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ORIGINAL RESEARCH ARTICLE

The dopamine D4 receptor gene (DRD4) modulates cultural variation in emotional experience

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Abstract Prior work suggests that people who carry a 7- or 2-repeat allele of the dopamine D4 receptor gene (*DRD4*) are more sensitive to environmental influences than those who do not carry this allele. Since culture is an important aspect of the environment for all humans, the carriers of this allele may be more likely to show culturally typical response patterns than non-carriers. The current work tested this hypothesis in the domain of emotional experience. Whereas European Americans typically report experiencing positive emotions more than negative emotions, this positivity bias is atypical for East Asians. Accordingly, we predicted that the positivity bias in emotional experience would be moderated by both *DRD4* and culture. 194 European Americans and 204 East Asians rated the frequency of actually experiencing various positive and negative emotions in a typical week. As predicted, we found a significant culture × *DRD4* interaction for emotional experience. East Asian carriers (versus non-carriers) of the 7/2R allele of DRD4 reported experiencing greater emotional balance (i.e., weaker positivity bias), than non-carriers of these alleles. For European Americans, however, the pattern was reversed such that the positivity bias was stronger, albeit non-significantly, among the carriers than among the non-carriers. Of note, the culture × *DRD4* interaction effect was absent for desirability ratings of experiencing the same set of emotions. Implications for cultural acquisition processes are discussed.

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How people experience, express, and regulate their emotions is closely tied to the rules, norms, and beliefs of their cultural environment. People from East Asian cultures (e.g., China, Korea, Japan) are more likely to value modesty, dampen positive emotions, and report experiencing balanced emotions (e.g., combinations of positive and negative emotions; Kitayama et al. 2000; Miyamoto and Ma 2011). In contrast, people from Western cultures such as the United States are more likely to value positivity of emotional experience and work to maintain emotional positivity (Kitayama et al. 2000; Miyamoto and Ma 2011). Although these culturally typical response patterns are likely to be learned through social norms, this cultural learning is purportedly grounded in biological processes (Kitayama et al. 2016; Kitayama and Salvador 2017). Hence, biological processes involved in cultural learning may modulate the systematic differences in how people from different cultural backgrounds report experiencing positive versus negative emotions. In the current study, we hypothesize that genetic factors that modulate cultural learning may also influence how culturally typical the emotions they experience are.

Are some individuals more prepared to respond in accordance with norms and values of cultural environments? And is this difference in the preparedness to respond in culturally typical ways influenced by biology? Research on gene-environment interactions suggests that individuals who carry certain genetic alleles, often called "plasticity" alleles, are more likely to be influenced by their environment. Specifically, individuals with these "plasticity" alleles who are exposed to chronic negative environmental influences show amplified negative outcomes, but the same individuals exposed to positive environmental influences show amplified positive outcomes (Belsky and Beaver 2011; Belsky and Pluess 2009; Richards et al. 2017; Suomi 2002). Thus, genetic factors may be expected to strongly influence the degree to which individuals learn and acquire implicit psychological tendencies that are unique to their culture.

One prominent "plasticity allele" has been identified in the dopamine D4 receptor gene (*DRD4*). In Exon 3 of the *DRD4* gene, there is a polymorphic region in which a sequence of 48 amino acids repeats itself anywhere from 2 to 11 times. Since the polymorphism is defined by varying number of repeats, the polymorphisms are called the varying number tandem repeat (VNTR) polymorphisms. The 2-repeat and 7-repeat versions of the *DRD4* VNTR polymorphism have greater dopamine signaling capacity than the other alleles (Wang et al. 2004). Since increased dopamine signaling is thought to enhance the efficiency of reinforcement-based learning (Kitayama et al. 2016; Kitayama and Salvador 2017), we may hypothesize that as compared to non-carriers, carriers of the 7/2R *DRD4* VNTR polymorphism are more prepared to learn reward contingencies implicit in social or cultural norms and, thus, these carriers are more likely to show culturally characteristic patterns of emotional experience.

Existing evidence is consistent with this hypothesis. For example, Sasaki et al. (2013) found that when religion was primed, people tended to engage in a prosocial action, but this effect of religious priming was more pronounced for carriers of the 7/2R *DRD4* VNTR polymorphism than for non-carriers. Thus, as compared to non-

carriers, carriers appear to acquire the culturally typical response of linking religiosity to prosocial behaviors. This interpretation is consistent with another recent study that directly tested cultural values and beliefs across cultures. In this study, the researchers assessed endorsement of independent or interdependent cultural values and beliefs with a set of validated scales, and found that carriers of the 7/2R alleles of the *DRD4* VNTR polymorphism were more likely to show the culturally typical response patterns (Kitayama et al. 2014). That is, European American carriers were more independent and individualistic than European American non-carriers, but East Asian carriers were more interdependent and collectivistic than East Asian non-carriers.

To date, the hypothesis that carriers of the 7/2R *DRD4* VNTR polymorphism are more likely to respond in accordance with cultural norms and values has yet to be extended to emotional experience. Emotion is a dynamic process that is defined by patterns of cognitive appraisals that provide meanings to somatic sensations of arousal and pleasantness (Ellsworth and Scherer 2003; Scherer et al. 2001; Smith and Ellsworth 1985). Even though arousal and pleasantness of the experience are biologically hardwired, their activations are conditional to cognitive appraisals, which are known to be responsive to cultural norms and beliefs (Mesquita 2001; Mesquita et al. 2016; Mesquita and Frijda 1992).

One known cultural difference in emotion norms concerns emotional positivity versus emotional balance. Specifically, independent cultures, such as the United States, promote cultural norms that sanction maximizing positive emotions and minimizing negative emotions, whereas interdependent cultures such as Japan promote cultural norms that instead sanction maintaining emotional balance (Kitayama et al. 2000; Miyamoto and Ryff 2011). Indeed, Westerners tend to report experiencing positive emotions far more frequently than negative emotions, whereas people from East Asian cultures report experiencing similar amounts of positive and negative emotions (Kitayama et al. 2000; Miyamoto and Ryff 2011; Sims et al. 2015). Recent research has found that cultural differences in the degree to which individuals report finding emotional positivity versus balance desirable drive cultural differences in the degree to which people report experiencing positive versus negative emotions (Sims et al. 2015).

How will emotion norms such as positivity in Western cultures and balance in East Asian cultures be acquired? Kitayama and colleagues (Kitayama et al. 2016; Kitayama and Salvador 2017) have argued that this process of cultural acquisition is likely mediated by reinforcement-based learning. Within this theoretical framework, the degree to which patterns of emotional experience are shaped by emotion norms of a culture is likely to depend on efficiency in reward processing, that is, how effectively individuals can register social rewards (and punishments) that are contingent on their emotional responses and then monitor and tally the reward contingencies over an extended period. We hypothesize therefore that people will vary in the degree to which they exhibit patterns of emotional experience that are typical of the emotion norms of their cultures. Further, as noted earlier, the tendency of responding in accordance with cultural norms is likely to depend on *DRD4* VNTR polymorphisms. Carriers of the 7- or 2-repeat allele of *DRD4* will be more

likely to respond in accordance with their culture's emotion norms than non-carriers.

In the current work, we tested these predictions using a validated instrument (Tsai et al. 2006) to measure how frequently European American and East Asian young adults report experiencing 13 positive emotions, nine negative emotions, and eight neutral emotions. We asked participants to report both how much they actually experience each emotion in a typical week (actual affect) and how much they would ideally want to experience each emotion in a typical week (ideal affect).

Method

Participants

In this study, we had 398 college students at the University of Michigan complete a battery of surveys and provide us with a saliva sample. This sample included 194 European American (68 males and 126 females) and 204 East Asian (71 males and 133 females) students. Participants received course credit or $25 for participating. To qualify as a European American participant, a person had to be of European ancestry and born and raised in the United States, whereas to qualify as East Asian participant, a person had to have been born in an East Asian country (i.e., China, Japan, Korea, and Taiwan) and have spent less than 10 years in the United States. Genotyping of the *DRD4* VNTR failed for 21 participants, and so these participants were excluded from further analyses. Of the remaining 377 participants, 189 were European American and 188 were East Asian.

Procedure

Participants were recruited using fliers posted at various campus locations, emails, and online postings. Eligible participants were invited to participate in a study on the relationship between personality, genes, and well-being either individually or in small groups of 2–10 individuals. They were asked to complete a series of questionnaires on the computer. Upon completion of the surveys, participants provided a saliva sample. Mean age of the participants was 20.3 years (SD = 1.2). A majority of East Asian participants (82%) spent less than eight years in the US, with an overall sample mean of 4.6 years (SD = 3.5).

Genotyping

Oragene Saliva kit OG-500 was used for saliva collection (DNA Genotek, Ontario, Canada). Genomic DNA was extracted using a high-capacity membrane-based column (QuickGene810, AutoGen, Inc., Holliston, MA), and was quantitated using A260/A280 ratio (Nanodrop), and agarose gel electrophoresis. The *DRD4* variable number tandem repeat (VNTR) polymorphism was amplified using 0.2 μM of each primer *DRD4* forward 5′-GCGACTACGTGGTCTACTCG and *DRD4* reverse 5′-AGGACCCTCATGGCCTTG (Lichter et al. 1993), using the Roche "GC-Rich

PCR System" amplification buffer (Roche Applied Science, Inc., Mannheim, Germany) and 20 ng of genomic DNA in a volume of 25 µl. The samples were heated in a Stratagene thermocycler (Life Technologies, Inc. Grand Island, NY) at 95 C for 3 min, then cycled 40 times at 95 °C for 20 s, 57 °C for 20 s, and 72 °C for 1 min, followed by 72 °C for 3 min. PCR products were separated and visualized on a 2% agarose gel (type 1-A, Sigma, St. Louis, MO) stained with ethidium bromide.

In line with previous findings (Chen et al. 1999), frequencies of common *DRD4* VNTR alleles in European Americans were 2R (7%), 3R (7%), 4R (64%), 5R (1%), 7R (17%), 8R (2%), 10R (2%); and in East Asians they were 2R (17%), 3R (2%), 4R (77%), 5R (2%), 7R (2%). As in previous work (Sasaki et al. 2013), the 7R and 2R allele carriers (associated with relatively higher dopamine signaling) were compared to a "lower dopamine signaling" group of 7/2R allele non-carriers (mainly 4/4 genotype, as well as more rare alleles including 3R, 5R, 6R, 8R, and 10R. Restricting our analyses to only individuals who carried the common 2R, 4R, or 7R alleles did not change the results reported below. Our high dopamine signaling group consisted of 84 European American and 63 East Asian carriers of at least one 2R or 7R alleles. Our low dopamine signaling group consisted of 105 European Americans and 125 East Asians.

Materials

We administered a series of questionnaires including self-construal, self-esteem, self-expression, self-efficacy, and cognitive style (previously reported in Kitayama et al. 2014). The packet also included two emotion scales examining actual emotional experience and perceived desirability of emotional experiences, which is the focus of the present report.

Affect Valuation Index The Affect Valuation Index (AVI) consists of two subscales—the Actual Affect subscale and Ideal Affect subscale (Tsai et al. 2006). In the Actual Affect subscale, participants reported how frequently they actually experienced different emotions over the course of a typical week on a 5-point scale (1 = Never experience that emotion, 5 = Experience that emotion all the time). The emotions they were asked to rate varied in terms of both valence and arousal, such that 13 emotions were positively valenced (e.g., enthusiastic, happy, relaxed), 9 were negatively valenced (e.g., fearful, sad, sluggish), and the remaining 8 were neutral (e.g., astonished, rested, inactive). In each of the 3 valence categories, approximately 1/3 of the words were high arousal (e.g., enthusiastic, astonished, nervous, 1/3 were low arousal (e.g., serene, inactive, sleepy), and 1/3 were neutral arousal (e.g., content, strong, unhappy).

The Ideal Affect subscale was identical to the Actual Affect subscale with one notable difference. Instead of rating how frequently they *actually* experience each emotion, participants rated how frequently they would *ideally* want to experience each emotion. They completed this rating for the same 30 emotions that they rated for the Actual Affect subscale.

Analyses

To examine emotional positivity versus balance, we computed the average value for the 13 positive items and 9 negative items in each subscale to yield the following subscales: average positive actual affect ($\alpha = .845$ for European Americans, $\alpha = .822$ for East Asians), average negative actual affect ($\alpha = .832$ for European Americans, $\alpha = .790$ for East Asians), average positive ideal affect ($\alpha = .883$ for European Americans, $\alpha = .896$ for East Asians), and average negative ideal affect ($\alpha = .877$ for European Americans, $\alpha = .834$ for East Asians). We then ran a mixed ANOVA with *DRD4* (carrier versus non-carrier) and culture (European American versus East Asian) as between-subjects factors, valence of emotion (positive versus negative emotion) as a within-subjects variable, and mean desirability ratings from the ideal affect scale as the dependent variable. Finally, we also ran identical analyses with the mean desirability ratings from the actual affect scale as the dependent variable. The results reported below did not change when we controlled for cultural differences in response style (Chen et al. 1995) by using the ipsatized values for each item in the Actual Affect and Ideal Affect subscales (i.e., for each participant, we calculated the overall mean and standard deviation for each subscale and subtracted the mean from each item and then divided by the standard deviation).

Results

Ideal affect: desirability of positive versus negative emotions

In order to ensure that there was a cultural difference in emotion norms, we first examined the desirability ratings from the Ideal Affect scale. We computed separate mean desirability ratings for positive and negative emotions (see detailed description above) and ran a mixed ANOVA with *DRD4* (carrier versus non-carrier) and culture (European American versus East Asian) as between-subjects factors, valence of emotion (positive versus negative emotion) as a within-subjects variable, and mean desirability ratings from the Ideal Affect scale as the dependent variable.

We found a significant main effect of valence [$F(1373) = 1265.07$, $p < 0.001$, $\eta^2 = 0.74$] and a culture × valence interaction [$F(1373) = 72.84$, $p < 0.001$, $\eta^2 = 0.14$; see Fig. 1]. The desirability rating was higher for positive (vs. negative) emotions in both groups (European Americans: $M = 2.65$, $SD = 1.03$; East Asians: $M = 1.61$, $SD = 1.28$), but the effect of valence was more pronounced for European Americans than for East Asians. The pattern suggests that there is a strong norm encouraging positive emotional experience among European Americans, which is diluted among East Asians.

As predicted, the culture × valence interaction was not qualified by *DRD4* [$F(1373) = 0.38$, $p = .538$, $\eta^2 < 0.001$], nor was there a main effect of *DRD4* [$F(1373) = 0.07$, $p = .789$, $\eta^2 < 0.001$]. Note that our finding does not show the hypothesized existence of a norm toward emotional balance among East Asians. We will return to this point in the Discussion.

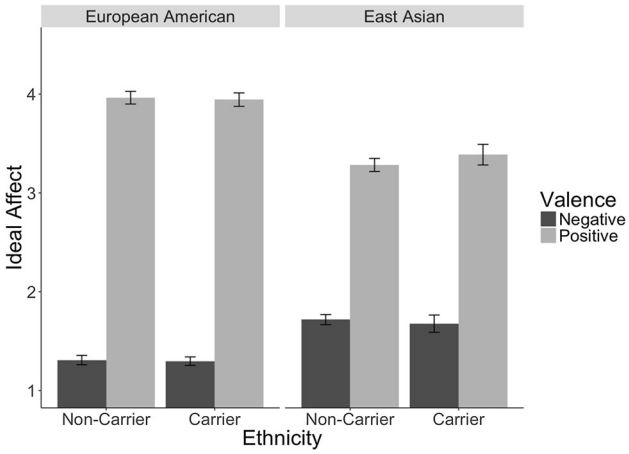

Fig. 1 Ideal affect is influenced by culture but not *DRD4*

Actual affect: experience of positive versus negative emotions

Next, we tested our central prediction that positivity in actual emotional experience would be modulated by *DRD4*. We computed separate mean actual experience ratings for positive and negative emotions (see detailed description above) and ran a mixed ANOVA with *DRD4* (carrier versus non-carrier) and culture (European American versus East Asian) as between-subjects factors, valence of emotion (positive versus negative emotion) as a within-subjects variable and mean actual experience ratings as the dependent variable.

We anticipated stronger emotional positivity (reporting significantly greater positive emotions than negative emotions) for European American carriers of the *DRD4* 7/2R polymorphism, but a stronger balance or weaker positivity (reporting similar levels of positive and negative emotions) for East Asian carriers. This predicted culture × *DRD4* × valence interaction proved significant [$F(1, 373) = 7.81$, $p = .005$, $\eta^2 = 0.02$; see Fig. 2], as was the main effect of valence [$F(1, 373) = 56.29$, $p < .001$, $\eta^2 = 0.10$]. We did not find a significant main effect for culture [$F(1, 373) = 0.74$, $p = .391$, $\eta^2 < 0.001$] or *DRD4* [$F(1, 373) = 0.90$, $p = .344$, $\eta^2 < 0.001$].

We then examined the results in each culture. First, among Asians, the predicted 2-way interaction between valence and *DRD4* was significant [$F(1, 186) = 7.15$, $p = .008$, $\eta^2 = 0.03$], such that carriers reported experiencing significantly more balanced emotions than non-carriers. Indeed, East Asian carriers reported experiencing positive emotions ($M = 2.50$, $SD = 0.50$) no more strongly than negative emotions [$M = 2.35$, $SD = 0.62$; $t(62) = 1.22$, $p = .229$, $d = 0.15$]. In contrast, non-carriers reported experiencing positive emotions ($M = 2.77$, $SD = 0.55$) more than negative emotions [$M = 2.21$, $SD = 0.61$; $t(124) = 6.40$, $p < .001$, $d = 0.57$]. As predicted, the pattern was reversed for European Americans (as is evident in Fig. 2). Emotional positivity tended to be stronger for carriers than for non-carriers, although caution is needed because the predicted valence × DRD4 interaction was

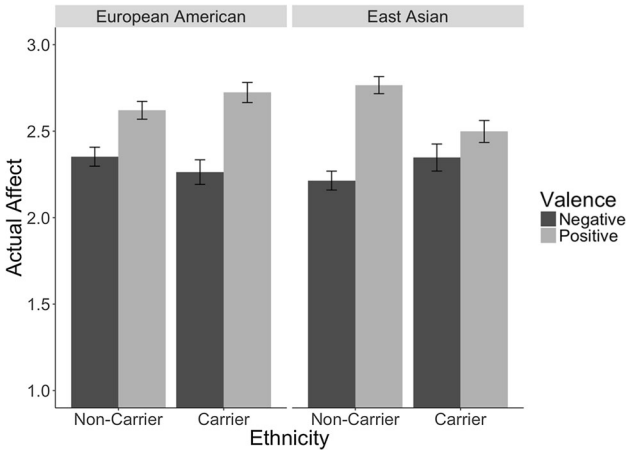

Fig. 2 Actual affect is influenced by the interaction between culture and *DRD4*

not significant for European Americans [$F(1, 187) = 1.65$, $p = .201$, $\eta^2 = 0.01$]. European American carriers reported experiencing more positive emotions ($M = 2.72$, $SD = 0.53$) than negative emotions [$M = 2.26$, $SD = 0.65$; $t(83) = 3.93$, $p < .001$, $d = 0.43$]. Although the effect was slightly weaker, European American non-carriers also reported experiencing more positive emotions ($M = 2.62$, $SD = 0.53$) than negative emotions [$M = 2.35$, $SD = 0.56$, $t(104) = 2.80$, $p = .006$, $d = 0.27$]. It is informative that emotional positivity (stronger experience of positive vs. negative emotions) was quite pronounced for European American carriers and East Asian non-carriers, whereas it was weaker for both European American non-carriers and East Asian carriers. We return to this pattern in the Discussion.

Discussion

Based on the theory that cultural norms, including emotion norms, are acquired through reinforcement-based learning (Kitayama et al. 2016; Kitayama and Salvador 2017), we hypothesized that *DRD4* VNTR polymorphisms would moderate the likelihood of experiencing culturally typical emotions. Two critical findings provide support for this hypothesis. First, emotional experience was moderated by a *DRD4* × culture interaction. Emotional positivity was significantly weaker (indicating a tendency toward emotional balance) among East Asian carriers of the 7/2R *DRD4* polymorphisms than for East Asian non-carriers. This pattern was reversed for European Americans, with a non-significant trend toward emotion positivity for carriers than for non-carriers. These results suggest that genetic predisposition to reinforcement learning influences the degree to which emotion norms are reflected in actual emotional experience.

Importantly, predisposition to demonstrate culturally typical patterns of emotional experience need not overlap with perceptions of those norms. In the context of emotional experience, people carrying 7/2R alleles of the *DRD4* VNTR may be

more sensitive to cultural norms about which types of emotional experiences are more or less valued, but that does not mean that they perceive those cultural norms as being more ideal (i.e., common, stronger, or more frequent) in the society. Our second key finding was consistent with this reasoning. We showed that the reported desirability of positive versus negative emotions showed a clear cultural difference. Whereas European Americans reported it more desirable to experience emotional positivity (stronger positive than negative emotions), this effect was significantly weaker for East Asians. Importantly, this effect was not moderated by *DRD4* VNTR polymorphisms.

The current work provides additional evidence for the general hypothesis that *DRD4* VNTR polymorphisms modulate reinforcement-based learning of cultural values and norms. As noted earlier, these polymorphisms amplify environmental influences. Thus, carriers of 7/2R *DRD4* VNTR polymorphisms are more sensitive to religion priming (Sasaki et al. 2013), peer affiliation (Richards et al. 2017), rearing environment (Bakermans-Kranenburg et al. 2011), and neighborhood socioeconomic status (Silveira et al. 2016). Most pertinent to the current work, we had recently shown that learning of cultural values and beliefs is also moderated by the same polymorphisms (Kitayama et al. 2014). Thus, among European Americans, carriers tend to be more independent (rather than interdependent), but among Asians, carriers tend to be more interdependent (rather than independent).

Our work built on these diverse findings to suggest the central significance of *DRD4* VNTR polymorphisms in the acquisition of cultural norms, standards, and beliefs. This study also shows that there may be important boundary conditions for the effect of *DRD4* on psychological tendencies and beliefs, such that *DRD4* moderates the effect of cultural norms on individuals (i.e., actual affect) without influencing their perceptions of the norms, standards, and beliefs themselves (i.e., ideal affect). Future work should attempt to capitalize on these findings by examining in more detail the specific neuro-biological pathways of reinforcement-based learning that are thought to mediate the effect of *DRD4* on acquisition of cultural norms.

Before closing, we wish to point out three potentially puzzling findings. First, in the current work, East Asian non-carriers showed a quite strong positivity in emotional experience and, in fact, reported slightly stronger emotional positivity than European American carriers. We speculate that this may be due, in part, to the fact that all of the East Asian participants were Asian-born sojourners in the United States. Most of the East Asian participants were 16 years old or older at the time they moved to the United States and had lived in the United States for fewer than 5 years. To the extent that East Asian non-carriers were less likely to be sensitive to reinforcement of the cultural norms in their home culture, they might have been more open to American emotion norms when having arrived in the United States. Although this particular question is beyond the scope of the current paper, future work could follow participants throughout the transition from High School in an Asian country to college in the United States (and vice versa) in order to test this possibility.

Second, the desirability ratings show that both European Americans and East Asians valued positive emotions more than negative emotions, although this effect

was weaker for East Asians relative to European Americans. In this case, balance is relative, in that East Asian participants clearly value balance more than European Americans, although they still want to experience positive emotions more than negative emotions. By definition, positivity in general is more desirable than negativity in general (Osgood, 1954, semantic differential reference). It may be the case that there are more situations where East Asians value negative emotional experience, even though they still report finding positive emotions more desirable overall. Future work should extend our current findings with diary and other experience sampling methods (Kitayama et al. 2006; Sims et al. 2015).

Third, research on the function of the *DRD4* VNTR polymorphism suggests that dopamine signaling capacity of the 2R allele falls in between the 7R and 4R alleles (Asghari et al. 1995; Reist et al. 2007). Moreover, the 7R allele is predominantly found in Western populations whereas the 2R allele is predominantly found in East Asian populations (Ding et al. 2002; Wang et al. 2004). Given the slightly greater difference between the 4R and 7R alleles than between the 2R and 7R alleles, and the greater prevalence of the 7R allele in Western populations, one might expect that the difference between carriers and non-carriers would be greater for European Americans than East Asians. However, we found that the effect of *DRD4* on actual affect was actually somewhat greater among East Asians than European Americans. As noted above, this effect was primarily driven by greater emotional positivity in East Asian non-carriers, suggesting that the discrepancy in the effect of *DRD4* on actual affect is not due to signaling differences between 2R and 7R alleles. These differences are difficult to test given the small percentage of European Americans 2R carriers and East Asians 7R carriers, but future work might investigate this more directly using neuroimaging measures of dopamine signaling in reward regions of the brain.

To conclude, the most important contribution of the present study is to provide the first evidence that emotional experience is moderated by a gene × culture interaction. We find that European Americans carriers of the 7/2R *DRD4* VNTR polymorphism experience more positive and less negative emotions, whereas East Asian carriers experience more balanced emotions. Both carriers and non-carriers from the US report ideally wanting to experience emotional positivity whereas carriers and non-carriers from East Asian countries report ideally wanting to experience more balanced emotions. This research also has important implications for how quickly people might adapt to a new cultural context, which requires learning and acquisition of new cultural beliefs and values (Mesquita et al. 2017). This study contributes to a growing body of evidence that genes may be an integral part of how culture is learned and acquired.

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