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Cultural evolution: integrating psychology, evolution and culture Alex Mesoudi

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, for example, 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.

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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 freeriders, 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 domainspecific mechanisms corresponding to certain recurrent ancestral challenges, cultural evolution researchers $[5,6^{\circ},7,8^{\circ},9]$ argue that something more is needed to explain the complex technological and social traits that seem to underlie our species' success, from the bow-andarrow 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

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, for example, 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, for example, 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.

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 [5,6°,7,8°,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 sociocognitive 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.

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