Cultural Evolution: Integrating Psychology, Evolution and Culture

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Alex Mesoudi
Human Biological and Cultural Evolution Group
Department of Biosciences
College of Life and Environmental Sciences
University of Exeter
a.mesoudi@exeter.ac.uk

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Abstract

Cultural evolution represents a body of theory and findings premised on the notions that (i) human cultural change constitutes a Darwinian evolutionary process that shares key characteristics with (but is not identical in details to) genetic evolution; (ii) this second evolutionary process has been instrumental in our species' dramatic ecological success by allowing the rapid, open-ended generation and accumulation of technology, social institutions, knowledge systems and behavioural practices far beyond the complexity of other species' socially learned behaviour; and (iii) our psychology permits, and has been shaped by, this cultural evolutionary process, e.g. through socio-cognitive mechanisms such as imitation, teaching and intentionality that support high-fidelity social learning, and biases governing from whom and what we learn.

Introduction

In just 60,000 years our species has colonised virtually every terrestrial environment on the planet [1], and transformed the planet so greatly that it is claimed we are now living in the “Anthropocene”, a geological epoch defined by human activity [2]. How has our species been able to so rapidly adapt to and transform such diverse environments? Beyond a few anatomical and physiological traits such as skin colour, human populations are not genetically adapted to different environments, as underlined by our relative genetic homogeneity [1]. Instead, our species’ success lies in our learning and cognition, capacities which allow the rapid acquisition of information stored in brains, rather than genes. Hunter-gatherers, for example, survive in diverse environments, from the Kalahari desert to the Arctic, not primarily due to genetic adaptations to those environments, but due to technology (e.g. bows, harpoons, clothing), knowledge (e.g. of predator behaviour or celestial navigation) and social customs (e.g. food-sharing norms, childrearing practices) that are all learned. Agriculture, city-states, the industrial revolution and other major human-related activities all rely on learned knowledge.

But what exactly is it about human learning and cognition that underlies this ecological success? Some evolutionary psychologists emphasise aspects of cognition that evolved to solve specific adaptive challenges in our species’ ancestral past (typically the Pleistocene), such as our ability to identify dangerous animals, to identify kin and free-riders, or to use our folk physics to manipulate objects to solve foraging problems ‘on-the-fly’ [3, 4]. According to this approach, humans uniquely occupy a ‘cognitive niche’ [3] in which content-rich, genetically-guided cognitive modules allow us to solve problems primarily via individual learning (Box 1).

While not denying that the human mind contains domain-specific mechanisms corresponding to certain recurrent ancestral challenges, cultural evolution researchers [5–9] argue that something more is needed to explain the complex technological and social traits that seem to underlie our species’ success, from the bow-and-arrow to the internet, from money and agriculture to laws and democracy. Such traits, it is argued, are primarily acquired from others via *social learning*, often with little understanding of how and why they work. These traits gradually evolve over successive generations not genetically but

culturally, as occasional beneficial modifications are selectively preserved and accumulated via non-random social learning biases. A full understanding of the evolutionary basis of human psychology therefore requires an understanding of these mechanisms and pathways of social learning, and how these in turn generate and guide the cumulative cultural evolution of technology, institutions, knowledge and practices. According to this view, humans uniquely inhabit not just a cognitive niche, but also a 'cultural niche' [7]. We are not just intelligent, we are 'culturally' intelligent [10]. Here I review recent research that stems from, and supports, these claims.

Humans possess uniquely high-fidelity social learning

Within a cultural evolutionary framework, the key biological adaptations that underlie our species' ecological success are the socio-cognitive mechanisms that permit high-fidelity social learning such that traits can be selectively preserved, shared and accumulated without degradation or loss. While many species exhibit some form of social learning, from honeybees' waggle dances to chimpanzees' nut-cracking, only humans seemingly possess social learning of high enough fidelity to support the long-term accumulation of cultural traits over successive generations [11].

Accordingly, comparative and developmental psychologists have found that while human children and other great apes differ little in their individual cognitive abilities (e.g. their 'folk physics' understanding of physical causality, or spatial cognition), only human children spontaneously and effectively copy others' actions [10, 12]. In a recent study comparing children, chimpanzees and capuchins in a foraging-like task with increasingly difficult solutions [13], children out-performed the other species due to multiple socio-cognitive abilities (imitation, teaching, communication and prosociality) that supported the high-fidelity transmission of successful solutions from child to child.

Moreover, both children and adults across diverse societies 'over-imitate', copying actions that are causally irrelevant to obtaining rewards [14–16]. This tendency to copy actions exhibited by others who possess greater expertise or experience, with no understanding of why those actions should be copied, is thought to be a broadly adaptive means of acquiring traits from others that are beyond any single individuals' inventive

capacity or understanding - the hallmark of cumulative cultural evolution [11].

High-fidelity social learning supports cumulative cultural evolution

If social learning is sufficiently faithful to support the long-term transmission of cultural information, then cultural change becomes an evolutionary process, sharing key characteristics with (but also differing importantly from) genetic evolution [5–9]. In *The Origin*, Darwin defined evolution as comprising three basic processes: variation, competition and inheritance. If cultural traits (ideas, beliefs etc.) exhibit variation, if they are subject to some kind of competition (e.g. due to differences in their memorability or effectiveness), and if they are relatively faithfully inherited from person to person (via social learning mechanisms like imitation or language), then we can say that culture evolves [5]. This parallel, non-genetic evolutionary process permits the rapid cultural adaptation to, and creation of, novel environments via the open-ended generation and accumulation of adaptive knowledge, technology and social institutions.

The task then is to identify the details of this cultural evolutionary system: where cultural variation comes from, why some traits are more likely to be learned or remembered, and how cultural traits are transmitted via social learning. Importantly, these processes need not operate identically to genetic evolution [5]. For example, while genetic mutation is random with respect to fitness, cultural 'mutation' may well be non-random and directed. While genetic inheritance is often 'vertical' (parent to offspring) and follows specific Mendelian rules, cultural inheritance is frequently 'horizontal' (between peers) and non-Mendelian (e.g. weighted towards certain individuals: see below).

Cultural micro-evolution: Learning dynamics within populations

Cultural micro-evolution comprises the details of who people learn from, how they learn from others, how they transform traits as they are learned, and other socio-cognitive processes that cause changes in cultural traits within populations over time. Numerous quantitative models, lab experiments and field studies have explored the pathways and processes of cultural microevolution [5, 17]. There is much overlap here with social, developmental and cognitive psychology [18], albeit with added rigour due to the use of formal evolutionary models that explore both the adaptiveness and consequences of

learning biases. Key micro-evolutionary processes include (see also Figure 1):

- *Content biases.* Here certain traits are more likely to be acquired than others due to their intrinsic characteristics. This may be because they fit better with genetically-evolved features of cognition, such as content biases to acquire information about animals' dangerousness [19], social interactions [20, 21], or disgusting, potentially disease-carrying stimuli [22]. There is much overlap here with evolutionary psychology [4], and this is a strong point of intersection between the two fields. Other content biases might arise from the effectiveness of a particular trait (e.g. the bow that fires an arrow furthest), as evaluated via more flexible criteria for which there are no domain-specific genetically-evolved biases.
- *Model-based biases.* Experimental and field evidence demonstrates that people preferentially learn from individuals who possess certain characteristics such as skill or success [23–25], prestige [26–28], age [29] or ethnic markers like dialect [30]. Model-based biases are a useful short-cut to acquiring adaptive behaviour without needing to directly evaluate the behaviour itself, although this may allow the occasional copying of neutral or maladaptive traits [27].
- *Frequency-dependent biases.* Here people preferentially copy traits based on the trait's frequency in the population. Positive frequency-dependence ('conformity') entails being disproportionately more likely to copy the most common trait [24, 31]. Negative frequency-dependence ('anti-conformity') entails disproportionately copying rare traits. Here 'conformity' and 'anti-conformity' are used more precisely than in social psychology, where conformity often cannot be distinguished from random copying [18, 31]. Conformity has received particular attention as a means of generating persistent between-group differences.
- *Guided variation.* This occurs when individuals transform an acquired trait in a specific, non-random direction, then pass on that modified trait to others [32]. This can generate cross-cultural regularities when biases are common across individuals. For example, colour terminology has been shown experimentally to converge on the same small number of terms due to intrinsic regularities in our perceptual systems [33]. Another experiment showed that repeated transmission of social information spontaneously generated social stereotypes [34]. Individual

transformation has sometimes been labelled ‘cultural attraction’ [35] or Bayesian ‘inductive biases’ [36]. Transformation may occur due to similar cognitive processes as those that constitute content biases. However, it is useful to distinguish them because while content biases depend on the extent of cultural variation in the population (much like natural selection depends on the extent of genetic variation) and cannot generate new cultural variation, guided variation does not depend on existing variation and can generate new cultural variation [32].

Cultural macro-evolution: Linking psychology to culture

Many of the aforementioned learning biases have also been studied within social psychology (e.g. conformity) or evolutionary psychology (e.g. content biases). A benefit of placing them within a cultural evolutionary framework, however, is that we can formally explore – using modelling techniques borrowed from biology – the large-scale, population-level (or ‘macro-evolutionary’) consequences of these learning biases. Examples include:

- *Cumulative cultural evolution.* Recent work has focused on explaining the cumulative dynamics of human culture, in particular for domains such as science and technology where there is clear accumulation of knowledge over successive generations. Models suggest that cumulative culture requires high-fidelity social learning [37], model-based or content biases that selectively preserve and accumulate beneficial traits [38], and large enough populations such that beneficial traits are not accidentally lost [37, 39]. These predictions have been tested using real-life datasets [40] and experiments [41–43].
- *Cultural phylogenies.* One of Darwin’s key insights was that descent plus modification can generate tree-like ancestries, now called ‘phylogenies’. Biologists have since developed sophisticated methods for reconstructing genetic phylogenies from extant species diversity. Cultural traits may exhibit similar tree-like structure due to the same process of descent with modification, and cultural evolution researchers have used phylogenetic methods to reconstruct the past cultural evolution of languages [44, 45], tools [46, 47], and folk tales [48]. Phylogenetic patterns are increasingly linked to specific micro-evolutionary

learning dynamics, such as conformity (frequently used words undergo less change [49]), and content biases (easily learned words undergo less change [50]).

- *Cross-cultural regularities.* As noted, where individuals all share similar cognitive features, and consequently all transform representations in a similar direction, then guided variation and/or content biases can result in cross-cultural regularities [51]. Examples include colour terminology [33] or portrait eye-gaze orientation [52].
- *Large-scale cooperation.* Humans cooperate in large groups of non-kin, often in one-shot interactions with no possibility of reciprocity. Some argue that this large-scale cooperation arose via cultural group selection [32, 53], wherein more internally-cooperative societies historically out-competed less internally-cooperative societies. Various micro-evolutionary biases have been proposed as mechanisms for this, such as conformity maintaining between-group variation, or payoff-biased social learning driving inter-group competition [32, 53].

Conclusions

The field of cultural evolution provides an integrated set of findings, methods and concepts for understanding the links between psychology, evolution and culture. While major questions remain concerning the causes and consequences of cultural evolution (Box 2), recent research is already shedding light on the psychological mechanisms that permit the generation and accumulation of socially-learned knowledge, and the long-term dynamics of cumulative cultural evolution.

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Box 1: Glossary of key terms

- *Cultural evolution:* the idea that Darwin's theory of evolution – comprising variation, competition and inheritance – applies to cultural change, where inheritance derives from social learning rather than genetic transmission.
- *Cumulative cultural evolution:* the preservation of cultural traits over successive generations such that individuals acquire knowledge that exceeds what any single individual could invent alone.
- *Individual (or asocial) learning:* acquisition of information with no direct social input, e.g. through associative learning (classical or operant conditioning) or the manipulation of mental models to solve problems 'on-the-fly'.
- *Social learning:* acquisition of learned information from another individual non-genetically, e.g. through imitation, teaching or spoken/written language.
- *Social learning biases:* non-random rules governing from whom people learn, what they learn, and how they transform what they learn during the process of learning.

Box 2: Current research questions

- To what extent is cultural change driven by selection-like processes (e.g. content or model-based biases) versus transformative processes (e.g. guided variation or cultural attraction) [54]?
- What socio-cognitive capacities (e.g. imitation, pro-sociality, language) and/or demographic factors are present in humans but absent in other species such that only humans possess cumulative cultural evolution [11, 37]?
- Is large-scale human cooperation a product of cultural group selection [53], or scaled-up versions of standard evolutionary processes like reciprocity [55]?
- To what extent is there cross-cultural variation in the dynamics of social learning [56], and what generates and maintains this cross-cultural variation?
- How is socially-learned information stored and represented in brains at a neural level?

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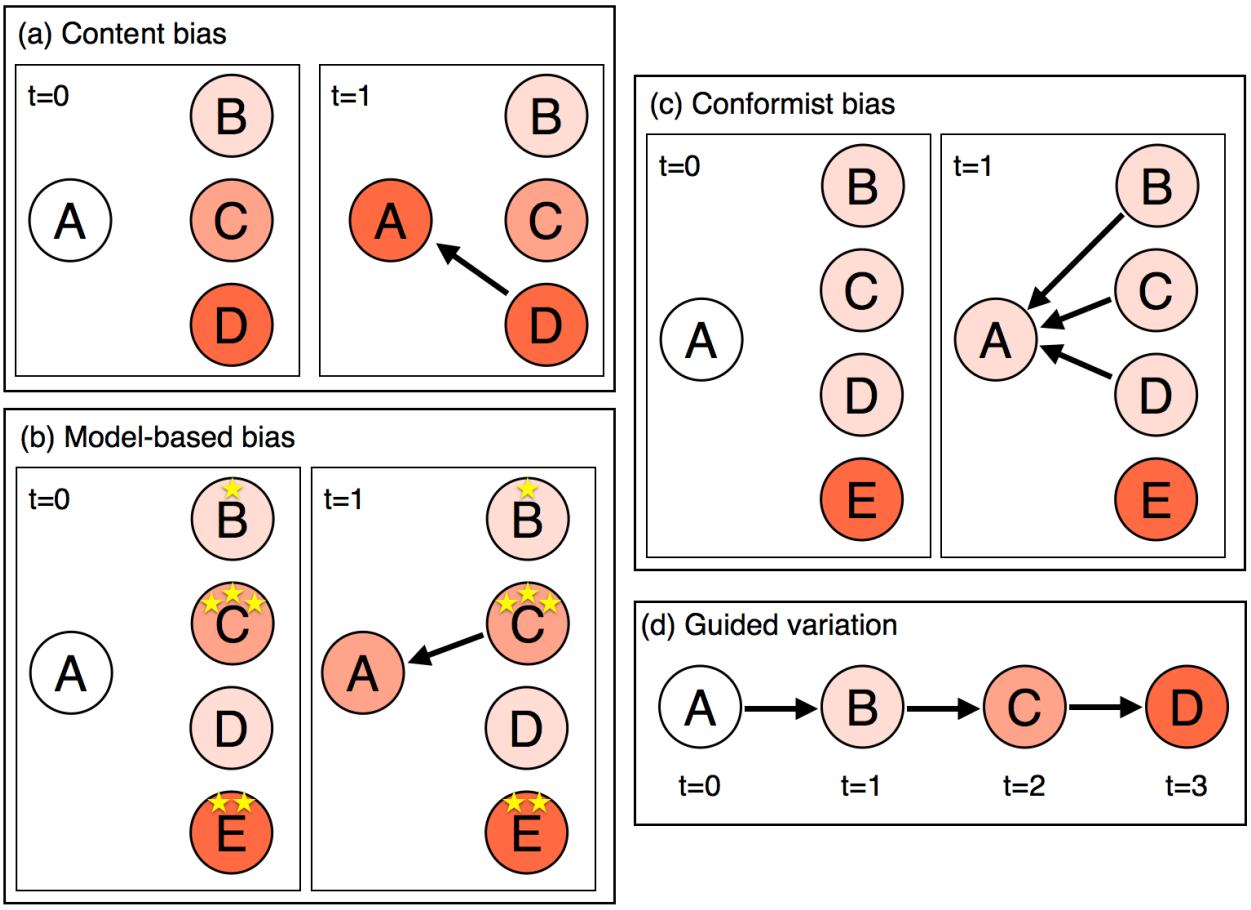

411 **Figure 1 – Cultural micro-evolutionary learning dynamics.** Schematic diagrams
412 illustrating four commonly studied biases that generate cultural change. Circles with
413 letters represent different individuals. Different shadings indicate different cultural traits.
414 (a) Individual A exhibits a content bias favouring dark-shaded traits, so preferentially
415 adopts the darkest-shaded trait from individual D. (b) Individual A exhibits a model-based
416 bias to preferentially learn from the most prestigious individual, as indicated by number of
417 stars, in this case individual C. (c) Individual A exhibits conformist bias so preferentially
418 adopts the most common trait in the population, which here is the lighter-shaded trait. (d)
419 Successive individuals gradually transform a trait via guided variation, each one making
420 the trait darker.