLPR Predictive Properties

We have not tested the predictive powers of S-allele prevalence for all significant correlations against those of all plausible independent variables. As we indicated, this would be a daunting task that should generate much future research. However, the fact that some of the most intriguing correlations remain, or are actually enhanced, after controlling for the most typical conflating variable—national wealth—which is highly correlated with nearly all major socioeconomic indicators, suggests that controlling for such indicators is unlikely to reduce all the reported correlations to insignificance.

Imperfect Replicability of Results in Individual-Level Studies in Sociogenetics

Most of the reported individual-level associations between 5-HTTLPR alleles and cognition were found in studies of European populations. At least some of these findings may fail to replicate in studies of other populations. For example, the better performance of S-allele carriers on the Iowa Gabling Task was not replicated in He et al.'s (2010) study of Chinese college students. As the body of literature on SLC6A4 and other brain–activity regulating genes expands, we should be able to provide increasingly better estimates and explanations of the relationship between genes and societal traits.

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Notes

1. The appropriateness of GLOBE's methodology, especially their "as is" measurement approach, has been challenged in various publications (for instance, McCrae, Terracciano, Realo, & Allik, 2008;

Minkov, 2013; Minkov & Blagoev, 2012) as it elicits national auto-stereotypes. Yet, some of the critics indicate that these stereotypes may be valid in specific cases—when the respondents are familiar with what they are describing (Minkov & Blagoev, 2012). Because managers deal with power issues on a daily basis, their aggregated assessments of power distribution in their societies (apparently based on power distribution in their organizations) may contain a high degree of validity.

2. We discovered two 5-HTTLPR studies from Colombia: Escobar, Calderon, and Moreno (2011), and Ospina-Duque et al. (2000). The first of these was done in the department of Caldas, apparently in the capital city Manizales, where the population is predominantly White (Wikipedia, 2014). The prevalence of the S allele in healthy controls can be calculated from Table 2 in that publication: 44%. (Note that the prevalence of an allele is not the percentage of people who carry the allele but the ratio of occurrence of this allele relative to the total occurrence of all alleles of the same gene in the studied population.) Ospina-Duque et al. (2000) studied an isolated Colombian population. Their data (provided in Escobar et al., 2011) show that the S-allele prevalence in that population is 55.3%. This suggests that Colombia has approximately the same average S-allele prevalence as the other Spanish-speaking, Latin American countries.

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