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GENES, SECURITY, TOLERANCE AND HAPPINESS

This paper discusses correlations between certain genetic characteristics of the human populations and their aggregate levels of tolerance and happiness. We argue that a major cause of the systematic clustering of genetic characteristics may be climatic conditions linked with relatively high or low levels of parasite. This may lead certain populations to develop gene pools linked with different levels of avoidance of strangers, which helped shape different cultures, both of which eventually helped shape economic development. Still more recently, this combination of distinctive cultural and economic and perhaps genetic factors has led some societies to more readily adopt gender equality and high levels of social tolerance, than others. More tolerant societies tend to be happier because they create a more relaxed environment conducive to happiness.

Keywords: genetic research, World Values Survey, happiness, tolerance.

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Evidence that people's happiness levels are influenced by genetic factors has been growing ever since neuroscientists first discovered close linkages between happiness and dopamine and serotonin levels in the brain, and that genes seem to play a major role in regulating these levels.^{1 2} An early study of over 3,000 identical and fraternal twins found that genetically identical twins reported much more similar levels of happiness even when they had different life experiences than fraternal twins.³ If genetic factors are involved, this could help explain why given individuals tend to have relatively high or low levels of happiness; though recent events can raise or lower these levels, in the long run, people tend to return to a baseline level of subjective well-being.⁴

Subsequent twin-based studies have found further evidence of genetic influences on happiness,⁵ but twin studies do not identify which genes might be involved. Only recently has the linkage with happiness been traced to a specific gene, the serotonin transporter gene *5HTT*. Variation in the promoter region of this gene (5-HTTLPR) has been linked with personality and mental health and selective processing of positive and negative emotional stimuli.^{6 7 8} And previous research suggests that the short allele is linked with depression and anxiety.^{9 10 11} Analyzing data from 2,574 American students, De Neve found that individuals with the transcriptionally more efficient long allele of the 5-HTTLPR gene reported substantially higher levels of happiness, as measured by life satisfaction, than did individuals with the short allele.¹² Both alleles produce the same protein, but the long allele is associated with approximately three times higher basal activity than the short allele, resulting in increased gene expression and alteration of serotonin availability in the synaptic cleft for signaling. De Neve's analysis indicates that individuals with two long alleles of the 5-HTTLPR gene are about 17 percentage points likelier to report being very satisfied with their lives than those with two short alleles.

Previous studies of the linkages between genetic factors and happiness have been based on twin studies, but De Neve analyzes data from the ACT, a survey of individuals who provided DNA samples as well as questionnaire responses. This article examines data from another source: in recent years, research on the serotonin transporter gene has been carried out in many countries and the published reports provide evidence of the distribution of the respective alleles in many countries. In 48 of these countries,

representative national samples of the publics were also interviewed in the World Values Survey, providing data on life satisfaction and other attitudes, together with information about each country's economic and social characteristics. Analysis of this cross-national database sheds new light on previous work, making it possible to examine the impact of societal characteristics such as the country's level of economic development or social tolerance. These factors are constants in studies carried out within any one country, so their impact cannot be analyzed in those studies. As we will see, these factors vary a great deal cross-nationally, and seem to have considerable impact.

Moreover, we also have data from published sources on the allele frequencies of Val158Met (rs4680) polymorphism in the COMT gene, and can examine its linkage with the happiness levels of the populations of 48 countries. This gene plays an important role in the inactivation of dopamine, which is linked with pro-social behavior such as empathy, cooperativeness and altruism.^{13 14} The evidence examined here suggests that 158Met allele frequencies vary cross-nationally along with level of happiness.

Evidence of national-level linkages does not refute findings from individual-level analysis. If two variables go together at the individual level, they usually go together at the level of large groups, but this is not necessarily true. National-level linkages can be considerably stronger or weaker than individual-level linkages and under some circumstances they can even have opposite polarity. We repeat: national-level findings do not refute individual-level findings-- but they can shed light on how individual-level genetic factors interact with societal factors, to shape a society's level of happiness. As we will see below, societal-level phenomena seem to play at least as important a role as genetic differences in shaping the happiness level of a given country's people. Moreover, the national-level linkage that we find between happiness and the Val158Met polymorphism in the COMT gene is strong enough to suggest that it merits further analysis at the individual level.

Twin studies have consistently found that individual differences in major personality dimensions are significantly influenced by genetic factors.^{15 16} But it is difficult to determine which genes are involved. Various studies have found evidence indicating that polymorphism in both the 5-HTT gene and the COMT gene are linked with differences in the Big Five Personality traits (Extraversion, Agreeableness,

Conscientiousness, Neuroticism and Openness).^{17 18 19 20 21 22 23}

(Table 1 about here)

Table 1 shows the correlations found between the mean scores on the Big Five personality traits and the frequencies of the 5-HTTLPR S-allele and COMT 158Met allele in all countries for which data on both variables are available. It also shows the linkages with the first principal component underlying the Big Five personality traits. The results support previous findings based on individual-level data, that these genes are linked with key personality traits. Both genetic polymorphisms show statistically significant linkages with several of the personality traits, and their linkages with the underlying personality dimension (on which Neuroticism shows negative loadings while the four other traits show strong positive loadings) are particularly strong, with the COMT Val158Met polymorphism showing a .52 correlation, and the 5-HTTLPR polymorphism showing a -.72 correlation with this dimension.

(Table 2 about here)

To what extent are these personality traits linked with happiness? This article uses the respondent's reported satisfaction with life as a whole as an indicator of happiness or overall subjective well-being; this indicator has been validated extensively²⁴ and was also used by De Neve (2011) in analyzing the impact of the 5-HTTLPR polymorphism on happiness. As Table 2 indicates, the Big Five personality traits are only weakly linked with life satisfaction, with none showing a statistically significant correlation. And surprisingly, the linkage of the 5-HTTLPR polymorphism with life satisfaction not only fails to reach statistical significance, but has the wrong sign. In previous individual-level research within single countries, the short allele of this gene was negatively linked with life satisfaction; but at the national level, it shows a weakly *positive* correlation—despite the fact that (as Table 1 demonstrates) it shows significant negative linkages with agreeableness, extraversion, conscientiousness and openness, all of which would be expected to go with happiness. On the other hand, the COMT 158Met allele does show a statistically significant linkage with life satisfaction, and in the expected direction: this is logical since it is conducive to relatively high levels of dopamine, which are linked with feelings of well-being. Moreover, in previous studies the 158Met allele has been linked with pro-social behavior, empathy and cooperativeness, which one would expect to be

conducive to subjective well-being.

(Figure 1 about here)

Figure 1 shows the relationship between mean life satisfaction levels and the percentage of the population having the short allele of the serotonin transporter gene. The right-hand side of this figure shows a cluster of East Asian and Southeast Asian countries in which very high percentages of the population have the short allele-- but these countries do not show the lowest happiness levels (they are about average). On the left-hand side of the figure, several African countries plus Trinidad (in which about half the population is of African origin) have the lowest percentages of the short allele; some of them show low levels of happiness but others show rather high levels. Though De Neve has presented convincing evidence that within a sample of U.S. students, those with the short allele tend to be significantly less satisfied with their lives than those with the long allele, countries in which a large share of the population has the short allele do *not* show relatively low levels of happiness. Let us repeat, we do not view this as refuting De Neve's findings-- but it does have significant implications about the interaction between societal-level and individual-level influences on happiness.

(Figure 2 about here)

Figure 2 shows the relationship between happiness and the distribution of the A allele in the dopamine receptor polymorphism. It shows a clear tendency for the A allele to be linked with high levels of happiness, which is consistent with what physiological evidence would lead one to expect, since this allele is linked with higher dopamine levels in the brain. On the left side of this figure, we find a group of East Asian, Southeast Asian and African countries in which the populations tend to have low percentages of the A allele. This distribution of the gene does not seem to reflect the distance a given population has traveled in moving out of Africa, since it groups populations located far from Africa with populations still in Africa. The life satisfaction levels of this group range from very low to above the mean, but the overall tendency is for countries having a high percentage of the A allele to show the highest happiness levels. Here again, simple geographic determinism doesn't seem to work. Although many Northern European countries such as Denmark, Norway, Iceland and the Netherlands rank high on both variables, this is also true of such Latin American countries as Colombia, Mexico and

Brazil. Since a substantial percentage of the population in the latter countries is of non-European descent, racial origin can not readily explain this pattern. We will propose an alternative explanation, which has a better fit with the empirical evidence.

Evidence from surveys carried out in scores of countries from 1981 to 2007 indicates that a sense of security is conducive to happiness and life satisfaction. Economic security is certainly important—one finds a .61 correlation between a country's per capita GDI and its mean life satisfaction score. But social tolerance is also important, so that rising levels of gender equality and tolerance of outgroups contributed to rising life satisfaction in most countries during 1981 to 2007.²⁵ Why is it that societies in which the 158Met allele of the COMT gene is widespread, are happier than others—while the populations of societies where the long allele of the 5-HTTLPR gene is widespread do not show relatively high happiness levels? This may reflect the fact that the COMT polymorphism has been found to be linked with pro-social behavior, while the 5-HTTLPR polymorphism has not.

(Table 3 about here)

Table 3 provides societal-level evidence that supports previous findings from individual-level studies that the 158Met allele of the COMT gene is linked with pro-social behavior. It shows the correlations between the two respective polymorphisms and two attitudinal measures, and two measures of the extent to which a society actually *is* tolerant. The first is an eight-point index of legislation concerning homosexuality, with scores ranging from “1” which indicates that (as of 2012) same-sex marriage was legal, moving through various stages of diminishing tolerance to a score of “8,” indicating that homosexuality punishable by death. The A allele shows a -.60 correlation with this indicator, significant at the .001 level, while the short allele of 5-HTTLPR has no significant linkage. The second indicator is the UN Gender Empowerment Measure, which is based on the proportion of women holding positions of authority in government, business and academic life in a given country. Here again, the COMT Val158Met polymorphism shows a statistically significant relationship with an indicator of tolerant, pro-social behavior while the 5-HTTLPR polymorphism does not. Next, we examine a measure of tolerant attitudes based on representative national surveys carried out by the World Values Survey in scores of countries. The COMT Val158Met polymorphism shows

a correlation that is significant in the expected direction at the .001 level while the 5-HTTLPR polymorphism has no significant linkage. Finally, we show the correlation with Materialist/Postmaterialist values, a widely used measure of basic values that reflects the extent to which given respondents give top priority to economic and physical security, or to autonomy and self-expression. Postmaterialists tend to have grown up under relatively secure conditions and are significantly more tolerant of outgroups and more politically active than Materialists. Again, the COMTval158Met polymorphism shows a correlation that is statistically significant at the .001 level while the 5-HTTLPR polymorphism has no significant linkage.

We see no reason to doubt De Neve's finding that the long allele of the serotonin transporter is linked with relatively high levels of happiness at the individual level in the U.S.-- but it seems to act only at the individual level. Moreover, De Neve's finding is based on data from the U.S. only. While the s-allele of the 5-HTTLPR is the risk allele for inferior mental health in most studies,²⁶ in some countries the l-allele has been reported to be the "risk allele"^{27 28 29}. These findings have led to the concept that *5-HTT* is a "plasticity gene"³⁰-- that both alleles offer advantages but in different environments³¹. If these two different patterns existed in roughly equal numbers of countries, it would explain the neutral overall effect. The evidence examined here suggests that the A allele of COMTval15Met has cross-nationally consistent effects. Apparently, societies in which a large share of the population carries the A allele of COMTval158Met, have larger numbers of pro-social actors—and they consistently show significantly higher levels of social tolerance. As previous research indicates,³² and as we will further demonstrate below, social tolerance is conducive to happiness. It establishes a less stressful, more congenial environment. The populations of societies in which the 158Met allele of the COMT gene is widespread, not only have more tolerant attitudes—their societies themselves tend to be more tolerant, which is conducive to higher levels of life satisfaction. The long allele of 5-HTTLPR seems to raise the happiness levels of individuals within a given society but it does not seem conducive to the pro-social behavior that is linked with the COMT Val158Met polymorphism—and at the societal level, the positive effects of the serotonin transporter gene may be submerged by even stronger economic and social factors, such as democratic institutions or a high level of

economic development, that are constants *within* any given society, and consequently can not be analyzed in one-country studies.

The Impact of Societal-level factors on happiness

Massive societal-level factors can have a strong impact on virtually everyone within a given society, as recent Russian history illustrates. . Most societies that experienced communist rule show relatively low levels of subjective well-being, even in comparison with societies at a lower economic level, such as India, Bangladesh, and Nigeria. Are these low levels of well-being a permanent baseline characteristic, possibly linked with genetic feature of their societies, or are they a relatively recent phenomenon linked with the collapse of communism? Time series data from Russia demonstrates that, under extreme conditions, life satisfaction levels can vary dramatically, as Figure 3 illustrates. Data from representative national samples of the Russian public are available from 1990 to 2011, and we can extend the time series even farther back to if we accept a 1982 survey in Tambov oblast as a proxy for Russia.⁸

(Figure 3 about here)

The results indicate that, already in 1982, the subjective well-being of the Russian people was even lower than that of much poorer countries such as Nigeria, Bangladesh, Turkey, and India. Russia was experiencing rising alcoholism, absenteeism, and the collapse of the communist belief system-- and the subjective well-being of its people was lower than that of countries with a fraction of their income. From this already- low level, Russian subjective well-being fell sharply, so that by 1990 the Russians manifested extreme malaise. Over half the population said they were dissatisfied with their lives as a whole. Within a year the communist system had collapsed, and the Soviet Union had broken up into successor states. Well-being continued to fall after the collapse, and in 1995 the overwhelming majority of the population said they were dissatisfied with their lives. Life satisfaction is normally very stable in advanced industrial societies. But it can and does

⁸ It was not possible to carry out the first wave of the Values Surveys in Russia, but our Soviet colleagues were able carry it out in Tambov oblast, a region they considered representative of Russia as a whole. In order to verify this assumption, we surveyed Tambov oblast again in 1995, along with a separate survey of the Russian republic. The results from Tambov and Russia in 1995 were similar: for example, on life satisfaction, Russia ranked 61st and Tambov 62nd among the 65 societies surveyed. Our Russian colleagues' belief that Tambov was reasonably representative of Russia as a whole seems justified.

show sharp declines-- and it seems significant that the dramatic decline of subjective well-being in Russia was followed by the collapse of the political, economic and social welfare systems, and the breakup of the Soviet Union. The sharp decline in subjective well-being experienced by the Russian people since 1982 is linked with traumatic historical events.

These findings in no way refute the claim that genetic factors play an important role in subjective well-being-- there is compelling evidence that they do. But these findings indicate that we are not the slaves of our genes. Happiness levels vary a great deal and in part they vary with cultures and institutions that are constructed by human beings. Thus, the pursuit of happiness is not necessarily futile. Genetic factors seem to play an important role, but they do so in interaction with societal-level factors. To fully understand the implications of individual-level genetic findings, one must also take into account the impact of societal-level factors.

Multivariate analysis

(Table 4 about here)

Life satisfaction levels vary greatly from one country to another. The percentage indicating they were “dissatisfied” with their lives as a whole (placing themselves on the lower half of a 10-point life satisfaction scale) ranges from 6 percent in The Netherlands, to 76 percent in Tanzania. Table 4 examines the impact of genetic variation on life satisfaction—together with the impact of economic development, social tolerance and other influences. As we have already seen, the 5-HTTLPR polymorphism has no significant impact on life satisfaction at the societal level. As Model 1 indicates, its linkage is weak and (if one expects the short allele to have a negative) even shows the wrong sign. But the 158Met allele of the COMT polymorphism shows a highly significant impact in the expected direction (Model 2). By itself, it explains 22 percent of the cross-national variation in life satisfaction. The two polymorphisms are negatively correlated, and when entered in the same regression equation this inflates the variance considerably, producing misleading results.

The distribution of both the short allele of 5-HTTLPR and the COMT158Met allele predict that East Asian societies should be very low on life satisfaction, but in fact, the Far Eastern societies fall in the middle of the happiness range. Moreover, when both genes are included in the regression model, their effects are much stronger than in bivariate

models. This curious effect is driven by the four East Asian societies in the sample (China, Japan, Singapore, and South Korea), which have extreme positions on the distribution of both genes and therefore have a strong leverage effect. But their leverage effects (very high on 5-HTTPLR and very low on COMT) sum close to zero in the multiple regression and the resulting fit is good, bringing their predicted life satisfaction to the middle of the range of life satisfaction.

Dropping the Far Eastern societies drastically changes the bivariate correlation between the short allele of 5-HTTPLR and the COMT 158Met allele: although the correlation is $-.66$ when they are included, the correlation becomes positive and mild when they are excluded. In the reduced subset of cases, the COMT gene retains its predictive value whereas the effect of the short allele on Life Satisfaction becomes even weaker.

It is possible that both genes have an impact on life satisfaction. African societies and East Asian societies are low on the COMT 158Met allele, but the Far Eastern societies, unlike the African ones, are also high on 5-HTTPLR. Caucasian societies are in the upper range on both genes. This roughly fits the empirical variation on life satisfaction. However, most of the cases for which we have data on both genes, come from societies with large proportions of Caucasian populations. Therefore we do not have enough variation to be certain of the effect of 5-HTTPLR, although we do have enough variation on COMT to proceed with the analysis. For this reason and because it has very little explanatory power, we exclude the 5-HTTLP R polymorphism from subsequent analyses.

As previous analyses have found, the transition from subsistence-level poverty to a fair degree of economic security brings a considerable increase in life satisfaction. When we add a society's per capita GDP to the regression, it and the COMT158Met polymorphism explain fully 43 percent of the cross-national variation in life satisfaction (Model 3). The prevalence of Postmaterialist values has fully as much explanatory power: together with the COMT158Met polymorphism, it explains 44 percent of the cross-national variance (Model 4). These three variables combined explain fully half of the variance (Model 5) and when we add the indicator of tolerance of homosexuals, Model 6 explains 58 percent of the cross-national variation in life satisfaction. As expected, the two indicators of tolerant, pro-social conditions have strong impacts on a society's

happiness level; they overlap with the genetic factor and with GDP per capita to such an extent that the contributions of the latter two variables drop below significance in Model 6. Model 7 drops GDP per capita and adds a Composite Political Risk indicator that reflects to the degree to which given societies have stable, non-corrupt governments with low levels of internal and foreign conflict, bringing the explained cross-national happiness variance up to 63 per cent. In this model, the indicators of tolerance, Postmaterialist values and stable polities explain almost all of the variance-- but these characteristics are most likely to be present in prosperous societies where the COMT 158Met allele is relatively widespread.

Geographic Clustering

Let's consider the impact of geographic clustering. If it is present, the correlations we find between COMT alleles and happiness (for example) might simply reflect population segmentation, in which given populations became geographically separated and then by genetic drift, came to differ on many genes -- so that any correlation between a specific gene and a given attribute might not reflect a causal linkage but simply the fact that they happen to go together in different populations.

Commenting on Chiao and Blizinsky's ³³ analysis of the cultural impact of cross-national variation in the serotonin transporter gene 5-HTTLPR, Eisenberg and Hayes³⁴ point out that their units of analysis may not be independent: the linkage between individualist-collectivist cultures and the 5-HTTLPR gene mainly reflects the contrast between a cluster of five East Asian societies that are high on both the short allele of this gene and on collectivist cultures; and a cluster of 22 countries that are low on both attributes—and are populated mainly by people of European/Caucasian descent. Within these two clusters, they find no significant linkage between the short allele of 5-HTTLPR and collectivist cultures. Similarly, De Neve et al. (2012) note that the association between Life satisfaction and the 5-HTTLPR gene that they find, might be due to population stratification rather than reflecting a causal link between genes and happiness. To deal with this possibility, they control for the respondent's race in their analysis, finding that the linkage does not disappear.

A larger and more diverse set of 48 countries is examined here than the 29 countries analyzed by Chiao and Blizinski; and, as Figure 2 indicates, the relationship between happiness and the COMT 158Met allele does not break down into an East Asian vs. European cluster.

Nevertheless it is evident that the populations of East Asian, Southeast Asian and African countries do have a significantly lower incidence of the Met allele than the populations of European, South Asian and Latin American countries. To partly control for the impact of population stratification, Models 8 and 9 introduce a variable that measures the percentage of each country's population that is of Caucasian descent (including those living outside Europe). By itself, this variable explains less than one percent of the cross-national variance in life satisfaction, and when added to the regression equation in Model 8, it raises the explained variance by only one point, from 62 percent to 63 percent, and is not statistically significant. Models 9 and 10 reduce the number of variables included by dropping first the COMT 158Met allele, and then the percentage of the population that is of Caucasian descent. Doing so does not reduce the amount of explained variance: our most parsimonious model, Model 10, still explains 63 percent of the cross-national variance with only three independent variables. The explanatory models presented here do not seem to reflect a European/non-European dichotomy.

As Model 10 indicates, we can explain a large proportion of the cross-national variation in happiness with three variables (1) Postmaterialist values, which reflect the extent to which the population was raised under relatively high levels of economic and physical security; (2) social tolerance— itself, an indicator of relatively secure social conditions; and (3) relatively secure political conditions. But the evidence also indicates that these factors are linked with prosperity and genetic factors, which by themselves explain 43 percent of the cross-national variance.

Though the COMT factor eventually drops out of the model, the evidence is consistent with the interpretation that a high frequency of the relevant COMT 159Met allele helps make pro-social and tolerant attitudes and institutions more likely to emerge. Though the latter attributes are closely linked with the COMT Val158Met polymorphism, they have emerged only recently and cannot have caused the genetic phenomenon. But what did cause it?

(Figure 4 about here)

Neither a country's distance from Africa nor its racial composition seem to explain the prevalence of the COMT 158Met allele. But historic parasite prevalence may play an important role.³⁵ It has been argued convincingly that, in societies where the threat of infectious disease is strong, avoidance of strangers is conducive to survival, conferring an evolutionary advantage on any genes that happen to be linked with avoidance of strangers.

This relatively inward-looking and xenophobic outlook would be conducive to survival in these circumstances, but it would come at a cost: it would be less conducive to the pro-social behavior that seems to be linked with higher levels of life satisfaction. Conversely, societies with lower levels of parasite prevalence would have higher levels of pro-social behavior, which is linked with cooperative activities and higher levels of happiness. Thus, it seems possible that genetic factors were involved in the selection of such behavior. As Figure 4 indicates, the populations of societies that historically have high prevalence of infectious disease tend to show lower levels of the 158Met allele than societies that were low parasite prevalence. The overall correlation is $-.71$, which suggests that as much as half of the cross-national variation in the prevalence of the 158Met allele might reflect the historic parasite load or related factors.

The impact of economic development on happiness

Though family income explains only about 3 percent of the variance in life satisfaction at the individual level, we find a $.61$ correlation between per capita GDP and mean life satisfaction scores at the national level, as Table 2 indicates. This suggests that economic development might explain as much as 37 percent of the cross-national variance. In other words, there is a huge difference between the apparent impact of economic factors on life satisfaction at the individual level and at the societal level. In part, this reflects the fact that there is a much wider range of variation between nations than within nations. For example, within the U.S., the richest state (Connecticut) has a per capita income twice as high as that of the poorest state (Mississippi). But on the cross-national scale, World Bank data indicates that the world's richest nation (Norway) has a per capita income (adjusted for purchasing power parity) that is 300 times as high as that of the poorest nation (Democratic Republic of the Congo). Moreover, the data cited by De Neve et al. concerning the modest impact of income on subjective well-being are from high-income countries. But the impact of income on life satisfaction follows a curve of diminishing returns: among the publics of low-income countries it has a considerably stronger impact than it does among the publics of high-income countries. This does not refute the finding that income has a relatively modest impact on happiness *within* the U.S. today-- it does. But this finding has somewhat misleading implications for policy makers: the fact that economic development has a $.61$ national-level correlation with life satisfaction suggests that economic development can have a considerable impact on human happiness. If massive social changes

raise or lower the happiness levels of almost everyone in a society, one would continue to observe relatively weak correlations between income and happiness within that society—although the society as a whole experienced traumatic changes in happiness levels. This is precisely what seems to have occurred in Russia during the past four decades.

Things do not necessarily work in the same way at the individual level and the societal level. The long allele of the 5-HTTLPR polymorphism seems significantly linked with happiness at the individual level, but the populations of countries in which this allele is widespread do not seem to be happier than the populations of countries in which it is rare. On the other hand, evidence from 48 countries indicates that populations in which the 158Met allele of the COMTval158Met polymorphism is relatively widespread, are significantly happier than the populations of countries in which it is relatively rare. This suggests, but does not prove, that the COMTval158Met polymorphism may complement the 5-HTTLPR polymorphism in helping to shape the life satisfaction levels of individuals; individual-level analysis will be needed to demonstrate whether this is true. In any case, there is evidence that the COMT 158Met encourages pro-social behavior that is conducive to higher life satisfaction levels in given societies.

(Figure 5 about here)

Let us perform a still more demanding test of geographic genetic clustering. Building on earlier exercises in genetic mapping,³⁶ we gathered data on 79 STR allele frequencies of five genetic markers used in forensic genetic testing to identify people's origins. We obtained data from the 39 countries shown in Figure 5 (countries such as the U.S., Australia or Argentina, whose population are mainly immigrants from other countries on this map, are not included). Figure 5 shows the genetic relationships between the populations of these countries, based on a principal components factor analysis of each country's mean score on the 79 STR alleles. The horizontal dimension shows each country's loading on the first principal component, which explains 42% of the cross-national variance. The vertical dimension reflects the second principal component, which explains 20% of the cross-national variance. We used the forensic STR system because these data are available for many populations, including some not studied for other genes.³⁷

The MDS plot in Figure 5 shows five clear geographic clusters, grouping countries in

sub-Saharan Africa, South America, South Asia and North Africa, East and Southeast Asia, and Europe. The distances on this Figure can be interpreted as reflecting in general the geographic distance traveled in humanity's emigration out of Africa, though South America—geographically the most remote region—is relatively close to the African cluster and East Asia is closer than Europe

But the horizontal dimension, based on the first principal component, could be interpreted as reflecting the degree of parasite prevalence, to which it is correlated at $r = -.86$. This dimension is also correlated rather strongly with a society's per capita GDP ($r = .55$). And it is even more strongly correlated with the distribution of the COMT polymorphism, at $r = .76$. Consequently, when both variables are entered in a multiple regression on Life Satisfaction, both effects become insignificant.

Conclusion

The analysis in Figure 5 supports other findings indicating that genetic variation tends to be geographically clustered. This implies that any correlation between gene X and a given attribute might not reflect a causal linkage, but simply the fact that they happen to go together in different populations. The real cause might be another gene that is closely linked with gene X—or even some cultural or political or economic factor that is closely correlated with gene X.

This is certainly possible. We find strong correlations between the COMT allele and a whole cluster of genetic polymorphisms *and* certain cultural zones *and* high levels of economic development *and* high levels of social tolerance. At this point, we can not be certain which of many related genes is driving the process if any. It is conceivable that certain types of pre-modern societies might have been able to affect genetic pools by encouraging pro-social behavior and suppressing its opposite. But it seems unlikely that high levels of economic development or a specific culture is the root cause of the genetic variation, which almost certainly preceded the emergence of these relatively recent phenomena. And it is even more implausible that the strong correlations that we find between the COMT alleles and current societal features such as the UN Gender Empowerment Measure, and legislation concerning

homosexuality simply reflect population segmentation and genetic drift. These are recent developments in which the publics of 48 different countries independently decided to allow gender equality and to tolerate homosexuality in varying degrees. The strong correlations that we find between this wide range of genetic, economic and social phenomena seem too strong to result from random drift: there is almost certainly an underlying causal process, though we have only begun to sort it out.

The fact that we find a correlation of $-.60$ between the 158Met allele and the degree to which homosexuality is repressed in given countries, suggests that there may be a causal link between the distribution of this allele and social tolerance. This supposition is supported by the fact that we also find highly significant correlations between this allele and other indicators of social tolerance. We know that economic security is conducive to tolerance, but these societies are not more tolerant simply because they are relatively prosperous: the linkages persist when we control for per capita GDP. These linkages do not prove that the COMT polymorphism causes tolerance, but they provide prima facie evidence that this genetic factor may be involved—perhaps in connection with other genes that have not yet been identified. Logically, the next step is to seek individual-level evidence that the COMT polymorphism is linked with happiness.

We suggest that a major cause of the systematic clustering of genetic characteristics may be climatic conditions linked with relatively high or low levels of parasite prevalence in accordance with results of Fumagalli et al., 2011.³⁸ This may lead certain populations to develop gene pools linked with different levels of avoidance of strangers, which helped shape different cultures, both of which eventually helped shape economic development. Still more recently, this combination of distinctive cultural and economic and perhaps genetic factors has led some societies to more readily adopt gender equality and high levels of social tolerance, than others.

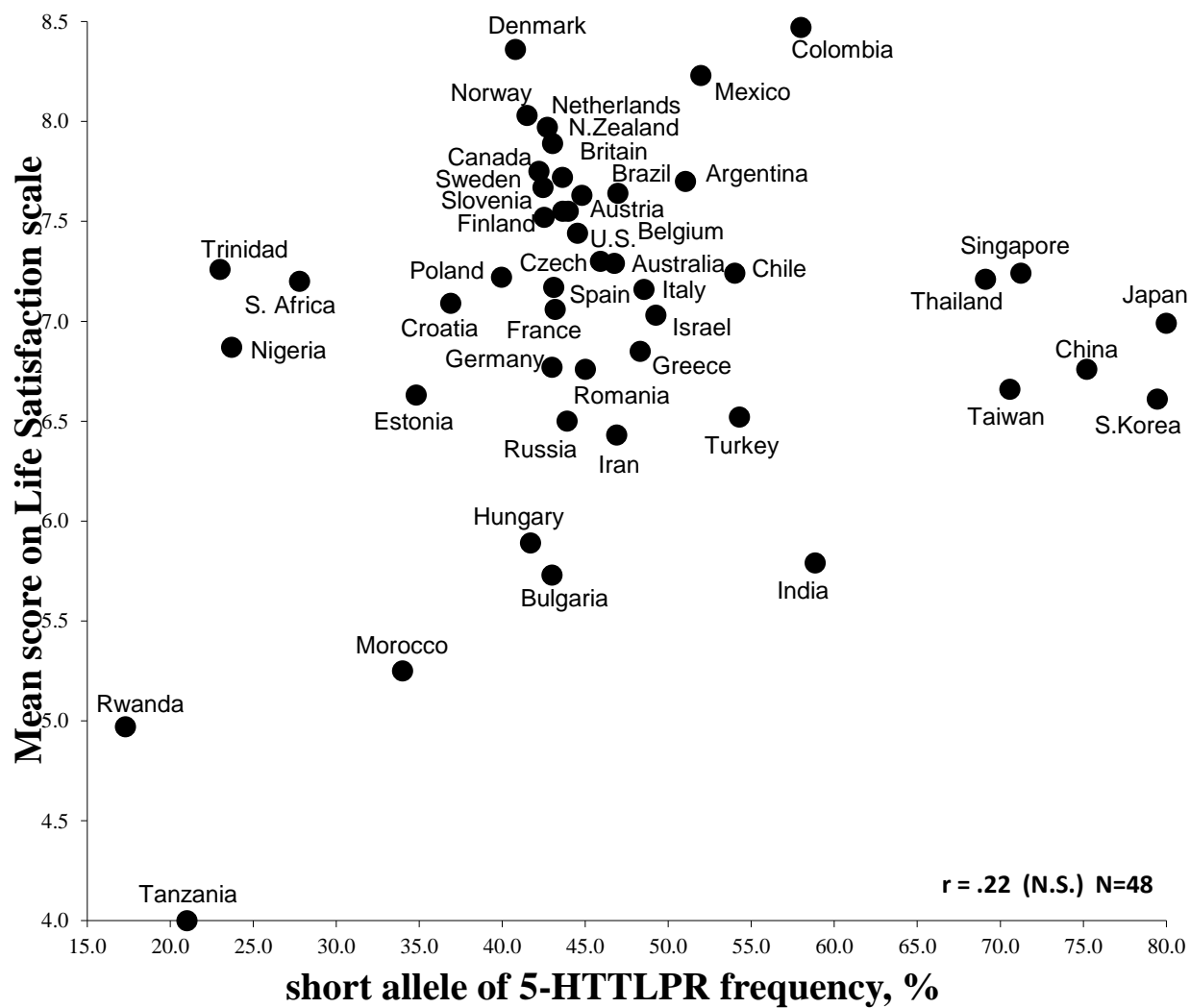


Figure 1. Life Satisfaction by 5-HTTLPR short allele frequency, %.
 $r = .22$ (n.s.) $N = 48$.

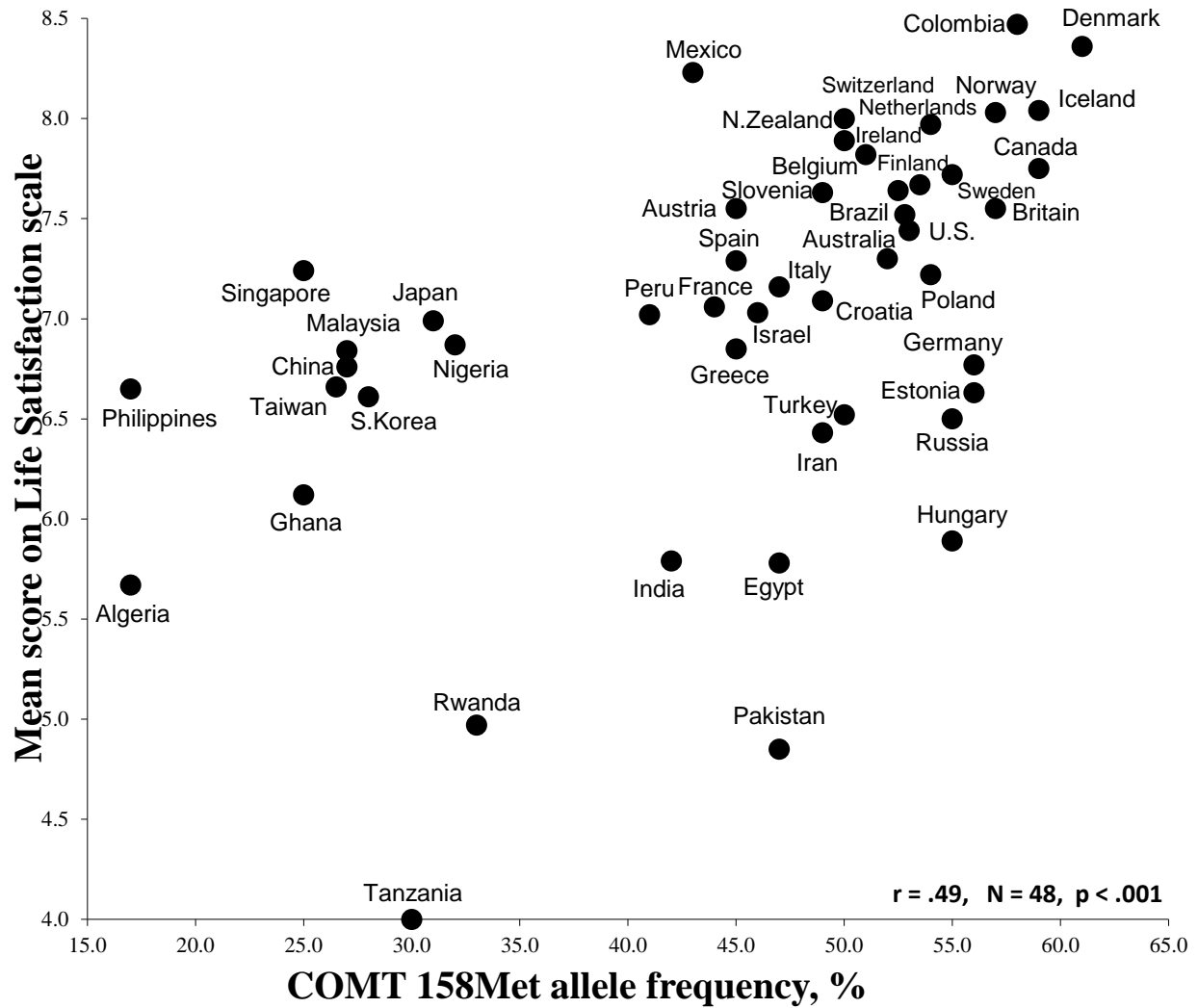


Figure 2. Life Satisfaction level by on COMT 158Met allele frequency
 $r = .49$, $p < .001$ ($N=48$).

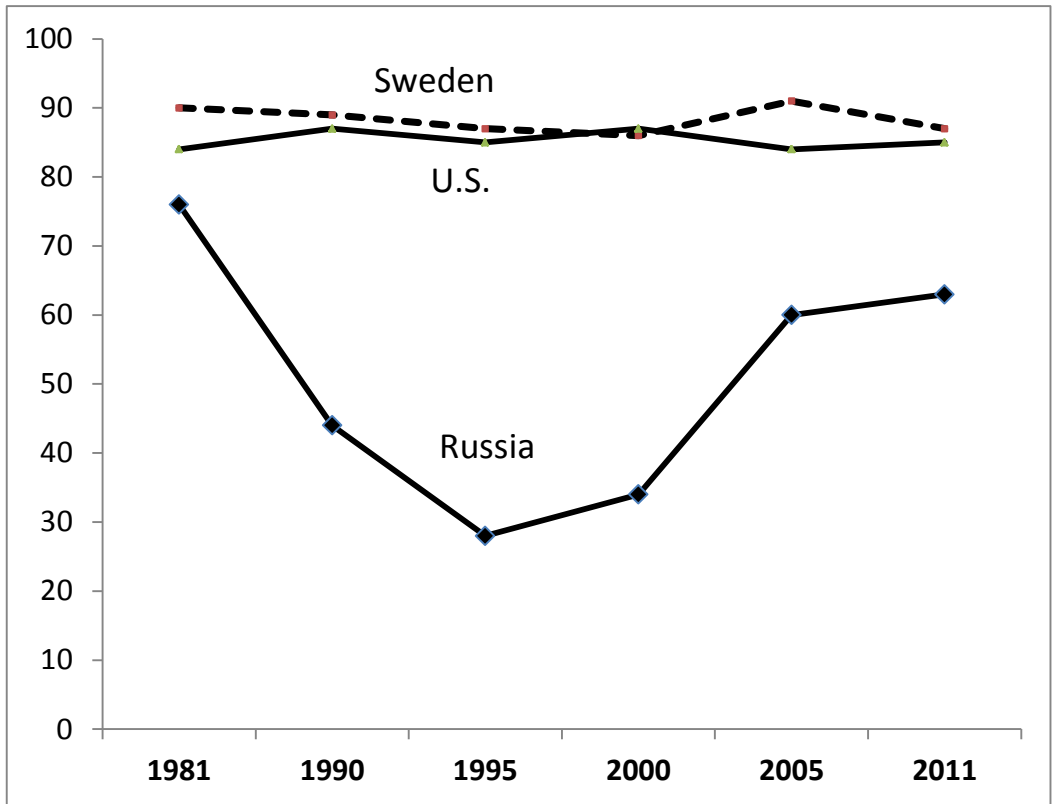


Figure 3. Life Satisfaction levels in Russia, United States and Sweden, 1981 – 2011.
 (percentage describing themselves as “satisfied” with their lives as a whole, i.e., choosing points 6-10 on 10-point scale on which 1 = completely dissatisfied and 10= completely satisfied).

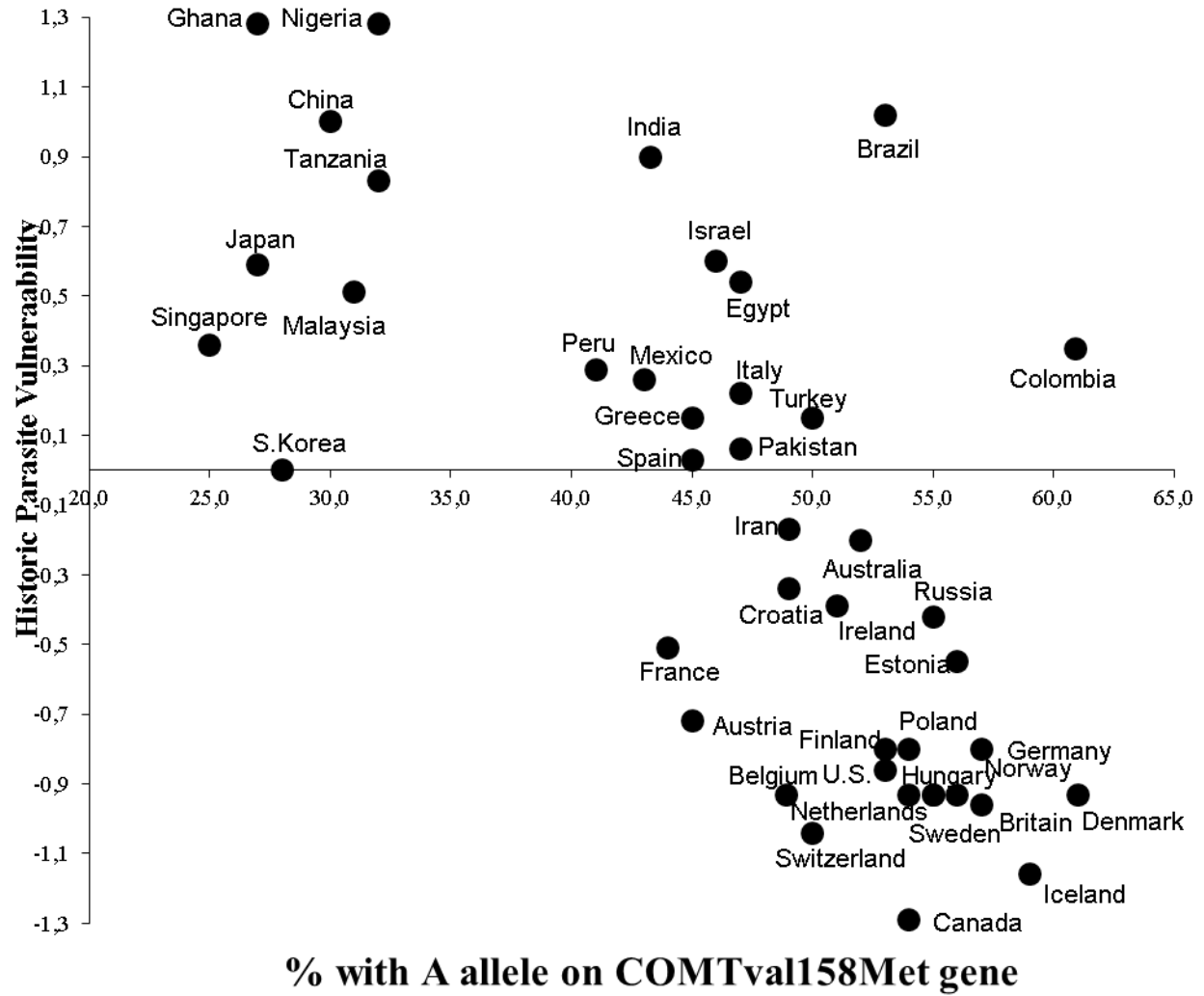


Figure 4. Frequency of COMT 158Met allele and historical parasite prevalence. $r = -.71$ $p < .000$ (N=45). Historic parasite prevalence from Fincher et al., 2008.

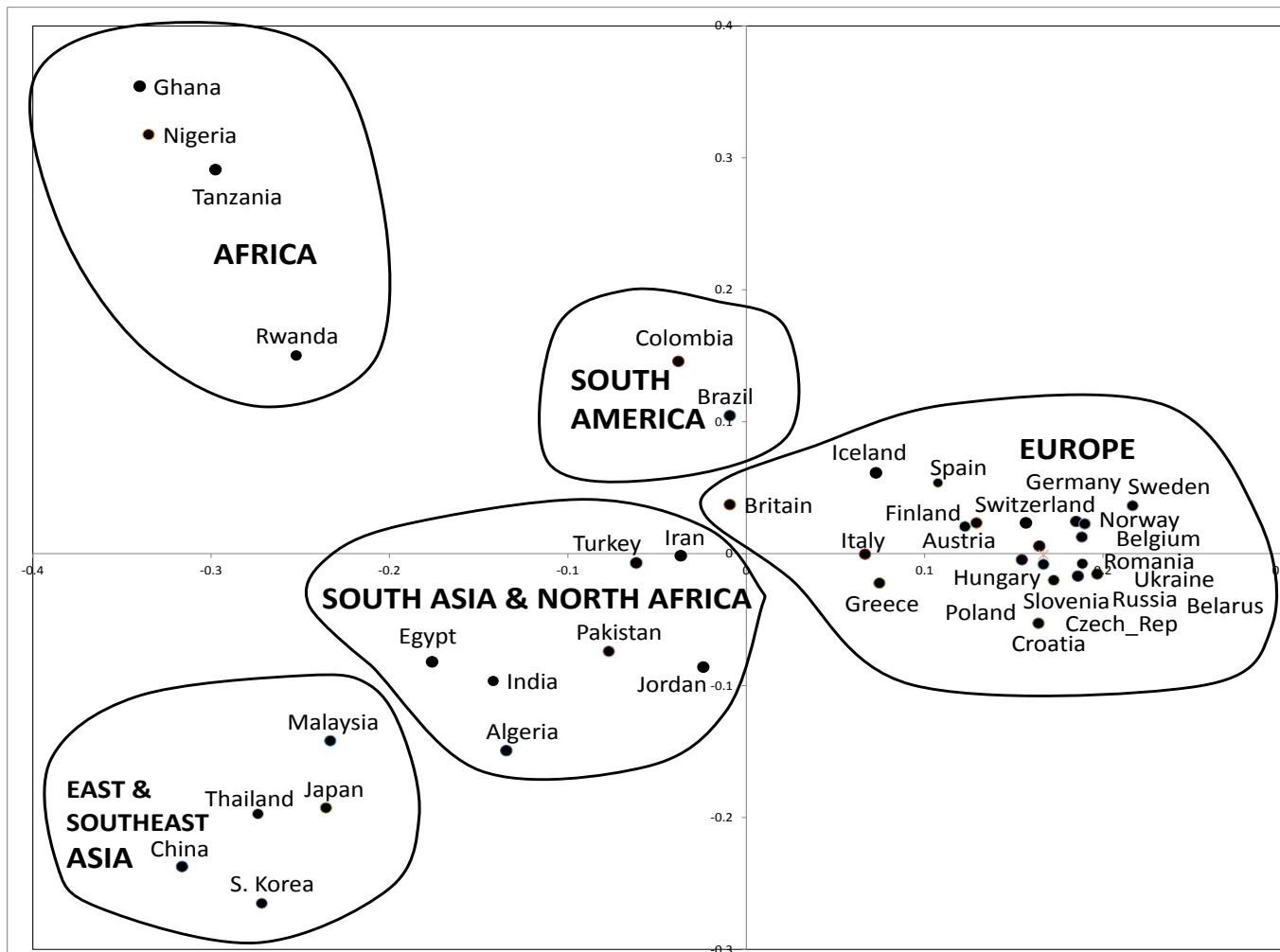


Figure 5. Multidimensional Scaling Plot Depicting Genetic Relationships between Populations of 39 Countries.

The horizontal dimension shows each country's loading on the first principal component from a factor analysis of 39 countries' mean scores on each of 79 STR alleles; the vertical dimension reflects the second principal component.

Table 1. Correlations between national mean scores on personality variables, values and societal traits, and 5-HTTLPR and COMT 158Met allele frequencies

	Frequency of short allele of 5-HTTLPR polymorphism	Frequency of 158Met allele of COMT gene
Big 5: Extraversion	-.41 * (32)	.38 * (30)
Big 5: Agreeableness	-.61 ** (32)	.38 * (30)
Big 5: Conscientiousness	-.55 ** (33)	.31 (30)
Big 5: Neuroticism	.28 (33)	-.28 (30)
Big 5: Openness	-.43 * (33)	.43 * (30)
Big 5: 1 st principal component	-.72 ** (32)	.52 * (30)

* significant at .05 level; ** significant at .01 level

Number of countries is in parentheses

Table 2. Correlations between national mean scores on personality variables values and societal traits, and Life Satisfaction

	Correlation with Life Satisfaction:	
Big 5: Extraversion	.24	(51)
Big 5: Agreeableness	.01	(51)
Big 5: Conscientiousness	-.25	(51)
Big 5: Neuroticism	.14	(52)
Big 5: Openness	.18	(52)
Big 5: 1 st principal component	.01	(50)
5-HTTLPR short allele frequency, %	.22	(48)
COMT 158Met allele frequency, %	.49***	(48)

* significant at .05 level; ** significant at .01 level; *** significant at .001 level
Number of countries is in parentheses.

Table 3. Correlations between gene allele distributions and indicators of tolerant, pro-social behavior

	5-HTTLPR short allele frequency, %	COMT 158Met allele frequency, %
Legislation concerning homosexuality scale: Same Sex Marriage is legal = 1 ...death penalty for homosexuality = 8	-.13 (48)	-.60 *** (48)
UN Gender Empowerment Measure (% of women in high-level positions in government, business and academic life)	-.18 (44)	.42 ** (43)
General tolerance factor: respondent supports gender equality in jobs, is relatively tolerant of homosexuality, accepts foreigners as neighbors (positive pole)	-.03 (44)	.54 *** (43)
Materialist/Postmaterialist values index (Postmaterialist values are high)	-.10 (48)	.47 *** (48)

* $p < .05$ ** $p < .01$ *** $p < .001$

Number of countries is in parentheses

Table 4. Predictors of Life Satisfaction: national-level regression analysis (dependent variable is nation's mean on 10-point life satisfaction scale, 1=completely dissatisfied... 10=completely satisfied)

Independent Variables:	Mod. 1	Mod. 2	Mod. 3	Mod. 4	Mod. 5	Mod. 6	Mod. 7	Mod. 8	Mod.9	Mod.10
5-HTTLPR short allele frequency, %	.22	—	—	—	—	—	—	—	—	—
COMT 158Met allele frequency, %	—	.49***	.25*	.24*	.17	.03	.09	.23	—	—
GDP/capita in 2000	—	—	.53***	—	.33*	.12	—	—	—	—
Materialist/ Postmaterialist values	—	—	—	.54***	.36**	.26*	.26*	.25*	.28*	.28*
Tolerance: Legislation concerning Homosexuals	—	—	—	—	—	-.48**	-.37*	-.37*	-.46**	-.43**
Composite Political Risk Score	—	—	—	—	—	—	.27*	.28*	.24*	.25*
Caucasian race as % of country's population	—	—	—	—	—	—	—	-.18	-.07	—
Historical parasite vulnerability (Fincher)	—	—	—	—	—	—	—	—	—	—
Constant	6.58	5.26	5.38	1.32	2.71	5.15	2.85	2.66	3.45	3.29
Adjusted R-squared	.01	.22	.43	.44	.50	.58	.62	.63	.62	.63
N =	47	47	47	47	47	47	47	47	47	47

Cell entry is standardized regression coefficient. Signif. levels:***p< .001; ** p < .01; * p<.05

Source: genetic data compiled from articles in scientific journals; attitudinal variables from latest available survey from 1981-2011 World Values Surveys and European Value Study; economic data from World Bank, *World Development Indicators*; Legislation concerning homosexuals from LGBT Portal; Composite Political Risk scores from *International Country Risk Guide*.

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