Review

Endless forms: human behavioural diversity and evolved universals

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Human populations have extraordinary capabilities for generating behavioural diversity without corresponding genetic diversity or change. These capabilities and their consequences can be grouped into three categories: strategic (or cognitive), ecological and cultural-evolutionary. Strategic aspects include: (i) a propensity to employ complex conditional strategies, some certainly genetically evolved but others owing to directed invention or to cultural evolution; (ii) situations in which fitness payoffs (or utilities) are frequency-dependent, so that there is no one best strategy; and (iii) the prevalence of multiple equilibria, with history or minor variations in starting conditions (path dependence) playing a crucial role. Ecological aspects refer to the fact that social behaviour and cultural institutions evolve in diverse niches, producing various adaptive radiations and local adaptations. Although environmental change can drive behavioural change, in humans, it is common for behavioural change (especially technological innovation) to drive environmental change (i.e. niche construction). Evolutionary aspects refer to the fact that human capacities for innovation and cultural transmission lead to diversification and cumulative cultural evolution; critical here is institutional design, in which relatively small shifts in incentive structure can produce very different aggregate outcomes. In effect, institutional design can reshape strategic games, bringing us full circle.

Keywords: adaptation; cultural evolution; game theory; institutions; social behaviour

1. INTRODUCTION

Evolutionists from Darwin on have faced the daunting task of trying to explain the tremendous diversity of living things in terms of a relatively small set of principles. In most respects, they have been successful in showing, as Darwin [1, p. 489] put it, that 'elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us.' In the case of humans, the evolutionary task is both simpler—we are, after all, only one species among millions—and more challenging still, if we consider the unprecedented diversity and rates of change found in human social behaviour and its products (such as technology and religious belief systems). Can evolutionary social science [2] account for such diversity with the tools at hand? Is neo-Darwinian theory up to the task of analysing the tremendous variation found in human social behaviour, and the apparently open-ended ability to generate new social forms at often rapid rates?

In this short essay, I sketch out an optimistic view of these challenges. I begin by discussing the relationship between human genetic diversity and variation in behaviour (particularly complex social behaviour); I argue that the relationship is quite minimal—most

variation in human social behaviour appears to be independent of genetic variation. This solves one problem—how to square high behavioural diversity with relatively low genetic diversity—but raises another. If variation in human behaviour does not arise from natural selection on genes, then what makes it vary adaptively? For answers, I examine various strategic, ecological and (cultural) evolutionary processes and mechanisms that can generate rich behavioural variability while guiding that variability in adaptive directions.

2. SIMPLE RULES AND COMPLEX BEHAVIOUR

It is an anthropological commonplace that people have constructed tremendously varied ways of organizing their lives, and of conceptualizing their surroundings and their place in it. As an evolutionist, I seek ways in which we can understand such diversity through application of unifying principles of variation, competitive struggle and adaptation. Evolutionary theory has thus far proved quite capable of comprehending and explaining the incredible diversity of life on Earth, with its millions of species and seemingly endless variety of niches. What tools does it offer for understanding human behavioural diversity? What tools, if any, do we need to add beyond those used by students of other species?

(a) *What role does genetic variation play?*

One seemingly straightforward evolutionary approach to understanding diversity is to look for underlying

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genetic diversity that may have been shaped by a history of natural selection. There is certainly much genetic diversity to be found in our species, some of it undoubtedly contributing to behavioural diversity (via heritable differences between individuals in temperament, physical and cognitive capabilities, etc.). But there are good reasons to doubt that differences in social behaviour from one human population to the next are owing to genetic differences between them, for at least three reasons. First, the very high behavioural diversity of *Homo sapiens* is not matched by a correspondingly high genetic diversity. In fact, it is just the opposite: our species has remarkably *low* genetic diversity for a large, widely dispersed mammal [3], even compared with other much less abundant and more localized species of hominoids, such as chimpanzees [4–6].

Second, most of the genetic diversity in our species is found within regional populations rather than between them. In fact, repeated studies (reviewed in [7,8]; see also [9]) have confirmed Lewontin's [10] original finding that about 85 per cent of genetic diversity is within populations, with only 10–15% left over for between-population differences. Furthermore, the whole approach of apportioning genetic diversity into within-population and between-population components assumes that population boundaries (once called 'races') are clear; but the bulk of the genetic evidence now available (as reviewed in [11]) reveals a clinal (continuous) geographical distribution of genetic variation. Indeed, Lawson Handley *et al.* conclude that 'no step decrease(s) in genetic diversity were found that could be interpreted as evidence for genetic discontinuities, even at continental boundaries' [11, p. 433]. They go on to note that geographical distance from East Africa (the probable source for the original worldwide expansion of modern humans) 'explains an impressive 85 per cent of the smooth decrease in gene diversity (Hs) within human populations' [11, p. 433]. This last point highlights the independence of genetic variation from variation in social behaviour, since there is no corresponding decrease in variation of social institutions, ideologies, economic lifeways or the like as one moves from Africa to other regions of the world.

But the most compelling evidence against a major role for genetic variation in explaining variation in social behaviour across human populations concerns the dynamics of such variation. Put simply, the rate of change in genetic parameters is too slow to account for most of the observed and inferred change in human social behaviour. The archaeological, historical and ethnographical records document thousands of natural experiments that contradict the hypothesis that between-population genetic differences explain any substantial portion of the observable inter-population diversity in human behaviour, particularly social behaviour. Put simply, these accounts reveal that substantial changes in every realm of human social behaviour—mating practices, political systems, patterns of cooperation, warfare, cuisine, gender norms and on and on—often occur far too rapidly to be driven by underlying genetic change [12]. At the level of individuals, one can point to the many documented cases of transcultural adoption that indicate essentially no genetic 'canalization' of the substantial and enduring behavioural differences between the adopter and adoptee societies (reviewed in ref. 13, pp. 39–42). In other words, children (and sometimes even adults) born into one society generally have no difficulty at all in becoming enculturated into a different society, even one with very different social practices, norms of temperament and sometimes a long time depth of genetic divergence.

This is all basic anthropology, and it would almost seem silly to repeat it here, but for the recurrent scholarly claims that major behavioural differences between human populations can be attributed to genetic differences (e.g. [14,15]; and the scandal over J.B. Watson's 2007 remarks to *The Sunday Times* [16,17]). To be sure, recent studies (e.g. [18–21]) reveal that portions of the human genome have evolved much faster than once believed. But most cases of rapid human genetic evolution with known function involve simple gene substitutions in blood antigens, lactose metabolism, skin pigmentation and the like, which, as Sabeti *et al.* note indicate 'a response to pathogens or other causes of illness, or to new diet and environmental conditions' [21, p. 1620]. In addition, there is considerable debate as to how much of the observed genetic differentiation between human populations reflects positive selection as opposed to drift and bottleneck/founder effects [19]. Thus, these data offer no challenge whatsoever to the position articulated in the previous paragraph.

It would be going too far to say that it is the nature of humans to have no nature. But the kernel of truth in that statement is that our species has extraordinary capabilities for generating behavioural diversity independently of underlying genetic variation. These capabilities, and their consequences, can be grouped into three categories: strategic, ecological and evolutionary.

3. THE STRATEGIC BASIS OF BEHAVIOURAL COMPLEXITY

If much behavioural variation in our species—particularly in social behaviour and in differences between groups—is independent of genetic variation, does it mean that evolutionary analyses are irrelevant? Not at all; but such analyses have to be conceptualized differently than in the classical view of evolution as changes in gene frequencies. In terms of strategic behaviour (individual decision-making), there are several useful ways of generating behavioural variation from evolved universals. Leaving discussion of cognitive mechanisms to the psychologists, I focus here on the somewhat more abstract language of game theory. There are at least three game-theoretical concepts relevant to the problem of generating behavioural variation from pan-human capabilities: conditional strategies, frequency-dependent payoffs and multiple equilibria.

(a) *Frequency-dependent payoffs*

While a single strategy may be dominant (i.e. offer the highest payoff, including when played against itself) in some payoff environments, often the Nash equilibrium

or evolutionarily stable strategy (ESS) mix will consist of two (or more) strategies. This is a standard result in game-theoretical analyses; examples include such iconic games as Chicken (also known as Hawk–Dove or Snowdrift), Battle of the Sexes, Assurance/Stag Hunt and the Prisoner's Dilemma—payoff structures that capture a large proportion of the game-theoretical models for social behaviour.

Thus, the very structure of social interactions may create conditions for the maintenance of behavioural variation. In games with no dominant strategy, the mixed equilibrium results because the rare strategy has an advantage—an advantage that diminishes as it becomes more numerous in the population, until it no longer does better than the alternative strategy. A classic example of such frequency-dependent advantage is found in the Hawk–Dove game [22]. Here, both Hawks and Doves gain higher payoffs than the alternative when rare; the result is an evolutionary equilibrium that maintains a mix of strategies in the population, and hence behavioural diversity. While the real world is far more complex than simple models such as Hawk–Dove, these do provide insight into some of the conditions that probably help generate empirical complexity. One possible empirical example is the equilibrium between right-handedness (common) and left-handedness (rare), an equilibrium that might be maintained by advantages in hand-to-hand fighting [23,24], by cultural preferences [25] or by a combination of factors favouring and disfavouring left-handedness [26].

(b) *Multiple equilibria*

Many games have multiple equilibria; this is particularly the case for games involving coordination, competition or cooperation [27]. For example, the Iterated Prisoner's Dilemma (IPD, where two players interact repeatedly, with no definite endpoint) has at least two equilibria, all-defect and conditional reciprocity; in fact, there are potentially infinite equilibria in the IPD, including varying mixes of cooperation and defection [28, p. 264]. In games with multiple ESSs, which one will end up prevailing may depend greatly on the particulars of the initial conditions, chance events (such as drift) or the like. For example, in a well-mixed population, reciprocity is an ESS in the IPD only if the initial frequency of reciprocators is quite high; thus, the spread of reciprocity from a non-cooperative state requires subdivision of the population into very small interacting groups, and chance multiple occurrences of the cooperative (reciprocity) strategy in one or more of these groups.

The ubiquity of multiple equilibria in social games has two important implications for behavioural diversity. First, it provides a reason to expect that such diversity will be more widespread than deterministic (in the mathematical sense) accounts would lead us to believe. Thus, even if Tit-for-Tat [29] were a stable equilibrium in the IPD (but see [30,31] for evidence that it is not), we could expect various chance events to produce many cases where other equilibria (such as all-defect) prevailed. Second, to get some purchase on which ESS will prevail in games with multiple

equilibria, we need to look outside the game itself for equilibrium selection mechanisms [32]. These mechanisms may include (i) additional games (social interactions) linked to the first game, such as reputation or signalling games (e.g. [33,34]); (ii) group selection (genetic or cultural) favouring ESSs with higher average fitness [27]; or (iii) institutional devices that reward some strategies over others (examined in a latter section of this paper).

(c) *Conditional strategies*

In game theory, a strategy is a rule for responding to some perceived situation with an action. Invariant strategies (where an individual always responds to a situation with a fixed action) are conventional in the simplest games, such as Hawk–Dove (where a player plays either Hawk or Dove, but not both). Useful as such fixed-strategy games can be, ones in which (i) multiple responses are possible and (ii) these provide different payoffs (in utility or fitness) are probably more relevant to social behaviour in complex organisms. The simplest way to incorporate variable responses into game-theoretical models is to assume that each individual is equally capable of expressing each of the alternative responses, with the difference in *net* payoff (i.e. subtracting the cost of the response, which could vary over the set) being solely determined by external factors. For example, one could play Hawk if the resource being contested was very valuable, but otherwise play Dove.

Alternatively, individuals may differ phenotypically (but not genetically) in their capabilities to win a contest: one is well-nourished while another is weakened by a short-term illness. In such cases, we often find that selection has favoured the evolution of conditional strategies [35,36]. In essence, such strategies are rules that specify behaving in one manner under condition 1, a second manner under condition 2 and so on. Unlike the case for a standard strategy, the conditions that determine payoffs are not (purely) external to the actor, instead being at least partially dependent on the actor's state, endowment, knowledge or relative standing. Probable examples of conditional strategies in human social behaviour are numerous. Local ecological conditions and economic endowments are often major predictors of mating strategies, parental investment, dispersal patterns and other life-history variables. An example involving variation in mating strategy concerns age at marriage or reproductive onset, which in subsistence farming societies facing land scarcity can be very sensitive to availability of arable land [37,38]. Mate preferences can also vary conditionally, whether the criteria be wealth [39,40], health [41,42], or even physical attractiveness [43,44].

In many cases, payoffs are determined by the actions of other actors: if other plays strategy *x*, respond with *α*; if other plays *y*, respond with *β*. Strategies conditional on the moves (implicitly, the strategies) of other players generate another rich source of behavioural variation, an insight that has been central to the development of evolutionary game theory [45–47]. Again, examples of this in human populations abound, with the realm of cooperation and reciprocity being a particularly rich source (reviewed in [48–50]).

It is important to note that conditional strategies generate behavioural variation (often extremely broad variation) with no underlying genetic variation. This is despite the fact that many strategies (and the biological mechanisms associated with producing them) are certainly dependent on genes, and must have evolved via natural selection. Like phenotypic variation in general, then, and various forms of learning, conditional strategies are an important means of generating adaptive variation without relying on genetic change (or differences across individuals).

Although conditional strategies are found to one degree or another in most species, there are reasons to believe they are particularly important in *Homo sapiens*. First, our species possesses very complex cognitive machinery that allows us to gather extremely detailed information about our social and natural environments, and adjust our behaviour accordingly. Second, humans occupy a very diverse set of environments, and have been ecological generalists for at least 60 000 years (since the expansion of *Homo sapiens* out of Africa began); this provides a selective environment favouring conditional strategies not only in subsistence, but also in myriad related aspects of social organization, technology, settlement pattern and so on (discussed further in §4). Third, the human capacity for cultural innovation and transmission (see §5) means that conditional strategies can evolve culturally, creating a vastly expanded space for evolution of conditional strategies as compared with organisms with more limited cultural capacities.

Useful as the concepts and models of the evolutionary game theory may be for analysing behavioral diversity, they apply equally well to any social animal with reasonably complex cognitive capabilities. Hence, by themselves they cannot really explain the much greater variation in behavioural strategies seen in humans as compared with other species. For this challenging task, we need some additional tools.

4. NICHE DIVERSIFICATION

Modern humans began expanding out of East Africa some 65 000 years ago [51]. Within at most 50 000 years later, populations had established themselves on every continent around the globe, in habitats ranging from tropical forest and savannah to temperate and subarctic woodlands to desert and arctic tundra. Note that this massive expansion into highly diverse habitats and correspondingly diverse niches was accomplished prior to any plant or animal domestication (except for dogs). Following the gradual domestication of plants and animals in various independent locations around the world some 4–11 millennia ago [52], various forms of agricultural and pastoral systems developed that greatly expanded both the diversity of human niches and their rates of change via niche construction [53,54].

Although modern humans remain physiologically very similar to our closest relatives, the large African apes, we exhibit a degree of niche diversity as well as a range of social behaviour that is orders of magnitude greater than those of our genetic cousins. These two dimensions of variation are intricately related. Research in ecological anthropology, as well as related fields, such as archaeology, geography, historical ecology and environmental history has documented the coevolution of ecological niches with social behaviour and cultural institutions that mark human history over the past 60 millennia. A classic example is agricultural intensification to extract surplus (in the form of labour as well as goods) that can support various forms of economic specialization as well as an elite class [55]. A recent study demonstrates that the organization of agricultural production in prehistoric Hawai'i evolved in ways that maximized agricultural surplus production (controlled by elites) and enhanced elite wealth and power at the expense of commoner life expectancy [56].

The diversification of human niches and social behaviour has resulted in surprisingly little genetic change, both because of the rapidity with which it has arisen and because of the powerful mechanisms of non-genetic adaptation outlined in §3. Put another way, if humans had never expanded out of sub-Saharan Africa, being limited to its small range of environmental diversity in comparison to what they eventually colonized, we can infer that human social and ecological diversity would be very much lower than it was even 10 000 years ago, whereas genetic diversity would be nearly the same.

Of course, humans do not simply adapt to their environments; they also adapt their environments to their own ends. Thus, behavioural change (particularly technological innovation) often drives environmental change, a process some have termed niche construction [57,58]. Examples abound, particularly in the realm of agricultural intensification. The landscapes of Java and Bali are testaments to the ability of humans to transform habitats into complex agroecosystems that support increasingly dense populations [59,60]. These wet-rice systems depend on engineering feats (terracing and irrigation canals), as well as diverse crops and other domesticates (fish and fowl) designed to feed people or to consume pests. But they also depend on a range of institutional structures to coordinate irrigation cycles, handle conflicts between different local groups and buffer variability in harvests [60,61]. These institutions have coevolved with agroecosystems in complex ways [62,63]. Broadly similar systems and dynamics can be found elsewhere, including the various Polynesian islands [64,65].

This positive-feedback process of productive intensification, ecological change and adaptation to this change has been a hallmark of our species, allowing vast increases in population density and niche diversification [53,66]. In the end, augmented by industrialization and fossil-fuel consumption, it may prove to be our undoing. Be that as it may, my main point here is that a substantial portion of the behavioural diversity we find in the archaeological, historical and ethnographic records is a consequence of human niche diversity. That diversity is in turn owing to global expansion into diverse environments as well as cultural evolution within environments—which brings us to the topic of §5.

5. INSTITUTIONAL EVOLUTION

There is a rich literature on cultural evolution; some of it is reviewed in other papers in this volume. Here, I wish to highlight an aspect of cultural evolution that is both critical for explaining behavioural diversity (across space and through time) and somewhat under-developed in the evolutionary literature—the evolution of institutions.

Anthropologists usually define institutions quite broadly; for example, 'locally stable, widely shared rules that regulate social interaction' [67, p. 326]. In other social sciences, a narrower meaning is often employed that specifies a set of explicit roles assigned to individuals, as well as rules governing their behaviour. For the discussion here, it does not really matter which meaning we adopt. Something akin to institutions may structure social interactions in other species (e.g. dominance hierarchies and alliances), but institutions are clearly much more variable (yet 'locally stable') in the human species. This is presumably because of much greater rates of cultural transmission and resultant cultural diversification as well as cumulative cultural evolution [68]. These in turn are made possible by language (symbolic communication), which is the medium *par excellence* for high-volume information flow.

Systems of marriage and inheritance are one important domain of institutional variation. Looking at small, relatively homogeneous social groups (rather than the very large, heterogeneous nation-states that have come to predominate during the past few centuries of human existence), we find some that practice patrilineal inheritance, others matrilineal (plus other possibilities, such as nonlineality or ambilineality). In addition, most pre-modern societies allow or even encourage (when economically viable) polygynous marriage, while some prescribe monogamy and a few polyandry. Evolutionary analysis of this variation, both functional and phylogenetic, has recently been quite productive [69–73], and is discussed elsewhere in this volume. This research, as well as older anthropological analyses, indicates that institutions regulating marriage and inheritance evolve (culturally) quite readily in response to changes in subsistence and transmissible property. A key illustration of this concerns the effects of agricultural and pastoral subsistence, where (oversimplifying for brevity) reliance on agriculture is associated with patrilineality (transmission of wealth and kin affiliation to sons) and monogamy when arable land is scarce, but matrilineality and polygyny when land is abundant (e.g. under low population densities and systems of shifting cultivation), whereas reliance on herd animals favours patrilineality and polygyny (wealthier men marrying multiple wives).

This institutional variation occurs despite certain mating preferences and kin-support biases that we have reasons to believe are a pan-human heritage from our mammalian ancestry. Importantly, it appears that once a particular form of marriage and inheritance is institutionalized, it becomes self-reinforcing and locally stable. This is because such systems, like institutions generally, involve forms of coordination or strategic action that reward conformity to the local

rules (e.g. [74]). If most of my neighbours endorse polygynous marriage and pass on wealth to their sons (who then use this wealth to attract wives in the local marriage market), my children will be at great disadvantage should I insist upon monogamous marriage and transmission of wealth to daughters. The nature of enduring ('locally stable') institutions is that actors within them are responding with their best moves, given the constraints they face, and in particular the moves of other actors.

But this focus on stability begs the *evolutionary* question of why any given institution manages to become established, in competition with other ways of organizing social life (e.g. alternative rules of marriage or inheritance). On this topic, there is much current exciting work in evolutionary dynamics, and on the coevolution of preferences and institutions (e.g. [67,75–78]). Here, I will only highlight two aspects of this current work. First, institutional design features are critical for shaping patterns of social behaviour. For example, Ostrom [79–81] and others have published extensively on design features that are critical for the success of systems for managing common-pool resources that do not rely on third-party (e.g. state) enforcement. These designs include elements such as clearly defined user groups (access control), simple rules for user rights and monitoring and sanctioning of rule-breaking. Groups that have arrived at these institutional solutions to managing common-pool resources and communally owned lands, whether these be grasslands, forests, irrigation water or fisheries, generally avoid any tragedy of the commons. However, not all collectives can or do develop such institutions, for a variety of reasons. Interestingly, a number of natural as well as artificial experiments demonstrate that even quite small differences in institutional design can produce widely different aggregate outcomes (see [82] for some exemplary cases).

Second, it is fruitful to view the evolution of institutions as a process of redefining social games (i.e. the rules and payoffs) to facilitate improved outcomes—improved, that is, either for the collective playing the game, or for those with the power to define game structure. In essence, institutions change the rules and payoffs—for example, from a Prisoner's Dilemma to a game of Assurance [83]. As argued by Bergstrom *et al.* [75, p. 142], people 'engage in a process of mechanism design, selecting the rules of the strategic games in which they will be involved. These rule choices give rise to conventions of behaviour—and where such conventions are granted normative force, they may appear to us as values.' Whether through intentional design (as implied by the wording just quoted) or through processes of cultural evolution (as proposed in [67], among others), institutions are crucial means for creating new rules and possibilities for social interaction. Regardless of how new institutions (and the norms that support them) come into being, once established as facts on the ground they serve to structure and constrain individual action. Just as the built environment of a wet-rice terracing system changes the ecological setting for present and future generations of farmers, institutions governing

property rights and inheritance, political decision-making and many other domains of social life usually outlive the people who created them, and shape the choices and opportunities of future generations in a given social system. Accidents of history as well as local adaptation mean that institutions differ from place to place, even among societies descendant from a single ancestral system. Thus, institutions play a major role in generating and perpetuating human behavioural diversity.

The realm of property rights provides many examples of the importance of institutional design and variation. Comparative ethnographic and archaeological evidence suggests that rights to land (or the resources found there) were held communally or were simply 'open access' for most of human (pre)history. A shift to land ownership at the level of households or larger kin groups entails claims that must be defended at some cost in time, risk and social conflict; these costs must be offset by greater benefits to the 'owners', and the theory of economic defensibility predicts that net benefits will require key resources to be dense and predictable [84,85]. Such conditions are not simply a matter of the development of agriculture: some hunter–gatherer systems are known to have had well-developed property rights over resource areas (e.g. northwest Coast Indians and salmon streams), and conversely many low-density farming systems worldwide feature usufruct (use rights) and abandonment of depleted gardens for newly cleared sites rather than land inheritance and alienability [86,87]. The principle of economic defensibility has been very successful in explaining where and why property rights in land (territoriality) will develop [85,88,89]. Yet, the specific institutional forms and associated norms found in each case are variable, reflecting cultural history and local circumstances; for example, northwest Coast Indian property rights were instituted through a system of hereditary titles and supernatural charters, whereas the family hunting territories that developed among subarctic Algonkians during the fur-trade era emphasized trapping rights and rotating stewardship of family groups. This institutional diversity is perhaps an inevitable outcome of a process of descent with modification, in the same way that biologically transmitted characters (e.g. avian feather colour) exhibit both general adaptive patterns and phylogenetic contingency.

In sum, far from being tightly constrained by an evolved human nature, institution-building (in conjunction with other factors discussed above, such as conditional strategies and niche diversification) can provide a mechanism for the evolution of patterns of social behaviour that have never existed before—for the generation of endless forms, both beautiful and terrible, that constitute the diversity of human social behaviour.

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