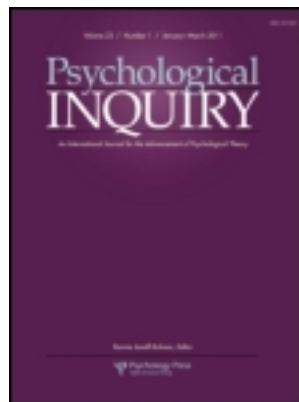


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Promise and Challenges Surrounding Culture-Gene Coevolution and Gene-Culture Interactions

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Promise and Challenges Surrounding Culture–Gene Coevolution and Gene–Culture Interactions

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Advances in neuroscience have heavily influenced many areas of psychological research in recent years, and cultural psychology is no exception. In fact, as Joan Y. Chiao, Bobby K. Cheon, Narun Pornpattananangkul, Alissa J. Mrazek, and Katherine D. Blizinsky emphasize in the target article, cultural psychology and neuroscience may have formed a particularly strong partnership in the business of explaining human diversity. Cultural psychology provides an explanatory framework for understanding meaningful variation in thought and behavior across cultures, and neuroscience offers explanations of how the brain and genes underlie psychological processes. By combining these two perspectives into a new field, cultural neuroscience may be well equipped to investigate the mind more completely, as arising from multiple, interacting forces from within and beyond the individual.

A particularly powerful factor to consider within the realm of cultural neuroscience comes from genetics, and although the study of culture and genes may be especially promising, with this unique opportunity for scientific growth comes specific challenges. Chiao and colleagues (this issue) put forth an important and impressive model of cultural neuroscience, the center of which is culture–gene coevolution theory (Chiao & Blizinsky, 2010; Feldman & Laland, 1996; see also Cavalli-Sforza & Feldman, 1981; Durham, 1990, 1991; Fincher & Thornhill, 2012; Lumsden & Wilson, 1981), or the dual inheritance theory of human behavior (Boyd & Richerson, 1985). The promise of this theory for contributing to progress in cultural neuroscience is undeniable. Yet some of the key challenges, necessary as they may be for a field in its infancy, are perhaps understated in the target article. Discussing both the promise and theoretical challenges of culture–gene coevolution theory in relation to another prominent framework in the study of culture and genes—that of gene–culture interactions (e.g., Kim et al., 2011; Kim, Sherman, Sasaki, et al., 2010; Kim, Sherman, Taylor, et al., 2010)—may be important for ultimately pushing the field toward greater potential.

Unprecedented Growth of Gene–Related Research in Psychology

Individual variation in genes is arguably one of the fastest growing biologically relevant factors stud-

ied in the field of psychology. As illustrated in Figure 1, the past dozen years have witnessed unprecedented growth in this area, more so than practically any other biological method or measure, including functional magnetic resonance imaging (fMRI), electroencephalography (EEG), hormones, heart rate, and galvanic skin response (GSR). This recent boom may be due, in large part, to technological advances in genotyping; that is, scientists are now able to conduct gene–related research more thoroughly, faster, and at a lower cost. Since the completion of the Human Genome Project in 2003, scientists have been hurriedly digging through the treasure trove of human DNA, searching for any sign of genetic answers to questions ranging from, “Why do some people despise cilantro?” to “Are my children predisposed to autism?” As evidenced by the vast number of publications in psychology that have incorporated genes in recent years, psychologists are likely among the most eager in the quest to understand what it all means.

The year 2003 was a seminal year for genetics, not only due to the mapping of the human genome but also because of a particularly influential paper that employed an elegant, nuanced approach to behavioral genetics. In their article on the link between genes, stress, and depression published in *Science*, Caspi and colleagues (2003) demonstrated a striking effect that rang true to many psychologists: that some aspect of the person (in this case, a genetic predisposition to stress reactivity) interacted with something about the situation (frequency of stressful life events) to predict psychological outcomes (depressive symptoms and clinical diagnosis of depression). This new framework of gene–environment interaction ($G \times E$; see also Caspi et al., 2002) is consistent with classic frameworks that psychologists tend to find quite familiar. For instance, the Person \times Situation approach from personality and social psychology (Lewin, 1936; Mischel, 1990; Mischel & Shoda, 1995) has substantial conceptual overlap with the $G \times E$ framework in that they both address questions of why the same person with a given predisposition may behave differently across two different situations and also why two people with different predispositions may behave differently given the same situation. To date, the 2003 finding by Caspi and colleagues has been cited thousands of times, and it has

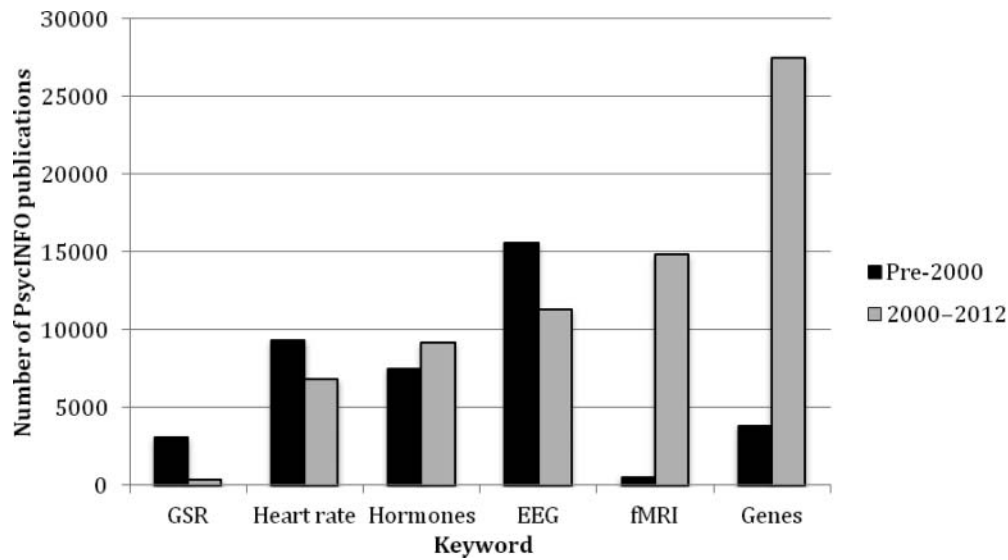


Figure 1. Number of publications in PsycINFO for biologically relevant methods or measures pre-2000 and from 2000–2012. *Note.* GSR = galvanic skin response; EEG = electroencephalography; fMRI = functional magnetic resonance imaging. *Source.* Adapted from Sasaki (2012).

set the stage for countless subsequent investigations on $G \times E$ in the field of psychology.

Promise of Culture–Gene Research for Explaining Human Diversity

Although not without its limitations (Munafò & Flint, 2009, 2011; Risch et al., 2009; but also see Karg, Burmeister, Shedden, & Sen, 2011), $G \times E$ is a promising new research direction with great potential for answering important questions in both general psychology and cultural psychology. Already, numerous investigations have made great impacts by demonstrating that features of the environment may interact with genes to predict psychological outcomes, including social support seeking (Kim, Sherman, Sasaki, et al., 2010), political ideology (Settle, Dawes, Christakis, & Fowler, 2010), aggression (McDermott, Tingeley, Cowden, Frazzetto, & Johnson, 2009), prosocial behavior (Bakermans-Kranenburg & van IJzendoorn, 2011; Knafo, Israel, & Ebstein, 2011; Sasaki et al., 2013), and health-related outcomes (Taylor et al., 2006; Way & Taylor, 2010). The specific outcome measures and candidate genes used in $G \times E$ studies may be broad, but a common theme emerging again and again across many of these studies is one of *environmental susceptibility*. It is possible, some have argued, that certain genes are linked to susceptibility or plasticity, and thus, people who carry particular variants of these genes may be predisposed to be sensitive to some environmental inputs “for better or for worse” (Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2007; Belsky et al., 2009; Obradović & Boyce, 2009).

For instance, people with certain genotypes of a susceptibility gene may suffer through negative outcomes in one environment, whereas in another environment they may thrive and achieve some of the best outcomes, even better than the outcomes of those without susceptibility genotypes.

Researchers have recently built on the $G \times E$ framework with that of gene–culture interaction, which considers culture as a specific form of environment that can interact with genes to predict psychological outcomes (e.g., Kim et al., 2011; Kim, Sherman, Sasaki, et al., 2010; Kim, Sherman, Taylor, et al., 2010; Sasaki, Kim, & Xu, 2011). According to this Gene \times Culture framework, even the same genetic predisposition can lead to different outcomes depending on the norms that permeate the broader culture, and likewise, culture may not have the same influence on people with different genetic predispositions. An important if implicit assumption of the gene–culture interaction framework, and of $G \times E$ more broadly, is that genes do not solely determine behavior but rather can provide people with the capacity to move toward a range of different outcomes depending on the specific conditions of the environment.

The promise of cultural neuroscience, and of the study of genes and culture in particular, is great. This culture–gene research may help scientists better understand population health disparities, as Chiao and colleagues point out, and achieve a more nuanced, and ultimately more accurate, view of the human mind. The target article also highlights the gene–culture interaction framework, in addition to culture–gene co-evolution theory, as playing an important role in understanding variation in psychological outcomes. Yet

for culture–gene research more broadly to continue to make an impact, there are some important challenges that should be addressed.

Challenges of Culture–Gene Research

As cultural psychologists venture ahead into new terrain, we should aim to address some of the real challenges involved in culture–gene research. Here I discuss a few specific challenges that culture–gene researchers (myself included) should consider as we reach across research areas and lay the foundation for a new, exciting field: 1) defining key theoretical components, 2) integrating more experimental research, and 3) bridging existing theories and frameworks.

Defining Key Theoretical Components

Particularly at the early stages of developing a new field, it is crucial to clearly define the key components of its foundation theories. In the culture–gene coevolution theory outlined by Chiao and colleagues (this issue), one term in particular that could be more explicitly defined is “adaptation.” When the authors state that “cultural traits are adaptive and emerge due to environmental and ecological pressures that vary across geography under which genetic selection occurs” (Boyd & Richerson, as cited by Chiao et al., this issue, p. 4), what do they mean by “adaptive”? Do they mean it in the biological sense of increasing “evolutionary fitness,” having the best chances of passing on one’s genes via natural selection? Or rather, that dominant cultural traits can perhaps have general benefits for health, make people successful in society, or keep them happy? It seems likely that they mean to use “adaptive” as it is used in evolutionary biology, but there are some potential problems that arise from this usage.

Although the capacity to learn and transmit culture itself may be essential for evolutionary fitness (Boyd, Richerson, & Henrich, 2011), one potential confusion with asserting “cultural traits are adaptive” is that it may seem to imply that normative traits in a culture are always adaptive and that nonnormative traits are not. It is unclear whether frequency of a behavior in a society can be used as a direct indicator of evolutionary fitness given that some seemingly “adaptive” traits (say, the desire to have many children) may not be the norm in a given place, yet the trait itself may still appear to increase the likelihood of successfully passing on one’s genes. Conversely, other normative traits—for instance, wanting just one child, if at all—may not seem so “adaptive.” Now it is possible that not wanting children is associated with other traits that do confer fitness advantages, such as having greater resources to care for close relatives, including those who have children, and thus passing on shared genes through kin.

However, it is not clear in this case whether fitness advantages lie with the normative or nonnormative trait regarding child–wanting given that the “adaptive” case can potentially be made for both. Although behavioral norms may at times reflect psychological or biological adaptations, the reality is that adaptations can lead to both normative and nonnormative behaviors (or traits) under different conditions. Thus, it may not be possible to always expect frequent genotypes to correlate with the phenotypes of normative behaviors (see, e.g., Tooby & Cosmides, 1990, for discussion of genetic variation in relation to differences in personality). If the authors instead intended to state that nonnormative traits could also be adaptive (or selected), then it may be necessary to clarify how the cultural selection component of culture–gene coevolution theory is distinct from the broader theory of natural selection, which acts on traits in general—not just normative ones in a culture—in order to build adaptations.

Another related problem is that it is not entirely clear whether the theory intends to make the “adaptive” claim about normative traits of *any* culture, or whether it pertains more to certain ones, such as ethnicity or nationality. Given that there are many forms of culture (A. B. Cohen, 2009), including but not limited to socioeconomic status (SES; Snibbe & Markus, 2005), region of country (D. Cohen, Nisbett, Bowdle, & Schwarz, 1996), and religious tradition (A. B. Cohen & Rozin, 2001), it may be useful to specify the extent to which culture–gene coevolution theory should apply equally to these other forms of culture. For instance, in the case of SES, does culture–gene coevolution theory predict that the culturally adaptive (normative?) traits of individuals low in SES should be reflected in their genes because “genetic selection causes further refinement of core cognitive and neural architecture necessary for the storage and transmission of adaptive cultural capacities” (Boyd & Richerson, 1985; Chiao & Blizinsky, 2010; Mrazek et al., as cited by Chiao et al., this issue, p. 2)? If not, then future research should determine the key aspects of a culture that must be present in order for culture–gene coevolution theory to most effectively apply.

Finally, it may be critically important for researchers to know approximately how long a given cultural trait must be stable before it can significantly influence genetic selection and become “adaptive.” As in the cases of higher lactose tolerance in postagriculture societies (Beja-Pereira et al., 2003) and greater collectivism in regions with higher frequencies of short (S) alleles of the serotonin transporter polymorphism 5-HTTLPR (Chiao & Blizinsky, 2010) and with historical pathogen prevalence (Fincher, Thornhill, Murray, & Schaller, 2008), some evidence for culture–gene coevolution theory comes from times not so long ago in the scope of human history (Richerson, Boyd, & Henrich, 2010). Yet cultures are dynamic, ever-changing systems that

evolve faster than genes (Richerson & Boyd, 2005; Tooby & Cosmides, 1989). Especially with recent exponential increases in globalization, cultural ideas and behaviors can spread faster now than ever before, creating the potential for particularly strong and widespread selection pressures in the environment (e.g., see Feldman & Laland, 1996). Meanwhile, the speed of genetic change must be limited by certain biological constraints. Thus, how fast can genes be expected to change in response to culture?

In sum, to effectively advance understandings of culture and genes, the theory of culture–gene coevolution eventually needs to address not only which traits are adaptive (normative traits or also nonnormative traits?) and what forms of culture can have adaptive cultural traits (any type or certain types?) but also when cultural traits can become adaptive. And what exactly is meant by “adaptive?”

Integrating More Experimental Research

The studies on culture–gene coevolution presented in the target article (e.g., Chiao & Blizinsky, 2010) are impressive given their broad cultural and geographical representation, substantial sample sizes, and large effects. However, one serious limitation of research on culture and genes is the reliance on survey data that are correlational. Aside from supplemental data from experiments that manipulate levels of gene–related hormones (e.g., serotonin; Beacher et al., 2011), the argument that a particular gene and a cultural trait mutually influence each other rests heavily on nonexperimental research. There is a clear need for more experimental research in this new area, yet there are points at which Chiao and colleagues (this issue) make strongly causal claims based on largely noncausal evidence.

It may be particularly difficult to conduct experiments well suited to test culture–gene coevolution theory. Other theories, however, may be able to incorporate causal data and complement culture–gene coevolution research. For instance, in a recent study of $G \times E$ (Sasaki et al., 2013), we examined a dopamine receptor gene (exon III region of DRD4), religion, and prosocial behavior and utilized a quasi-experimental design. By manipulating whether people were implicitly primed with religion or not, we demonstrated that religion priming interacted with DRD4 variant such that people with susceptibility variants of DRD4 (2- or 7-repeat alleles) were influenced by the religion prime to behave more prosocially, whereas people without DRD4 susceptibility variants were not affected by the religion prime. This pattern of results is an interesting reworking of previous understandings of DRD4, which had characterized people with DRD4 susceptibility variants as “antisocial” compared to people without these susceptibility variants (e.g., Bachner-Melman et al., 2005). In fact, when people in our

study were not primed with religion, we indeed found that those with DRD4 susceptibility variants seemed to be less prosocial than those without susceptibility variants, consistent with the “antisocial” characterization of past research. However, among those who were primed with religion—an environmental condition which should have given them sufficient situational pressure to behave appropriately—people with susceptibility variants were actually the most likely to act prosocially compared to all the other groups. This study used classic experimental methods from social psychology in combination with the $G \times E$ framework in order to build on past correlational studies of Gene \times Culture and $G \times E$ more broadly (e.g., Sasaki et al., 2011). The experimental component of studies such as this may allow for a better understanding of how the environment causally leads to differences in psychological outcomes, and how this effect may vary depending on genetic predispositions.

Bridging Existing Theories and Frameworks

When possible, we should bridge existing theories and frameworks to advance new research areas. Here I discuss culture–gene coevolution theory and the framework of gene–culture interaction together because these are among the most prominent in this new field of cultural neuroscience. Whereas the gene–culture interaction framework addresses how human psychological diversity stems from interacting aspects of biological and cultural diversity, the theory of culture–gene coevolution aims to tackle the question of how that biological and cultural diversity came to be. In statistical terms, the Gene \times Culture framework makes a claim of moderation such that the same genetic predisposition can predict different outcomes depending on culture, whereas the culture–gene coevolution theory makes a claim of cyclical mediation regarding cultural selection and genetic selection. More specifically, culture–gene coevolution theory posits that cultural traits are adaptive and, thus, cultural selection occurs due to higher frequency of certain genotypes in a culture, which are influenced by other environmental or ecological pressures (Boyd & Richerson, as cited by Chiao et al., this issue). At the same time, culture can allow humans to modify the environments that influence genetic selection, thus resulting in greater frequency of particular genotypes in a culture (Odling-Smee, Laland, & Feldman, as cited by Chiao et al.). Both these perspectives move the field forward by integrating genetics with cultural psychology, but a more explicit comparison may help clarify where they make complementary or diverging predictions.

Gene \times Culture research demonstrates that genetic predispositions interact with culture to predict a variety of outcomes, such as social support (Kim, Sherman, Sasaki et al., 2010), locus of attention (Kim, Sherman,

Taylor et al., 2010), and emotional suppression (Kim et al., 2011). Across psychological outcomes, these studies suggest that a particular genotype may predict different outcomes depending on culture, and furthermore, many of the “culturally normative” responses found in cultural psychology research seem to be stronger for people with certain genotypes than others. In particular, this research finds that genes and culture interact over and above an association between genotype frequency and cultural traits. Contrary to what one might expect from the description of culture–gene coevolution theory by Chiao and colleagues (this issue), Gene \times Culture findings indicate that the people who *most strongly* exhibit cultural traits, or those who have the greatest expression of psychological phenotypes that are normative in a particular culture, may not always represent the most frequent genotype of a particular gene. Therefore, it may be important to clarify when we should expect to find genetic correlates, and when we should expect to find susceptibility genes that interact with the environment.

Thus far, our Gene \times Culture research has found evidence that the oxytocin receptor gene (OXTR rs53576) may be linked to differential susceptibility. For example, in a study on culture, OXTR, and emotional support seeking (Kim, Sherman, Sasaki et al., 2010), we proposed that OXTR might be sensitive to culture–specific input about the relational norms of social support. Given that East Asian and mainstream American cultures differ systematically in the way they seek social support from their relationships (Kim, Sherman, & Taylor, 2008; Taylor et al., 2004), we expected that people with a stronger predisposition for social sensitivity (i.e., G allele vs. A allele carriers) would show the strongest culturally normative response or “cultural trait.” As predicted, we found that culture interacted with OXTR such that, when under high psychological distress, European Americans with the G allele reported seeking emotional support more than European Americans without the G allele, whereas Koreans did not significantly differ in support seeking by genotype, though there was a trend for Koreans with the G allele to report seeking less support than Koreans without the G allele. In this study, we also found that the European American and Korean samples differed significantly in genotypic distributions of OXTR. Consistent with past investigations on ethnically similar samples (Bakermans-Kranenburg & van IJzendoorn, 2008; Wu et al., 2005), we found that the G allele was more common than the A allele among European Americans, whereas the A allele was more common than the G allele among Koreans. In line with what one might predict from culture–gene coevolution theory (e.g., Chiao & Blizinsky, 2010), European Americans with GG or GA genotypes not only had the more common genotype but also showed the more culturally normative response: When under high psycho-

logical distress, they sought more emotional support than European Americans with the AA genotype. For Koreans, however, the same culture–gene association did not hold. Among Koreans with the AA genotype, the genotype more frequent in their culture, they did not significantly differ from Koreans with GG or GA genotypes in support seeking, and if anything, they tended to seek slightly more emotional support than GG or GA carrying Koreans. This means that Koreans with the AA genotype tended to show the *less* culturally normative response even though AA is the most frequent genotype in their culture.¹

Besides OXTR, we found that other genes produce a pattern of results suggesting genetic susceptibility. For instance, in our investigation of culture, a serotonin receptor gene [C(-1019)G 5-HTR1A], and locus of attention (Kim, Sherman, Taylor et al., 2010), we examined whether people with the G allele (vs. the C allele) of 5-HTR1A would be more sensitive to culture-specific norms regarding broad versus narrow scope of attention. Of importance, we found the predicted interaction of genes and culture such that the cultural difference in locus of attention was greatest among those with the GG genotype, followed by the CG genotype (for whom the cultural difference was still significant but smaller than the GG genotype), and finally the CC genotype (for whom there was no significant cultural difference). In terms of genotype frequency distributions, we did find a significant cultural difference: GG was the most frequent genotype of 5-HTR1A among Koreans compared to the other genotypes (CG and then CC), whereas CG was the most frequent among European Americans, followed by GG and CC. Yet there was no main effect of 5-HTR1A, and the significant main effect of culture was qualified by the gene–culture interaction. Koreans with the GG genotype most strongly exhibited the East Asian culturally normative response of broad locus of attention. At the same time, the culturally normative response for European Americans—that of narrow locus of attention—was strongest among European Americans with GG, not CG or CC genotypes, despite the finding that GG was not the most frequent genotype in their cultural group. In this case, the cultural trait of broad versus narrow locus of attention did not correlate with frequency of 5-HTR1A genotype across cultures. Rather, it was predicted by an interaction of culture and genes.

Because these Gene \times Culture studies compare two groups that differ not only in cultural background but also potentially in genetic makeup (i.e., their relative proportions of alleles at different genetic loci), one possible alternative explanation for these findings is

¹In another study of culture and OXTR, we again found that the most frequent genotype did not necessarily correspond with the most normative response regarding emotional suppression in one culture (Kim et al., 2011).

that the reported gene–culture interactions are actually gene–*gene* interactions. To address this possibility, in most of our gene–culture interaction studies, we use the triangulation method of comparing the results against a third cultural group, such as Korean Americans, who should be more similar in their genetic makeup to one group (e.g., Koreans more than European Americans) but were raised in the cultural context of the other group (e.g., mainstream American culture). Across three studies (Kim et al., 2011; Kim, Sherman, Sasaki, et al., 2010; Kim, Sherman, Taylor, et al., 2010), we found that Korean Americans, the third cultural group, showed a pattern of results resembling that of European Americans more than Koreans, suggesting that genes are interacting with the cultural environment rather than another gene or set of genes to predict different psychological outcomes.

Yet how can it be that a normative trait within a culture does *not* correspond to relative frequency of a dominant genotype in that culture? According to evidence from evolutionary psychology and biology, changes within cultures may occur much faster than changes in genes (Richerson & Boyd, 2005; Tooby & Cosmides, 1989), and thus, one possibility is that there are a number of cultural traits not yet directly reflected in the genes of a given population because of a time lag. Another possibility is that for some cultural traits, there may appear to be no correlation with genotypes across groups because a particular gene or set of genes codes for environmental susceptibility within a domain (e.g., locus of attention), and then specific input from a culture shifts phenotypes of that group in one direction or another (e.g., broader or narrower loci). If this is the case, then a major task in the study of culture and genes is to establish when to expect cultural environments to correlate with genes and when to expect them to interact. To be clear, the gene–culture interaction framework and the theory of culture–gene coevolution can be complementary, but as a field, we need to delineate the conditions under which one or both of these should apply.

Concluding Remarks

Chiao and colleagues (this issue) have significantly contributed to a more complete understanding of how human diversity may be impacted by both genetic and cultural selection with an ambitious theory of culture–gene coevolution, and I commend the authors for bringing these very important issues to the forefront. Although some key challenges remain to be addressed in future research—such as which cultural traits are adaptive, whether culture–gene relationships are causal, and when genetic variants should correlate and/or interact with the cultural environment—the promise of cultural neuroscience is evident. The integration of biological and neuroscientific perspectives with cultural psychol-

ogy will continue to be crucial for advancing understandings of the mind, brain, and behavior.

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Note

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