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Pathogen prevalence predicts human cross-cultural variability in individualism/collectivism

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Pathogenic diseases impose selection pressures on the social behaviour of host populations. In humans (*Homo sapiens*), many psychological phenomena appear to serve an antipathogen defence function. One broad implication is the existence of cross-cultural differences in human cognition and behaviour contingent upon the relative presence of pathogens in the local ecology. We focus specifically on one fundamental cultural variable: differences in individualistic versus collectivist values. We suggest that specific behavioural manifestations of collectivism (e.g. ethnocentrism, conformity) can inhibit the transmission of pathogens; and so we hypothesize that collectivism (compared with individualism) will more often characterize cultures in regions that have historically had higher prevalence of pathogens. Drawing on epidemiological data and the findings of worldwide cross-national surveys of individualism/collectivism, our results support this hypothesis: the regional prevalence of pathogens has a strong positive correlation with cultural indicators of collectivism and a strong negative correlation with individualism. The correlations remain significant even when controlling for potential confounding variables. These results help to explain the origin of a paradigmatic cross-cultural difference, and reveal previously undocumented consequences of pathogenic diseases on the variable nature of human societies.

Keywords: collectivism; human culture; individualism; infectious disease; pathogens; social behaviour

1. INTRODUCTION

Disease-causing pathogens represent significant ecological hazards that must be managed or avoided all together. Selection pressures imposed by pathogens appear to have had an influence on the psychology and social behaviour of many species, including primates (Freeland 1976; Møller *et al.* 1993; Loehle 1995). Humans are no exception. Infectious diseases have been agents of morbidity and mortality throughout human history (Anderson & May 1991; Ewald 1994; Dobson & Carper 1996; Wolfe *et al.* 2007), and a growing body of empirical research indicates that people possess psychological mechanisms that serve the function of antipathogen defence. For instance, ethnocentrism, xenophobia and other specific forms of interpersonal prejudice appear to result, in part, from the operation of these mechanisms (e.g. Faulkner *et al.* 2004; Navarrete & Fessler 2006; Park *et al.* 2007).

As is the case with immune defence more generally (Zuk & Stoehr 2002; Hanssen *et al.* 2004), there are potential costs as well as benefits associated with psychological and behavioural antipathogen defences. One consequence is the activation of these mechanisms contingent upon cues indicating vulnerability to the transmission of pathogens. To the extent that individuals are more vulnerable (or perceive themselves to be more vulnerable) to the hazards posed by infectious diseases, those individuals show stronger evidence of cognitions and attitudes that serve an antipathogen defence function (Faulkner *et al.* 2004; Navarrete & Fessler 2006; Navarrete *et al.* 2007; Park *et al.* 2007; Schaller & Duncan 2007).

This sort of contingency may manifest not merely in differences between individual persons, but in differences between human cultures. To the extent that particular forms of social behaviour (and the specific psychological mechanisms underlying those behaviours) serve an antipathogen defence function, then those behaviours (and the underlying mechanisms) are more likely to characterize the cultural populations within which there has historically been greater prevalence of disease-causing pathogens. Prior research shows that worldwide variability in pathogen prevalence predicts specific kinds of cultural differences, including differences in food preparation (Sherman & Billing 1999), marriage structures (Low 1990), parenting practices (Quinlan 2007) and mate preferences (Gangestad *et al.* 2006). We focus here on the multifaceted value systems of individualism and collectivism, which are fundamental to social scientists' descriptions of culture and cross-cultural differences (e.g. Triandis 1995; Hofstede 2001). Indeed, it has been suggested that the individualism/collectivism dimension 'may ultimately prove to be the most important dimension for capturing cultural variation' (Heine 2008, p. 189). But it has remained largely a riddle as to why some cultures are more individualistic while others are more collectivistic. We suggest that collectivism (in contrast to individualism) serves an antipathogen defence function, and thus is

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more likely to emerge and persist within populations that historically have been characterized by a greater prevalence of pathogens.

The logical basis of this hypothesis is evident in at least two defining features of collectivistic (versus individualistic) value systems. First, collectivists make sharp distinctions between coalitional in-groups and out-groups, whereas among individualists the in-group/out-group distinction is typically weaker (Gelfand *et al.* 2004). A consequence is that collectivists are more wary of contact with foreigners and other out-group members (Sagiv & Schwartz 1995). This xenophobic attitude can serve an effective antipathogen function by inhibiting exposure to novel pathogens. A second, but no less critical, distinction between these cultural value systems lies in their different emphases on conformity versus the tolerance for deviance. Collectivism is characterized by a strong value placed on tradition and conformity, whereas individualism is characterized by a greater tolerance for (and encouragement of) deviation from the *status quo* (Oishi *et al.* 1998; Cukur *et al.* 2004). Given that many specific traditions and norms (such as those pertaining to food preparation; e.g. Sherman & Billing 1999) can serve as buffers against pathogen transmission, deviance from the *status quo* may pose a contagion risk to self and others, whereas conformity helps to maintain the integrity of these ritualized buffers against disease. In sum, the behavioural manifestations of collectivism (compared with the behavioural manifestations of individualism) are more likely to provide defence against the dangers posed by pathogens.

Individualistic values may promote other kinds of functional benefits. For example, the discovery or spread of beneficial new technologies may occur more frequently when individuals are encouraged to deviate from existing traditions and engage in interactions with non-group members. In geographical regions characterized by relatively low pathogen stress, the benefits of collectivism (in terms of antipathogen defence) may be minimal, compared with the benefits associated with individualism. Under these ecological circumstances, individualistic values may be more adaptive. However, within geographical regions characterized by a greater prevalence of pathogens, the functional benefits of collectivism would also be greater, and may outweigh whatever benefits are conferred by individualistic tendencies. Under these circumstances, collectivistic values are likely to be more adaptive. It follows that worldwide variation in the historical prevalence of pathogens should predict contemporary cultural tendencies towards individualistic versus collectivistic values.

Indirectly consistent with this hypothesis is the observation that, just as infectious diseases are typically more prevalent in equatorial regions (Guernier *et al.* 2004), equatorial societies also tend to be more collectivistic than societies at higher latitudes (Hofstede 2001). However, to date, no empirical evidence has directly tested the hypothesis linking worldwide variability in pathogen prevalence to cultural variation in individualism/collectivism.

2. MATERIAL AND METHODS

For our analyses, geographical regions served as the unit of analysis. The majority of these regions are countries (e.g. Nigeria), but the sample also included several culturally distinct geopolitical regions within a nation (e.g. Hong Kong). Although geopolitical boundaries are not strictly synonymous with cultural boundaries, there is abundant evidence that geopolitical regions can serve as useful proxies for societal cultures (e.g. Schwartz 2004).

Regional scores on pathogen prevalence were assigned using methods that are modelled after previous investigations (e.g. Low 1990; Gangestad *et al.* 2006). Given that pathogen prevalence is hypothesized to be causally precedent to cultural values, and that any effect of ecology on culture requires some time lag, our primary measure of pathogen prevalence was based on historical indicators of disease prevalence in each region. For the sake of reliability and comparison, we also computed a second measure of pathogen prevalence, based on contemporary epidemiological data.

Regional scores on individualism/collectivism were obtained from previously published cross-cultural studies. To avoid dependence on any single assessment method, we examined four different indicators of individualism/collectivism in our analyses.

Our entire sample included 98 regions for which we had at least one measure (and in most cases, multiple measures) of individualism/collectivism. For 93 of these regions we had an indicator of historical pathogen prevalence. For 97 regions we had an indicator of contemporary pathogen prevalence. Statistical analyses tested whether, as predicted, pathogen prevalence correlates negatively with measures of individualism and positively with measures of collectivism. To help rule out alternative causal explanations, we also assessed (and conducted follow-up analyses to statistically control for) several additional variables that might be correlated with pathogen prevalence and cultural differences in individualism/collectivism. Appendix 1 in the electronic supplementary material contains the values for our pathogen prevalence measures and the different individualism/collectivism measures.

(a) *Measures of pathogen prevalence*

To create our primary measure of pathogen prevalence, we were able to estimate the prevalence of nine pathogens detrimental to human reproductive fitness (leishmanias, trypanosomes, malaria, schistosomes, filariae, leprosy, dengue, typhus and tuberculosis) within each of the 93 geopolitical regions worldwide. By necessity, a contemporary source was used to estimate the prevalence of tuberculosis (National Geographic Society 2005), but the prevalence of the remaining eight pathogens was estimated on the basis of old atlases of infectious diseases and other historical epidemiological information (Simmons *et al.* 1944; Rodenwaldt & Jusatz 1952–1961). The nine individual prevalence estimates (coded on either three- or four-point scales) were standardized (transformed into z-scores), and the mean of these nine standardized scores served as the estimate of the historical prevalence of pathogens in each region.

We used similar methods to create a second measure of pathogen prevalence within each of the 97 geopolitical regions. This measure was based explicitly on contemporary epidemiological information. Data were obtained from the Global Infectious Diseases and Epidemiology Online Network (http://www.gideononline.com/), which reports current distributions of infectious diseases in each country of the world. (The database is updated weekly; our data were obtained during the period April–June 2007.) We focused on seven classes of pathogens (leishmanias, trypanosomes, malaria, schistosomes, filariae, spirochetes and leprosy) and coded the relative prevalence of each specific pathogenic disease within each class. A total of 22 specific

pathogenic diseases were coded, each on the same three-point prevalence scale. These values were summed within each region to create a composite index estimating the contemporary prevalence of pathogens.

The reliabilities of the two pathogen prevalence indices are indicated by high correlations with a similar index created by Gangestad & Buss (1993) to assess pathogen prevalence within a smaller sample of 29 regions (r's = 0.89 and 0.83, for the historical and contemporary pathogen prevalence indices, respectively). Intercorrelation between our two indices was $r = 0.77$.

(b) *Measures of individualism and collectivism*

The results of four previously published cross-cultural surveys provided us with regional scores on four different measures of individualism/collectivism.

Hofstede (2001) assessed attitudes and values from over 100 000 IBM employees worldwide. He also consulted other published reports, observations and descriptive information. From these data Hofstede estimated individualism/collectivism scores for 68 specific geopolitical regions included in our analyses. Higher scores indicate greater individualism.

Suh *et al.* (1998) computed a measure of individualism/collectivism for 58 regions included in our analyses. Their index is a combination of Hofstede's individualism scores, and the numerical ratings of Harry C. Triandis—a pioneering researcher in the field of cross-cultural psychology with a particular expertise on individualism and collectivism. As with Hofstede's index, higher values on this index indicate greater individualism.

Gelfand *et al.* (2004) reported the 'Global Leadership and Organizational Behavior Effectiveness Research Program (GLOBE)' measures of individualism/collectivism, based on responses from 17 370 individuals worldwide. From these data, several conceptually distinct kinds of region-specific scores were computed. Our analyses focus specifically on 'in-group collectivism practices'. Gelfand *et al.* reported that these particular scores showed the greatest convergent validity with other independent indicators of individualism/collectivism. Moreover, compared with the alternative measures summarized by Gelfand *et al.* this particular measure is the one most clearly based on actual behaviour. Regional values ($N = 57$) were scored in such a way that higher values indicated greater collectivism.

Kashima & Kashima (1998) reported that cultural value differences are strongly reflected in a simple linguistic convention: whether or not it is acceptable to drop first- and second-person pronouns in spoken language. Pronoun drop in a region's dominant language is much more prevalent in more highly collectivistic cultures. Kashima & Kashima reported on the pronoun-drop conventions within 70 regions included in our analyses. We coded this binary variable such that a higher score indicates the allowance of pronoun drop and so reflects greater collectivism.

Given that our pathogen prevalence indices were computed based on contemporary geopolitical boundaries, we had to exclude from our analyses several of the individualism/collectivism values reported by these prior researchers. Kashima & Kashima (1998), Suh *et al.* (1998) and Gelfand *et al.* (2004) reported values for both East and West Germany, a distinction not made by our pathogen prevalence indices. Similarly, our indices did not distinguish between French-speaking and German-speaking Switzerland, for which Gelfand *et al.* reported separate scores. In these cases, we chose one regional value (West Germany, German-speaking Switzerland) to represent the current country, and excluded the other values (East Germany, French-speaking Switzerland). Gelfand *et al.* also reported separate values for White versus Black South Africans—a non-geographical distinction that cannot be sensibly mapped onto our pathogen prevalence indices. We excluded both of these values from our analyses. Hofstede reported separate values for three former Yugoslavian nations (Croatia, Serbia and Slovenia; for each of which we computed pathogen prevalence scores), as well as a value for Yugoslavia more generally (for which we did not compute scores). We retained the former but excluded the latter. (Kashima & Kashima also reported a pronoun-drop value for Yugoslavia, and specifically indicated Croatian as the regional language; thus, rather than excluding this datum, we ascribed it to Croatia.) The results reported below remain virtually unchanged even if different inclusion/exclusion criteria are applied to these special cases.

Within our dataset, the two 'individualism' scores (Hofstede, Suh) were highly positively correlated ($r = 0.91$), as were the two 'collectivism' scores (Gelfand, Kashima; $r = 0.80$). Correlations between the individualism and collectivism scores were highly negatively related (r's ranged from -0.72 to -0.85).

(c) *Other variables*

To address alternative causal explanations for the hypothesized relationship between pathogen prevalence and individualism/collectivism, we also examined several other variables that might be expected to predict individualism/collectivism.

Some social scientists (e.g. Hofstede 2001) have suggested that increased individualism may be a cultural consequence of economic development and urbanization (both of which might also be correlated with pathogen prevalence). Therefore, we obtained measures of variables bearing on these constructs: gross domestic product *per capita* (GDP *per capita*), inequity in the distribution of wealth (Gini index) and population density (computed from population size divided by land area and then log transformed). Region-specific data on these variables were obtained from the World Factbook 2007 (http://www.cia.gov/).

One could also speculate that differences in individualism/collectivism might be predicted by pathogen-irrelevant influences on health and mortality. That is, just as collectivistic values may maintain cultural buffers against pathogen transmission, they might also maintain cultural buffers against other sources of morbidity and mortality independent of the direct effects of pathogens (e.g. interpersonal violence). To create a measure of pathogen-independent health threats, we regressed average life expectancy (obtained from the World Health Organization; http://www.who.int) on our index of historical pathogen prevalence and saved the residuals. These region-specific residual values represent variation in life expectancy that cannot be attributed to variation in pathogen prevalence.

(d) *Alternative analysis strategy*

Although contemporary geopolitical boundaries can be useful proxies for cultural boundaries, there is often considerable cultural overlap between neighbouring geopolitical regions (i.e. neighbouring countries tend to be relatively similar along the individualism/collectivism dimension). According to our hypothesis, such spatial autocorrelation is expected given that

Table 1. Correlations between two measures of pathogen prevalence, and four measures of individualism/collectivism. ($^{*}p<0.001$; the number of geopolitical regions in each analysis is indicated in parentheses following each correlation coefficient.)

	pathogen prevalence index	
	historical	contemporary
individualism (Hofstede)	-0.69^{*} (68)	-0.59^{*} (68)
individualism (Suh)	-0.71^{*} (58)	-0.58^{*} (58)
collectivism (Gelfand)	0.73^{*} (52)	0.56^{*} (57)
collectivism (Kashima)	0.63^{*} (70)	0.44^{*} (70)

neighbouring regions typically have similar pathogen prevalence profiles. Still, given these strong spatial autocorrelations, it might be argued that country-level values are not statistically independent units of analysis. Therefore, in addition to our primary analyses that focused on countries as the units of analysis, we also conducted additional (more statistically conservative) analyses, in which we divided the world into a small number of more encompassing cultural regions and treated these distinct cultural regions as the units of analysis.

One set of additional analyses was informed by Murdock's (1949) designation of six world regions based on shared historical and geographical ranges. We computed mean values for pathogen prevalence and individual/collectivism within each of these six world regions (see electronic supplementary material for the classification of countries into world regions), and tested our hypothesis by computing correlations between these region-level composite values. Another set of additional analyses was informed by a more recent division of the world into cultural regions. Gupta & Hanges (2004) divided the GLOBE sample of countries into 10 distinct regional clusters based on 'the history of the societies under consideration as well as the religious, linguistic, and economic similarities' (p. 183). We computed mean values for pathogen prevalence and Gelfand *et al.*'s collectivism measure within each of these 10 culture clusters, and computed correlations between these composite values.

3. RESULTS

We predicted that pathogen prevalence would correlate negatively with measures of individualism and positively with measures of collectivism. Results testing that hypothesis are summarized in table 1.

Across both measures of pathogen prevalence, and all four measures of individualism/collectivism, the results are consistent with the hypothesis. Historical pathogen prevalence was an especially strong predictor of both individualism and collectivism (absolute magnitude of the r's ranged from 0.63 to 0.73; all p's <0.001; see figure 1 for one illustrative scatter plot). Contemporary pathogen prevalence showed the identical pattern of results, although the magnitude of the correlations was somewhat less strong.

The fact that cross-cultural variation in individualism/collectivism was predicted more strongly by the index assessing historical (rather than contemporary) pathogen prevalence is consistent with the expected causal relation between pathogen prevalence and cultural value systems. It also renders less plausible any reverse causal explanation.

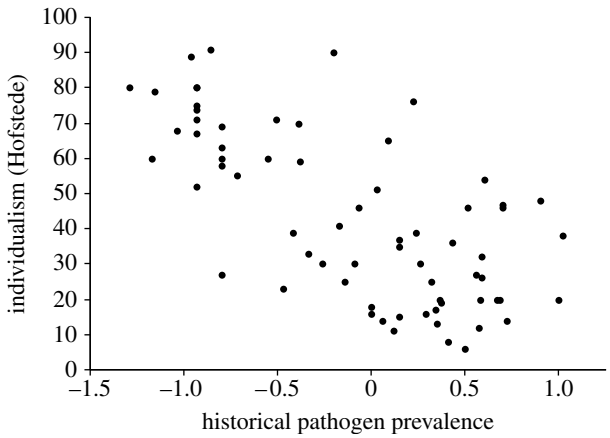

Figure 1. The correlation between historical pathogen prevalence and individualism (Hofstede 2001; $r=-0.69$, $p<0.001$, $n=68$).

To address additional alternative causal explanations, we assessed the relation between pathogen prevalence and individualism/collectivism while statistically controlling for other variables that consistently predicted individualism/collectivism. Of the four additional variables assessed (GDP *per capita*, Gini, population density and residual life expectancy), only GDP *per capita* and Gini were reliably correlated with individualism/collectivism. (Residual life expectancy correlated significantly with only one of the four individualism/collectivism measures, and population density failed to correlate significantly with any of the four measures. By contrast, GDP *per capita* and Gini were substantially and significantly correlated with all four individualism/collectivism measures, all p's <0.05.) Consequently, we conducted four multiple regression analyses, in which historical pathogen prevalence, GDP *per capita* and Gini were entered simultaneously as predictors of each individualism/collectivism measure. An identical pattern of results emerged across all four measures: there were no unique effects of Gini (all p's >0.05). By contrast, GDP *per capita* did exert unique predictive effects (all p's <0.05; greater wealth was associated with greater individualism and less collectivism). And, of primary interest, pathogen prevalence also uniquely predicted all four measures of individualism/collectivism (all p's <0.05). Thus, while other variables (like economic development) may also predict cultural value differences, these other variables cannot account for the predictive effects of pathogen prevalence.

The pattern of results reported above is replicated when broader cultural regions (rather than countries) are treated as the units of analysis. Regardless of whether the world is divided up according to Murdock's (1949) 6 world regions, or Gupta & Hanges' (2004) 10 cultural regions, composite scores on pathogen prevalence correlated negatively with composite scores on individualism, and positively with composite scores on collectivism. These correlations were strong in some cases. For example, when Murdock's six world regions were treated as the units of analysis, the correlation between historical pathogen prevalence and the Gelfand *et al.* collectivism measure was 0.93 ($p=0.004$, $n=6$); and when Gupta & Hanges' (2004) 10 cultural regions were treated as the units of analysis, the correlation was 0.80 ($p=0.003$, $n=10$).

4. DISCUSSION

Across multiple measures, we found that worldwide variation in pathogen prevalence substantially predicted societal tendencies towards individualism/collectivism. Within ecological regions characterized by higher prevalence of infectious diseases, human cultures are characterized by greater collectivism. The size of this effect was substantial and remained significant even when controlling statistically for potential confounding variables. The effect also remained strong when broader cultural regions (rather than individual countries or territories) were treated as the units of analysis.

These findings are consistent with the conjecture that, while individualism may confer certain kinds of benefits upon individuals and the societies they create, the behaviours that define individualism may also enhance the likelihood of pathogen transmission, and thus may be functionally maladaptive under conditions in which pathogens are highly prevalent. By contrast, the behaviours that define collectivism may function in the service of antipathogen defence, and thus be especially adaptive under conditions of high pathogen prevalence.

These results complement and substantially extend previous results linking regional variation in pathogen prevalence to the evolution of cross-cultural differences. Sherman & Billing (1999) suggested a link between pathogens and regional differences in cuisine. Several sets of research results have linked pathogen prevalence to cross-cultural differences in values and norms pertaining to mating and parenting behaviour (Low 1990; Gangestad & Buss 1993; Gangestad *et al*. 2006; Quinlan 2007). There is also recent evidence that worldwide variation in pathogen prevalence predicts cultural differences in personality traits, like extraversion (Schaller & Murray in press). Our results reveal that the predictive effects of pathogen prevalence are not limited to isolated cultural traits; indeed, the effects of pathogen prevalence are observed on a paradigmatic element of culture that, in the eyes of many social scientists, is fundamental to any understanding of cross-cultural differences (Triandis 1995; Heine 2008).

These findings also help to explain additional variables that are correlated with individualism/collectivism. A correlation between individualism/collectivism and latitude has frequently been noted, but never fully explained (Cohen 2001; Hofstede 2001; Kashima & Kashima 2003). Our results imply that this correlation is substantially, albeit not completely, accounted for by pathogen prevalence: the meteorological and ecological conditions associated with lower latitudes provide the ideal circumstances for the proliferation of pathogens (Guernier *et al*. 2004), which in turn constrain cultural values towards collectivism. Similarly, there is a correlation between individualism and mean levels of extraversion, which has led to some speculation about the possible causal relations between cultural values and personality traits (Hofstede & McCrae 2004). Our results, in conjunction with those reported by Schaller & Murray (in press), suggest that the correlation between individualism and extraversion is largely spurious, resulting from the fact that both individualism and extraversion are strongly predicted by pathogen prevalence.

Many researchers have observed a strong positive correlation between economic affluence (i.e. GDP *per capita*) and individualism and have articulated specific psychological and societal mechanisms through which affluence might lead to individualism (Triandis 1995; Hofstede 2001). Our results suggest that the sizeable correlation between affluence and individualism results in part from shared variance with pathogen prevalence. Even the apparently unique effect of GDP *per capita* may indirectly reflect some causal role of pathogens, given that infectious diseases are powerful inhibitors of economic development (Sachs & Malaney 2002). Thus, the extant literature on individualism/collectivism may overestimate economic influences, while underestimating the causal influence of pathogens.

It follows from our analysis that pathogen prevalence may also predict additional cross-cultural differences that are yet to be investigated. If the effects on individualism/collectivism result in part from the antipathogenic consequences of conformity, then explicit behavioural indicators of conformity may be predicted by pathogen prevalence. Pathogen prevalence may also explain cultural differences in ideological tendencies, such as authoritarianism and political conservatism (e.g. Thornhill & Fincher 2007). And it may predict cross-cultural differences in practices pertaining to learning and education: where pathogens are prevalent, cultures are likely to encourage modes of learning that emphasize imitation and emulation of prestigious in-group members (whereas in less pathogenic environments, there may be greater encouragement for individual experimentation and trial-and-error learning). Pathogen prevalence may also predict cross-cultural variation in other characteristically collectivistic behaviours, such as extended nepotism and in-group care more generally. Existing cross-cultural analyses provide limited evidence consistent with some of these hypotheses (e.g. Bond & Smith 1996; Georgas *et al*. 2001), but rigorous empirical tests have yet to be conducted.

It will also be important for future research to determine the mechanism(s) through which regional variability in pathogen prevalence produces cultural variability along the individualism/collectivism dimension. At least three different kinds of mechanisms can be envisaged; they are not mutually exclusive and may coexist. One is that of cultural transmission. Among humans, culturally specific cognitive and behavioural tendencies can emerge over time as a consequence of local ecological pressures on the information that individuals learn from and teach each other (Richerson & Boyd 2005). For instance, in regions characterized by high pathogen prevalence, individuals may make deliberate efforts to encourage others to adopt collectivistic (rather than individualistic) behavioural tendencies. Regional differences in individualism/collectivism might also have emerged through locally adaptive allelic differences. As with many other attitudes and behavioural dispositions, individual tendencies towards individualism or collectivism are likely to be substantially heritable (Bouchard & McGue 2003). It is possible that in regions characterized by a high level of pathogen prevalence, there has been a selection process favouring alleles probabilistically associated with collectivism (whereas alleles associated with individualism may be relatively favoured in regions with low prevalence of pathogens). We suspect that a different kind of genetic adaptation might also be at work. Because individual tendencies towards either individualism or collectivism may confer either fitness costs or benefits, depending on ecological circumstances, some of the genetic and associated

developmental substrates for these tendencies may be characterized by a species-typical, evolved sensitivity to informational inputs from the immediate environment—including input indicating the prevalence of pathogens.

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