analysis didn't find any genes of large effect; candidate gene studies didn't find any genes of medium effect; genome-wide association study (GWAS) didn't find any genes of tiny effect; GWAS was able to estimate human heritabilities without twins, but they were much smaller than twin heritabilities; GWAS was used to sum tiny DNA effects into polygenic scores (PGSs), which were modestly correlated with behavioral phenotypes; those PGSs are able to make genetic discriminations within families in ways that twins are not; in particular they are able to separate genetic effects on parents transmitted environmentally to offspring from genetic effects originating directly in the offspring genome; and all of these analyses are confounded in complex ways by genetic, ethnic, and phenotypic clustering, that is, culture.

But in the newest genomic studies of human behavior, something remarkable has happened. Chastened, perhaps, by the absence of any actionable genes, by the diminishing heritabilities, by the elusiveness of meaningful biology, by the less than practical performance of PGSs, yet spurred on by the deep fractal complexity of modern genomics, the most recent behavior genetic papers include no nature–nurture content whatsoever. Consider, for instance, the recent GWAS of sexual orientation (Ganna et al., 2019). A few single-nucleotide polymorphism (SNP) hits were identified, some small heritability was quantified, and on a charitable reading some interesting biological and behavioral pathways were suggested. All of which is fine, and may or may not lead to insight in the long run. But in the meantime, the paper contains absolutely zero Bouchardian litigation of nature–nurture issues as regards sexual orientation.

When I first wrote in these pages (Turkheimer & Gottesman, 1991), we were responding to a target article by Plomin and Bergeman (1991) that, ironically, had a great deal in common with the current one. Where the current article notes that the transmission of differences across generations often occurs along cultural rather than strictly genetic pathways, Plomin and Bergeman (1991) argued that ostensibly environmental modes of transmission often encompass genetic variance. From the point of view of a social scientist trying to sort it all out, it is the same conclusion viewed through the nature–nurture looking glass. In response, Gottesman and I concluded,

> Our concern is about where all this will lead. Behavior is influenced by genotype and environment. The environment provided by a parent is influenced by the parent's (not to mention the child's) genotype, and the parent's rearing environment, which had its own tangle of reciprocal genetic and environmental influences. Everything is intercorrelated; everything interacts. Where does this leave the columns of "model-fitting heritabilities," meticulously computed to two decimal places and starred for statistical significance on the basis of path models that cannot hope to keep pace with the reciprocal causal structures described in the target article?

We now know where it led: To the end of nature–nurture as a serious question to be debated by genetically informed social scientists. Good riddance.

References

Bouchard, Jr, T. J. (2004). Genetic influence on human psychological traits: A survey. *Current Directions in Psychological Science*, 13(4), 148–151.

Ganna, A., Verweij, K. J., Nivard, M. G., Maier, R., Wedow, R., Busch, A. S., … Zietsch, B. P. (2019). Large-scale GWAS reveals insights into the genetic architecture of same-sex sexual behavior. *Science*, 365, eaat7693. doi: 10.1126/science.aat7693.

Plomin, R., & Bergeman, C. S. (1991). The nature of nurture: Genetic influence on "environmental" measures. *Behavioral and Brain Sciences*, 14(3), 373–427.

Turkheimer, E. (2000). Three laws of behavior genetics and what they mean. *Current Directions in Psychological Science*, 9(5), 160–164.

Turkheimer, E., & Gottesman, I. I. (1991). Is $H^2 = 0$ a null hypothesis anymore?. *Behavioral and Brain Sciences*, 14(3), 410–411.

Hidden clusters beyond ethnic boundaries

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Abstract

Hidden cluster problems can manifest when broad ethnic categories are used as proxies for cultural traits, especially when traits are assumed to encode cultural distances between groups. We suggest a granular understanding of cultural trait distributions within and between ethnic categories is fundamental to the interpretation of heritability estimates as well as general behavioral outcomes.

The target article argues that accounting for human social categories is essential for understanding aggregate measures of ostensibly non-social phenomena, such as the heritability of intelligence. Uchiyama et al. rightly highlight what they call the "hidden cluster problem," (sect. 3), in which geopolitical or ethnolinguistic boundaries often used by geneticists to account for culture may fail to accurately represent important cultural and even environmental clustering. We agree that this is a problem, and further propose that the hidden cluster problem creates challenges not only for behavioral genetics, but also for social scientists who want to better understand the full spectrum of influences to cultural and behavioral traits. We draw particular attention to the classic anthropological work of Barth (1969) in outlining the importance of developing more granular understandings of human cultural trait distributions.

As the human behavioral sciences have expanded over the last several decades, special attention to sampling and methodological issues, such as the WEIRD (western, educated, industrialized, rich, and democratic) sampling and causal locus problems discussed by Uchiyama et al., have been extensively explored. In contrast, the hidden cluster problem has received less attention outside of the social sciences despite recurrent examples of cultural clustering in social-scientific and ethnographic accounts (Colleran, 2020; Henrich, Heine, & Norenzayan, 2010; Richerson & Boyd, 2008; Schulz, Bahrami-Rad, Beauchamp, & Henrich, 2019). Hidden clusters represent a particularly pernicious problem because the categories that individuals use to socially identify themselves may not necessarily map onto well-defined cultural trait distributions. Consider, for

example, caste and ethnicity in India and differentiation *within* these categories: Biswas and Pandey (1996) found that traditionally defined categories of identity in India did not map well onto self-perceived economic condition or social status once one accounts for economic mobility (also see Schooler, 2010). This means that using these endemic social categories with the aim of controlling for cultural differences between individuals does not ensure that the cultural differences represented by those categories are the ones most relevant for studying the problem at hand.

Hidden clusters can confound behavioral analysis when self-ascribed ethnicity is used as a proxy for culture, especially when there is scarce information about the distribution of cultural traits within and across ethnic groups in a society. In the case of estimating heritability, this can potentially blind us to the extent of cultural heterogeneity in the social environment, as outlined in the target article. Scholars going back as far as Barth (1969) have warned that self-ascribed ethnicity should not be used as a proxy for substantive cultural trait distributions between ethnic groups. Rather, because ethnicities emerge in the interactions between groups and cluster around particular cultural dimensions that give rise to demarcation, they do not reflect the entirety of the cultural trait distribution of a group, only the part of it that is relevant to the boundaries of group membership. Knowing these boundaries means knowing across which cultural dimensions groups differentiate from one another, which relates directly to the degree of heterogeneity of the social environment and its effect on heritability estimates.

Consider a society where two ethnic groups are differentiated by their cooking practices, but share other cultural traits, such as kinship norms, in common. These self-ascribed ethnic categories, demarcated by differences in cooking practices, tell us nothing about the clustered nature of kinship norms across ethnic groups. If (for the purposes of this example) kinship norms are causally intertwined with political preferences, and we want to study the genetic heritability of political preferences, researchers may be presented with hidden environmental homogeneity, which would increase the measured genetic heritability of political preferences, leading to the erroneous conclusion that one is accounting for cultural differences in the behavioral dimensions of interest. Using self-ascribed ethnicity as a proxy for culture opens us up to the risk of ignoring hidden clusters, leading us to overestimate the heritability of political preferences because of the residual variation explained by genes in our example.

In its moment (and beyond), the Barthian notion of ethnic identity was important for proposing ethnic ascription as an indicator of group-level interactions at work. In the study of cultural evolution, this way of thinking about identity has been generalized beyond ethnicity, particularly in contemporary notions of social identity and its relation to behavioral clustering (McElreath, Boyd, & Richerson, 2003; Smaldino, 2019; Smaldino & Turner, 2021). Social identities emerge in an evolving ecology of groups, and thus are driven by potential patterns of coexistence, cooperation, competition, domination, dependence, hierarchization, and so on. In human societies, where social identities can be nested and multidimensional (in great part owing to the possibility of multiple group membership), understanding which cultural clusters correlate with which facets of social identity is necessary in order to construct a sufficiently clear view of a society's cultural trait landscape. For example, the social identity dimension of social class can be defined, at least in part, by the bounded set of cultural traits that correlate with socioeconomic status (Bourdieu, 1987). Certain traits, in this example, may be shared by all high socioeconomic status members of a society, regardless of ethnicity (even though ethnicity is often non-

independent of socioeconomic status across groups). From this view, it becomes clear that, if the aim is to explain where a particular behavior comes from and the extent to which it is genetically heritable, the goal of understanding a society's cultural dynamics with fine granularity in regards to its unique traits – and even more critically, the extent to which these traits overlap with other cultural groups – must be incorporated into the research process.

Understanding the emergence of cultural clusters is a work in progress, with both theory and methodology still under construction. That said, turning a blind eye to cultural clustering in societies of interest is a potential problem for any science of human behavior that seeks to account for the effects of cultural differences. Accounting for the existence of hidden cultural clusters should be a default aim for *all* behavioral sciences, including but not limited to behavioral genetics.

References

Barth, F. (1969). *Ethnic groups and boundaries: The social organization of culture difference*. Little, Brown.

Biswas, U. N., & Pandey, J. (1996). Mobility and perception of socioeconomic status among tribal and caste group. *Journal of Cross-Cultural Psychology*, 27(2), 200–215.

Bourdieu, P. (1987). *Distinction: A social critique of the judgement of taste*. Harvard University Press.

Colleran, H. (2020). Market integration reduces kin density in women's ego-networks in rural Poland. *Nature Communications*, 11, 266.

Henrich, J., Heine, S., & Norenzayan, A. (2010). Most people are not WEIRD. *Nature* 466, 29. https://doi.org/10.1038/466029a.

McElreath, R., Boyd, R., & Richerson, P. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology*, 44(1), 122–130.

Richerson, P. J., & Boyd, R. (2008). *Not by genes alone: How culture transformed human evolution*. University of Chicago Press.

Schooler, C. (2010). Culture and social structure: The relevance of social structure to cultural psychology. In D. Cohen (Ed.), *Handbook of cultural psychology* (pp. 370–388). Guilford.

Schulz, J. F., Bahrami-Rad, D., Beauchamp, J. P., & Henrich, J. (2019). The church, intensive kinship, and global psychological variation. *Science*, 366, eaau5141.

Smaldino, P. E. (2019). Social identity and cooperation in cultural evolution. *Behavioural Processes*, 161, 108–116.

Smaldino, P. E., & Turner, M. A. (2021). Covert signaling is an adaptive communication strategy in diverse populations. *Psychological Review*, 129(4), 812–829. https://doi.org/10.1037/rev0000344.

Culture is reducing genetic heritability and superseding genetic adaptation

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