

different forms of intercourse is believed to produce culturally distinct beings (Kelly, 1974). Such traits marking identity stand fast at boundaries regardless of rates of interaction.

Traits that mark identity obscure many essential commonalities across cultures. Complex cultural packages that confer strong selective advantages spread rapidly across boundaries allowing people from distinct linguistic and cultural groups to share many behaviors and adaptations. I will give three examples. (1) Sweet potatoes, introduced to Highland Papua New Guinea cultures some 400 years ago, released constraints on agricultural production and spread widely in response to environmental pressures long before first contact with Europeans (Ballard, Brown, Bourke, & Harwood, 2005). Utilization of the new crop created homogeneity in subsistence practices and pig husbandry across vast areas, similarities which could be obscured by linguistic differences and expressions of cultural identity. (2) Among the Enga, bachelors' cults to discipline and educate cohorts of youths arose before European contact in some clans of central Enga under conditions of intense competition in trade, ceremonial exchange, and warfare. Big-men along trade routes identified successful clans from whom to purchase the transformative rites to improve clan fortune, while bachelors raised the wealth and went on journeys to do so (Wiessner & Tumu, 1998). Within two to three generations, bachelors' cults were adopted by 500 or more clans in the five dialect groups of Enga, fostering group loyalty and masking individualistic agendas. Meanwhile influential big-men exerted pressures to proclaim their enterprising sons as marriageable years before others to jump start their polygynous careers, creating reproductive inequalities. (3) Intraclan institutions applying restorative justice were adopted across linguistic groups in most Highland societies where intergroup competition was fierce. Social selection drove their development to bring potentially productive transgressors back into community, compensate for harm done, restore cooperation, and avoid the grudging conformity that ensues from punishment. Restorative measures fostered tolerance, openness, and innovation (Wiessner, 2020).

The many selection pressures that operate on agents who steer the course of cultural evolution must be considered to understand how cultural heterogeneity and homogeneity are generated and whether their content is significant for masking or unmasking genetic inheritance. For this purpose, the ethnographic record is most valuable.

Conflict of interest. None.

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Cultural evolution may influence heritability by shaping assortative mating

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doi:10.1017/S0140525X21001801, e181

Abstract

Uchiyama et al. productively discuss how culture can influence genetic heritability and, by modifying environmental conditions, limit the generalizability of genome-wide association studies (GWASs). Here, we supplement their account by highlighting how recent changes in culture and institutions in industrialized, westernized societies – such as increased female workforce participation – may have increased *assortative mating*. This alters the distribution of genotypes themselves, increasing heritability and phenotypic variance, and may be detectable using the latest methods.

Nearly 50 years ago, mathematical concepts from population genetics were first applied to understand how cultural evolution could shape genetic heritability (Cavalli-Sforza & Feldman, 1973). Building on those efforts and much subsequent work, Uchiyama et al., productively fuse modern *dual-inheritance theory* (Henrich & McElreath, 2007; Laland, Brown, & Brown, 2011) – which can account for how cultural evolution has shaped our environments in specific ways – with prevailing ideas from behavioral genetics, including approaches to studying how the effects of large numbers of genetic variants additively combine to shape heritable phenotypes in genome-wide association studies (GWASs). Stated simply, any dataset of phenotypes is shaped by two landscapes of variation, one genetic and another cultural, that were generated by different evolutionary processes and transmission rules.

The authors' ideas imply that much of the *exposome* (Wild, 2012) is shaped by transmissible cultural traits and therefore possesses its own population history, structure, and dynamics. Because the environment influences genetic effects, either in aggregate (e.g., Amin et al., 2017) or for single genes (Gauderman et al., 2017; e.g.,

Rask-Andersen, Karlsson, Ek, & Johansson, 2017), the tendency of GWASs to focus on populations that have evolved culturally in ways that minimize certain kinds of variation – through mechanisms such as universal schooling, social safety nets, and parasite-free environments – limits the scope of their inferences and biases variant discovery toward those that impact the phenotype in this limited environmental range.

One important mechanism by which culture evolution can drive up genetic heritability, which the authors only allude to, involves covariation between genes and sociocultural environments caused by the sorting of genotypes into specific environments (“reciprocal causation,” Dickens & Flynn, 2001). Recent cultural and institutional changes in western, educated, industrialized, rich, and democratic (WEIRD) societies are especially likely to have strengthened such sorting. In fact, purely cultural changes (no natural selection), by increasing social sorting, may even alter genotype distributions themselves through *assortative mating* – which occurs whenever spouses resemble each other phenotypically and genetically.

Assortative mating increases the additive genotypic variance directly (recall, $h^2 = V_g/V_{total}$). Additionally, culturally induced assortative mating can – if it occurs *across* traits (e.g., if tall men marry educated women) – create a genetic correlation between two different traits (Keller et al., 2013). If a genetic correlation was induced by assortment, it would have arisen purely from population-level phenomena and not from physiological or developmental processes. Such effects are notable for two reasons: (1) through assortative mating, cultural change can systematically alter, sometimes quite rapidly, a statistic-like genetic variance or genetic correlation without influencing natural selection; (2) Uchiyama et al. largely focus on the denominator of the expression for heritability, that is, the cultural contribution to the total phenotypic variance ($V_{culture}$ in $V_{total} = V_E + V_{culture}$), and less on what we highlight here – heritability’s numerator.

How assortative mating increases genotypic variance is well-understood (Peyrot, Robinson, Penninx, & Wray, 2016). Intuitively, more people would have extreme genotypic values for height if the tall mated with tall and the short with short. However, why should assortative mating have increased in recent cohorts? First, a growing proportion of those populations typically sampled in genetic studies participate intensively in institutions that have an explicit sorting function – such as schools, universities, specialized occupations, and labor markets; this is accelerated by the dismantling of social barriers (e.g., during the entry of women into the workforce; Breen & Andersen, 2012; Greenwood, Guner, Kocharkov, & Santos, 2014). Relative to traditional forms of communality such as religious institutions or neighborhoods, such institutions also increasingly shape our social lives – and our mating opportunities. Second, with social liberalization, WEIRD people have an increasingly homogeneous exposure to the set of social niches and behavioral choices offered by those aforementioned institutions, in addition to those offered by consumption, lifestyle, and entertainment markets, increasing the scope for *self-selection* into specific social environments. Third, major shifts in norms, technology, and economic behaviors lead to increased urbanization and increased geographic and relational mobility (Ancestry.com, 2020; Maas & Zijdeman, 2010). It also changes in how people meet their mates, with social contexts possessing low relational mobility such as church or neighborhood declining in importance relative to high relational-mobility social environments such as bars, the workplace, or dating apps (Rosenfeld, Thomas, & Hausen, 2019). This grows the pool of potential mates, increasing the efficiency of assortative mating.

These effects have not been directly demonstrated, but a growing body of evidence indicates that the requisite conditions exist. Some social groups in modern industrialized societies, such as occupational groups, are behaviorally differentiated at both the phenotypic and genotypic levels. For example, individuals employed in STEM have increased autism spectrum quotients (Daysal, Elder, Hellerstein, Imberman, & Orsini, 2021; Ruzich et al., 2015), and the incidence of autism among newborns is elevated in regions with high-occupational participation in STEM, suggesting some genetic sorting (Roelfsema et al., 2012). In an Icelandic dataset, high polygenic scores for schizophrenia and bipolar disorder strongly predict participation in creative industries and membership in artistic societies (Power et al., 2015); these correlations were replicated in Sweden (MacCabe et al., 2018). High polygenic scores for these two disorders also contribute to increased time in the educational system (Bansal et al., 2018; Demange et al., 2021); and relatives of tenured university academics suffer elevated rates of these disorders (Parnas, Sandsten, Vestergaard, & Nordgaard, 2019). If mating within such behaviorally differentiated groups has increased over time because of the sociocultural and institutional changes we highlighted previously, assortative mating would strengthen, which indeed has happened for educational and occupational specializations (Eika, Mogstad, & Zafar, 2019). High rates of within-trait and cross-trait assortative mating for psychiatric diagnoses at the phenotypic level were found in a dataset drawn from the Swedish population register (Nordsletten et al., 2016).

Together, these theoretical insights and empirical facts suggest that culture can, and likely has, influenced genetic heritability through multiple pathways, including – in addition to the effects suggested by Uchiyama et al. – assortative mating. The target article presents a window into fascinating processes entangling genes and culture that deserve to be studied empirically with the newest methods. Such a program would represent the flowering of a dual-inheritance theory that has been fortified by modern data and research designs.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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