Why cultural and genetic group selection are unequal partners in the evolution of human behavior

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While both cultural and genetic evolution are necessary components of human social life, they are not always equal participants in the evolution of human behavior. The formal basis for the evolution of altruism is briefly reviewed along with arguments why cultural evolution is a stronger force in the evolution of large-scale cooperative societies.

Introduction

“It deserves notice that, as soon as the progenitors of man became social... the principle of imitation, and reason, and experience would have increased, and much modified the intellectual powers in a way, of which we see only traces in the lower animals.”

“...a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.”—Charles Darwin in The Descent of Man and Selection in Relation to Sex.1

When taking measures to explain human behavior, Darwin may have envisioned an evolutionary synthesis that not only included biological but also cultural evolution. Perhaps it came easy to imagine how the complexities of human social life can only be adequately addressed by a study of both of genetic and cultural traits. With the New Synthesis of the 1920s motivating almost a century’s worth of ongoing genetic research, we should expect the relatively recent formalization of culture to similarly have far-reaching implications in the study of human behavior.2-4

First of all, it provides a solution for the human propensity to cooperate in large societies. Controversy surrounds this puzzle as most hypotheses include natural selection to work at a level above the individual, termed group selection. Group selection for genetic variants was considered very weak and the term became almost heretical for many evolutionary biologists since the debate 50 years ago.5 For reasons reviewed below, the revival of group selection we see today is best attributed to cultural rather than genetic evolution. This gives culture, not genes, the upper hand in solving the problem of human prosocial tendencies among non-relatives.

What Makes Group Selection Viable?

Theoretical developments in multilevel selection unified separate approaches to the evolution of altruism. Hamilton’s breakthroughs on kin selection6,7 and why popular group selection arguments up to the 1960s were wrong can be understood by learning the covariance mathematics of George Price8 (reviewed in ref. 9). The rules for the evolution of cooperation also follow the same principle: positive assortment.10 Social groups must be formed such that altruists interact more frequently with other altruists than with non-altruists. Operationalizing the concept means asking what is the focal group, the costs and benefits of cooperation at the individual and group level, and how variance is partitioned within and between groups.
Let \( p \) be the global frequency of any trait and \( V_g \) and \( V_w \), the variance of the trait found between and within groups respectively. Then the global change in trait frequency, \( p \), can be expressed as,

\[
\Delta p \propto \beta_g V_g + E[\beta_w V_w]
\]

\( \beta_g \) and \( \beta_w \) are regression coefficients if you regressed group and individual fitness on the frequency of the trait at the group and individual level, respectively. In the altruism case, \( \beta_g \) is negative and \( \beta_w \) positive. What now matters is how variance is partitioned in the population i.e., the values of \( V_g \) and \( V_w \). The more of the total variation is found between groups, the greater scope natural selection will work at the group level (see Table 1). Natural selection works on heritable variation, at whatever level it is found.

Because there are few assumptions behind the Price equation, groups can be defined liberally and anything that is transmitted a trait. For Hamilton’s rule, groups are close relatives. Recent work on cultural drift and related processes, selection for locally adaptive variants and migration, which is vital to the question of group selection. An outcome of some social learning biases is the maintenance of between-group differences in the face of heavy migration. While migration between groups can eliminate between-group genetic variation rather quickly, some social learning biases may maintain high levels of between-group variation despite it. Prestige, conformity and guided variation, are important candidate learning preferences for this reason. Though mainstream socio-cultural anthropology’s departure from quantitative analysis has left many evolutionary anthropologists unanswering, a growing number of investigators have gathered data motivated by cultural evolutionary models through experiments on social learning preferences and data collected in the field. Other social scientists, however, have also gained interest in the effects of social learning, though motivated by social network theory (reviewed in ref. 21).

### Fueling Empirical Work on Social Learning

The theory behind cultural evolution is far ahead of the empirical studies on cultural transmission, which is vital to the question of group selection. An outcome of some social learning biases is the maintenance of between-group differences in the face of heavy migration. While migration between groups can eliminate between-group genetic variation rather quickly, some social learning biases may maintain high levels of between-group variation despite it. Prestige, conformity and guided variation, are important candidate learning preferences for this reason. Though mainstream socio-cultural anthropology’s departure from quantitative analysis has left many evolutionary anthropologists unanswering, a growing number of investigators have gathered data motivated by cultural evolutionary models through experiments on social learning preferences and data collected in the field. Other social scientists, however, have also gained interest in the effects of social learning, though motivated by social network theory (reviewed in ref. 21). Momentum behind research motivated by cultural evolutionary models is increasing, promising a future synthesis of both genetic and cultural inheritance in human behavior.

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