Culture is Reducing Genetic Heritability and Superseding Genetic Adaptation

Comment on target article: Cultural Evolution of Genetic Heritability**,** by R Uchiyama, R Spicer and M Muthukrishna, 2021

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Abstract

Uchiyama, Spicer, and Muthukrishna reveal how group-structured cultural variation influences measurements of trait heritability. We argue that understanding culture's influence on phenotypic heritability can clarify the impact of culture on genetic inheritance, which has implications for long-term gene-culture coevolution. Their analysis may provide guidance for testing our hypothesis that cultural adaptation is superseding genetic adaptation in the long term.

Uchiyama, Spicer and Muthukrishna have made an important contribution to dual inheritance theory. To date, dual inheritance theory has focused mainly on the coevolution of a pair of genetic and cultural traits (e.g. Gerbault et al., 2011) or on the genetic evolution of cultural evolution itself (e.g. Henrich & McElreath, 2003). The question of how genetic evolution might itself evolve culturally has received less rigorous inquiry. Uchiyama *et al.* broach this issue, showing how cultural adaptation (especially group level cultural adaptation) can change genetic heritability by intervening between genes and their effects on survival and reproductive outcomes. In a recent article, two of us explore this same dynamic from the perspective of long-term gene-culture coevolution (Waring & Wood, 2021). Here we consider the implications of the insights of Uchiyama *et al.* on long-term gene-culture coevolution.

The authors argue that cultural contributions to phenotypes can modify genetic heritability, an important and often overlooked point. Phenotypic variation in humans is the result of genetic, environmental, and cultural factors, and their interactions. Genetic heritability can be given as:

$$V_G/(V_G + V_c + V_e)$$

where V_G, V_c, *and* V_e denote phenotypic variation with a genetic, cultural, and environmental basis, respectively. Our capitalization is consistent with Uchiyama *et al*, but our formulation differs in order to highlight the idea that cultural effects on phenotype are not limited to acting through environmental variation.

The influence of culture on genetic heritability is complex, and the result of indirect feedbacks by which one *V* component affects another. Culture may generate phenotypic variation directly (increasing V_c), affect environmental (or ecological) variation indirectly (changing V_e), and mask or unmask genetic variation (decrease or increase V_G). For example, medicine can reduce the effect of diseases (an environmental variable) on health, reducing the role of immunity genes in determining phenotypic outcomes, but making health contingent on the health system one is part of. In this example, the novel cultural adaptation decreases V_e and V_G and increases V_c. These changes would decrease genetic heritability if changes in V_G and V_c outweigh those in V_e. Therefore, the overall impact depends on the relative phenotypic contribution of each type of variation.

Uchiyama *et al*. appear to assume that cultural evolution tends to decrease cultural and environmental variation within groups, citing mechanisms such as conformist learning (Henrich & Boyd, 1998), prestige-biased learning (Henrich & Gil-White, 2001), and success-biased learning (Baldini, 2012). However, structured group-level cultural traits complicate the argument (Smaldino, 2014). Because of specialization and divisions of labor, social learning mechanisms often generate adaptive cultural complexity within a society, rather than merely homogenize it. For traits that mask genetic effects, increases in cultural variation, V_c, cause decreases in genetic heritability. Thus, there may be more scenarios which decrease genetic heritability than previously thought.

Cultural influences on genetic heritability have major consequences for human evolution well beyond those discussed by Uchiyama *et al.* A key point they omit is how these cultural influences would alter genetic adaptation and evolution. Increased heritability strengthens the evolutionary response of functional genes to selection, while decreased heritability weakens this response (Lush, 1943). Laland (1992) has shown how the transmission of an adaptive behavior via social learning can preempt adaptation by natural selection on genes. This effect should be the expected result. Therefore, students of human evolution should ask whether there is any average long-term trend in culturally mediated changes to heritability.

We hypothesize a general directionality to the role of culture in determining phenotypic variation in the long term: culturally determined phenotypic variation is increasing (V_c is growing), and cultural evolution is simultaneously decreasing genetically determined phenotypic variation by breaking the link between genotype and phenotype (V_G is shrinking). For example, educational attainment depends on both genetic and cultural factors, and generally comes at a reproductive cost. But, as Hong (2020) shows, educational attainment

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is likely to continue to increase even while the genetic component declines.

We think that V_c has increased, not for all traits at all times, but as part of a long-term average trend across human societies over the course of evolution. Evidence for this comes from the broad and striking increase in the emergence, diversification and refinement of cultural systems and technology that improve human fitness outcomes in food production, collective defense, health and so on. Such complex group-level cultural adaptations increase cultural variation and, thus, V_c, in the human species. When V_c increases, then genetic heritability decreases. Thus, we suspect, along with Uchiyama *et al.* and others, that cultural adaption has already been replacing genetic adaptation in humans (e.g. Mathew & Perreault, 2015). However, we also hypothesize that this trend, highlighted by decreasing genetic heritability, will continue in the long term.

Together, cultural preemption (or masking) and increased V_c are expected to reduce genetic heritability, and this has dramatic implications for the future of human evolution (see Waring and Wood, 2021). As the response of any trait to selection depends in part on that trait's heritability, culturally mediated reductions in genetic heritability could weaken the role of genetic evolution in shaping human fitness and adaptation. At the same time, reductions in genetic heritability and genetic adaptation in humans could pave the way for a more predominant role of culture in human evolution, creating an accelerating positive feedback (Crespi, 2004). This trend is not just a curious possibility but represents a dominant and growing mode in human gene-culture coevolution over long time scales (Waring and Wood, 2021).

We feel that Uchiyama *et al*. help geneticists and social scientists better understand how genes and cultures interact to shape human heritability. But we believe the most important implication of their work is the emergence of culture as our primary system of evolutionary adaptation, a long-term pattern which uniquely defines the human species in the past, present and future.

Conflict of interest statement

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