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Cultural and Genetic Influences on Emotion: The Role of Motivational Processes in Gene-Culture Interactions

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Imagine you have just arrived in a country you have never visited before. The language spoken is different from yours, and yet you find that you are able to communicate at least some of your sentiments with the local people. You can express your feelings of excitement, perhaps from being in an exotic environment, as well as your frustrations from getting a little lost. Through your facial expressions, gestures, and physiological responses—sweating palms, a racing heart, and rapid breathing—some of your basic emotions come across to the people you meet. Although the general meaning of certain emotions may be shared, are emotions experienced and expressed in the same way across cultures? How do biological factors, such as genetic and physiological processes, interact with social and cultural factors to influence emotions? In this chapter, we first review research on culture and emotional experience and expression. Next, we review the theoretical background for gene-culture interaction research, and we put forward a novel hypothesis that considers the role of motivational processes in these interaction effects: the motivational setting hypothesis. We then discuss gene-culture interaction research with cultural psychological findings in the area of emotion.

CULTURE AND EMOTION

Research on culture and emotion can be traced to the origins of facial expression research, and it is proposed that emotions have the evolutionarily adaptive value of communication. Darwin once said, "We have also seen that

expression in itself, or the language of the emotions, as it has sometimes been called, is certainly of importance for the welfare of mankind" (Darwin, 1872/1965, p. 366). According to Darwin, emotions evolved to protect the body and to signal it from threats or acts of force, suggesting that emotions are biologically based and not highly influenced by cultural modes. He also noted that there are basic emotions and that they are universally expressed.

Darwin's point was followed up by Ekman (1972, 1977) and Izard (1971), whose studies provided further support for Darwin's notion of basic human emotions. The basic discrete and universally recognized emotions include anger, disgust, sadness, fear, joy, and surprise. In some of their most well-known studies on basic emotions, Ekman and Friesen took photos of individuals posing with different emotional facial expressions and then sent them to different universities across the world (Ekman & Friesen, 1971; Ekman et al., 1987). Participants in these different cultures were asked to match the emotional facial expression in the photos with one emotion from the list of emotional words. As expected, high agreement was found across cultures, supporting the universality position.

However, other research findings question the universality of facial expressions of emotion (Jack, Garrod, Yu, Caldara, & Schyns, 2012; Russell, 1994). In recent work by Jack et al. (2012), researchers used a computer graphics program to generate three-dimensional simulations of human facial movements. When Western and Eastern culture individuals were asked to categorize the facial animation by the six emotions (or indicate "do not know"), researchers found cultural differences in facial expression categorization such that Easterners tended to show lower recognition levels for negative faces compared to Westerners.

In addition to potential differences in emotion recognition, there is good evidence for cultural differences in emotion processes (see Mesquita & Walker, 2003). For example, growing evidence shows how specific emotions, such as shame, can show different patterns of experience and expression (e.g., D. Cohen & Nisbett, 1994; Eid & Diener, 2001; Elfenbein, Beaupré, Lévesque, & Hess, 2007; Fischer, 1999). Cultural differences have been observed with respect to emotion appraisals, emotion norms, emotion types, and emotion regulation (Butler, Lee & Gross, 2007; D. Cohen, Nisbett, Bowdle, & Schwarz, 1996; Eid & Diener, 2001; Elliot, Chirkov, Kim, & Sheldon, 2001; Kitayama, Markus, & Matsumoto, 1995; Kitayama, Mesquita, & Karasawa, 2006; Markus & Kitayama, 2003; Matsumoto & Kupperbusch, 2001; Mesquita & Frijda, 1992; Mesquita & Karasawa, 2002; Oishi, Diener, Scollon, & Biswas-Diener, 2004; Scherer, 1997; Schimmack, Oishi, & Diener, 2002; Scollon, Diener, Oishi, & Biswas-Diener, 2004; Tamir et al., 2016; Tsai, Knutson, & Fung, 2006). The key findings are that the same event is experienced more positively in individuals from Western cultures than Asian cultures and that Asian culture encourages emotion

suppression more than Western culture (Matsumoto et al., 2008; Mesquita, & Karasawa, 2002). Emotions are individual's lived experiences that are shaped by individual experiences, attributes, and social contexts. Thus, human dynamics and social interactions are crucial for the formation and experiences of emotions. Next, we define emotion, describe the cultural model of independence and interdependence, and review traditional research findings on culture and emotion.

Emotion Definitions and Cultural Models

We consider emotion to broadly encompass both conscious and unconscious multifaceted phenomena, defined as "transient, bio-psycho-social reactions to events that have consequences for our welfare and potentially require immediate action," taking into account both biological and sociocultural influences on emotion (Matsumoto & Hwang, 2012, p. 92). Emotions are composed of physiological arousals, are consciously experienced feelings and thoughts, and are experienced differently depending on the sociocultural context. Emotions are conceptualized as multifaceted, entailing subjective experiences of the self that might change depending on the cultural meaning system.

Considerable research on emotion has focused on the independent and interdependent self-construal models to describe the ways individuals understand the self. The independent self-construal is most characteristic of individualistic cultures and characterizes the self as a bounded, self-sufficient, and autonomous self that is separate from others (Markus & Kitayama, 1991). On the other hand, the interdependent self is associated with collectivistic cultures. Individuals with an interdependent self-construal often define themselves based on their relationships with others and emphasize the relatedness between people. Importantly, their actions are guided by the relationship the self has with others, and its primary goal is to strengthen interpersonal bonds (Markus & Kitayama, 1991). Therefore, individuals with dominant independent self-construals are expected to emphasize and feel more ego-focused emotions, such as pride, and use emotions as a way to express themselves and enhance their self-esteem. In comparison, individuals with dominant interdependent self-construals may be more likely to emphasize and feel other-focused emotions, such as shame and empathy, to nurture social harmony within the ingroup, and use emotions to regulate appropriate social behavior.

Positive and Negative Emotional Experiences

Are different emotions experienced to the same degree across cultures? Research shows that good feelings are more emphasized in North American

contexts, resulting in a relative prevalence of positive emotions compared to East Asian contexts (Heine, Lehman, Markus, & Kitayama, 1999; Mesquita, & Karasawa, 2002; Oishi, 2002; Tsai & Levenson, 1997). Cultural models appear to explain the findings across cultures. The rationale is that people with a predominantly independent self tend to highlight good feelings and engage in self-enhancement and, as a result, experience more frequent positive emotions than people with a predominantly interdependent self (Heine et al., 1999; Triandis, Marin, Lisansky, & Betancourt, 1984).

For example, Tsai and Levenson (1997) asked dating European American and Asian American couples to describe their greatest relationship conflict while being recorded in the laboratory. Couples then watched the videotape of their conflict conversation and provided continuous reports of positive and negative emotions while watching the video. European American couples reported more positive emotions compared to Asian American couples, whereas no cultural differences were observed in negative emotions. In a study using experience sampling, American, Japanese, and Taiwanese students reported the last emotion they had experienced and rated the pleasantness of the event (Mesquita & Karasawa, 2002). The questionnaires were administered four times a day for 1 week. Japanese and Taiwanese students evaluated their lives, on average, as neither positive nor negative, whereas American students evaluated their lives as better than neutral. Taken together, these two studies suggest that people from Western cultures (e.g., North Americans) compared to Eastern cultures (e.g., Asians) generally experience more positive emotions (Diener, Suh, Smith, & Shao, 1995; Oishi, Schimmack, Diener, Kim-Prieto, Scollon, & Choi, 2007).

Yet some research suggests that this cultural difference in emotional experience may be more robust for judgments that are retrospective rather than online or in the moment. Another experience sampling study, for instance, found cultural differences in retrospective judgments of emotions but no differences in online judgments of emotions (Oishi, 2002). Across four studies, European Americans tended to be more positive in their retrospective judgments of emotions and life satisfaction, despite the lack of differences in positive and negative experiences at the time of the event. Participants provided daily reports of emotions and retrospective judgments at the end of week, and the results showed that European Americans tended to remember events more positively than Asian Americans. This study provides some evidence that people may similarly experience both positive and negative emotions at the moment of the experience but that cultural differences arise in reports over time. It also seems to be the case that the differences lie in the ways individuals experience or evaluate positive emotions (but not negative emotions), suggesting that, over time, European Americans are more likely to focus on positive events and provide higher positive emotions.

Socially Engaging and Disengaging Emotions

While previous research has mostly focused on overall positive or negative feelings,[1] some researchers have expanded to other important dimensions of emotion, such as degree of sociality. Kitayama and colleagues (2006) examined whether emotions involve social disengagement versus engagement,[2] which refers to the "degree to which an emotion affirms the identity of an individual as a distinct, separate entity (disengaged) versus the individual as part of a social group (engaged)" (Scollon et al., 2004, p. 307). The expectation is that particular emotions will be more emphasized and meaningful in cultures in which they support the cultural meaning system. Thus, socially engaging emotions, such as feelings of social harmony, may be highlighted in interdependent cultures, whereas socially disengaging emotions, such as feelings of personal achievement and self-focus, may be highlighted in independent cultures. Indeed, Kitayama and colleagues (2006) found that North Americans reported higher frequencies of socially disengaging positive and negative emotions (e.g., pride and anger), whereas Japanese reported higher frequencies of socially engaging positive and negative emotions (e.g., respect and shame). Culturally relevant emotions also seem to have downstream implications, as they more strongly predict subjective well-being in their respective cultures. Japanese subjective well-being was more strongly related to the experience of socially engaging positive emotions than with disengaging emotions and the reverse pattern was observed for North Americans. In general, these cultural differences provide evidence supporting the cultural shaping of emotional experiences.

Emotion Regulation

Emotions involve not only the expression and experience of strong feelings but also the suppression of feelings, or inhibition of emotional expression. Are there differences in the ways individuals regulate their emotions across cultures (e.g., inhibit feelings of negative emotions)? Are there differences in default regulation strategies? Do individuals with different self-construals use different strategies depending on the context? According to recent findings on emotion regulation, individuals with different cultural lenses use different emotion regulation strategies, and these different strategies may have different implications depending on the cultural context (Butler et al., 2003, 2007; Cole, Bruschi, & Tamang, 2002; Gross, 2002; Gross & John, 2003; Richards, Butler, & Gross, 2003).

Earlier work on emotion suppression was mostly conducted in a North American context. In independent cultures, inhibiting negative emotions has been linked to poor social consequences, such as avoidant attachment styles and poorer peer-rated likability, and elevated physiological markers

of stress (Butler et al., 2003; Gross 1998). For example, individuals who inhibited their emotions were more likely to be evaluated poorly by informants (Butler et al., 2003). Furthermore, high emotion suppression in facial expression has been linked to more physiological reactivity to stressful situations than high emotion expression. The argument is that suppression makes individuals feel inauthentic and bad about themselves because outward expression of a negative emotional experience is suppressed. As a result, individuals are more likely to experience negative emotions.

More recent attempts have documented cultural differences in emotion regulation and questioned the effectiveness of emotion suppression (Butler et al., 2007; Gross & John, 2003; Mauss & Butler, 2010; Soto, Levenson, & Ebling, 2005). These findings provide some evidence that context plays a key role in determining the effectiveness of certain emotion regulation strategies. Interdependent individuals may consider suppression of emotions as a valuable self-regulation strategy to maintain social harmony, and thus downplay feelings of negative emotions (Matsumoto et al., 2008). In comparison, independent individuals may value the expression of emotions (especially positive emotions) as a way to boost self-assertion and independence.

One study from the United States showed that individuals who held more collectivistic values were more likely to suppress their emotions in daily life than individuals who held more individualistic values, and furthermore, cultural values moderated the association between emotion suppression and social consequences (Butler et al., 2007). In this study, researchers randomly assigned participants to either the suppression group or control group and examined their emotion suppression during a face-to-face interaction with a partner after watching a documentary war film. In contrast to earlier findings, suppression was linked to fewer negative outcomes for people who held Asian rather than European American values. Interestingly, individuals with Asian (vs. European American) values who were instructed to suppress their emotions were less likely to be seen as hostile and withdrawn by their interaction partners.

Current Gaps in Culture and Emotion Research

Although the literature on culture and emotion is rich, there are certain areas that should be developed further in order to continue making progress on this topic. Most research on culture and emotion has compared North Americans to East Asians, and thus, we focus mostly on these cultural groups in this chapter. However, we do not want to suggest that emotions are experienced in the same way within all independent or interdependent cultural groups. For instance, Mexico is a more collectivistic culture than North America (Hofstede, 1980); however, their interdependent self differs from East Asians' interdependent self (Klein, 2001; Valdes, 1996). In order

to understand emotional experiences, it is important to move beyond the dimensions of the independent and interdependent self and contextualize emotions within other aspects of the broader cultural context (e.g., hierarchical nature of the society and gender role). Furthermore, research should consider potential interactions of self models with the broader society, which may result in unique forms of independence (e.g., American independence vs. German independence) and interdependence (e.g., Korean interdependence vs. Japanese interdependence) across societies.

Perhaps most relevant to this chapter, empirical evidence of cultural differences in emotion has often been kept separate from understandings of the biological underpinning of emotion, despite calls to integrate these perspectives (Mesquita & Frijda, 1992). One missing piece in this literature on culture and emotion is the link to physiological and neurological responses, as well as genetic influences. Examining individuals' physiological responses to particular types of emotions as well as their genetic composition may facilitate understandings of the nature and range of emotional experience. It is likely that experiences of particular emotions have at least some genetic basis, and thus, a more nuanced understanding of emotion may come from considering not only sociocultural influences but also biological influences such as genes.

BIOLOGY AND EMOTIONS

The idea that emotions are intrinsically tied to biology dates back to William James. "[B]odily changes," he writes, "follow directly the perception of the exciting fact, and [. . .] our feeling of the same changes as they occur IS the emotion" (James, 1884, p. 190). His insistence on considering the body in emotional experience was prescient, as advances in genetics, neuroscience, and physiology today continue to uncover the importance of these underlying factors in understanding emotion. Certain genetic variants, for instance, seem to be linked to higher physiological stress reactivity as evidenced by increased heart rate (Rodrigues, Saslow, Garcia, John, & Keltner, 2009), and the expression of these genes can influence fear and anger response in the brain (Puglia, Lillard, Morris, & Connelly, 2015), suggesting that genetic factors may form the basis for a cascade of neural and physiological events that contribute to emotional experience.

Why Study Genes?

If scientists can measure emotion not only explicitly by asking people what they are feeling but also implicitly by measuring their physiological and neurological responses, what does it add theoretically to also know their genotype and expression of particular genes? First, humans are biological

beings, so psychological questions such as those involving emotional experience need to consider more than just what people say if we want to understand what people do and why (Nisbett & Wilson, 1977). Second, to the extent that genes contribute to first building the body and with it, the brain, genes may be ultimate explanations for emotional experience. Finally, biological systems are complex and ultimately need to be studied at multiple levels, including at the level of genes, in order to achieve a more complete understanding of how humans develop and function.

Yet the influence of genes cannot be understood separately from the cultural inputs that shape the brain, and thus, the mind. Humans are biological beings, but they are also social beings. Most human experiences, including emotions, unfold in the context of a broader social or cultural environment. People with certain genetic predispositions may be more likely to perceive emotion-eliciting events and experience physiological changes that are interpreted as emotion. At the same time, what people consider "emotion eliciting" and the way they interpret certain physiological experiences can be influenced by culture. Therefore, perspectives that integrate both genetic and cultural factors may be useful for predicting what people feel and what they want to feel.

Reconciling Gene-Culture Interactions with the Differential Susceptibility Hypothesis

According to the gene-culture interaction model, culture is a form of environment that can interact with genes to predict psychological outcomes (H. S. Kim & Sasaki, 2014; H. S. Kim et al., 2010). Because the cultural context provides information about what is valued and normative, the same genetic predisposition may manifest itself in different ways depending on culture. While the gene-culture interaction model builds on some previous frameworks, a growing collection of gene-culture interaction findings also raises important questions about how nature and nurture interact in different psychological domains.

The gene-culture interaction model is based on the framework of gene-environment interactions, which suggests that people with the same genetic predispositions may have different outcomes depending on variation in the environment and that the same environment may lead to different outcomes depending on variation in genetic predispositions (Caspi et al., 2002, 2003). Recent research has further theorized that gene-environment interactions may have particular evaluative consequences. According to the *differential susceptibility hypothesis*, the same people who are more sensitive to negative environments and experience worse outcomes may also be the ones who are more sensitive to positive environments and enjoy better outcomes (Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2007; Belsky et al.,

2009; Obradović & Boyce, 2009; Way & Taylor, 2010). As Belsky and colleagues (2007) suggest, people with certain genetic predispositions may be susceptible to both helpful and harmful environments around them, "for better and for worse." Importantly, the perspective of differential susceptibility shifted the focus away from sensitivity to only negative environments, as highlighted by the diathesis-stress framework, and demonstrated instead that the people once assumed to be "at risk" in non-supportive environments may actually fare the best when placed in supportive environments (Belsky et al., 2009).

However, it is difficult to say that being in one cultural environment is largely "for better" while being in another is "for worse." Cultural psychology emphasizes that the way people respond to the environment can be shaped by socially shared meanings about that behavior or event. Culture exists in every environment, whether positive or negative, providing meaning to actions. Across a number of gene-culture interaction studies, it seems that certain people tend to be more "culturally sensitive" than others in particular domains, including for positive outcomes such as social support (H. S. Kim et al., 2010) or prosocial behavior (Sasaki et al., 2013). At first glance, these findings seem consistent with the differential susceptibility hypothesis because it is clear that genetic susceptibility to environments is not solely negative. Yet, because culture is not an environment that can be clearly conceptualized as solely beneficial or harmful, the differential susceptibility hypothesis does not fully capture findings of gene-culture interactions.

The Motivational Setting Hypothesis

We propose the *motivational setting hypothesis* as a possible alternative for reconciling findings of gene-environment or gene-culture interactions together with those of differential susceptibility. There are a number of assumptions under this hypothesis: (1) According to the motivational setting hypothesis, genetic variation may predict how motivated people are to achieve goals within a particular psychological domain (e.g., anxiety, reward, and sociality). (2) Within a given domain, people with certain genotypes may be highly motivated to distinguish whether a stimulus is relevant to anxiety, reward, sociality, and so forth, compared to people with other genotypes. Therefore, people may exhibit one psychological response as a "default" because it best meets their goal, but they will move away from the default response according to relevant input from the environment if this behavioral change would better suit their goal. In general, people will behave in the way that matches their genetically predicted motivation. (3) The environment is to some extent uncertain across evolutionary history, so there are different default strategies within a population, and within any given population,

people with different genotypes may be using different strategies in response to the sociocultural environment.

This hypothesis differs from the differential susceptibility hypothesis because it does not state that some genotypes are more sensitive to environmental pressures and will conform to positive or negative environments with similarly positive or negative outcomes. Rather, a person's "default" strategy could be good, bad, or neutral—valence is irrelevant. Even when an environment is not understood as clearly positive or negative, the cultural meaning of the event may predict one set of behaviors in one culture versus another because there will be different ways to meet one's goals depending on inputs from the environment. The motivational setting hypothesis thus accounts for findings showing that people can exhibit seemingly negative outcomes even when the environment is not clearly negative. While it is likely that other factors aside from motivation are involved in gene-environment interaction effects, the motivational setting hypothesis provides one possible explanation for *why* people appear sensitive to certain environmental inputs by stating that they are motivated to achieve particular goals. People with different genotypes may show varying psychological responses at the level of cognition or perception, but crucially, the motivational setting hypothesis explains that the reason for these differences may be at least partially motivational.

For example, people with certain genotypes may be more motivated toward rewards, which results in behaviors with high risk (and high-potential short-term benefit) as a default strategy. However, in an environment that is resource rich, they may change their behavior to be less risk taking because they may ultimately reap the most benefits or rewards with a low-risk (but high long-term benefit) strategy. People with other genotypes may not be as motivated toward rewards, so they do not take a particularly high- or low-risk strategy, and their behavior does not drastically change according to resources in the environment. These strategies may reach an equilibrium in a population because having both strategies buffers the population against times of great suffering (because of those with low motivation toward reward) but still allows the population to grow in times of prosperity (because of those with high motivation toward reward).

Three important considerations arise from the motivational setting hypothesis: What is the default strategy based on genetic predispositions? What is the relevant situation (in a particular domain) that evokes a potential shift in response? What is the broader cultural context that gives meaning to that situation?

In the next section, we discuss empirical evidence for gene-culture interactions on emotion-relevant outcomes. We provide a review of past research demonstrating that genes may influence emotional experience via physiological responses. We also integrate gene-culture research with cultural

psychological research on emotional experiences, highlighting potential implications for theory on gene-environment interactions and cultural psychology more broadly.

GENE-CULTURE INTERACTIONS IN THE DOMAIN OF EMOTION

A number of emotion-relevant processes, including the expression of fear, aggression, and sexual behaviors, are regulated by the limbic system, which consists of numerous interconnected brain structures such as the amygdala, hippocampus, hypothalamus, nucleus accumbens, and cingulate cortex. These brain regions are central not only to reward processing, motivation, and memory, but also to emotion (Heimer, 2003; Morgane, Galler, & Mokler, 2005). In this section, we will discuss literature on emotion-relevant processes in relation to serotonin, dopamine (DA), and oxytocin (OXT). An understanding of how serotonin, DA, and OXT all interact is crucial in order to capture the full essence of emotion-based social behavior. However, because research examining the interaction of these systems in relation to emotion is limited, we focus our attention on gene-culture interactions for serotonin, DA, and OXT separately in this chapter.

Serotonin and Negative Emotions

The serotonin system is highly involved in processing emotion, including negative affects such as anxiety or stress (Sen, Burmeister, & Ghosh, 2004) and fear (Hariri et al., 2002). Serotonin, or 5-hydroxytryptamine (5-HT), is produced and stored within the raphe nuclei of the brainstem, from where it is dispersed throughout the entire central nervous system (CNS) (Ciranna, 2006). Its levels are particularly enriched in certain brain regions, including limbic forebrain structures (Hensler, 2006). 5-HT is involved in many facets of emotional information processing, such as attentional bias. For instance, individuals with depression, which is characterized by disrupted 5-HT neurotransmission (Deakin, 2003; Lucki, 1998), tend to exhibit negative biases in the processing of emotional cues (Leppänen, 2006). Perhaps not surprisingly, studies have shown that following treatment with a selective serotonin reuptake inhibitor, this bias toward negative emotional cues attenuates (Fu et al., 2004). Many other facets of emotion processing have been linked to 5-HT as well (Harmer, 2008; Merens, Van der Does, & Spinhoven, 2007).

Serotonin may be important to consider for predicting how people process potentially stressful emotional experiences, but in addition to that, the meaning of emotional experiences is shaped by the sociocultural context. Based on research in cultural psychology, we know that the broader culture can change the way people interpret emotionally relevant stimuli (e.g., Ishii,

Miyamoto, Mayama, & Niedenthal, 2011), but how does this interface with gene-environment interaction findings? In one study, Ishii, Kim, Sasaki, Shinada, and Kusumi (2014) examined how Japanese and Americans perceived changes in emotional expressions depending on their own genotypes of the serotonin transporter gene polymorphism (5-HTTLPR), a commonly studied polymorphism that modulates transcription of the serotonin transporter gene (SLC6A4). Participants in this study viewed faces that first looked either happy or sad and then slowly morphed into a neutral expression, and their task was to judge the point at which they perceived a smile or frown had disappeared. First, this study showed that, consistent with other research on 5-HTTLPR in similar samples, the frequency of the s (vs. l) allele is higher in Japanese than Americans. There has been some research investigating why allele frequencies may vary across cultures (see Chiao & Blizinsky, 2010 for evidence of gene-culture coevolution in the case of 5-HTTLPR), but this study showed that, crucially, there was an interaction between genes and culture on the perception of emotional expressions. Among Japanese, people with s/s genotypes (vs. s/l or l/l genotypes) of 5-HTTLPR were especially quick to judge that a smile had disappeared, while there was no difference for frowns. Americans with s/s genotypes (vs. s/l or l/l genotypes), on the other hand, were actually slower to judge that a smile disappeared, while again there was no difference for frowns. This is an instance of gene-culture interaction because the effect of 5-HTTLPR genotype on sensitivity to changes in expressions critically depended on cultural background. For Japanese participants—who may experience higher attachment anxiety and avoidance (Ishii et al., 2011), social anxiety (Norasakkunkit & Kalick, 2002), and concern for social approval compared to European Americans (Suh, Diener, Oishi, & Triandis, 1998)—a disappearing smile may be a meaningful sign of social disapproval and a source of anxiety. This gene-culture interaction study (Ishii et al., 2014) showed that Japanese may be especially vigilant to a disappearing smile if they are genetically predisposed to be sensitive to anxiety, carrying the s/s versus s/l or l/l genotype of 5-HTTLPR. Crucially, Americans with the same "sensitive" s/s genotype showed the opposite pattern of results compared to Japanese, suggesting that culturally variable norms surrounding social expectations may be integrated into their judgments of emotional expressions. Based on this research, people with s/s genotypes of 5-HTTLPR may be sensitive to the experience of anxiety, but culture shapes the way they interpret an event or stimulus as a cause for concern in the first place.

This research may be particularly interesting to consider within broader theories of gene-environment interactions. The diathesis-stress model predicts that people with one genotype—in this case, s/s genotypes of 5-HTTLPR—may be at risk when put in stressful environments. Considering the Japanese results in isolation, this study seems consistent with

the diathesis-stress model given that s allele carriers in a potentially stressful environment (i.e., when faced with a disappearing smile) are quick to identify it as such. However, the American pattern of results is not accounted for by this model, which does not predict that another environment would push responses in the opposite direction. According to the differential susceptibility hypothesis, however, some genotypes may be sensitive to stressful environments, as could potentially be the case in the Japanese context of high social anxiety, while being simultaneously sensitive to supportive environments, as could be occurring in the American context of relatively lower social anxiety. This pattern of results is also consistent with the motivational setting hypothesis, as people with the s allele could be characterized as having a default strategy that is vigilant to distinguishing anxiety-relevant information. In cultures such as East Asia, the best way to detect anxiety-relevant stimuli is to have a more cautious strategy, that is, even the slightest signal of a change in approval could be a sign of stress or anxiety in a culture where social approval is of high concern. However, in North America, where concerns for social approval are not as strong, people with the s allele may not increase their accuracy at detecting anxiety by reading even small changes as true signals of anxiety.

DA and Positive Emotions

DA seems to be strongly implicated in reward motivation and receipt. Positive affect can be viewed as the result of motivated behaviors that depend on activation of the DA system (Ashby, Isen, & Tuken, 1999). DA is produced in the ventral tegmental area (VTA) and substantia nigra (SN) of the midbrain (Gerfen, 2010), from where it is distributed to various regions of the brain through three major pathways. The mesolimbic pathway in particular, which transmits DA mainly from the VTA to the nucleus accumbens, plays a critical role in reward reinforcement and motivation (Robbins, 2010). Reward-seeking behaviors may be reinforced through a mesolimbic DA-amplification system that enhances the positive affective states underlying motivational behaviors (Burgdorf & Panksepp, 2006), demonstrated by some studies positively linking mesolimbic DA levels to amphetamine-induced feelings of euphoria (Drevets et al., 2001). Affect may thus be central for understanding the behavioral manifestation of reward motivation.

A commonly studied gene in the DA system is the DA receptor gene DRD4. In particular, the exon III region of DRD4 contains a 48-base pair variable number tandem repeat polymorphism that has alleles ranging from 2- to 11-repeats (Van Tol et al., 1992). DRD4 has been studied in connection to a number of reward-relevant behaviors, including novelty and sensation seeking (Ebstein et al., 1996), gambling (de Castro, Ibanez,

Torres, Saiz-Ruiz, & Fernandez-Piqueras, 1997), alcohol use (Laucht, Becker, Blomeyer, & Schmidt, 2007), and financial risk taking (Kuhnen & Chiao, 2009). Although DRD4 has more commonly been studied in relation to specific traits or behaviors that tend to elicit a reward response, one study recently examined DRD4 in relation to the broad social orientation of independence and interdependence (Kitayama et al., 2014). Because adherence to culturally sanctioned norms are likely to be rewarded and reinforced, the authors argued that people with susceptibility genotypes (in this case, 7-repeat or 2-repeat allele carriers) were more likely to show the culturally dominant social orientation. This is an instance of gene-culture interaction because the same susceptibility genotype (2-/7-repeat carriers) was linked to independence in one cultural context (i.e., for European Americans) and to interdependence in another cultural context (i.e., for East Asians), and there was no difference in cultural orientation among non-susceptibility genotypes (non-2-/7-repeat carriers). The underlying rationale for this research is that acting in accordance with cultural norms is often reinforced by the broader culture, and to some people, this reinforcement may feel particularly good. That is, people with genetic predispositions to be sensitive to reward should be the most motivated to behave in a way that is consistent with cultural norms because they are continuously reaping psychological benefits from these behaviors. Consistent with the motivational setting hypothesis, this research suggests that the default strategy of DRD4 susceptibility carriers may be culturally shaped because there are different ways to reap social rewards depending on the cultural context. In one culture, 2-/7-repeats (who are sensitive to rewards) can optimize rewards by behaving consistently with a more independent social orientation, while in another culture, they need to optimize rewards by behaving consistently with a more interdependent orientation. In both cases, 2-/7-repeat carriers are likely drawn to the reinforcing nature of culturally consistent norms and practices, while non-susceptibility carriers do not reap any special benefits from behaving more or less in line with cultural norms.

As a form of culture (A. B. Cohen, 2009), religion is another meaningful source of information that can guide thoughts and behaviors. A study examining the influence of religion and genes on prosocial behavior found some evidence that religion may motivate reward-relevant behaviors for people with certain variants of DRD4 compared to others (Sasaki et al., 2013). Specifically, this study showed that an implicit prime of religion increased prosocial behavior for people with 2-/7-repeat allele variants, who are more reward sensitive, while there was no effect of the religion prime on prosocial behavior among those without the 2-/7-repeat allele variants. Interestingly, people with 2-/7-repeat allele variants showed the highest levels of prosocial behavior overall when there was a compelling reason to do so—perhaps the prospect of reward from being reminded of a God or higher power—while

those with these same variants showed the lowest levels of prosocial behavior when there was none. People with the 2-/7-repeat allele variant of DRD4 may have lower baseline DA signaling, meaning that they may need to experience higher levels of DA increase in order to achieve "normal" levels of cyclic AMP reduction, and thus it is possible that they need greater external reasons to behave prosocially to experience satisfactory feelings of reward. However, for people without the 2-/7-repeat allele variant, who experience higher baseline DA signaling, the prosocial act itself may feel good enough for them. Therefore, in this study, it seems that people with the susceptibility variant of DRD4 are more motivated to behave prosocially when there is an immediate prospect of reward, perhaps because their motivation is set on optimizing rewards. Without a compelling reason to behave prosocially, people with the DRD4 susceptibility variant may optimize rewards more by holding onto their resources (in this case, their time) rather than giving it away. This finding is consistent with the motivational setting hypothesis because it was not the case that people with 2-/7-repeat allele variants were just more sensitive to any environmental input, thus increasing any effect of the religion prime. At a perceptual level, DRD4 genotype did not moderate the initial perception of the prime itself. The implicit religion prime increased levels of self-reported religiosity for participants overall, and this effect was not any stronger among people with 2-/7-repeat allele variants compared to those without these variants. Instead, once the concept of religion was salient in people's minds, the downstream behavioral effect was to be more prosocial only for those who were motivated to optimize rewards. While the concept of religion itself is not particularly relevant to reward, the act of behaving prosocially because "God is watching" (Shariff & Norenzayan, 2007) does have potential implications for reward, and thus, it is people's behaviors in this case that are relevant for their different motivations toward rewards.

An interesting possibility is that the DA receptor gene could be implicated in the link between culture and positive emotions. A common finding in research on culture and emotion is the emphasis on positive emotions in Western culture relative to Eastern culture (Heine et al., 1999; H. Kim, Schimmack, & Oishi, 2012; Markus & Kitayama, 1991; Suh et al., 1998), and recent research suggests that the dopaminergic system, which plays a key role in approaching rewards, is related to *plasticity*—defined as "a general tendency to explore and engage with possibilities" (DeYoung, 2010, p. 1170). This plasticity trait is comprised of extraversion and openness to experience and is highly focused on personal growth and self-actualization (DeYoung, 2010, 2013), and importantly, these traits have been suggested to be associated with certain hormones (such as DA) and brain structures. A few other studies directly implicated DA function in the personality trait extraversion (Depue & Collins, 1999; Wacker, Chavanon, & Stemmler,

2006). Thus, it is possible that different cultures may focus on positive emotions to different degrees due to differences in personality traits, such as extraversion and openness to experience, perhaps via variation in certain DA-related genes. Indeed, certain traits, such as extraversion, seem to be more strongly related to positive emotions in independent cultures than interdependent cultures (Schimmack, Radhakrishnan, Oishi, Dzokoto, & Ahadi, 2002; Tsai et al., 2006). However, further empirical observations are needed before any definite inferences can be made about the moderating role of genes.

Following the motivational setting hypothesis, people with susceptibility genotypes in both independent and interdependent cultures may have the goal of receiving social rewards but may achieve this goal in different ways. In independent cultures, people with susceptibility genotypes may be more sensitive to rewards and behave consistently with the respective independent social orientation, while in interdependent cultures, those with susceptibility genotypes may behave consistently with their interdependent social orientation. In both cultures, people with susceptibility genotypes may seek and optimize rewards: they are all motivated to engage in adaptive behaviors, and these motivated or goal-directed behaviors may serve the same function of improving general well-being, although perhaps via different routes. Another interesting possibility is that the domain (e.g., seeking rewards) might be more consistent with certain cultural norms, and thus, the reinforcement not only may be adaptive but also may feel good to a person in certain contexts more than others.

OXT and Socially Relevant Emotions

OXT is a neuropeptide that is linked to socioemotional sensitivity. Produced in the hypothalamus, OXT is released both centrally, to various brain regions including limbic structures (Loup, Tribollet, Dubois-Dauphin, & Dreifuss, 1991), and peripherally, into circulation, where it plays a role in regulating uterine contractions during labor and milk release during lactation (Gimpl & Fahrenholz, 2001). In the CNS, OXT facilitates a variety of behaviors related to social cognition and affiliation, such as social recognition, parent-offspring attachment, mating behaviors, and even aggression (Burkett & Young, 2012; Crespi, 2015; Donaldson & Young, 2008; Kemp & Guastella, 2011; Love, 2014). Some researchers have theorized that OXT is involved in increasing socially engaging motivations ("social approach"), whether positive (e.g., trust) or negative (e.g., anger), and decreasing socially disengaging ("social withdrawal") motivations (e.g., fear; Kemp & Guastella, 2011). Therefore, OXT may promote both positive *and* negative social interactions (e.g., aggression) depending on the social context and implications for connecting with others socially.

In one study of the oxytocin receptor gene (OXTR), H. S. Kim et al. (2011) examined emotion regulation in three distinct cultural groups: Koreans, U.S.-born Asian Americans, and European Americans. This gene has a polymorphic site, OXTR rs53576, localized in a single copy to chromosome 3 of the human genome (Gimpl & Fahrenholz, 2001). People with the G allele of OXTR rs53576 tend to show higher socioemotional sensitivity overall, exhibiting greater empathic accuracy (Rodrigues et al., 2009) and more sensitive parenting (Bakermans-Kranenburg & van IJzendoorn, 2008), compared to those with the A allele. Yet the way people show socioemotional sensitivity may be shaped by culture. Indeed, research in cultural psychology suggests that East Asians are more likely to use emotion suppression to regulate their feelings compared to European Americans (Gross & John, 2003; Tsai & Levenson, 1997). In order to integrate gene-environment and cultural perspectives, H. S. Kim et al. (2011) showed that Americans (both European American and Asian American) with the susceptibility (G/G) genotype were the least likely to report suppressing emotions compared to Americans with A/G or A/A genotypes. In comparison, Koreans with the G/G genotype reported suppressing emotions more than Koreans with A/G or A/A genotypes. The opposite patterns of genetic effects between the two cultural groups demonstrate a gene-culture interaction on emotion regulation.

Another study examining OXTR rs53576 and culture found that the relationship between the G allele and empathy was even stronger for individuals with dominant interdependent self-construal than independent self-construal within the Chinese cultural context (Luo et al., 2015). Based on the findings linking OXTR and social emotions, it can be expected that individuals with the G allele will exhibit more socially engaging emotions compared to individuals without the G allele. A further research question is whether the association can be found across cultural contexts. However, the association might not be as straightforward as anticipated because culture not only can covary with certain gene frequencies in a population but also can influence gene expression patterns (H. S. Kim & Sasaki, 2014).

Overall, it seems that for people who carry the G allele of OXTR, the default strategy is to socially engage, whether the resulting emotion is positive or negative. For people in North America, the way to draw closer to others is to express emotions, while in East Asia, the way to maintain connections is to suppress emotions (Butler et al., 2007). We can see in the gene-culture interaction study on emotion suppression (H. S. Kim et al., 2011) that for people who are motivated to socially engage, those with G/G genotypes of OXTR, the effect on emotion regulation changes depending on the cultural meaning of expressing or suppressing emotion. For both cultural groups, people with the G/G genotype may be trying to maintain socioemotional connections with others, but the way to achieve this goal depends

on cultural norms. Although this research focused on positive socioemotional outcomes, other researchers have emphasized that OXT may play a role in facilitating both positive and negative social emotions (see Kemp & Guastella, 2011 for explanation of the social approach/withdrawal hypothesis). Future research may investigate whether the link between OXT and negative socioemotional outcomes shows a similar interaction with culture.

CONCLUSION AND FUTURE DIRECTIONS

Two decades of research on genes have produced a wealth of new knowledge with special relevance for cultural psychology, especially when it comes to variations in gene expression patterns and their relations to psychological outcomes for people around the world. There is an apparent disconnect in the literature between these two areas of research—genetics and cultural psychology research—perhaps due to the novelty of the research area and methodological issues in combining cultural genomic data with behavioral and cognitive data. Still, research integrating these perspectives is growing, and in this chapter, we reviewed evidence from two research traditions that may jointly inform our understanding of different emotion processes.

There are a number of concrete recommendations we can offer for future research on culture, genes, and emotion. First, to adequately examine gene-culture interactions in the domain of emotion, it is important to compare individuals within and across cultures. Although there are more genetic variations across individuals, genetic variation differences that exist at the population level are often ignored. Second, there is no single gene that solely predicts a complex behavior or emotional process. Thus, more research should examine how culture interacts with multiple genes to predict psychological and behavioral outcomes. For example, examining serotonin-DA-OXT interactions with environmental factors may provide us with a clearer picture of emotion-based social behavior. Third, examining individuals' physiological and neurological responses to particular types of emotions, as well as genetic influences, may facilitate understanding of the nature and structure of emotions. For example, if it feels good to experience socially engaging emotions and if people in certain cultures continue highlighting these emotions, it may be not only psychologically beneficial but also physiologically beneficial. For people who are more interdependent, experiencing socially engaging emotions, and not socially disengaging emotions, may be linked to less stress reactivity in general (e.g., smaller increases in heart rate and cortisol levels; see Kogan et al., 2014; Stellar, Cohen, Oveis, & Keltner, 2015, for evidence of the link between socially engaging emotions and lower stress reactivity).

We also set forward a new hypothesis, namely the motivational setting hypothesis, to reconcile findings across different gene-environment

interaction studies. The theory posits that certain genes predict the level of motivation to achieve goals in a particular domain, and individuals with different genotypes use different strategies to achieve these goals across sociocultural contexts. Environmental conditions within a psychological domain will thus trigger different psychological responses because of differences in genetically linked motivations. This theory may not only help explain the current gene-culture findings on emotions but also guide future research uncovering what people feel in different situations and why.

NOTES

1. It is worth noting that many studies tend to assess positive and negative feelings with single-item measures of pleasantness/unpleasantness instead of multi-item measures, and most studies with multi-item measures use averages across items pertaining to positive and negative emotions rather than analyzing specific emotions (e.g., fear, anger, and happiness) separately.
2. Socially engaging and disengaging emotions are typically measured with multiple items.

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