CHAPTER 3

# Infectious Disease and the Creation of Culture

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## I. INTRODUCTION

The study of cultural psychology is a massive scientific enterprise. Cultural psychology is defined by two conceptually distinct bodies of scientific research, each of which explores a different set of causal connections between psychology and culture.

One body of research examines the influence of psychology on culture. That is, it addresses questions about exactly how psychological processes (defined at an individual level of analysis) exert causal consequences on cultural outcomes (measured at a collective level of analysis). There are many different investigations that, in one way or another, fit into this broad program of research. In doing so, they provide many different insights into the effects of individual-level psychological processes on the rituals and norms and collective beliefs that define cultures in the first place (e.g., Conway & Schaller, 2007; Heath, Bell, & Sternberg, 2001; Latané, 1996; for an overview, see Schaller & Crandall, 2004). Of course, when people think about "cultural psychology," this is not typically the first body of research that comes to mind.

Rather, for most people, the concept of "cultural psychology" conjures up a rather different body of research, in which the arrow of causality reverses and the research questions pertain to the influence of culture on psychology. The results of these investigations describe the myriad ways in which

individuals' cultural backgrounds influence the specific ways in which they perceive, think about, and respond to the world around them. The vast majority of empirical research in cultural psychology is this particular kind of cultural psychology: the study of cross-cultural differences. Indeed, for many people the phrase "cultural psychology" probably equates immediately to "cross-cultural psychology."

Research on cross-cultural differences typically begins with the recognition that cultures differ in many profound ways—some human populations are characterized by norms, values, and belief systems that are demonstrably different from the norms, values, and belief systems that define other human populations. For instance, it is recognized that some geographically defined populations (East Asians, for example, or aboriginal Native Americans) have relatively collectivistic ideologies, whereas other populations (Northern Europeans and the descendants of European immigrants to the Americas) tend to have more individualistic ideologies. Based on the assumption of cultural difference, specific empirical investigations proceed to examine specific ways in which those cultural differences manifest in the perceptions, thoughts, emotions, and actions of individuals. Thus, we witness flourishing literatures documenting specific ways in which East Asians and Euro-Americans differ in visual perception, logical reasoning, self-concept, and many other fundamental aspects of psychological functioning (Heine, Lehman, Markus, & Kitayama, 1999; Lehman, Chiu, & Schaller, 2004; Masuda & Nisbett, 2006; Nisbett, Peng, Choi, & Norenzayan, 2001). Of course, the study of cross-cultural differences in psychology is hardly limited to this one prototypical comparison between East Asians and Euro-Americans. There now exists a burgeoning psychological database documenting—across many small-scale societies as well as dozens and dozens of countries worldwide—substantial cross-cultural differences in all kinds of fundamental kinds of psychological phenomena, including behavioral decision making (Henrich et al., 2005), interpersonal attachment (Schmidt et al., 2004), sexual attitudes and behavior (Schmidt, 2005), personality traits (McCrae, Terracciano, & Members of the Personality Profiles of Cultures Project, 2005), and, of course, the sorts of attitudes, ideologies, and values implied by the individualism/collectivism distinction (Gelfand, Bhawuk, Nishii, & Bechtold, 2004).

However, despite this immense body of research on cross-cultural differences, a fundamental question of long-standing interest (e.g., Berry, 1979) remains largely unanswered: Exactly *why* do these cross-cultural differences exist in the first place?

In this chapter, we provide an overview of a program of research that identifies one possible answer to that question: Many contemporary cross-cultural differences may result from the fact that, historically, people living under ecological circumstances have been differentially vulnerable to the threat posed by infectious diseases. We begin with a very brief overview of previous work on the origins of cultural differences, emphasizing especially the ecological and evolutionary perspectives from which this particular research program has emerged. We then summarize the conceptual basis for predicting causal relations between *(a)* the prevalence of disease-causing pathogens in the local ecology and *(b)* cultural outcomes pertaining to dispositions, values, and behavior. This conceptual framework has provided the foundation for many hypotheses linking pathogen prevalence to specific kinds of cultural differences, including differences in social attitudes, personality traits (e.g., extraversion, openness to experience), value systems (e.g., individualism versus collectivism), and political ideologies. We summarize these hypotheses and review recent empirical evidence that tests (and supports) the hypotheses. Finally, we discuss additional research questions that are raised by these results, including important questions about the exact causal mechanisms through which the differential prevalence of infectious diseases might create cross-cultural differences.

## A. Origins of Cross-Cultural Differences

There are many specific features that define any particular culture—its language and literature and religious practices, its arts and crafts, its folklore, its cuisine, and the countless numbers of popular beliefs, attitudes, expectations, and behavioral tendencies that distinguish its people from those in other cultures. Many of these diverse defining features may be attributable to quirky causes—ecological features unique to the local geography, singular events specific to the history of the local people, and a variety of other things that are idiosyncratic to a particular population and the particular place that they populate. These idiosyncratic causes may be revealed by intensive ethnographies or cultural histories, but they do not lend themselves to the systematic, quantitative, and comparative methods employed by psychological scientists. Any rigorous psychological inquiry into the origins of cross-cultural differences must rest upon the assumption (or hope, perhaps) that lurking within the noise of idiosyncratic cultural causes is some systematic signal of a causal process that applies widely across the entire human landscape.

Psychological inquiry into the origins of existing cross-cultural differences is also constrained by substantial methodological and inferential limitations. First of all, this kind of research is correlational. This is not to say that experimental methods are entirely off the menu. Experimental methods can certainly be used to test hypotheses, at an individual level of analysis, that bear *indirectly* on the roots of cultural differences. Illustrative examples include experiments showing that manipulations of perceptual context activate specific cultural identities (Hong, Morris, Chiu, & Benet-Martinez, 2000), and experiments showing that manipulations of social ecological circumstances can produce temporary psychological responses that mimic those of existing cultural differences (Chen, Chiu, & Chan, 2009). But any inquiry into the origins of already-existing cross-cultural differences is necessarily correlational (no one is randomly assigned to be, say, East Asian.) Moreover, existing cultural differences are rarely of recent origin. Consequently, it is difficult to unambiguously measure a presumed causal variable that temporally precedes the cross-cultural difference itself. Therefore, even if one finds a strong correlation between a presumed causal variable and an existing cross-cultural difference, it is difficult to rule out alternative explanations based on reverse causal processes, or on the presumed existence of correlated third variables. Plus, of course, when we talk about causal processes through which cross-cultural differences might arise, we are talking about processes that presumably played out across a substantial chunk of historical time—the kind of longitudinal time scale that cannot be tracked with any typical psychological methodology.

Line 13: transpose period and parenthesis.

So, while questions about the origins of cross-cultural differences in psychological functioning are of fundamental interest and importance, these questions are also perhaps fundamentally unanswerable. Or, at least, they cannot be answered with the degree of methodological rigor and inferential confidence to which psychological scientists (and other empirically minded scholars) typically aspire.

These constraints have not stopped scientists from speculating. Over the years, many types of explanations have been offered to explain the origins of contemporary cross-cultural differences. Some of these explanations may ultimately prove to be right. Of course, while they are typically compelling on logical grounds, given the substantial methodological problems that must be overcome to put them to empirical test, these hypotheses are typically buttressed by only modest smatterings of actual empirical results.

## *1. Migration-Based Perspectives*

Across several different scholarly contexts, one can encounter suggestions that specific cross-cultural differences may be the result of specific human migrations. Within the economics literature, for example, it has been argued that contemporary regional differences in wealth and sociopolitical values associated with wealth (e.g., individual rights, democracy) have their roots in specific patterns of European migration and colonization over the past several hundred years (Acemoglu, Johnson, & Robinson, 2001).

A rather different—and more psychological—migration-based perspective has been offered by Kitayama and his colleagues to help explain geographical variation in individualistic versus collectivistic value systems (Kitayama & Bowman, 2010; Kitayama, Ishii, Imada, Takemura, & Ramaswary, 2006). They suggest that, compared to other people, individuals who choose voluntarily to migrate from their homeland to settle frontier regions are more likely to be characterized by independence of thought and nonconformist behavioral tendencies. Consequently, the cultures that emerge within frontier populations are also more likely to be characterized by individualistic (rather than collectivistic) values and ideologies. Consistent with this "voluntary settlement" hypothesis is evidence that, within one prototypically individualistic nation (the United States), especially high levels of individualism are observed in western regions that historically comprised the North American frontier (Vandello & Cohen, 1999). Similarly, within one prototypically collectivistic nation (Japan), the area that historically comprised the frontier (the northern province of Hokkaido) is characterized by a relatively "un-Japanese" tendency toward individualism in both thought and behavior (Kitayama et al., 2006).

A third migration-based perspective focuses not on human culture, nor even on human psychology, per se, but instead on genetic information that has been linked to human psychological outcomes. There is a particular variant of the DRD4 dopamine receptor gene that has been found, in some studies, to be predictive of novelty seeking (Bailey, Breidenthal, Jorgensen, McCracken, & Fairbanks, 2007; Schinka, Letsch, & Crawford, 2002). Intriguingly, the frequency of this DRD4 allele varies across different aboriginal populations in North and South America. The frequency is relatively low among populations living relatively close to the place (the now-submerged Bering land bridge) where humans first migrated out of Asia and into North America over 12,000 years ago, and the frequency is higher in places that represent further reaches of that migration, with the highest frequencies of all

found among populations in the southernmost regions of South America (Chen, Burton, Greenberg, & Dmitrieva, 1999).

## 2. Ecological Perspectives

Another broad category of conceptual perspectives on the origins of cultural differences focuses on ecological diversity (Nettle, 2009). The basic idea is straightforward: Just as specific features of the natural and/or social ecology may incline people inhabiting those ecologies to engage in particular types of habitual behaviors (e.g., people populating coastlines will be especially likely to build boats and to cook fish; people populating deserts will not), specific features of the ecology may also incline people toward particular ways of perceiving, thinking, and interacting—and these differences may manifest in the behavioral norms, expectations, and value systems that define a culture (Berry, 1979; Cohen, 2001). Different ecological perspectives have focused on different kinds of ecological circumstances. Some work focuses on physical elements of the local ecology, such as ambient temperature and other variables pertaining to climate (e.g., Tavassoli, 2009; Van de Vliert, 2009). Other work emphasizes specific aspects of the local social ecology, such as the relative ease of residential and/or vocational mobility (e.g., Chen et al., 2009; Oishi, Lun, & Sherman, 2007).

A classic example is evidence that the perceptual susceptibility to the well-known Müller-Lyer optical illusion varies cross-culturally and may do so in part because of differences in the geometric properties of local architecture (Segall, Campbell, & Herskovits, 1963). Another well-known example links a specific set of social economic variables to the emergence of contemporary cultural differences in norms pertaining to honor and male violence (Cohen, Nisbett, Bowdle, & Schwarz, 1996; Nisbett & Cohen, 1996; see also Daly & Wilson, 2010). A third illustrative example focuses on ecological niches that constrain particular kinds of economic and social systems, and it suggests that these ecological differences may have contributed to the emergence of well-documented cultural differences in holistic perception and thought (Nisbett et al., 2001; Norenzayan, Choi, & Peng, 2007). This speculation is supported by evidence showing that, compared to herders, farmers and fishermen show a greater natural tendency toward holistic perception and thought (Uskul, Kitayama, & Nisbett, 2008).

More broadly, ecological variables have been conceptually linked to the potential for cultural variability of any kind. It has been suggested, for instance, that cultural diversity is especially likely to persist under conditions in which

the ranges of cultural groups are geographically constrained, and that the size of these ranges is influenced by ecological variables pertaining to seasonality and temporal variation in food supply. This hypothesis is supported by evidence linking the mean length of the growing season within a region to that region's linguistic variability (Nettle, 1996, 1998).

### *3. Evolutionary Perspectives*

Within the broad category of ecological approaches to cross-cultural variability, a subset of research has been informed by a conceptual approach that draws on the tools of evolutionary psychology (e.g., Gangestad, Haselton, & Buss, 2006; Nettle, 2009; Schmitt, 2005; Tooby & Cosmides, 1992). The program of research that we describe in detail later in this chapter fits within this evolutionary framework. The broad assumptions underlying this conceptual approach are explained next.

A culture is defined, in part, by the behavioral tendencies of the people who populate that culture. Those behavioral tendencies (and the psychological processes that produce them) are, to some extent, the product of evolutionary processes. Behavioral tendencies that inhibited reproductive fitness within ancestral ecologies would, over time, have become less prevalent within the population, whereas behavioral tendencies that promoted reproductive fitness within those ecologies would have become more prevalent. The consequence is that cross-cultural differences may emerge for any particular behavioral tendency (and the psychological processes that produce it) simply because that particular behavioral tendency has somewhat different implications for reproductive fitness under somewhat different ecological circumstances.

It is within this general framework that researchers with backgrounds in both the biological and psychological sciences have deduced, and empirically supported, hypotheses suggesting that that different kinds of cross-cultural differences (ranging from differences in food preparation and sexual behavior to differences in personality traits and value systems) may result from the fact that, in some places more than others, there has existed a greater prevalence of pathogens that cause debilitating infectious diseases.

## B. The Evolutionary and Psychological Power of Pathogens

There are hundreds of different human infectious diseases, caused by hundreds of different pathogens. Some of these infectious diseases (e.g., human immunodeficiency virus [HIV]) have found their way into human populations

only relatively recently, whereas other infectious diseases (e.g., malaria, tuberculosis, and many others) are of considerable antiquity (Ewald, 1993; Wolfe, Dunavan, & Diamond, 2007). Research on the antiquity of disease compels the inescapable conclusion that disease-causing pathogens have posed a threat to human (and prehuman) welfare and reproductive fitness throughout much of human evolutionary history.

Because pathogens have posed such a powerful threat to reproductive fitness, they have imposed an enormous force in guiding human evolution (McNeill, 1976; Ridley, 1993; Zuk, 2007). For instance, biologists have theorized that sexual reproduction itself emerged as an adaptation to the threat of disease, due to the disease-buffering benefits offered by the genetic and phenotypic diversity that is more readily promoted by sexual rather than asexual reproduction (Hamilton & Zuk, 1982; Zuk, 1992). The evolutionary power of pathogens is indicated also by the presence in humans (and across virtually all other species too) of anti-pathogen defense mechanisms that help to mitigate the threats posed by the presence of pathogens.

The most obvious form of anti-pathogen defense is the immune system. The immune system is comprised of a highly sophisticated set of mechanisms that are able to identify, and subsequently form a counterattack against, parasitic intruders within the body. This system, however, is far from perfect. Its detection mechanisms are prone to be outfoxed by pathogenic species that, because of their relatively short life cycle, evolve much faster than mammalian hosts (Ridley, 1993). In addition, for many pathogenic infections, activation of an immune response is initiated only after specific cells have detected its specific antagonist, by which time the invading pathogens may have already begun to cause considerable damage. Further, despite the benefits of defense against potentially deadly pathogens, the activation of an immune response is not without costs as well. It can be metabolically taxing to mount an immune response, robbing individuals of caloric resources that might otherwise be devoted to other fitness-promoting tasks such as caring for one's kin (Brown, 2003; Klein & Nelson, 1999). Specific features of an immune response, such as fever, may be even further debilitating. The logical upshot is that people (and other animals) benefit from the existence of their immune systems, but they are still better off when that immune system is engaged as infrequently as possible.

It follows logically that there would be additional adaptive benefits associated with a very different kind of anti-pathogen defense system—a system designed to promote behavioral avoidance of contact with pathogens

in the first place. Consistent with this evolutionary speculation is evidence of anti-pathogen behavioral defense observed across the animal kingdom. Chimpanzees react aversively, and sometimes violently, to other chimpanzees infected with polio (Goodall, 1986). Rodents avoid mating with other rodents who produce olfactory cues connoting disease (Kavaliers & Colwell, 1995). Bullfrog tadpoles selectively avoid swimming in the vicinity of other tadpoles suffering from bacterial infections (Kiesecker, Skelly, Beard, & Preisser, 1999). Even whitefish *eggs* respond to waterborne cues of a virulent egg parasite from other infected eggs by hatching earlier than usual (Wedekind, 2002).

Humans too are characterized by a suite of mechanisms that serve to provide a first line of behavioral defense against pathogens—a sort of "behavioral immune system" (Schaller, 2006; Schaller & Duncan, 2007). These mechanisms are designed to detect the presence of infectious pathogens in the immediate environment, to trigger specific kinds of affective and cognitive responses, and to promote motor responses that facilitate avoidance of pathogen transmission. There is now a considerable body of evidence bearing on these mechanisms and their psychological implications, including implications for emotion (Oaten, Stevenson, & Case, 2009), person perception (Ackerman et al., 2009), interpersonal prejudice (Faulkner, Schaller, Park, & Duncan, 2004; Navarrete, Fessler, & Eng, 2007; Park, Faulkner, & Schaller, 2003, Park, Schaller, & Crandall, 2007), and interpersonal social contact in general (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010).

### *1. Flexibility and Context Contingency*

One of the important general conclusions to emerge from this body of research is this: Not only are there a wide variety of everyday psychological responses that can have the functional consequence of inhibiting pathogen transmission, but these particular psychological responses are especially likely to be produced under conditions in which individuals perceive themselves to be especially vulnerable to pathogen transmission. For instance, it is postulated that the avoidance of pathogens is facilitated by aversive reactions to individuals characterized by gross morphological anomalies. Consistent with this conjecture, morphologically anomalous individuals are not only implicitly associated with disease-connoting semantic concepts, but these implicit associations tend to occur more strongly among perceivers who feel especially vulnerable to the potential transmission of infectious diseases (Park et al., 2003, 2007). Similarly, it is postulated that the avoidance of pathogens is facilitated

by an avoidance of social interaction more generally. Consistent with this conjecture is recent research showing that when people feel more vulnerable to disease transmission, they report lower levels of extraversion and produce more socially avoidant motor responses (Mortensen et al., 2010).

The implication is that the behavioral immune system evolved not only to have the capacity to produce responses that inhibit contact with pathogens, but that it evolved in a way such that it produces these responses in a functionally flexible and context-contingent manner. These responses are especially likely to be produced under conditions in which people are (or merely perceive themselves to be) vulnerable to pathogen infections. They are less likely to be produced under conditions in which people are less vulnerable.

This implication—the context contingency of pathogen-relevant psychological responses—may play out not only at an individual level of analysis but also at a cultural level of analysis. In making this logical transition to a cultural (rather than individual) level of analysis, we must consider the fact that, just as there is variability in the perceptual contexts that influence individuals' cognitions and behaviors, so too there is variability in the ecological contexts that are home to entire human populations.

## *2. Ecological Variability in the Threat Posed by Pathogens*

Pathogens—and the infectious diseases that they cause—may have been ubiquitous throughout human history, but that does not mean that they pose an equal threat to all people worldwide. Rather, there is considerable geographical and ecological variability in the distribution of human infectious diseases and in the burden they place on human welfare.

Many pathogens depend on warm, wet environments for survival and reproduction. Therefore, the prevalence of pathogens depends fundamentally on geographical and climatological variables (temperature, humidity, rainfall, etc.). Compared to cooler and drier climates, for instance, there is greater diversity and density of infectious pathogens in the tropics. More generally, the prevalence of pathogens is an inverse function of absolute distance from the equator (Guernier, Hochberg, & Guégan, 2004). Indeed, given the high correlation between absolute latitude and pathogen prevalence, and the precision with which absolute latitude can be measured, it could serve as a reasonable proxy for the prevalence of pathogens in a particular location.

This unequal distribution of pathogens has profound implications for predicting regional differences between human populations—differences

not just in overt health outcomes but in psychological and behavioral outcomes as well.

## II. PATHOGEN PREVALENCE AND THE PREDICTION OF CROSS-CULTURAL DIFFERENCES

The basic logical template is as follows: To the extent that a particular behavioral tendency increases the likelihood of pathogen transmission, that behavioral tendency has negative implications for reproductive fitness. Those fitness costs are likely to be greater within ecologies characterized by higher levels of pathogen prevalence. Therefore, all else being equal, to the extent that a particular behavioral tendency *increases* the likelihood of pathogen transmission, that particular behavioral tendency (and psychological characteristics associated with it) is expected to be *less* characteristic of human populations in geographical regions with historically higher levels of pathogen prevalence. Similarly, to the extent that a particular behavioral tendency *decreases* the likelihood of pathogen transmission, that particular behavioral tendency (and psychological characteristics associated with it) is expected to be *more* characteristic of human populations in regions with historically higher levels of pathogen prevalence. Therefore, any psychological or cultural characteristic that has consequences for pathogen transmission is likely to be predictably variable across human populations, as a function of pathogen prevalence within the local geographical region.

At this point, some readers might object and observe that, despite the fact that infectious diseases are relatively more prevalent in some places compared to others, infectious diseases have posed some threat everywhere. And so, therefore, one might argue that behaviors facilitating pathogen transmission should be inhibited within every culture, whereas behaviors inhibiting pathogen transmission should be celebrated and encouraged within every culture. This argument may seem sensible on the surface, but it ignores a very important point: Many behavioral tendencies that facilitate pathogen transmission (and so are costly in that one specific way) may actually be beneficial in other ways. These benefits may outweigh the relatively modest costs that occur in low-pathogen environments. But, as pathogen prevalence increases (along with the baseline likelihood of pathogen transmission), the costs are more likely to increase to the point that they outweigh the benefits. Similarly, behavioral tendencies that inhibit pathogen transmission (and so provide functional

benefits of this very specific kind) may impose costs of other kinds. These costs may outweigh the modest benefits that are likely to emerge in environments with a low baseline level of pathogen transmission. But, as pathogen prevalence increases, the benefits are more likely to increase to the point that they outweigh the costs.

## A. An Illustrative Example: Use of Spices in Food Preparation

The use of culinary spices offers a good example. Spices have natural disease-buffering properties; most culinary spices (such as garlic, onion, and rosemary) inhibit or kill foodborne bacteria (Billing & Sherman, 1998). Thus, the use of spices in food preparation is functionally beneficial specifically because of these antibiotic consequences. However, the use of spices can be costly as well. For instance, spices typically offer little nutritive value, and the resources (e.g., arable land) consumed in the cultivation or procurement of spices could presumably be used to cultivate or procure more nutritionally valuable foodstuffs. These costs are likely to outweigh the anti-pathogenic benefits of spice use under ecological circumstances in which there is a relatively low prevalence of foodborne bacterial diseases. But, under ecological circumstances characterized by a high prevalence of food-borne bacterial diseases, the anti-pathogenic benefits of spice use will be considerably greater, and are more likely to outweigh the costs. The logical upshot is a hypothesis specifying a relationship between pathogen prevalence and the use of culinary spices: The use of spices in food preparation should be a positive function of the prevalence of pathogens within the local ecology.

This hypothesis was tested by Sherman and Billing (1999). Sherman and Billing analyzed the contents of over 4500 meat-based recipes from traditional cookbooks in dozens of countries around the world. For each country, they computed mean annual temperature as a proxy measure indicating the threat posed by foodborne bacterial infections. The results were clear: In hotter, more tropical geographical regions, people traditionally employ a greater number of culinary spices. The same effect was also observed in analyses that examined regional differences within geographically vast countries such as the United States and China. Compared to cooler regions in northern China, for example, one finds spicier Chinese food in the hotter, more tropical regions of southern China.

Of course, a measure of temperature is just a measure of temperature. Does the same effect hold if one employs a more direct measure of pathogen prevalence? Yes. We reanalyzed these data using a country-level index of

pathogen prevalence derived from old epidemiological data (we describe this pathogen prevalence index in more detail later). The results revealed that, compared to the correlation between temperature and spice use (reported by Sherman & Billing, 1999), the correlation between pathogen prevalence and spice use is, if anything, even stronger ($r$ = .58; Murray & Schaller, 2010).

## B. Another Illustrative Example: Mate Preferences

A more prototypically psychological illustration of this research strategy is offered by inquiry into the relation between pathogen prevalence and cross-cultural differences in mate preferences—specifically preferences for mates who are physically attractive. Physical attractiveness is universally prized, of course, but there are cross-cultural differences in the extent to which physical attractiveness is valued relative to other desirable traits (Buss, 1989). Why might this preference for physical attractiveness vary as a function of pathogen prevalence? The argument proceeds from two bodies of evidence. First, subjective appraisals of physical attractiveness are influenced by objective psychophysical characteristics such as feature prototypicality and bilateral facial symmetry (Rhodes, 2006; Thornhill & Gangestad, 1999). Second, these objective features, as well as subjective appraisals of attractiveness, appear to be somewhat useful indicators of an individual's health status, as well as their immunological functioning in general (Møller, 1996; Thornhill & Møller, 1997; Weeden & Sabini, 2005). The upshot is that another person's level of physical attractiveness may provide useful inferential information about the extent to which that person is *(a)* currently free from pathogenic infections, *(b)* likely to successfully fend off pathogen infections in the future, and *(c)* likely to produce offspring with the ability to fend off pathogen infections. A disease-free mate is beneficial to one's own reproductive fitness; and so, by implication, it is also reproductively beneficial to prefer mates who are physically attractive.

Of course, mate selection almost always involves trade-offs. To the extent that one places a high value on the physical attractiveness of a mate, one may place a relatively lower value on other traits (such as wealth, intelligence, or agreeableness) that are also desirable and functionally beneficial in a mate. Given these inevitable trade-offs, the underlying evolutionary logic implies that that individuals are most likely to place a high value on physical attractiveness under conditions in which the benefits signaled by attractiveness (good health and a strong immune system) are most especially beneficial: under conditions in which the threat from pathogens is especially high.

This leads directly to the hypothesis that pathogen prevalence within a region should predict the value placed on a mate's physical attractiveness.

And, in fact, it does. In a data set that included responses from 29 different countries, Gangestad and Buss (1993; see also Gangestad et al., 2006) found that the historical prevalence of pathogens within a country was positively correlated with the contemporary value that people within that country place on their mate's physical attractiveness. This effect occurred among both men and women and held when controlling for a variety of additional social and economic variables that also influence mate preferences.

## C. Important Methodological and Inferential Issues

These examples illustrate not only the basic conceptual logic that links pathogen prevalence to the origin of cross-cultural differences, but they also illustrate some of the nontrivial methodological and inferential issues that must be addressed in pursuing this line of inquiry. We quickly summarize some of these issues here, so that readers might bear them in mind when evaluating the body of research evidence that we review later.

One issue arises from the use of contemporary geopolitical entities (e.g., countries) as units of analysis in research on cross-cultural differences. Almost no one would claim that country is synonymous with culture, and some scholars (e.g., many ethnographers and other cultural anthropologists) might strenuously object to the use of a country as a proxy for a culture. After all, many countries (especially those that are geographically vast and/or ethnically varied, such as China, India, Russia, and the United States) are home to multiple distinct cultures. These within-country cultural differences are possibly more profound than many differences between countries. But there are certain methodological advantages associated with the use of geopolitical entities as units of analysis. Political borders offer both a convenient and a geographically objective means of dividing up the worldwide human population into culture-like categories. Because of this, many important forms of worldwide cultural variability have been and continue to be categorized according to these geopolitical boundaries, such as documentation of worldwide differences in personality traits and cultural values. If one is to conduct empirical inquiries into the origins of these particular differences, one must employ the same unit of analysis. And, even if geopolitical borders are not truly identical to cultural boundaries, extensive empirical evidence suggests that they can still serve as useful proxies for cultural boundaries (e.g., Schwartz, 2004).

The use of countries as stand-ins for cultures also introduces a statistical issue: nonindependence of the units of analysis. Peoples move and migrate through geographical space, and aspects of their culture move with them. The closer that any two countries are in geographical space, the more likely those two countries are to have cultural elements in common, simply as a result of historical migrations and cultural borrowing. For highly focused forms of cross-cultural comparison (e.g., the prototypical study in which responses from a western European sample are compared to responses from an east Asian sample), this statistical nonindependence is a nonissue. But in the kinds of inquiries of the sort described here (exemplified by Sherman & Billing, 1999, and Gangestad & Buss, 1993), in which countries themselves are the units of analysis, one cannot easily ignore this statistical independence (which is sometimes referred to as autocorrelation or "Galton's problem"). Scholars in other disciplines that are accustomed to treating cultures and/or countries as units of analysis (e.g., anthropology, economics, political science) are highly sensitive to this issue, and they have developed a variety of statistically sophisticated strategies for dealing with it (e.g., Dow, 2007; Ross & Homer, 1976). At the very least, it can be inferentially informative to supplement analyses that treat countries as units of analysis with additional analyses that combine country-level data into a smaller set of geographical categories that correspond to regions of the world that have historically been culturally distinct (e.g., Eastern Eurasia, Western Eurasia, Africa, etc.; see Gupta & Hanges, 2004; Murdock, 1949).

Regardless of the units of analysis, this kind of inquiry is strictly correlational. From a positivist Popperian perspective, this poses no problem: A simple zero-order correlation is sufficient to empirically test (i.e., to potentially falsify) a conceptual hypothesis specifying the effect of pathogen prevalence on some specific kind of cross-cultural variability. But we typically aim a little higher than that, inferentially, and simple zero-order correlations are not completely compelling on their own. We must consider alternative explanations and control for additional variables that may produce entirely spurious correlations. For instance, in the case of culinary spicing, one must address the possibility that more culinary spices are used in tropical countries simply because more species of spices can be successfully cultivated in those countries (in fact, Sherman & Billing, 1999, do report data that addresses this alternative explanation). More broadly, within any particular investigation, one must consider a variety of alternative processes—which may have nothing to do with infectious diseases whatsoever—that might lead to the same

cross-cultural differences, and one must ascertain whether variables bearing on those processes might covary with pathogen prevalence. If they do, they must be statistically controlled when testing whether pathogen prevalence actually predicts the cross-cultural difference of interest. Compelling support for any hypothesis about the effects of pathogen prevalence emerges only when pathogen prevalence uniquely predicts cross-cultural outcomes even when controlling for these additional variables.

These hypotheses about pathogen prevalence are clearly causal. But, of course, observation of correlation does not imply a particular direction of causality—at least not all by itself. Temporal precedence is therefore an important inferential ally in correlational studies. To infer that pathogen prevalence exerts a causal influence on culture (and not the reverse), it helps to obtain a measure of pathogen prevalence at a period of time substantially prior to the measure of the cultural outcome variable. Gangestad and Buss (1993) did exactly this. They employed old epidemiological atlases (documenting disease prevalence information from decades ago) to create a composite index of historical pathogen prevalence for the 29 countries included in their analyses. To further gain traction on this tricky inferential issue, it can be informative to also compute a measure of contemporary pathogen prevalence in exactly the same countries. If pathogen prevalence is a consequence (rather than a cause) of some cross-cultural difference, then the correlation with the contemporary pathogen prevalence measure would be expected to be greater than that with the historical pathogen prevalence measure. If not—if the historical measure predicts cross-cultural outcomes more strongly than the contemporary measure does—it lends credence to the argument that pathogen prevalence is the cause, rather than a consequence, of the cross-cultural difference.

## D. Quantitative Indices of Pathogen Prevalence

How does one measure the historical prevalence of pathogens within a country? In our research, we employed a methodological strategy adapted from Gangestad and Buss (1993), who followed an approach used earlier by Low (1990) who focused not on countries, but on small-scale societies that are part of the Standard Cross-Cultural Sample employed in much comparative ethnographic research (Murdock &White, 1969, 2006). Low (1990) used old epidemiological atlases to estimate the prevalence of a handful of prototypical human infectious diseases within each small-scale population and combined these estimates into a single index indicating pathogen prevalence. This index

has been proven to predict several cross-cultural differences observed in the ethnographic record, such as societal norms pertaining to marriage structures and parenting practices (Low, 1990; Quinlan, 2007). Similarly, in their study of mate preferences across 29 countries, Gangestad and Buss (1993) used old epidemiological atlases to estimate the country-level prevalence of seven specific kinds of prototypical pathogenic diseases. An overall index comprised by these prevalence estimates successfully predicts cross-cultural differences in the value accorded to physical attractiveness, as we described earlier, and differences in several additional kinds of mate preferences as well (Gangestad et al., 2006).

We extended this approach to cover a more complete set of 230 geopolitical regions worldwide (Murray & Schaller, 2010). Most of these regions are nations (e.g., Angola), whereas others are territories or protectorates (e.g., New Caledonia) or culturally distinct regions within a nation (e.g., Hong Kong). For the sake of expository ease, we use the word "country" to refer to all these regions. The nine diseases coded were leishmania, schistsoma, trypanosoma, leprosy, malaria, typhus, filaria, dengue, and tuberculosis. With one exception (tuberculosis), the prevalence of each disease was informed by epidemiological atlases and additional epidemiological information compiled in either the late nineteenth or early twentieth centuries. For the majority of countries (N = 160), prevalence data on all nine diseases were available, allowing the computation of a standardized nine-item index of historical pathogen prevalence. For all 230 countries, a standardized index of historical pathogen prevalence was computed based on data from either six or seven infectious diseases.

Line 16: insert the letter "o": it should be: "schistosoma"

Given that that pathogenic diseases are generally more prevalent in the tropics (Epstein, 1999; Guernier et al., 2004), it is no surprise that the nine individual disease prevalence ratings were all positively correlated, and the composite indices have good internal reliability (e.g., for the nine-item index, Cronbach's alpha = .84). Additional results reported by Murray and Schaller, 2010) attest to the index's construct validity. (For example, this index correlates strongly with other indices of pathogen prevalence computed on more limited samples, and it correlates strongly with other variables—such as absolute latitude—that have previously been shown to predict both prevalence and diversity of infectious diseases.) Thus, although this numerical index is inevitably crude (given the nature of the source materials), it does appear to offer a reasonably valid and reliable indicator of the historical prevalence of pathogens within any particular contemporary country.

Historical pathogen prevalence scores for each of the 230 countries worldwide are summarized in an Appendix presented by Murray and Schaller (2010). These values are available to any researcher who wishes to test hypotheses linking pathogen prevalence to contemporary cross-national differences.

Complementing this measure of historical pathogen prevalence are measures based on contemporary epidemiological data. The Global Infectious Diseases and Epidemiology Online Network (GIDEON; http://www.gideononline.com) reports current distributions of infectious diseases in each country of the world and is updated weekly. Using this GIDEON database, Fincher and Thornhill (2008a, 2008b) computed two different indices. One index offers a measure of the contemporary variety of different pathogenic species within a country. As such, it assesses biodiversity rather than the actual threat to human health and welfare posed by those pathogenic species, and its implications for cross-cultural differences are not straightforward. The other index, however, is conceptually analogous to our index of historical pathogen prevalence. Focusing on seven classes of pathogens (leishmanias, trypanosomes, malaria, schistosomes, filariae, spirochetes, and leprosy), Fincher and Thornhill coded the relative prevalence of 22 specific pathogenic diseases. These 22 values were summed to create a composite index estimating the contemporary pathogen prevalence within each of 225 countries. (Actual country-level values on this measure of contemporary pathogen prevalence can be found in Appendix 2 of the online data supplement accompanying Fincher & Thornhill, 2008b.)

Armed with these measures, we have empirically tested a number of conceptual hypotheses specifying causal consequences of pathogen prevalence for the emergence of cross-cultural differences.

## E. Pathogen Prevalence Predicts Cultural Differences in Sociosexual Attitudes

Epidemiologists define some human infectious diseases as sexually transmitted infections (STIs). The transmission of these pathogens depends upon (or, at least, is substantially facilitated by) human sexual intimacy. The more sexual partners one has, the greater the risk of disease transmission. Many other infectious diseases may not fit the epidemiological definition of an STI, but people are still more likely to contract those diseases if they engage in sexual contact with someone who is already infected—simply because of the prolonged interpersonal proximity that sexual contact entails. The implication

is simple: To the extent that people tend to be sexually promiscuous or "unrestricted," those people are more likely to contract infectious diseases themselves and to transmit those diseases to others.

Of course, these specific fitness costs associated with unrestricted sexual behavior must be weighed against any potential fitness benefits that may accrue as a result of unrestricted mating strategies (e.g., among men, promiscuous mating strategies confer benefits through the production of more offspring). The cost/benefit ratio is likely to vary depending upon the prevalence of pathogens in the immediate ecology. In places where the prevalence of pathogens is relatively higher, the costs associated with unrestricted mating strategies are more likely to outweigh the benefits. This hypothesis for cross-cultural differences is clear: In places that historically have had a high prevalence of pathogens, one expects a less promiscuous, more "restricted" approach to sexual relations.

To test this hypothesis we (Schaller & Murray, 2008) employed the results of a cross-national study devoted to the assessment of attitudes and behaviors bearing on restricted versus unrestricted approaches to sexual behavior (Schmitt, 2005). Along with an international team of researchers, Schmitt collected responses on a Sociosexual Orientation Inventory (SOI; Simpson & Gangestad, 1991) from over 14,000 people in 48 different countries and reported mean standardized SOI scores (for both men and women separately) for each country. Higher SOI scores indicate a tendency toward more unrestricted sexual behavior. There is considerable worldwide variability in these country-level SOI scores. People in Argentina and Austria, for instance, on average have higher SOI scores (indicating a more unrestricted attitude toward sexual relations) than people in Bangladesh or Botswana.

Given the hypothesis, we expect to see a negative relation between pathogen prevalence and SOI. And, in fact, that is exactly what the results show: In places with a higher level of historical pathogen prevalence, both men and women report more restricted attitudes toward sexual relations (*r*'s for men and women were –.27 and –.62, respectively; Schaller & Murray, 2008).

It is worth noting that this effect was substantially stronger for female SOI scores than for male SOI scores. And it was only on female SOI scores that the negative correlation remained statistically significant even after statistically controlling for other country-level variables (e.g., gross domestic product per capita, life expectancy). This sex difference in the effect sizes is consistent with the overall cost/benefit framework. Because of differential reproductive investment, the fitness benefits associated with unrestricted sexual behavior

are likely to be considerably greater among men than among women. Therefore, for men only, these benefits may outweigh the costs (disease transmission) even at relatively high levels of pathogen prevalence. Among women, however, the benefits of unrestricted sexuality behavior are relatively minimal, and so they are more likely to be increasingly outweighed by the disease-related costs as pathogen prevalence becomes increasingly greater.

It is also worth noting that country-level SOI scores were more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence. This pattern of findings is consistent with the hypothesized causal relation (in which pathogen prevalence is the cause, and cross cultural differences in sexual attitudes are the consequence) and is inconsistent with the reverse causal relation.

## F. Pathogen Prevalence Predicts Cultural Differences in Extraversion and Openness

An individual's inclination toward restricted versus unrestricted sexual behavior is a kind of personality trait. But it is a highly specific trait, with implications for a relatively narrow domain of behavioral contexts. Might pathogen prevalence also predict cross-cultural differences in more fundamental personality traits, such as those that comprise the so-called Big Five (agreeableness, conscientiousness, extraversion, neuroticism, and openness to experience)?

Several cross-national investigations have documented important cultural differences along each of the Big Five personality traits. McCrae (2002) summarized results from multiple independent studies that used the NEO-PI-R questionnaire (Costa & McCrae, 1992) to assess the self-reported personality traits in 33 different countries. In a separate study, McCrae and an international team of collaborators obtained observer reports on the NEO-PI-R questionnaire from almost 12,000 individuals in 50 different countries (McCrae et al., 2005). And, in a third international study, Schmitt and his colleagues assessed self-reports on the Big Five Inventory (John & Srivastava, 1999) from almost 18,000 individuals in 56 different countries (Schmitt et al., 2007). Each investigation produced a set of country-level scores on each of the Big Five personality traits, documenting many different kinds of cross-cultural differences. For instance, on average, people in Norway and New Zealand report higher levels of extraversion than people in India or Ethiopia.

Given the questionnaire methodologies employed, some of the differences in country-level personality scores must surely be attributable to noise

and/or methodological artifacts, such as nonequivalent linguistic translations or reference group effects. Indeed, some empirical evidence research suggests that country-level scores on conscientiousness in particular might be especially difficult to interpret (Heine, Buchtel, & Norenzayan, 2008). Nevertheless, to the extent that there is some validity associated with these country-level personality scores, they offer the potential to test conceptual hypotheses about the links between pathogen prevalence and cross-cultural differences in fundamental personality traits.

### *1. Extraversion*

There is ample basis to expect a causal link between pathogen prevalence and cultural differences in extraversion. Being high in extraversion implies a wider circle of acquaintances and social contacts and an increased frequency of contact with those people. These social contacts have the potential to expose individuals to interpersonally transmitted pathogens. Indeed, there is empirical evidence that a dispositional tendency toward extraversion may be associated with an enhanced risk of disease transmission (Hamrick, Cohen, & Rodriguez, 2002; Nettle, 2005).

Of course, extraversion can be associated with many positive outcomes as well, including higher levels of leadership effectiveness, higher levels of happiness, and increased opportunities for sexual reproduction (Berry & Miller, 2001; Fleeson, Malanos, & Achille, 2002; Silverthorne, 2001). These benefits of extraversion are likely to outweigh the disease-related costs under conditions in which the disease-related costs are relatively minimal: in ecological settings characterized by low levels of interpersonally transmitted pathogens. However, as pathogen prevalence increases, there is increased likelihood that the disease-related costs of extraversion will begin to outweigh the benefits of extraversion. It is worth noting that these costs of extraversion are likely to accrue not only to extraverts themselves but also to anyone (even an introvert) in the local population who happens to interact with an extravert. Therefore, in places characterized by high pathogen prevalence, one might expect that individuals will not only be less extraverted themselves but will also devalue extraversion more generally. In any case, the hypothesis is straightforward: Regional variation in pathogen prevalence is expected to be inversely related to population-level variation in extraversion.

We (Schaller & Murray, 2008) conducted multiple tests of this hypothesis, using the results from the three different cross-national surveys of the

Big Five personality traits summarized earlier (McCrae, 2002; McCrae et al., 2005; Schmitt et al., 2007). As predicted, across every measure, cross-cultural differences in extraversion were negatively correlated with historical pathogen prevalence (see Table 3.1). These relationships remained even when controlling for a variety of additional country-level variables (e.g., gross domestic product, individualism/collectivism). In addition, consistent with the causal relation specified by the hypothesis, extraversion was more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence.

### *2. Openness to Experience*

A similar cost/benefit analysis implies a causal link between pathogen prevalence and cultural differences in openness to experience. Openness is associated with creativity, willingness to experiment, and attraction to novel experiences and unfamiliar stimuli (Larsen & Buss, 2005). These behavioral dispositions can be associated with certain kinds of fitness benefits, in that they encourage innovation and adaptive problem solving. But these dispositions also connote potential fitness costs specific to pathogen transmission. This is because many familiar ways of doing things—particular in domains such food preparation, personal hygiene, and public health—actually serve as buffers against pathogen transmission. To the extent that individuals deviate from these accustomed norms (e.g., experiment with novel methods of food preparation, or take a "creative" approach to hygiene), those individuals expose themselves—and others in their local community—to an increased risk of pathogen transmission. These particular kinds of costs, of course, are likely to be greater (and more likely to outweigh the benefits associated with dispositional openness) under conditions of greater pathogen prevalence. Thus, regional variation in pathogen prevalence is expected to be inversely related to population-level variation in openness to experience.

We conducted multiple tests of this hypothesis too, using exactly the same source materials as we used in our investigations into extraversion (Schaller & Murray, 2008). Again, across every measure, cross-cultural differences in openness to experience were negatively correlated with historical pathogen prevalence (see Table 3.1). These negative relationships remained even when controlling for additional country-level variables. And, consistent with the causal relation specified by the hypothesis, openness to experience was more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence.

TABLE 3.1: **Correlations between Historical Pathogen Prevalence and Contemporary Cultural Outcomes Pertaining to Dispositions and Values**

| Cultural Outcome Variable | Correlation with Pathogen Prevalence |
|---|---|
| Sociosexual attitudes (for details see Schaller & Murray, 2008) | |
| Female sociosexuality scores | –.62 |
| Male sociosexuality scores | –.27 |
| Extraversion (for details see Schaller & Murray, 2008) | |
| Extraversion scores from Macrae, 2002 | –.67 |
| Extraversion scores from Macrae et al., 2005 | –.50 |
| Extraversion scores from Schmitt et al., 2007 | –.26 |
| Three-sample composite | –.59 |
| Openness to experience (for details see Schaller & Murray, 2008) | |
| Openness scores from Macrae, 2002 | –.45 |
| Openness scores from Macrae et al., 2005 | –.34 |
| Openness scores from Schmitt et al., 2007 | –.24 |
| Three-sample composite | –.59 |
| Individualism (for details see Fincher et al., 2008) | |
| Individualism scores from Hofstede, 2001 | –.69 |
| Individualism scores from Suh et al., 1998 | –.71 |
| Collectivism (for details see Fincher et al., 2008) | |
| In-group collectivism practices | .73 |
| Pronoun-drop indicator of collectivism | .63 |
| Conformity pressure (Murray et al., unpublished data) | |
| Behavioral conformity effect sizes | .49 |
| Percentage of people who prioritize obedience | .48 |
| Tolerance for nonconformity (Murray et al., unpublished data) | |
| Dispositional variability | –.52 |
| Percentage of left-handed people | –.73 |
| Political ideologies (for details see Murray & Schaller, 2010) | |
| Restriction of individual rights and civil liberties | .55 |
| Democratization | –.65 |

### *3. Negligible Effects on Other Big Five Traits*

In addition to testing hypotheses linking pathogen prevalence to cross-cultural differences in extraversion and openness, we also conducted additional analyses to explore whether there might be any relationships with the other three Big Five factors: agreeableness, conscientiousness, and neuroticism (Schaller & Murray, 2008). No consistent patterns emerged across the various measures, although there was some evidence that pathogen prevalence may predict more narrowly defined facets of these additional factors. (For two of the three cross-national surveys—those that employed the NEO-PI-R questionnaire—facet scores were reported by McCrae, 2002, and by McCrae & Terraciano, 2008). For instance, at a cross-cultural level, pathogen prevalence was consistently positively correlated with measures of deliberation (a facet of conscientiousness) and negatively correlated with measures of impulsiveness (a facet of neuroticism).

It would probably be wise to be very careful about interpreting any results on these underlying facets. That said, it is perhaps worth noting that the findings on deliberation and impulsiveness fit neatly within the conceptual analysis that gave rise to the hypothesis pertaining to openness. However, there is some useful inferential value associated with the negligible relations between pathogen prevalence and these additional three Big Five factors (agreeableness, conscientiousness, and neuroticism). These negligible relations suggest that the conceptually interesting results on extraversion and openness cannot easily be attributed to response biases (e.g., acquiescence bias) or other methodological artifacts that affect all traits assessed by the personality questionnaires. This improves our confidence that the observed correlations involving pathogen prevalence and personality are truly meaningful.

## G. Pathogen Prevalence Predicts Cultural Differences in Individualism and Collectivism

Just as pathogen prevalence is expected to predict worldwide cultural variability in personality style, it is also expected to predict variability in cultural values. There are many different kinds of cultural values (e.g., Hofstede, 2001; Schwartz, 2004), but there is one value construct in particular that has been the focus of an enormous amount of attention from cross-cultural researchers: values pertaining to individualism versus collectivism. This attention is warranted, as it has been suggested that individualism/collectivism "may ultimately prove to be the most important dimension for capturing

cultural variation" (Heine, 2008, p. 189). Despite the attention that this dimension has received (including a limited number of attempts to explore possible antecedents of cultural differences along this dimension; e.g., Kitayama & Bowman, 2010), it still remains largely a mystery as to exactly *why* some cultures tend to be individualistic, whereas others tend to be more collectivistic. One solution to this mystery may lie in ecological variation in pathogen prevalence.

Why might pathogen prevalence have a causal influence on cultural inclinations toward individualism versus collectivism? There are several reasons, each related to a distinct definitional element of this multifaceted value construct.

According to most definitions of individualistic and collectivistic value systems (e.g., Gelfand et al., 2004), collectivist cultural values (as opposed to individualist values) are characterized in part by an expectation of prosocial behavior among family members and other individuals within a local social alliance. There are costs associated with the obligatory prosocial expenditure of resources. But there are benefits too, which may accrue whenever one (or one's immediate kin) is in need of assistance from others. These benefits are likely to be especially pronounced under conditions in which the local ecology is characterized by a high level of threat to health and welfare. Thus, because of the emphasis on obligatory prosociality within families and local alliances, collectivistic value systems are likely to be relatively more advantageous under conditions of greater pathogen prevalence (whereas individualism may be relatively more advantageous under conditions of lower pathogen prevalence).

Another defining feature of collectivistic (compared to individualistic) value systems is a relatively sharper psychological boundary between ingroup and outgroup (Gelfand et al., 2004). This manifests in higher levels of ethnocentrism and xenophobia (e.g., greater wariness of, and reduced contact with, foreigners and other outgroup members; Sagiv & Schwartz, 1995). Xenophobic attitudes come at some cost (e.g., reduced opportunities for trade, reduced exposure to exotic-but-useful ideas and technologies), but there are also benefits specific to the domain of disease transmission. Compared to ingroup members, outgroup members are more likely to host exotic pathogens. If introduced to the local population, exotic pathogens pose an especially virulent threat to individuals' health and reproductive fitness, given the immune system's proclivity to be most effective against local pathogens (Mayer, 2006). In addition, compared to ingroup members, outgroup members are more likely to be ignorant of, and thus to violate, local norms that serve as buffers against

pathogen transmission. Thus, wariness and avoidance of outgroup members may be associated with disease-relevant benefits that must be weighed against the costs. These disease-relevant benefits are most likely to outweigh the costs under conditions of high pathogen prevalence. The implication is that, because the emphasis on sharp ingroup/outgroup distinctions, collectivistic value systems are likely to be relatively more advantageous under conditions of greater pathogen prevalence, whereas individualism may be relatively more advantageous under conditions of lower pathogen prevalence.

Line 4: insert the word "of": it should be "...because of the..."

A feature that accompanies collectivistic value systems is "tightness": a strong value placed on the upholding of cultural traditions and conformity to cultural norms, accompanied by a lack of tolerance for deviance from these established norms (Gelfand, Nishii, & Raver, 2006; Gelfand et al., 2004; Triandis, 1995). In contrast, individualist value systems are characterized by greater tolerance for deviation from established norms (Cukur, De Gusman, & Carlo, 2004; Oishi, Schimmack, Diener, & Suh, 1998). The cost/benefit implications are essentially identical to those for openness to experience, discussed earlier. While there are certain costs associated with values emphasizing tradition and conformity (decreased incidence of useful innovation), there are clear benefits specific to the domain of infectious diseases (decreased likelihood that individuals will violate the various norms and traditions that serve as buffers against pathogen transmission). These benefits are most likely to outweigh the costs under conditions of high pathogen prevalence. The implication is that, because of this emphasis on conformity and tradition, collectivistic value systems are likely to be relatively more advantageous under conditions of greater pathogen prevalence (whereas individualism may be relatively more advantageous under conditions of lower pathogen prevalence).

Thus, multiple complementary lines of deduction yield a single clear hypothesis linking pathogen prevalence to cultural values along the individualism/collectivism dimension: Regional variation in pathogen prevalence is expected to be inversely related to indicators of individualism and positively related to indicators of collectivism.

We conducted four tests of this hypothesis using two different country-level measures of individualism and two additional country-level measures of collectivism (Fincher, Thornhill, Murray, & Schaller, 2008). These measures included the following: *(a)* individualism scores reported by Hofstede (2001), which were based on extensive survey data along with a variety of additional observations; *(b)* individualism scores reported by Suh and colleagues (1998), which supplemented Hofstede's scores with the subjective assessments of a

scholarly expert on worldwide differences in individualism and collectivism; *(c)* "in-group collectivism practices" scores reported by Gelfand et al. (2004), based on extensive survey data; and *(d)* a binary variable indicating whether it is acceptable to drop first- and second-person pronouns in spoken language (pronoun-drop is more prevalent in highly collectivistic cultures, and so serves as a linguistic indictor of collectivism; Kashima & Kashima, 1998). The sample of countries varied with each measure, but every analysis included a substantial number of countries from around the world (N's varied between 58 and 70). The results were clear and consistent across all four sets of analyses: Consistent with the hypothesis, geographical variation in the historical prevalence of pathogens was strongly negatively correlated with individualism (*r*'s = –.69 and –.71) and strongly positively correlated with collectivism (*r*'s = .73 and .63).

Fincher et al. (2008) also reported the results of analyses in which culturally distinct world regions (e.g., Western Eurasia, Eastern Eurasia), rather than individual countries, were treated as the units of analysis. The results were essentially the same. In fact, some of the correlations were even stronger when treating large cultural regions as units of analysis.

Additional analyses revealed that the predictive effect of pathogen prevalence remained even when controlling for a variety of additional country-level variables that might plausibly have a causal influence on individualistic/collectivistic value systems (e.g., gross domestic product, non-disease-related threats to health and morality). And, consistent with the causal relation specified by the hypothesis, individualism/collectivism was more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence.

Overall, these results provide compelling evidence consistent with the hypothesized causal relation between pathogen prevalence and cultural value systems along the individualism/collectivism dimension. But recall that individualism and collectivism are multifaceted value systems, defined by a variety of more highly specific and conceptually distinct constructs. And recall that these different constructs are the foci of logically distinct conceptual analyses linking pathogen prevalence to individualism/collectivism. Evidence bearing on the broader value systems (individualism and collectivism) does not clearly indicate which—if any—of these more specific conceptual analyses might be right or wrong. In short, we still need to know about exactly what specific construct (or constructs) might be driving the effect. Do the individualism/collectivism findings reflect an effect of pathogen prevalence on obligatory prosociality? On ethnocentrism and/or xenophobia? On conformity pressures?

All of the above? Some of the above? None of the above? Answers to these questions require empirical analyses that focus more purely on indicators of these more specific underlying constructs.

Thus far, there is very little rigorous research addressing relations between pathogen prevalence and either obligatory prosociality, enthnocentrism or xenophobia. However, there are a couple of promising empirical beginnings. In one set of analyses, we examined the extent to which the prevalence of different categories of human-infecting pathogens (zoonotic, human-specific, multihost) might have differential relations with cross-cultural outcomes (Thornhill, Fincher, Murray, & Schaller, 2010). One finding that emerged is evidence that pathogen prevalence of all kinds (but especially the prevalence of human-specific and multihost pathogens) is positively correlated with cross-cultural differences in the strength of allegiance to one's immediate family (*r*'s = .58 and .50 for human-specific and multihost pathogen prevalence, respectively; N = 78). Separately, in an analysis that employed data from the World Values Survey, we also found that pathogen prevalence is positively correlated with the percentage of people in a country who explicitly indicate that they would not want "people of a different race" as neighbors ($r$ = .43, N = 67; Schaller & Murray, 2010). But these are just hints, at best. To our knowledge, no one has reported any comprehensive set of empirical analyses to test the hypothesized effects of pathogen prevalence on either of these two specific facets of collectivism.

In contrast, the hypothesized effect of pathogen prevalence on "tightness"—cultural conformity pressures—has recently been subjected to close empirical scrutiny, as will be discussed next.

## H. Pathogen Prevalence Predicts Cultural Differences in Conformity Pressure

It has been previously documented that there are cross-cultural differences in the pressure to conform, and that these differences covary with the broader cultural differences in individualism and collectivism (Bond & Smith, 1996). We recently conducted a series of analyses designed to address the hypothesis that these cross-cultural differences in conformity pressure may result, in part, from regional differences in pathogen prevalence (Murray, Trudeau, & Schaller, unpublished data). We examined four different country-level outcome variables.

One of these measures was taken from Bond and Smith's (1996) meta-analysis of social psychological experiments (such as those designed originally

by Asch, 1956) that assessed public conformity to majority behavior. In their results, they tabulated the effect sizes that emerged from over 100 experiments conducted in 17 different countries. For each of these countries it is possible to calculate the mean effect size. This mean effect size offers a crude, but direct measure of country-level behavioral conformity.

A second measure of conformity assesses not behavioral conformity per se, but rather the cultural value placed on a particular kind of conformity—obedience. This measure was obtained from the results of the World Values Survey (available at http://www.worldvaluessurvey.org). These results tabulate, for each of 83 countries, the percentage of survey respondents who indicated that obedience is a very important value for children to learn.

These two measures of within-country conformity pressures are complemented by two additional measures that, in different ways, provide indirect measures of tolerance for nonconformity. One of these measures follows from the logical implication that, in cultures characterized by stronger conformity pressure, there will be reduced tolerance for dispositional tendencies that deviate from dispositional norms within the culture (Gelfand et al., 2006). This in turn implies that tolerance for nonconformity may be indexed by within-country variability around mean values on basic personality traits. Exactly such an index was reported by McCrae (2002) who, in addition to reporting within-country means on the Big Five personality traits, also reported for each country (N = 33) the average standard deviation around mean values on the Big Five facet scores.

Finally, tolerance for nonconformity can also be measured indirectly by assessing the percentage of people within a country who are left-handed. In the words of Harry Triandis (1995, p. 56), "This works well because in all cultures the right hand is considered the correct one, but in cultures that are tight there is pressure for those who are naturally left-handed to become right-handed." And, in fact, evidence from many studies reveals that the percentage of left-handed people is greater—sometimes considerably so—within cultural contexts characterized by greater tolerance for nonconformity (e.g., Fagard, & Dahmen, 2004; Porac & Martin, 2007). Obtaining precise within-country estimates is not as straightforward as one might think. There are lots of different ways of measuring handedness, and these different measures sometimes produce rather different estimates. But, within the laterality literature, we were able to locate 20 different countries for which the same measurement techniques were employed to produce estimates of the percentage of people who are left-handed.

To what extent are these four variables (two measures of conformity pressure and the two measures of tolerance for nonconformity) predicted by pathogen prevalence? Substantially. The historical prevalance of pathogens correlated significantly positively with behavioral conformity effect sizes and the value placed on obedience (*r*'s = .49 and .48), and significantly negatively with personality variation and the percentage of left-handers (*r*'s = –.52 and –.73).

Of course, once again we must consider the possibility that these correlations are the spurious result of additional variables that covary with both pathogen prevalence and conformity. There are a variety of additional variables that have been linked either empirically or conceptually to conformity and/or nonconformity, including such things as non-disease-related threats, agricultural activity, and economic wealth (e.g., Berry, 1967, 1979; Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006). Additional regression analyses revealed, however, that the predictive impact of pathogen prevalence remained significant even when controlling these additional variables. Furthermore, consistent with the causal relation specified by the hypothesis, these various measures of conformity (and tolerance for nonconformity) were more strongly predicted by historical pathogen prevalence than by contemporary pathogen prevalence. In addition, the relations hold—and are even stronger in magnitude—when treating world regions (the six world cultural regions identified by Murdock, 1949), rather than individual countries as units of analysis. Thus, the results are consistent with the hypothesis specifying a causal impact of pathogen prevalence on cultural values promoting obedience, conformity, and the conservation of existing cultural traditions.

Line 15: insert the word "for": it should be "...controlling for these..."

## I. Pathogen Prevalence Predicts Cultural Differences in Political Ideology

Thus far we have focused on the role that pathogen prevalence may have had in shaping the sorts of cultural outcomes that are of particular interest to psychologists—personality traits, behavioral dispositions, and value systems. But there are additional implications that matter to other kinds of social scientists as well, including implications for economists and political scientists.

Economic and political outcomes within a country are influenced substantially by political ideologies. These ideological outcomes are likely to be influenced by the traits, dispositions, and values of the people living within a country. For instance, within any culture that prizes tradition and conformity, specific kinds of individual rights and freedoms (e.g., freedom of speech) may be perceived to pose a threat. Consistent with this analysis is evidence that

cultural tightness and collectivism are highly associated with the existence of authoritarian governments and legalized repression of civil liberties and individual freedoms (Conway, Sexton, & Tweed, 2006). An obvious implication is that these country-level differences in political ideology may have resulted, in part, from regional differences in pathogen prevalence.

Several empirical analyses provide preliminary support for this hypothesis. Thornhill, Fincher, and Aran (2009) found that contemporary pathogen prevalence was positively correlated with country-level measures that assess the repression of individual rights, negatively correlated with various additional measures of social and political liberalism, and negatively correlated with democratization in general. Further analyses (reported by Murray & Schaller, 2010) reveal that these ideological outcome variables are even more strongly predicted by historical pathogen prevalence (e.g., countries that historically have had a high prevalence of pathogens tend to be less democratic; see Table 3.1).

## J. Pathogen Prevalence Predicts Cultural Diversity Itself

The results that we have discussed so far have documented a variety of ways in which regional differences in pathogen prevalence predict cultural differences between regions. Some of these effects have logical implications also for cultural diversity *within* regions.

The logic is as follows: To the extent that people are extraverted and open and willing to interact with outgroup members, they are more likely to engage in the kinds of cross-cultural interactions that allow for cultural accommodation and/or assimilation. In contrast, to the extent that people are cautious and introverted and wary of strangers, they are relatively unlikely to interact with people who are culturally distinct. And, as a result, their own cultural norms (their language, their religious rituals, their traditional beliefs and behaviors) are relatively unlikely to encroach upon other cultural norms, and also unlikely to be encroached upon by those outside influences. Thus, the lack of cross-group cultural interaction preserves cultural diversity. In a sense, just as specific kinds of physical barriers (waterways, mountain ranges) create island biogeographies, specific kinds of psychological traits (low levels of extraversion, low levels of openness to experience) and specific kinds of value systems (collectivism) create insular social geographies. And just as island biogeographies promote high levels of biodiversity within a geographical region, island social geographies promote high levels of cultural diversity

within a geographical region. The logical upshot is that, because a high level of pathogen prevalence is associated with psychological traits and values that define island social geographies, it follows that a higher level of pathogen prevalence should also predict a higher level of cultural diversity within the broader region.

This appears to be the case. In two separate sets of analyses, Fincher and Thornhill (2008a, 2008b) examined the relationship between contemporary pathogen prevalence and two different indicators of cultural diversity: the number of different religions within a region, and the number of different languages spoken within a region. In both cases, as predicted, higher levels of pathogen prevalence were associated with higher levels of cultural diversity. These results suggest that not only might pathogen prevalence help to explain observed patterns in the contemporary record of worldwide cultural diversity, pathogen prevalence might also help to explain local cultural diversity.

## K. Implications, Limitations, and Future Directions

Not only do these findings collectively support a variety of conceptually derived hypotheses specifying relations between pathogen prevalence and cultural outcomes, these findings also help to provide a more complete explanation for various previously documented relations between different kinds of country-level variables. We provide three examples.

First, at a cultural level of analysis, extraversion is associated with individualistic (rather than collectivistic) value systems. Consequently, cross-cultural researchers have speculated about the possible causal influence of personality dispositions on cultural values, and about the possible influence of values on dispositions (Hofstede & McCrae, 2004). It turns out, however, that the correlation between individualism and extraversion disappears when statistically controlling for pathogen prevalence (Fincher et al, 2008; Schaller & Murray, 2008). Rather than extraversion leading to individualism, or vice versa, it appears that the relation between these two constructs is largely spurious, resulting from the fact that both are cultural consequences of pathogen prevalence.

Second, there are well-documented relations between economic conditions and cultural characteristics. For instance, the mean level of economic affluence within a country (as indicated by gross domestic product per capita) is a powerful predictor of values along the individualism/collectivism dimension (Hofstede, 2001; Triandis, 1995). This relation is substantially

diminished—although does not disappear entirely—when controlling for pathogen prevalence (Fincher et al., 2008). It appears, therefore, that the actual influence of economic conditions on cultural values may be considerably less substantial than has often been assumed. In fact, given that infectious diseases are powerful inhibitors of economic development (Sachs & Malaney, 2002), the indirect influence of pathogen prevalence may be lurking in the background behind even the unique effects of economic affluence on cultural outcomes.

Third, latitude is a strong statistical predictor of many different kinds of cross-cultural differences (Cohen, 2001; Hofstede, 2001; Kashima & Kashima, 2003). Of course, latitude is merely a cartographic abstraction; it cannot exert any direct causal influence on human behavior. The statistical effects of latitude require explanations that focus on more physically meaningful variables such as the higher temperatures, greater rainfalls, and other meteorological conditions associated with lower latitudes (e.g., Van de Vliert, 2009). Pathogen prevalence is profoundly influenced by these same meteorological variables, which is a major reason why the diversity and prevalence of pathogens is generally much greater in the tropics compared to higher latitudes (Epstein, 1999; Guernier et al., 2004). It appears likely that pathogen prevalence is an instrumental part of any complete causal explanation for the relation between latitude (and the meteorological variables that covary with latitude) and psychologically interesting cultural outcomes.

Of course, there are not only implications associated with this body of evidence but also limitations. It is important to bear these limitations in mind when interpreting the results that we have just reviewed and when proceeding with new research in the future.

One set of limitations arises from the fact that the units of analysis are countries, and not independent cultures per se. This analytic strategy raises the specter of Galton's problem, which we discussed at the outset of our review. To address this issue, some of the results summarized earlier were accompanied by additional analyses that focused not on countries as units of analysis, but instead on large world regions that, historically, have been culturally distinct. Reassuringly, the results from these additional analyses replicate those observed on the country-level data (e.g., Fincher et al., 2008). But not all the published findings have been accompanied by these additional analyses. For example, in our article reporting the effects of pathogen prevalence on personality traits (Schaller & Murray, 2008), we reported only country-level analyses, but no region-level analyses of the sort that might help address

Galton's problem. We are happy to report here that those region-level analyses have been done (we computed mean values on pathogen prevalence as well for each of the Big Five personality traits within each of the six world cultural regions identified by Murdock, 1949), and that the results do indeed replicate the primary effects by Schaller and Murray (2008): When treating world regions rather than countries as the units of analysis, the predictive effects of pathogen prevalence on extraversion and openness are identical in direction and even stronger in magnitude. More generally, across the various studies documenting relations between pathogen prevalence and cultural differences, there has emerged no evidence that the results—or conclusions—are compromised by the use of country as a unit of analysis.

Still, this inferential issue is a complicated one, and it would be unwise to dismiss it. There are a variety of methodological techniques that can be employed to address Galton's problem and the statistical issue of autocorrelation more generally (e.g., Dow, 2007; Mace & Holden, 2005). The issue itself might be minimized by inquiries that focus on cultural units of analysis that are more clearly independent, such as small-scale societies of the sort that have traditionally been the subject of ethnographic research in the anthropology literature. (It is worth noting, however, that even relatively isolated small-scale societies may not be as culturally independent as often assumed; Eff, 2004).

Another important inferential limitation arises from the twin facts that *(a)* the empirical methods are necessarily correlational, and *(b)* any one country-level variable is inevitably correlated with many other country-level variables. This is certainly the case for pathogen prevalence. In our research, we have drawn conclusions about the predictive effects of pathogen prevalence only when those effects remained after controlling for a variety of additional variables. But it is impossible to statistically control for every variable that might be correlated with pathogen prevalence. Any conclusion about the effects of pathogen prevalence on cultural outcomes must, logically, be accompanied by the familiar caveat that a causal inference cannot be claimed with absolute certainty.

Of course, this inferential issue applies equally to *any* investigation that tests hypothesized effects of any variable on cultural outcomes. Thus, regardless of whether a researcher has a conceptual interest in the effect of pathogen prevalence on culture, the results that we have reviewed suggest researchers must contend with the predictive effects of pathogen prevalence anyway. Before drawing conclusions about the alleged unique effects of other variables

on cultural outcomes, researchers must show that those effects remain even after controlling for the historical prevalence of pathogens.

Ultimately, as evidence accumulates bearing on the potential causal relevance of various different kinds of ecological and economic variables, it will become important to articulate the complex causal relations between the multiple variables that predict contemporary cross-cultural differences. Only by rigorously pursuing multivariate and multicausal strategies of inquiry are we likely to arrive at a true reckoning of the possible role that pathogen prevalence may have played in the origin of contemporary cross-cultural differences.

It may be important also to consider the possibility that cultural consequences *of* pathogen prevalence may have reciprocal causal implications *on* pathogen prevalence, and that these implications may be especially complicated as ecological circumstances change over time. For instance, while collectivistic value systems can promote specific kinds of behavioral buffers against endemic pathogens (e.g., conformity to existing norms of culinary spicing inhibits the transmission of foodborne bacteria), these same value systems might be counter-productive in the context of exotic pathogens (conformity to existing norms inhibits the development of novel behavioral strategies that might effectively respond to the threat posed by novel diseases).

These are just a few of the ways that future research must build upon and extend the findings that we have reviewed here. Another agenda for future research is to illuminate the causal mechanisms through which pathogen prevalence might actually exert its effects on cultural outcomes. We believe that this particular agenda is of such fundamental importance—and of such wide-ranging scientific interest value—that we close this chapter with a detailed discussion of the diverse kinds of processes that might be implicated, and the diverse kinds of scientific methodologies that might be used to implicate them.

## III. DEEPER CONSIDERATION OF UNDERLYING CAUSAL PROCESSES

Even if we allow ourselves to draw the tentative conclusion that many different kinds of cultural differences may indeed be the result, in part, of regional differences in pathogen prevalence, we must still contend with a huge question: Exactly how might this have occurred? What is the exact causal process—or set of processes—through which ecological variation in pathogen prevalence leads to cultural variation in human cognition and behavior?

There are at least four different kinds of processes through which pathogen prevalence might exert a causal influence on cross-cultural variability. These processes are all conceptually distinct—operating at four entirely different levels of analysis—and so they are not mutually exclusive. Each must be considered on its own terms and evaluated on the basis of both logical plausibility (which appears ample for all four) and available empirical evidence (which, thus far, is ample for none).

## A. Cultural Evolution: Ecological Influence on Interpersonal Communication and Social Learning

Human beings have considerable cognitive capacities that allow them to recognize both the dangers and the opportunities in their local environments, to pragmatically adjust their behavior accordingly, and to communicate their pragmatic wisdom to others. Even in the absence of any knowledge about the pragmatic considerations that may have informed others' behavior, people learn from others' behavior, they imitate and reproduce that behavior, and thus they reify and perpetuate those behavioral norms. Through these processes of interpersonal communication and social learning, cultural norms evolve. And, under different ecological circumstances characterized by different kinds of perils and prospects and pragmatic considerations, cultural norms evolve differently.

On logical grounds alone, cultural transmission processes provide a highly compelling means through which ecological variability in pathogen prevalence might lead to cross-cultural variability in traits, values, and other behavioral norms (Schaller, 2006). Cultural transmission processes provide a speedy and efficient means through which human populations adapt sensibly to their ecological circumstances. Indeed, because of this speed, an explanation rooted in cultural evolutionary processes is entirely compatible with evidence documenting rapid-but-not-overnight changes in cultural values (i.e., changes observed over the course of a generation or two) associated with immigrant populations who migrate from countries characterized by high pathogen prevalence to countries with substantially lower levels of pathogen prevalence (e.g., Hardyck, Petrinovich, & Goldman, 1976). And, of course, there are empirical literatures documenting the individual-level psychological phenomena that provide the raw materials for cultural evolution—including perceptual hypervigilance to cues connoting the presence of threat, selective communication about threat, social learning of avoidant responses to threat, and many different forms of selective behavioral mimicry and conformity.

On the other hand, there is scant evidence that bears specifically on the implications of pathogens for cultural evolution. Among the many studies that document hypervigilance to threat (Öhman, Flykt, & Esteves, 2001; Schupp et al., 2004), there are only a few that suggest hypervigilance to disease-connoting cues in particular (e.g., Ackerman et al., 2009). And while there are some empirical results suggesting that people are especially likely to communicate about threat-connoting information (Schaller & Conway, 1999; Schaller, Faulkner, Park, Neuberg, & Kenrick, 2004), there are none that focus on disease-relevant information in particular. Similarly, while there is evidence showing that humans and other primates learn from other individuals' aversive emotional responses to threats (Cook & Mineka, 1990; Hornick, Risenhoover, & Gunnar, 1987), none of this evidence pertains specifically to pathogens. And while there is evidence that collective human behavior is sensitive to emotionally charged communications connoting the threat of disease (Sinaceur, Heath, & Cole, 2005), this evidence does not link the nature of these communications to the actual prevalence of disease in the natural ecology. Thus, as yet, there is virtually no empirical evidence that directly tests the hypothesis that cultural transmission processes might mediate any of the observed relationships between pathogen prevalence and cultural characteristics.

## B. Neurocognitive Processes: Ecological Influence on Adaptively Flexible Cognition and Behavior

Human cognitive functioning is characterized by perceptual mechanisms that are highly sensitive to fitness-relevant information in the immediate environment. When this information is perceived, it triggers a cascade of neurochemical activity that ultimately influences how individuals respond affectively, cognitively, and behaviorally to their environment. In a relatively benign environment, these perceptual cues are likely to trigger approach-oriented cognitions and behaviors. In a more dangerous environment, however, these perceptual cues are likely to trigger more avoidant cognitions and risk-averse behaviors. Thus, for instance, under conditions in which threats are temporarily salient, people show less evidence of independent thinking and a greater tendency toward social conformity (Griskevicius et al., 2006).

Many of the cultural variables predicted by pathogen prevalence (including not only conformity but also basic personality traits and the endorsement of individualistic/collectivistic values) are, at an individual level of analysis, highly malleable in response to immediate contextual circumstances (e.g., Gardner, Gabriel, & Lee, 1999; Hong et al., 2000; Kunda & Santioso, 1989),

and there is now abundant evidence that the perceived threat of pathogen transmission has an immediate causal influence on human cognition. For instance, under conditions in which the threat of pathogenic infection is either especially high or especially salient, people respond by being more likely to display more xenophobic and ethnocentric attitudes toward foreigners (Faulkner, Schaller, Park, & Duncan, 2004; Navarette et al., 2007). The salience of infectious diseases also leads to reduced levels of self-reported extraversion and to behavioral withdrawal from social stimuli (Mortensen et al., 2010).

Thus, it is entirely plausible that a causal relation between pathogen prevalence and cultural outcomes could be mediated, in part, by the operation of adaptively flexible neurocognitive mechanisms. Under ecological conditions characterized by high pathogen prevalence, these mechanisms may induce individuals to think and behave in an adaptively cautious manner (characterized by lower levels of extraversion, higher levels of xenophobia and ingroup conformity, etc.) In contrast, under ecological conditions characterized by low pathogen prevalence, these neurocognitive mechanisms are less likely to be triggered by disease-connoting perceptual cues, and so individuals are likely to be more open-minded and approach-oriented instead.

However, while there is empirical evidence documenting the causal influence of disease salience on ethnocentrism, xenophobia, and extraversion (e.g., Faulkner et al., 2004; Mortensen et al, 2010), these are just a few of the many variables that, at a cultural level of analysis, have been linked to pathogen prevalence. There is no published empirical evidence showing that the mere perception of disease threat might lead people to be more conforming, to endorse more collectivistic values, to be more sexually restricted, or to be more likely to put spices in one's food.

Even if such evidence is eventually found, additional empirical considerations suggest that neurocognitive mechanisms are unlikely to offer a complete explanation for the cultural consequences of pathogen prevalence. The cognitive and behavioral consequences of these neurocognitive mechanisms occur very quickly. (In the typical experiment documenting the causal consequences of a disease salience manipulation, the effects are observed in mere minutes.) Thus, if the cross-cultural differences of pathogen prevalence were due solely to the operation of neurocognitive mechanisms, one would expect contemporary measures of pathogen prevalence to predict cultural outcomes more strongly than historical measures. This is not the case. Moreover, one would expect immigrants to show a virtually instantaneous change in dispositions and values upon migrating to a novel ecological niche. Such instantaneous

change is rarely observed. Thus, while there is a compelling conceptual case to be made for the mediating role of neurocognitive mechanisms, and this conceptual case is buttressed by some recent empirical results, it is also clear that other mechanisms, operating at different levels of analysis, must also be considered.

## C. Epigenetic Processes: Ecological Influence on Developmental Expression of Genes

A third plausible process that might account for an effect of pathogen prevalence on cultural outcomes is a developmental process—not "developmental" in the sense that the word is employed by psychologists, but instead in the sense that it is employed by developmental biologists. This is the kind of process to which evolutionary psychologists typically refer when they talk of "evoked culture" (e.g., Gangestad et al., 2006; Tooby & Cosmides, 1992). The basic idea is as follows: Attitudes, traits, and other dispositional tendencies are influenced by genes. The phenotypic consequences of genes depend, however, on whether (and how) the genes are expressed during the course of development. Gene expression is profoundly influenced—typically in functionally adaptive ways—by the ecological circumstances within which an individual organism develops.

When this developmental reasoning is applied to pathogen prevalence, the logic is straightforward: Under ecological circumstances characterized by higher levels of pathogen prevalence, genes associated with cautious dispositional tendencies (e.g., introversion, sexual restrictedness, the endorsement of conformist values) are relatively more likely to be expressed during development, and to exert a greater influence on individuals' eventual dispositional tendencies. Conversely, under ecological circumstances characterized by relatively fewer pathogens, genes associated with more risk-tolerant and approach-oriented dispositional tendencies (e.g., extraversion, openness, nonconformity) are relatively more likely to be expressed. This context-contingent developmental process results, inevitably, in regional populations characterized by somewhat different attitudes, values, and personality traits.

The plausibility of this epigenetic explanation is supported by a considerable body of evidence documenting gene–environment interactions in the prediction of human cognition and behavior (e.g., Cole, 2009). Its plausibility is also supported by an extensive literature in the biological sciences bearing on the evolutionary advantages associated with phenotypic plasticity and the

many ways in which phenotypic plasticity manifests in the natural world (Ridley, 2003). Among many mammal species, developing fetuses obtain information about postnatal environments via chemical cues obtained through the placenta; these cues influence gene expression in ways that promote the development of adaptive phenotypic responses (Gluckman & Hanson, 2005). Among meadow voles, for example, the placental transfer of melatonin (a chemical signal diagnostic of the length of the day) has the adaptive developmental consequence that, as winter (rather than summer) approaches, infants are born with thicker coats (Lee & Zucker, 1988).

Just as development is adaptively influenced by the placental transfer of melatonin, development may also be adaptively influenced by the placental transfer of chemical signals that are produced maternally when mothers are exposed to pathogens. These chemical signals include corticosteroids and other hormones associated with stress and immune response. In research with nonhuman mammals, prenatal exposure to maternal corticosteroids has been linked to dispositional tendencies later in life, including lower levels of sexual aggression, reduced social interaction, and less exploratory behaviors in novel environments (e.g., Takahashi, Haglin, & Kalin, 1992; see Edwards & Burnham, 2001, for a review). In one particularly notable study with mice, pregnant dams who were exposed to pathogen-infected conspecifics produced higher levels of corticosterone and produced offspring who, upon reaching adulthood, were meeker and less socially aggressive than controls (Curno, Behnke, McElligot, Reader, & Barnard, 2009). Analogously, among humans, pregnant mothers treated with a stress hormone (dexamethasone) gave birth to children who, compared to controls, were relatively more shy and less sociable (Trautman, Meyer-Bahlburg, Postelnek, & New, 1995).

These developmental results neatly parallel the cross-cultural findings reported by Schaller and Murray (2008), and so they give special credence to an explanation based upon the effects of pathogen prevalence on gene expression and development. Still, this evidence is indirect, at best. More compelling tests of this explanation must focus more specifically on human development and must consider a fuller range of the attitudes, traits, values, and behavioral tendencies that have been linked, cross-culturally, to pathogen prevalence.

## D. Genetic Evolution: Ecological Influence on Population-Level Gene Frequencies

Finally, we must consider the possibility of a genetic evolutionary process, such that alleles that predispose individuals to specific kinds of traits and

values are differentially likely to proliferate under different kinds of ecological circumstances. Thus, just as alleles promoting post-weaning production of lactase have been differentially selected for (and consequently have become relatively more common) within pastoral populations that domesticate milk-producing animals (Durham, 1991), alleles promoting extraversion, openness, and individualism may have been differentially selected for (and become relatively more common) within populations characterized by relatively low levels of pathogen prevalence.

Like the cultural evolution explanation, the genetic evolution explanation is consistent with findings showing that historical pathogen prevalence predicts cultural outcomes more strongly than contemporary pathogen prevalence. The plausibility of a genetic evolution process is supported by evidence of relatively rapid evolution of different gene frequencies within populations that differ in the prevalence of specific kinds of pathogens (Williamson et al., 2007). Its plausibility is supported also by evidence of a heritable basis for the kinds of attitudes, traits, and values that characterize worldwide cross-cultural differences. For example, the Big Five personality traits—including extraversion and openness to experience—all have substantial heritability coefficients (Henderson, 1982; Jang, Livesely, & Vemon, 1996), and there is also evidence of genetic influence on behavioral tendencies toward individualism and collectivism (Bouchard & McGue, 2003).

But in order to be truly compelling, the genetic evolution explanation must be tested directly against empirical data pertaining to specific genetic polymorphisms that *(a)* are statistically associated with specific kinds of dispositional tendencies, and *(b)* exist in at different frequencies within different cultural populations. Presumably, future genetics research will reveal many such genetic polymorphisms, but the extant literature has identified only a few promising candidates for consideration. One such candidate is a coding-sequence polymorphism on the DRD4 dopamine receptor gene. The long version of this polymorphism has been linked to novelty-seeking behaviors in humans and other primates (Bailey et al., 2007; Schinka et al., 2002), and there are widely different frequencies of this allele in different populations throughout the world (Chen et al., 1999). Another promising candidate is the 5-HTTLPR polymorphic region of the SLC6A4 serotonin transporter gene. The short allele version of this polymorphism has been associated with a variety of cautious and avoidant behavioral tendencies (e.g., Beevers, Gibb, McGeary, & Miller, 2007; Munafo, Clark, & Flint, 2005), and the relative frequencies of short versus long 5-HTTLPR alleles vary substantially across different populations (Gelernter, Kranzler, & Cubells, 1997). Although cultural

psychologists have speculated that variability in these (or other) gene frequencies might covary with psychologically meaningful cross-cultural differences (e.g., Chiao & Ambady, 2007), there has been almost no rigorous research addressing this possibility, nor the possibility that these gene frequencies might help to account for the relationships between pathogen prevalence and cultural outcomes.

This state of affairs may be changing. Recently, Chiao and Blizinksy (2010) reported a provocative result showing that, across several dozen countries worldwide, the relative frequency of short 5-HTTLPR alleles is strongly positively associated with country-level values of collectivism. Moreover, the frequency of short 5-HTTLPR alleles is also positively associated with country-level values of pathogen prevalence, and it partially mediates the relationship between pathogen prevalence and collectivism. These results provide the first empirical evidence to directly test, and support, a gene-frequency explanation for the effects of pathogen prevalence on cultural outcomes.

Of course, regardless of evidence such as this, genetic evolution can provide, at best, only a partial explanation. Even though pathogen prevalence imposes the kind of powerful selection pressure that can result in relatively fast changes in gene frequencies, the pace of genetic evolution is still slow compared to the pace of the other causal processes that may contribute to cross-cultural differences. Genetic evolution certainly cannot account for changes in cultural values that often occur over the course of just one or two generations. For example, compared to populations in East Asia, left-handedness occurs more frequently among populations of East Asian immigrants to North America (Hardyck et al., 1976). This particular difference is consistent with the broader pattern of evidence pertaining to the effects of pathogen prevalence, but a genetic evolution process cannot logically account for it. An additional explanation is required.

## E. Conclusion

So which of these four processes provides the best explanation for the relation between pathogen prevalence and cultural differences? All of them. Each process is conceptually compelling in its own right, and each is buttressed by either direct or indirect empirical evidence of one sort or another. Moreover, not a single one of these processes seems capable of accounting for all the different pieces of empirical evidence. And given that these processes are conceptually independent, there is no logically sensible reason to suppose that any

one process operates to the exclusion of others. All things considered, the most plausible conclusion to draw at this point is that, if pathogen prevalence does indeed exert causal influences on cultural outcomes, these effects are likely to be the result of multiple processes operating at multiple levels of analysis.

It is possible that some of these processes account for some cultural outcomes, but not others. For instance, while epigenetic and neurocognitive processes might mediate the relationship between pathogen prevalence and extraversion, that does not mean they must also play a role in mediating the relationship between pathogen prevalence and conformity, or the relationship between pathogen prevalence and culinary spicing. And while the effect of pathogen prevalence on collectivism might be partially explained by a genetic evolutionary process, the effect on culinary spicing might not reflect any kind of genetic mechanism whatsoever; it might instead reflect a cultural evolutionary process.

Of course, it is also possible that two or more processes might contribute jointly to any particular cultural outcome. Because these processes operate at different levels of analysis, they might operate entirely in parallel. Or, in some cases, they might be causally connected. There is considerable theoretical basis to expect that cultural and genetic evolutionary processes may be entwined in a more complicated coevolutionary process (e.g., Durham, 1991). For instance, within the domain of food preparation, the threat of bacterial infections might lead, through cultural evolutionary processes, to the emergence of cultural norms prescribing the liberal use of spices. Once established, these cultural norms may impose selection pressures on genes associated with a tolerance or craving for spicy foods.

Future research must probe much more deeply into all these possible processes, and it must find ways of more directly testing the implications of each. For example, it would be illuminating to conduct longitudinal studies that document changes in pathogen prevalence within a cultural region (e.g., epidemic outbreaks of infectious disease) and track the cultural effects over time (e.g., consequent changes in social behavior and value systems). This kind of methodology would not only help to identify *which* cultural outcomes are influenced by pathogen prevalence, but it also could document *when* those changes occur. The time frame for those changes could reveal clues to the underlying processes. Any change in population-level norms that transpires within days or weeks of a disease outbreak would indicate the operation of neurocognitive mechanisms. Changes that are specific to a one-generation lag

behind a disease outbreak are more likely to implicate an epigenetic process. And changes that accumulate across multiple generations would be more indicative of a cultural evolutionary process. If the selection pressure imposed by a disease outbreak is substantial enough, longitudinal studies might even be able to test genetic evolutionary processes as well, by assessing whether changes in population-level behavioral norms are accompanied by changes in gene frequencies as well.

This kind of study is ambitious, of course, and would require considerable resources and considerable patience as well, given that some of the most interesting results might take decades to emerge. But, as we noted earlier, it is no simple task to inquire empirically into the origins of cultural differences. For scientists who care about psychology and culture, it is important to ask big questions of this sort; however, we cannot expect the answers to arrive quickly, or easily.

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