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How the Study of Religion and Culture Informs Genetics and Vice Versa

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In some places, cultural and religious practices may be considered distinct parts of life that individuals can choose according to personal preferences. In others, the boundary between culture and religion may be blurred in such a way that being a part of a culture may necessarily include affiliating with a certain religion. Yet what seems shared in many places is the idea that culture and religion are part of the learned environment. Just as a child may learn that fireworks signal the start of the new year, she may also learn that prayer can send messages to a being she cannot see. While laypeople may generally agree that the study of culture and the study of religion have some common ground, when they are asked whether culture and religion have anything to do with genes the answer is likely to be "no." As part of the environment, culture and religion are perceived to be socially transmitted and subject to change. Genes, on the other hand, are rooted in the biological makeup of an individual, and are perceived to be fixed and unmalleable. These two sources of influence are thought to be incompatible with each other, reflecting a larger assumption that nature is incompatible with nurture. Although long-accumulating scientific evidence suggests that behavior is shaped by both nature *and* nurture, the idea that culture and religion are separate and independent from genes is still deeply rooted in lay beliefs about the origins of human behavior.

These lay beliefs also parallel common practices in academic communities. How culture and religion influence human behavior has long been studied within the social science disciplines of anthropology, sociology, and psychology, and have remained relatively independent of the field of genetics. Perhaps there is an underlying assumption that the field of

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genetics has nothing to gain from culture and religion research, and vice versa. Yet, more recently, there has been an emergence of multidisciplinary fields, such as cultural neuroscience, that have attempted to piece together the biological and environmental influences that shape human behavior and thought. Given the importance of culture and religion for a complete understanding of the human mind (Baumeister, 2002; Shweder, 1995), it seems crucial to study how these learned environmental influences, together with genes, jointly shape psychological processes.

In this chapter, our goal is to discuss foundational research on the influence of culture, religion, and genes on behavior while highlighting recent advances in this area. We first summarize psychological research on culture and religion, focusing on how these concepts in psychology can be studied alongside genetics. Next we explain how existing theoretical frameworks can be used to integrate research on culture and religion with genetics, followed by a review of empirical studies in genetics that examine the heritability of religiosity and genetic correlates of religious beliefs and behaviors, evidence of gene–culture coevolution in relation to morality, and gene–environment interaction research on prosocial behavior, immoral behavior, coping, and well-being. In the final section we provide suggestions for future research integrating culture, religion, and genes.

The Study of Culture and Religion in Psychology

People are necessarily cultural beings. Herskovits (1948) defined culture as the human-made part of the environment. Culture is a shared system of beliefs, ideas, and values passed down over generations that continuously informs people how to live their lives appropriately and meaningfully. From a cultural-psychological perspective, culture fundamentally changes how the mind perceives and manipulates environmental input (Shweder, 1995), leading to systematic differences in psychological processes across different cultures.

Beyond conventional conceptualizations of "culture" as synonymous with nationality or ethnicity, there are other forms of culture that may share similar definitional features to these but are not necessarily associated with a single country or ethnic group. Cohen (2009) states that there are other forms of culture, such as religion and social class, which can bind and impact groups of people in psychologically important ways. Religion, in particular, shares many key characteristics with national or ethnic culture. Religion and culture[1] both involve a set of passed-down beliefs

and ideas about how to live one's life appropriately, and both function as resources for making sense of the world. Religion plays a significant role across many cultures (Bloom, 2012; Manuti, Scardigno, & Mininni, 2016), and different religious traditions emphasize certain patterns of behavior or thought, just as culture does. For example, Cohen and Rozin (2001) examined differences in religious groups and found that Protestant Christians were more likely than Jews to condemn immoral thoughts. This finding probably stems from Protestant traditions that emphasize that immoral thoughts inevitably lead to immoral behavior, whereas Jewish traditions do not believe the two are equivalent (Cohen & Rozin, 2001). Other research has included non-Western religious comparisons by examining Buddhists and Christians in the United States. In one study, Tsai, Miao, and Seppala (2007) found that American Christians valued high arousal positive states (e.g., excitement) more than American Buddhists, whereas American Buddhists valued low arousal positive states (e.g., calm) more than American Christians. It is clear that religion can be as influential as more commonly studied forms of culture, such as ethnic and national culture. Understanding religion as a form of culture requires conceptualizing it as a mutually constituted part of the human mind, not just as non-shared individual difference or as "noise." Religion may fundamentally change how people conceptualize their world, and thus it may be useful to study religion as a meaningful form of the sociocultural environment.

Even though the cultural-psychological perspective can be used to study different forms of culture, each culture has unique features that should be highlighted. Religion, unlike other forms of culture, is uniquely centered on the supernatural. Specifically, religion draws from beliefs about sacred items, rituals, and the divine to derive a fundamental understanding of the world based in spirituality[2] (Silberman, 2005). Relatedly, an emphasis on morality, or beliefs about what is right or wrong, is often central to religion. For some, religion is an important source of moral guidance, explicitly prescribing appropriate ways to think or behave (Cohen & Rozin, 2001), and morality seems particularly emphasized in relation to the divine in general, via sacred order, sanctity, and purity (Bloom, 2012). This emphasis on purity is particularly reflected in beliefs and rituals about sex and food (Johnson, White, Boyd, & Cohen, 2011). Religious teachings often focus on specific aspects of morality, explicitly claiming to know what is moral and immoral concerning issues such as abortion and homosexuality (Bloom, 2012). Religion is also unique in that religious membership varies in how it is perceived to be acquired, from membership by birth (e.g., Judaism) to personal faith (e.g., Protestant Christianity; Cohen, Siegel, & Rozin, 2003).

These different aspects of religion may have a unique influence on behavior, above and beyond other forms of culture.

Recent evidence suggests that the effect of religion, as a unique form of culture, can change depending on the broader national culture. The same religious affiliation across different cultures may encourage different strategies to achieve similar goals. Individualistic cultures, such as the North American, emphasize that the self is unique, relatively stable, and distinctly separate from others, whereas collectivist cultures, such as the East Asian, emphasize that the self is inherently connected with close others, and maintenance of social obligations and harmony are highly valued (Markus & Kitayama, 1991). Sasaki and Kim (2011) examined the effects of religion (mainly Christianity) across American and East Asian cultural contexts, focusing on the religiously informed strategies used in each culture to cope with distressing situations. Using multiple methods, they found that religion within American culture promoted the use of more secondary control to cope (e.g., adjustment of the self to the situation, personal spiritual growth), reflecting the focus on the self in individualistic cultures, whereas religion within East Asian culture promoted more social affiliative strategies to cope (e.g., seeking support from religious communities, such as fellowships), reflecting the emphasis on social relationships in collectivist cultures. It is likely that certain teachings born of religion become valued and emphasized more than others over time, and that culture (at the ethnic or national level) is a meaning system that can change which aspects of religion are promoted. Because religion always exists within a greater cultural context, it is important to consider the interaction of religion and culture.

Whether or not religion is studied as a unique form of culture, it is clearly a prominent influence in some people's social environment. Studying religion as a systematic, meaningful aspect of the environment may also have important implications for the integration of research on religion with approaches perceived as very disparate, such as biology or genetics. In addition to the crucial influences of culture and religion on psychology, biological features of the body also need to be considered for a complete understanding of the human mind.

Integrating Culture and Religion with Genetics

Religion is often assumed to be irrelevant or counter to scientific knowledge (e.g., Rios, Cheng, Totton, & Shariff, 2015). Yet, regardless of whether

or not religious beliefs are valid, an understanding of human behavior may be incomplete without studying religion. Although the number of scientific investigations of religion has grown since around the early 2000s, there are still many gaps in basic scientific knowledge about religion and its effects on thoughts and behaviors. Especially when it comes to more "basic" scientific investigations such as biology, relatively few studies use approaches from, for instance, genetics to understand religion. Even though lay beliefs may typically keep religion from being studied together with genes, ironically these are exactly the sorts of investigations that hold the most promise for answering basic questions about how religion influences people, and why.

In the next section, we review research on the heritability and genetic correlates of religious beliefs and behaviors. We then discuss gene–culture coevolution theory by reviewing research on correlations between genetic variations and cultural norms at the societal level. Last, we review research on the interaction of genes with culture and religion, discussing how findings in this area may be relevant for understanding religion as a form of culture with unique features.

The Heritability of Religiosity and the Behavioral Correlates of Religion

What leads people to become more or less religious has often been thought of as a difference of family environment. In other words, religion is perceived to be learned from and socialized by the family at a young age and then carried throughout the lifetime. However, religiosity, or level of self-reported religiousness as indicated by factors such as religious values and attendance, may also be influenced by genes. In addition to providing evidence of the heritability of religiosity, research suggests that genes may also play a part in the etiology of religiosity over the lifespan and in other related constructs such as spirituality and meaning in life.

In a study by Koenig, McGue, Krueger, and Bouchard (2007), monozygotic ($N = 165$) and dizygotic ($N = 100$) adult male twins filled out a questionnaire on retrospective religiosity, current religiosity, antisocial behavior, and prosocial behavior. They found that prosocial behavior was positively correlated with both retrospective and current religiosity ($r = .24$) and antisocial behavior was negatively correlated with both retrospective ($r = -.15$) and current ($r = -.23$) religiosity. There was also shared genetic and environmental variability between religiosity and both

prosocial and antisocial behavior. Prosocial behavior and religiosity shared most of their genetic variability and about half of their environmental variability. Antisocial behavior and religiosity, however, shared nearly all of their genetic variability (indicated with a near-perfect negative multiple genetic correlation of $R = 1.0$), with a small, but significant amount of shared environmental variability). These results suggest a significant, common genetic component underlying religiosity and prosocial and antisocial behavior.

To examine how genes may play a role in religious affiliation, behavior, and attitudes, D'Onofrio, Eaves, Murrelle, Maes, and Spilka (1999) recruited a large US sample of monozygotic and dizygotic twins ($N =$ 14,781) from the Virginia Twin Registry and the American Association of Retired People. Participants filled out a questionnaire, including religious affiliation (65.8% Protestant, 15.5% Catholic, 3.9% Jewish, and 10.3% unspecified), a church attendance scale, and a 5-item subset from a larger inventory measuring social attitudes associated with the "Religious Right." Twin correlations among monozygotic and dizygotic twins on religious affiliation were not significantly different, suggesting an environmental influence underlying religious affiliation. In contrast, when it comes to religious behavior and attitudes, twin correlations were significantly smaller for dizygotic twins than for monozygotic twins. This reduction suggests that the factors underlying religious behavior and attitudes may have a genetic component.

Similarly, there is research that examines whether genetic factors play a role in how religiosity changes across the lifespan. Button, Stallings, Rhee, Corley, and Hewitt (2011) investigated genetic and environmental influences on religious values and attendance in a 5-year, longitudinal twin study in which they sampled monozygotic ($N = 685$) and dizygotic twins ($N = 739$) at two time points (ages ranged from 12 to 18 at wave 1, and 17 to 29 at wave 2). Religious values and attendance were both measured using a subset of items from Jessor's Adolescent Health and Behavior Questionnaire (Jessor & Jessor, 1977). They found that the heritability, or variability of phenotypic expression due to genetic variability of a trait in a population, of religious values and attendance was lower in adolescence and higher in early adulthood. The heritability of religious values, specifically, increased by only a small amount from adolescence, suggesting that religious values are relatively stable. However, the heritability of religious attendance increased significantly from adolescence to early adulthood. During adolescence, shared family environment between twins influenced religious attendance more than genetic factors did. This pattern of results is

consistent with previous research (Koenig, McGue, & Iacono, 2009), and is expected, because religious attendance while living with the family is often controlled by parents. Yet in early adulthood, when young adults gain independence from their parents, genetic factors are likely to predispose them to embrace religious values, which then increases the likelihood that they will attend religious services because of personal religiosity rather than because of parental control in the environment. These findings on the heritability of religious attendance over time are consistent with the findings of D'Onofrio and colleagues (1999) that religious behavior is more similar between monozygotic than dizygotic twins, highlighting the role of genes that underlie religious behaviors.

Button and colleagues (2011) also examined the factors that contribute to the stability of religious values and attendance over time. Shared environmental influences contributed the most to the stability of religious values and attendance for both younger and older adolescents, but there was a significant genetic influence for older adolescents as well. This is in line with the previous finding that the heritability of religiosity increases from adolescence to young adulthood, as well as with previous research that has found a decrease in environmental, and an increase in genetic, influence on religiosity over the lifespan (Kandler & Rieman, 2013; Koenig, McGue, & Iacono, 2008).

Steger, Hicks, Krueger, and Bouchard (2011) examined the relationship between religiosity and two other related concepts: meaning in life and spirituality. The similarity of these three concepts is derived from their common desire for meaning, but distinctions can be made. Meaning in life refers to a person's understanding and realization of the significance and role of his or her life in the greater world (Steger et al., 2011). Using an adult twin sample ($N = 343$), Steger and colleagues collected responses on the Expressions of Spirituality Inventory (the Religiousness and the Cognitive Orientations Towards Spirituality subscales for the religiosity and spirituality constructs, respectively) (MacDonald, 2000) and the Meaning in Life questionnaire (the Presence for Meaning and Search for Meaning subscales were both included) (Steger, Frazier, Oishi, & Kaler, 2006). They found, through biometric modeling, that there were moderate genetic correlations between the Presence of Meaning subscale and the Religiousness ($r = .38$) and Cognitive Orientations Towards Spirituality ($r = .42$) subscales. These results seem to suggest that religiosity, spirituality, and meaning in life share considerable underlying genetic influence. An interesting possibility proposed by Steger and colleagues (2011) is that these three related concepts may be specific features of a broader function that

compels humans to seek reasons for their existence, the significance of their roles in the greater world, and the overall meaning of life itself.

Previous research has also found evidence of genes interacting with some behavioral correlates of religion, such as cooperation. Schroeder, McElreath, and Nettle (2013) tested whether the mere possibility of punishment changes how people with different variants of the serotonin transporter gene (SLC6A4) and the serotonin 2A receptor gene (HTR2A) contribute in a cooperative economic game. They examined two variants of each of these genes within the serotonergic system, because they have been linked with an increased sensitivity to environmental and social threat cues and an increased tendency to experience negative affect (Hariri et al., 2002; Way & Taylor, 2010). In their study, participants ($N = 184$) played two versions (with or without punishment) of the Public Goods Game, a standard game used in experimental economics in which participants are given a certain amount of money and privately choose how much money to contribute to a collective pool that multiplies and is later split amongst the group. The version with no punishment in the current study was always played before the version with the punishment, and punishment was to be given by fellow group members. Results showed that SH2 homozygotes of SLC6A4 (SH2 was classified as having a short allele at 5-HTTLPR and a 10-repeat allele at serotonin transporter intron 2 variable number of tandem repeats (STin2 VNTR)) contributed less money to the pool in every round than SH1 homozygotes and heterozygotes (SH1 was classified as having a short allele at 5-HTTLPR and a 12-repeat allele at STin2 VNTR) in the no-punishment version, but in the presence of punishment they increased their contribution to about the level of SH1 homozygotes and heterozygotes. Overall, SH1 homozygotes and heterozygotes consistently contributed more money to the pool than SH2 homozygotes, which suggests that SH1 carriers internalized the group's norms and felt more social pressure from fellow group members to contribute. However, the difference in contributions between SH2 homozygotes and SH1 homozygotes and heterozygotes diminished once there was punishment. Interestingly, HH1 homozygotes and heterozygotes of HTR2A (HH1 was classified as G and C alleles at reference single nucleotide polymorphism rs6311 and rs6313) did not differ from HH2 homozygotes (HH2 classified as A and T alleles at rs6311 and rs313) in amount of contributions when playing the version with no punishment. However, the mere presence of punishment was enough to increase the contributions of those with HH1 compared with those homozygous for HH2, suggesting HH1 individuals were highly sensitive to potential punishment. This research raises the

question of whether the differences in genotypes that led to smaller group-level behaviors could have bigger consequences in large populations that differ in these genotypes, especially in religious communities that create pressures for punishment avoidance.

Taken together, these results suggest that religiosity and its behavioral correlates may be at least partially influenced by genes, and a consistent pattern seems to be that heritability of religious traits increases over time. While high heritability of traits highlights the importance of genes, it is also important to understand that genetic influence is not necessarily fixed. Genes often interact with the surrounding environment to lead to changes in traits and behaviors over the course of the lifespan. Thus, a possible explanation for the increase in heritability of religious traits may come from mutual influences between genes and the environment. Certain genes may predispose an individual to embrace religious values, which influence individuals to choose and shape the environment around them to suit and reinforce their predisposition. In the following sections, we discuss different theories and frameworks that have examined this gene–environment interplay.

Gene–Culture Coevolution

Although a number of studies suggest that there may be genetic predispositions for stable traits, such as religiosity, or for morally relevant behaviors, there is no evidence of one-to-one mapping between specific genes and religiosity. Like many complex social behaviors, "religion" is unlikely to be reduced to a single gene or set of genes. It is also important to recognize that most traits and behaviors are influenced by a complex interplay of genetic and environmental factors. Basing their research on the idea that cultural norms and genetic predispositions in a population can influence each other via processes of cultural and genetic selection (dual-inheritance theory, Boyd & Richerson, 1985; gene–culture coevolution theory, Chiao & Blizinsky, 2010; Feldman & Laland, 1996), Mrazek and colleagues (2013) examined whether gene–culture coevolution may account for differences in morality judgments across nations. Using pre-existing data from 21 countries, researchers in this study found, first, that the level of historical ecological threats predicted greater tightness (versus looseness) in a culture, which is characterized by more cautious behavior or preference for structure (Gelfand et al., 2011). It is theorized that normative behaviors related to tightness may have been adaptive as a response

to ecological threats, such as the prevalence of disease. Second, cultural tightness–looseness covaried with the proportion of s allele carriers of 5-HTTLPR, a polymorphic region on the serotonin transporter gene, which has been related to harm avoidance in previous findings (Munafo, Clark, & Flint, 2005). This finding crucially suggests that cultural norms surrounding harm avoidance are also reflected in dominant genetic predispositions in a population, perhaps because of processes of gene–culture coevolution. Finally, this study showed that the proportion of 5-HTTLPR s alleles in a population and cultural tightness–looseness predicted whether people justified a series of morally relevant behaviors from the World Value Survey, including divorce, prostitution, evading taxes, and avoiding a fare on public transit. Mediation analyses demonstrated that population-level s allele frequency predicted a lower likelihood that these morally relevant behaviors would be justified in a culture, and this association was explained by the degree to which a culture endorsed tight (versus loose) norms (Mrazek et al., 2013). In other words, it seems that normative endorsement of morally relevant beliefs, such as whether it is justifiable to evade taxes, may be linked to dominant genotypes in a population and culturally shared beliefs about avoiding harm. Genetic tendencies and cultural norms may mutually influence each other over time via gene–culture evolutionary processes, and both genes and culture may be ecologically influenced, for example by the historical threat of disease. This research is one of only a few studies that have examined how morality may be influenced by a complex set of macroevolutionary processes involving genes and culture.

Gene–Environment Interactions

While gene–culture coevolution theory aims to uncover the more macro-level processes that underlie cultural and genetic influence, the gene–culture interaction framework (G × C) is a complementary model that focuses on the more micro-level processes of gene–culture interplay. G × C is based on the broader framework of gene–environment interactions (G × E), demonstrating that the same environment may lead to different outcomes according to differences in genes, and, similarly, that the same genetic predisposition may lead to different outcomes according to differences in the environment (Caspi et al., 2003). Some recent research has used the G × E framework to conceptualize religion and culture as important aspects of the environment that may interact with genes. A few studies

have investigated how genetic predispositions interact specifically with different aspects of religion, whether it be the salience of the concept of religion, religious affiliation, or the level of religiosity, to predict different behavioral outcomes. These different ways of studying religion – as a form of culture with unique features (Sasaki et al., 2013), as a group identity with shared norms (Jiang, Bachner-Melman, Chew, & Ebstein, 2015), and as a level of involvement that can interact with other forms of culture (Sasaki & Kim, 2011) – can all be incorporated with genetics research in fruitful ways.

Implications for Prosocial Behavior

In one of the first experiments to directly examine a gene–religion interaction, Sasaki and colleagues (2013) found that genes may interact with religious information in the environment to influence prosocial behavior. In this study ($N = 178$), participants completed a sentence scramble task designed to implicitly prime concepts (that is, they were asked to make sentences from a string of words); about half the participants were exposed to religion-relevant words (e.g., God, spirit, divine, prophet, and sacred) and the other half were exposed to neutral words that formed no coherent theme (e.g., shoes, sky, holiday, worried; Shariff & Norenzayan, 2007). After the sentence scramble task was completed, the dependent variable – prosocial behavior – was measured in an ostensibly unrelated study. Participants read about a number of actual organizations which supported the environment on their college campus (e.g., the Green Campus Program), and prosocial behavior was measured by asking participants to complete a checklist to indicate whether they would like to get involved. They could indicate their wish to get involved by asking for more information about an organization, asking to be added to an organization's mailing list, and volunteering to get involved in organizational projects. Higher scores ("yes" responses) on the checklist indicated greater behavioral intentions to help society in general by volunteering their time to help these prosocial causes. This study showed that people with 2- or 7-repeat allele variants of a dopamine receptor gene (DRD4) were more prosocial when they were exposed to a religion prime than when exposed to a neutral prime. However, people without the 2-/7-repeat allele variant were not significantly influenced by the religion prime. Using an experimental manipulation of religious salience, this study was able to demonstrate that thinking about religion may causally influence prosocial behavior but that this effect crucially varies according to genetic predisposition. Given that the 2-/7-repeat

allele of DRD4 may be linked to reward sensitivity, it is notable that people with this DRD4 variant were the most likely to act prosocially when there seemed to be a compelling reason to behave in this way (that is, when they were given an implicit reminder of God, which has been shown in past studies to increase prosocial behavior: Shariff & Norenzayan, 2007; see Shariff, Willard, Andersen, & Norenzayan, 2016 for meta-analysis), yet those with this same variant were also the least likely to behave prosocially when there was no particular motivator present. Importantly, in this study participants with the 2-/7-repeat allele of DRD4 did not differ from those without it in baseline religiosity or in self-reported level of religiousness, yet they changed their level of prosocial behavior if they were reminded of religion.

A similar gene–religion interaction was found in a correlational study comparing different religious affiliations (only among men; Jiang et al., 2015). This study included a sample of 2,288 Han Chinese participants who identified as Buddhist/Tao, Christian, or without religious affiliation. Altruism was measured using a resource-allocation task (the Andreoni–Miller Dictator Game; Andreoni & Miller, 2002) in which participants were classified according to their sharing behavior in the task. Results showed that among men with more reward-sensitive variants of DRD4 (i.e., mostly 2-repeat alleles given the East Asian sample), Christians demonstrated more altruistic giving behavior than non-Christians. Specifically, Christians with this genotype were more likely to increase fair behavior (splitting resources equally) and deviate from selfish behavior (keeping all resources for themselves) than non-Christians with the same genotype. Among men with less reward-sensitive DRD4 variants (i.e., two 4-repeat alleles), however, there was no difference in giving behavior between Christians and non-Christians. Interestingly, this pattern of results seemed to hold only for Christians versus non-Christians and not Buddhists/Taoists versus non-Christians. These findings suggest that the content of religious beliefs may play an important role in promoting prosocial behavior, and that some behavioral implications of religious (versus non-religious) beliefs may only emerge among people with particular genetic predispositions. What are the possible explanations for this G × E effect on prosocial behavior? The DRD4 2-/7-repeat allele variant may be linked to lower baseline dopamine signaling, which may translate to a greater motivation to increase dopamine to reach "normal" levels of cAMP reduction. Therefore, people with this genotype may be more likely to seek external motivators for their prosocial behavior because, for them, this maximizes their feelings

of reward. For people without the DRD4 2-/7-repeat allele variant, who have higher baseline dopamine signaling and less motivation to increase dopamine, external motivators such as religion may not be as necessary for them to behave prosocially. Differences in motivation may explain why people with and without the 2-/7-repeat allele variant of DRD4 respond differently to religion in their environment. An interesting and as yet untested possibility is that people with different variants of DRD4 are all capable of behaving prosocially, but they do so for different reasons. People with the 2-/7-repeat allele may behave prosocially because they are motivated by the feelings associated with the reward that they might receive externally, while for people without the 2-/7-repeat allele the act itself may feel good enough.

Implications for Immoral Behavior

As mentioned previously, one of the features unique to religion is its emphasis on morality. Given that morality is an important feature of religion in certain contexts, it may be useful to consider research that has looked at the relationship between morality, culture, and genetics. Kong (2014) used a gene–environment perspective to examine relationships among corporate corruption, wealth, cultural endorsement of self-protective leadership, and 5-HTTLPR genotypes across cultures. Previous research has found that those with at least one s allele (s/s or s/l genotypes of 5-HTTLPR) attend more to negative affect and threat than those without the s allele (l/l genotypes of 5-HTTLPR) (Fox, Ridgewell, & Ashwin, 2009; Karg, Burmeister, Shedden, & Sen, 2011). Kong (2014) found that although low wealth increases corporate corruption in general (as low wealth leads to an environmental need to engage in self-protective behavior, such as corporate corruption), 5-HTTLPR moderated the relationship between wealth and corporate corruption. Societies with high 5-HTTLPR s allele frequencies tend to experience greater amounts of corporate corruption than societies with low 5-HTTLPR s allele frequencies. In addition, Kong (2014) found that wealth had a stronger relationship with cultural endorsement of self-protective leadership in societies with low 5-HTTLPR s allele frequencies than in societies with high 5-HTTLPR s allele frequencies. This research suggests that population genetics may interact with social and economic factors in ways that go above and beyond the individual influences of genes and the environment, and that, furthermore, these interactive effects may be linked with moral behavior at the societal level.

Implications for Coping and Well-Being

Some gene–religion studies have also demonstrated implications for coping behaviors and well-being. Sasaki, Mojaverian, and Kim (2015) examined the extent to which the DRD4-by-religion interaction found previously (Sasaki et al., 2013) was specific to prosocial behavior as an outcome. If people with the susceptibility variant of DRD4 are sensitive to any environmental input, perhaps they would just be more impacted by the religion prime in general, and any pre-existing relationship between religion and an outcome would be strongest among those with environmental susceptibilities, such as those with the 2-/7-repeat allele of DRD4. This recent investigation (Sasaki et al., 2015) put participants in a mildly distressing situation and tested whether the effect of religion priming on their coping behavior, which has been found in previous research in European-American samples (Sasaki & Kim, 2011), would be stronger among people who are supposedly more susceptible to the environment than those who are not. This was not the case. European Americans in this study were more likely to exhibit control-related coping behaviors, such as inhibiting their negative affect in front of the experimenter, when they were primed with religion versus not, replicating the initial finding (Sasaki & Kim, 2011); however, this effect of the religion prime on coping behavior was not moderated by the DRD4 genotype. But, interestingly, when a gene that is more relevant to socio-emotional sensitivity as a motivator of behavior was examined, a gene-by-religion interaction emerged. The G (vs. A) allele of the oxytocin receptor gene (OXTR) polymorphism rs53576 has been linked to more sensitive parenting (Bakermans-Kranenburg & van IJzendoorn, 2008) and greater empathy (Rodrigues, Saslow, Garcia, John, & Keltner, 2009). Sasaki and colleagues (2015) found that the effect of the religion prime on coping behavior was moderated by OXTR in such a way that among people with the G allele, who tend to be more socio-emotionally oriented, the religion prime increased their control-related coping behavior (that is, they inhibited their negative affect). However, among people with the A allele, who tend to be less socio-emotionally oriented, the religion prime did not influence their control-related coping (Sasaki et al., 2015). It is informative to consider these results together with the earlier findings on prosocial behavior (Sasaki et al., 2013), because it shows that it does not seem to be the case that one gene interacts with any environment indiscriminately to affect any psychological outcome. Instead it seems more likely that when people think about religion (versus not), people with certain predispositions to reward motivations may be

impacted psychologically in a way that is relevant to reward, while people with other predispositions linked to socio-emotional motivations may be influenced in a way that is relevant to expressing emotions in social interactions.

Most of the studies so far have examined how genes interact with culture (Kim et al., 2010) or with religion (Sasaki et al., 2013), but in this next study researchers integrated gene–environment interactions with perspectives on both culture and religion (Sasaki & Kim, 2011) to examine how the interaction of religion, culture, and genes has implications for well-being. Previous research has shown that religiosity seems to be generally associated with greater well-being (McCullough, Hoyt, Larson, Koenig, & Thoresen, 2000, but see Diener, Tay, & Myers, 2011 for evidence of nation- and state-level moderation of this effect), and that one of the key mechanisms explaining this relationship may be social affiliation, or spending time and interacting with close others (Thoits, 1995; Wills, 1998). The extent to which religion encourages social affiliation, however, may vary depending on the broader cultural context. In North American culture, religion tends to encourage social affiliation less than in East Asian culture (Sasaki & Kim, 2011), where social relationships with others are highly emphasized (Markus & Kitayama, 1991). Therefore, research suggests that the link between religiosity and well-being may be moderated by culture, so that it is stronger in East Asia than in North America because of the greater emphasis on social relationships in East Asia. In order to utilize a G × E perspective, a study ($N = 242$) examined whether the predicted cultural difference in the link between religiosity and well-being would emerge only among people who are predisposed to care about social relationships (Sasaki, Kim, & Xu, 2011). Religiosity in this study was measured by the Religious Commitment Inventory (Worthington et al., 2003). Well-being was indexed by lower scores on a composite of two psychological distress measures: the Brief Symptoms Inventory (BSI; Derogatis & Spencer, 1982) and the Perceived Stress Scale (PSS; Cohen, Kamarck, & Mermelstein, 1983). Results indeed showed that for people with the G/G genotype of OXTR, who should be more motivated to care about social connectedness, religiosity predicted greater well-being (or lower psychological distress) among East Asians, but this same relationship between religiosity and well-being did not occur for European Americans. In fact, among European Americans, religiosity predicted lower well-being for people with G/G genotypes. However, for people with A/G or A/A genotypes, who should be less motivated to care about social connectedness, there was no cultural difference in the link between religiosity and

well-being. Overall, this study demonstrates that religiosity may predict greater well-being only when the broader cultural context supports greater social affiliation in religious groups, and this matters more for people who are predisposed to care about social relationships in the first place.

Conclusions and Future Directions

Culture and religion, at first glance, may seem irrelevant to genetics. However, this lay assumption is unwarranted. There is increasing evidence that genes influence and interact with different cultures and religions. Our initial goal in this chapter was to familiarize the reader with how culture, religion and genetics research can be integrated with each other, and why this integration is important.

Although relatively few studies examine culture, religion and genes together, there is a growing awareness of the benefits of this type of cross-disciplinary research. There are a number of promising perspectives that can frame future research questions in this area. Gene–culture coevolution theory can examine whether dominant genetic tendencies in a population are linked to cultural norms (Chiao & Blizinsky, 2010), and the gene–culture interaction model can test whether genetic tendencies at the individual level can change according to differences in the cultural context (Kim et al., 2010). The broader gene–environment interaction framework (Caspi et al., 2003) can be used to test potential interactions between genetic tendencies and religious influences (Sasaki et al., 2013) by conceptualizing religion as a form of culture (Cohen, 2009) with a unique emphasis on the supernatural. The cultural shaping of religion (Sasaki & Kim, 2011) can also be examined simultaneously with the gene–culture interaction model to examine culture, religion, and genes together (Sasaki et al., 2011).

We offer this chapter as a way to provide the initial foundation for an understanding of gene–culture interactions, as well as to demonstrate how this framework can benefit culture and religion research by uncovering the underlying biological mechanisms of cultural and religious influence. Discoveries of gene–culture interactions can also benefit the field of genetics by showing that shared, complex social environments such as cultural and religious contexts can have significant downstream effects on behavior via their interaction with the biological body. We hope this not only informs future research in this area, but also encourages other seemingly unrelated areas to consider gene–environment interactions as a broader framework for explaining important processes in psychology.

Notes

1 Here, and later in the chapter, we use "culture" in the more conventionally understood way, to mean national or ethnic culture.
2 While religiosity and spirituality are both concerned with the pursuit of the sacred, the former is guided by existing communities and contextualized rituals, and the latter is often self-driven and individualized (Hill et al., 2000).

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