

## Research



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# Human nature, human culture: the case of cultural evolution

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In recent years, far from arguing that evolutionary approaches to our own species permit us to describe the fundamental character of human nature, a prominent group of cultural evolutionary theorists has instead argued that the very idea of 'human nature' is one we should reject. It makes no sense, they argue, to speak of human nature in opposition to human culture. The very same sceptical arguments have also led some thinkers—usually from social anthropology—to dismiss the intimately related idea that we can talk of human culture in opposition to human nature. How, then, are we supposed to understand the cultural evolutionary project itself, whose proponents seem to deny the distinction between human nature and human culture, while simultaneously relying on a closely allied distinction between 'genetic' (or sometimes 'organic') evolution and 'cultural' evolution? This paper defends the cultural evolutionary project against the charge that, in refusing to endorse the concept of human nature, it has inadvertently sabotaged itself.

## 1. The C word

Cultural evolutionists—at least the ones I focus on in this paper—are a diverse group of researchers who are interested in broad questions about the abilities of some organisms to learn from others [1–3]. They mainly, but by no means exclusively, focus on human organisms [4,5]. For example, they might ask how we need to supplement traditional evolutionary models that focus on the changing genetic profiles of species, when we realize that change and stasis in populations can be produced by forms of learning, as well as by well-known evolutionary processes like genetic drift and natural selection [6]. They might ask why the capacity for culture emerged in the first place, and what evolutionary rationale might account for the precise features of how we learn from others. More specifically, they might ask what explains our tendency to attend to particular types of organisms, and what explains our tendency to find some features of what we attend to especially memorable, while others are hard to learn [7,8,9]. They might try to document and account for the differences in cultural capacities displayed by different species, and they might try to explain what allows populations to sustain cultural traditions, and to build increasingly elaborate and effective bodies of know-how, over time [10,11].

None of these projects demands that we think of beliefs, behaviours, neural states or whatever as engaged in a Darwinian struggle for existence (although sometimes they may be). Nor do they demand that we conceive of these items in ways that make them close analogues of genetic replicators [12]. These forms of 'cultural selectionism' in general, and 'memetics' in particular, are just some of the ways in which we might try to understand social phenomena of learning, tradition or the acquisition of know-how, from an evolutionary perspective. In spite of these differences between the subvarieties of cultural evolutionism, cultural evolutionists do, more or less invariably, frame their questions in terms of coming to an understanding of *culture*: how does it work, what is it for, why are we so good at it? Here lies one source of conflict between natural scientific and social scientific approaches to what goes on in human groups. Many social

scientists—especially social anthropologists—have grown suspicious of the very idea of culture. The job for this essay is to understand what some of the sources are for this suspicion of culture itself, and to ask what trouble this creates for the cultural evolutionary project. The answer is that it leaves that project largely intact, but not wholly unscathed.

In particular, I want to illustrate one source of tension with respect to how cultural evolutionists use the culture concept and how that notion relates to the idea of human nature. The concept of human nature is innocuous if it merely draws attention to general truths about what humans are like, compared with general truths about what other taxa are like [13]. So we might say in a casual way that ‘Spider monkeys have prehensile tails; humans do not’; or perhaps ‘Many adult humans can digest lactose; the adults of other mammalian species cannot.’ These ways of picking out truths about what humans (and other species) are like are not threatened by the facts that not all humans can digest lactose, and not all spider monkeys have prehensile tails. The point of these assertions is to draw contrasts between striking traits that are systematically present in one group, but not in the other. That does not mean that all uses of ‘human nature’ are so unobjectionable, especially when we use ‘human nature’ not in contrast with the nature of other species, but when we contrast it with ‘human culture’ [14].

Partly in defence of their conviction that various forms of learning are, and have long been, of great importance in shaping many of the characteristic traits of our species members, several very prominent cultural evolutionists have argued that the very idea of human nature—when the notion is contrasted with human culture—is one we should abandon. To give just one example, Cecilia Heyes has made an empirical case for thinking that the capacity of humans to imitate others is a capacity that is itself acquired by learning from others [15–17]. Heyes is no sceptic regarding the idea of human nature in general. Instead, her view is that ‘human nature’ names all those evolved mechanisms that are responsible for the cognitive and behavioural traits that are typical of our species, regardless of what form those evolutionary processes take, and what kind of inheritance processes they rely on [18]. Heyes’s empirical work suggests that the capacity to imitate is an element of human culture, in that its reliable development and transmission owes itself to social interaction. This is also, however, a capacity that is very widely present across all human populations, which seems especially well developed in humans, and which may explain some distinctive features of human history compared with the histories of other species. If Heyes is right, it seems that we should say that imitation is both a part of human culture and a part of human nature. That, in turn, means that even if we do not need to give up on the idea of human nature, we do need to give up on the idea that human nature and human culture are categories that mark out different classes of traits.

We have seen that a prominent group of cultural evolutionists have argued that the very idea of human nature is a confusion; but now the question arises of whether this critique of the nature/culture distinction is damaging to the cultural evolutionary project itself. For if it makes no sense to talk of ‘human nature’ in a way that distinguishes it from ‘human culture’, then it also makes no sense to talk of ‘human culture’ in a way that distinguishes it from ‘human nature’. One might then worry about how cultural

evolutionists can possibly articulate their research project—which, as we have seen, is usually framed in terms of a series of questions about the adaptive advantages conferred by the capacity for culture, and about the ways in which cultural and genetic transmission affect each other—without falling foul of the very distinction they so often attack. The worry, in short, is that in attacking the very idea of human nature, cultural evolutionists have shot themselves in the foot.

As I have already indicated, I do not think the cultural evolutionary project is fatally damaged by worries about whether we can distinguish nature and culture. Instead I want to suggest that, first, understanding these worries about the nature/culture relation can help us to better appreciate some of the sources of scepticism of the cultural evolutionary project voiced by those social anthropologists who have long been suspicious of the culture concept; second, that some of these worries are already appreciated by those working in cultural evolution itself; and third, that the cultural evolutionary project is profiting from more nuanced understandings of the difficulties inherent in distinguishing nature from culture.

## 2. On human nature

The historian Roger Smith remarked 10 years ago that ‘Modern evolutionary accounts of human origins continue to reflect the belief that there is an essential human nature, the nature all people share through their common root’ [19, p. 27]. While this may have been true of some evolutionary approaches to humans, it was—and still is—by no means true of all of them. In particular, a small handful of the most prominent evolutionary thinkers have denied the value of the very idea of human nature. In a forthcoming publication, Kevin Laland and Gillian Brown express their scepticism in a very general way [20]:

There may be (‘universal’, or at least ‘typical’) human traits that are relatively stable across environments and cultures, but these derive their stability not solely from inherited genes but equally from extra-genetic inheritance, including constructive environmental/cultural processes.

Here, I take it that Laland and Brown—well known for their advocacy of the niche-construction perspective on evolution—are using a set of arguments very similar to those put forward by advocates of developmental systems theory (DST) in an effort to cast doubt on the idea that it makes sense to distinguish that which we owe to a shared nature from that which we owe to local culture. DST—the view of development and evolution pioneered by Paul Griffiths, Russell Gray and Susan Oyama—does not deny that genes can often have thoroughly stable effects on developmental outcomes over generations, of the sort that make alternative alleles subject to natural selection in just the way stressed by mainstream evolutionary theorizing [21–26]. Instead they caution that this stability of genetic effects is only possible because of the stable developmental context in which those genes act. As that developmental context itself includes stable features of environmental context whose very stability is a product of the collective behaviours of previous generations, we need to acknowledge that every trait is simultaneously ‘genetic’ and ‘cultural’. It is for these sorts of reasons that Laland and Brown’s recent article builds to

the conclusion that human nature is quite literally socially constructed: more-or-less universal and stable features of human phenotypes—the very traits we are tempted to think of as elements of human nature—are also artefacts of human culture.

At this point, I have neither endorsed nor attacked Laland and Brown's argument. My goal, so far, is merely to point out that at least one pair of researchers with a very prominent commitment to the programme of cultural evolution is also committed to drawing on DST to argue against the nature/culture distinction. This also means that it should be no surprise that thinkers from social anthropology have detected an instability in the cultural evolutionary programme. Christina Toren [27] remarks that the 'culture–biology' distinction has long been considered problematic among researchers in social anthropology. Maurice Bloch complains about work done by gene-culture co-evolutionists, on the grounds that culture and genetics are not distinct forces that can influence each other, but instead need to be thought of as 'a unified process' [28, p. 52]. Finally, Tim Ingold [29] characterizes humans as 'biosocial becomings': once again in an effort to reject any separation of what is biological or genetic from what is cultural or social.

The apparent problem for cultural evolution lies in the way that research programmes in 'dual inheritance theory' or 'gene-culture co-evolution'—both more or less synonymous labels for a highly influential element of the cultural evolutionary project—are sometimes framed. Research in these traditions aims to track the impact of cultural change on genetic evolution, and the reciprocal changes wrought by genetic change on culture. Perhaps the best known example of this type of research concerns the co-evolution of pastoralism and lactose tolerance [30]. In rough terms, the basic hypothesis—which is widely accepted and well confirmed—is that the adoption of dairying set up a modified niche in which the ability to digest lactose into adulthood was at an advantage. With dairying in place, our ancestors who were lactose tolerant could take advantage of a new source of calories. Hence, it is the learned acquisition of dairying which explains the natural selection of genes favouring lactase persistence, i.e. the continued production of the enzyme lactase beyond weaning [31,32].

This result—along with many others in this genre of research—is often expressed using the language of distinct inheritance 'channels'; hence 'dual inheritance theory'. Dairying is inherited, so the story goes, via a cultural channel; lactase persistence is inherited via a genetic channel. The research question for dual inheritance theory is to ask how these channels influence each other. Sometimes, researchers even go so far as to distinguish between genetic and cultural *traits*, as when Holden and Mace, in their widely cited paper on lactose tolerance, write that '...lactase persistence is a genetic trait, whereas pastoralism and milk-drinking are cultural traits' [31]. Generalizing from this specific example, Laland and collaborators write that 'Cultural evolutionists tend to view natural selection and cultural evolution as providing competing ultimate explanations' [33, p. 1515]. This suggests that it makes sense to distinguish the biological process of natural selection from the cultural processes that explain the spread of practices like dairying. This all makes it sound, on the surface of things at least, as though cultural evolutionists are committed to a fairly strong distinction between what we owe to nature and what we owe to culture.

How are we supposed to square all this with Laland and Brown's own more recent insistence that '...it is not possible to distinguish what is "biological" from what is environmental/cultural?' [20].

### 3. Primary resolution

It is perhaps not surprising that some have perceived a significant tension in a research programme whose adherents seem sometimes to insist that there is no distinction between what is biological and cultural, while elsewhere asserting that we should distinguish between different channels of inheritance, between natural selection and cultural selection, or between genetic and cultural traits. I have argued elsewhere that this apparent tension is merely apparent [34]. In the case of lactose tolerance, for example, the co-evolutionary hypothesis is committed only to the claim that, as individuals learned how to milk cows, a new selection pressure was established in which the ability to profit from this new source of calories by digesting lactose was favoured. This hypothesis does indeed require that we can distinguish comparatively rapid cycles of the reproduction of dairying, which have the ability to travel 'horizontally' between non-kin, from comparatively slower cycles of the reproduction of lactase persistence, which instead travel 'vertically' from parents to their offspring. In spite of this, the basic content of the co-evolutionary hypothesis does *not* demand that dairying be wholly 'cultural', in the manifestly absurd sense that it hops from mind to mind, independent of a physiological (and thereby genetic) background. Evidently dairying is a complex skill requiring suitable musculature and coordination, not to mention access to cows themselves. Dairying is not 'cultural', if one means by this that it is wholly or even mainly 'in the head'. Similarly, the co-evolutionary hypothesis does not require that lactase persistence be wholly 'genetic', in the sense that its development is unaffected by factors that vary across cultures. Diet itself, for example, appears to have an influence on the ability to digest lactose, and on the continued production of lactase into adulthood. Gut trauma, such as gastroenteritis, can result in loss of lactase, and social influence over diet can evidently bring about such traumas. Stress can result in individuals who are heterozygous for genetic variants that normally result in lactase persistence experiencing lactose intolerance instead [35]. Gut flora may explain lactose tolerance in Somali nomads who lack alleles associated with lactase persistence [36]. Finally, as Ruth Mace [37] herself has pointed out, in some other areas of Africa a comparatively low incidence of lactose tolerance may be explained by the adoption of techniques for processing milk that reduce the advantage of lactase persistence.

Gene-culture co-evolutionary hypotheses have no need of any strong distinction between that which is genetic and that which is cultural, and sceptics of the latter distinction need not be sceptics regarding the former research programme. Indeed, this way of having one's cake and eating it (or, in this case, having one's milk and drinking it) has always been part of the DST approach, whose foundational papers made it clear that it can make perfect sense to speak in terms of distinct inheritance 'systems', so long as we remember that in talking of (for example) the methylation 'system' or the genetic 'system', we describe a set of resources

affecting inheritance—varying methylation states, varying genetic sequences—whose stable effects on future cellular or organismic generations are contingent on the presence of a whole developmental system by virtue of which their phenotypic expressions are robust [26].

#### 4. Lessons learned

The previous section showed that, in spite of strong appearances to the contrary, it is possible to pursue the kind of research questions characteristic of dual inheritance theory at the same time as endorsing DST's scepticism of the nature/culture distinction. The cultural evolutionary project survives worries about the inability to draw a line between nature and culture. We should not conclude from this that cultural evolutionists have nothing to learn from those who are sceptical of the very idea of 'culture'. We can appreciate this if we begin by asking what cultural evolutionists typically understand by 'culture'.

Richerson & Boyd's [3, p. 5] definition is fairly typical of the cultural evolution community. They tell us that culture is 'information capable of affecting individuals' behaviour that they acquire from other members of their species through teaching, imitation and other forms of social learning'. So culture is information, with a very specific provenance. I will not worry here (although I have done elsewhere) about what one might mean by 'information' in this context [34]; instead, I want to put some pressure on how we should understand 'social learning'. This term is important for cultural evolutionists, because, in Richerson and Boyd's case, it is that which is learned socially that determines the scope of culture.

We have already seen that thinkers from the humanities and social sciences have expressed doubt about the nature/culture distinction. They have also expressed doubt about the related distinction between that which is social and that which is individual. Christina Toren [27], again, remarks that the very distinction between individual and social learning is one that social anthropologists have long regarded as problematic.

In a useful paper on culture in primates, Andrew Whiten [38] points to the variety of different forms of social learning. He notes that strict 'social learning' is a more demanding concept than mere 'social interaction'. In the case of what psychologists typically call 'stimulus enhancement', for example, a learner's attention is drawn to the object or site of the demonstrator's activity. In the case of 'local enhancement', the learner is attracted to the individual demonstrator. In both cases, the fact of being drawn to a demonstrator, or to the site in which the demonstrator is located, can have the result that the learner ends up learning what the demonstrator has learned, but not because the learner has imitated the demonstrator [39]. There are, as a consequence, numerous ways in which two apes may interact with each other, such that they learn similar things, but which fall short of full-blown imitation.

Even so, Whiten hints that unless two apes actually *meet*, it cannot be appropriate to think of one exerting social influence on the other. What he calls 'non-social processes' are defined so as to 'include all those cases that do not even require social interaction between A and B: for example, two apes who never meet but who are faced with similar fruits in their environments, may learn by their own

individual efforts (*individual learning*) how to peel the fruit in the same, perhaps optimal, fashion.' The structure of his taxonomy of learning processes makes clear that, in his view, there can be no cultural transmission via these 'non-social processes'.

The problem with this way of defining things is that we ignore the fact that, even when acting in a manner that appears to involve no direct interaction with other creatures, organisms nonetheless develop and learn in environments that have been affected by the prior actions of their conspecifics (and not just their conspecifics). This is precisely the sort of phenomenon stressed by the proponents of the niche-construction approach to evolution, and it is also stressed by developmental systems theorists [40,41]. Organisms grow in environments that have been constructed by the actions of previous generations: in that way, what an organism learns can be profoundly affected and enhanced by the collective activities of individuals it may never meet. In other words, we should not assume that there is any good distinction between individual learning and what we might call 'social transmission'. The latter can be achieved via the former.

These considerations make problems for simple efforts to define culture in terms of a supposed distinction between individual and social learning. That said, the problems inherent in assuming any simple individual/social learning distinction are already well understood by some researchers working on cultural evolution. Perreault *et al.* [42] proposed a formal model of the evolution of learning a few years ago that understood both 'social learning' and 'individual learning' as consequences of a single (Bayesian) inferential process. While denying a distinction between social and individual learning in terms of underlying cognitive process, that model remained committed to a distinction between 'social' and 'non-social' *cues* regarding the state of the environment. Other forms of work have cast further doubt on the notion that we can easily determine when the information an individual acquires is 'social' in provenance. For example, in a useful paper on learning in chimpanzees, Hobaiter *et al.* [43] looked at the spread of a new behaviour, which they call 'moss sponging', in a community of wild chimps. Previously, these chimps had used 'sponges' made from chewed up leaves in order to soak up water which they would then squeeze into their mouths and drink. Some chimps then began to make these sponges out of moss instead. They note that 'One individual [whom they called "KW"] acquired moss-sponging without any evidence of first observing another individual... However, KW acquired [moss sponging] after reusing another chimpanzee's sponge that contained moss, suggesting social learning mediated through the products of the moss-sponging behavior...'. In other words, while KW did not rely on any direct interactions with other chimps in her discovery that moss could be used as a sponge and, at least based on what the authors report here, simply learned for herself (based on what she had found around her) that this was indeed a good alternative sponging technique, the very fact that moss sponges were lying around her environment helped to explain how she was able to acquire this behaviour. The authors mention this example as part of what they describe as 'a growing literature that refutes a strong distinction between individual and social learning'.

Similarly, and again focusing on learning in primates, Frigaszy [44] describes a hybrid category of what she

revealingly calls, ‘socially biased individual learning’. Here again, an individual learns by interacting with her environment, but the environment itself is ‘biased’—in other words, structured in a manner that makes some learning outcomes easier than they would otherwise be—by prior social action. She cites a paper by Humle *et al.* [45] which explains how young chimps in Bossou, Guinea, learn to dip for ants. Again, the availability of discarded tools is important: ‘[I]nfants’ initial efforts to practice dipping were enabled by the availability of pre-used (and hence, pre-selected as suitable) tools’ [44,46].

In a recent overview of work on cultural evolution, Joseph Henrich begins by characterizing individual and social learning:

Throughout this book, *social learning* refers to any time an individual’s learning is influenced by others, and it includes many different kinds of psychological processes. *Individual learning* refers to situations in which individuals learn by observing or interacting directly with their environment, and can range from calculating the best time to hunt by observing when certain prey emerge, to engaging in trial-and-error learning with different digging tools. So, individual learning too captures many different psychological processes [11].

As we have seen, this way of characterizing things means that social learning and individual learning are not exclusive: an individual can learn by interacting directly with its environment—hence a case of ‘individual learning’—but in an environment that has itself been influenced by others, hence ‘social learning’. In other words, it is not merely the case that ‘individual’ and ‘social’ learning both involve ‘many different psychological processes’. Rather, if we focus solely on psychological events, they may involve precisely the same processes. That said, Henrich’s immediate follow-up indicates that he is aware of this consequence, and is untroubled by it: ‘Thus, the least sophisticated forms of social learning occur simply as a by-product of being around others, and engaging in individual learning.’

These considerations voiced from within the cultural evolution community can help us to understand why it is that some social anthropologists have dismissed the very idea of culture. Christina Toren, for example, takes:

... the radical view that one can conceive of all aspects of the world, including crucially all dimensions of human being, indeed of all living things, as historically constituted. This perspective does away with ideas of ‘human nature’ and ‘culture’ as analytical categories, but it does not entail any denial of the science of biology and its ever more remarkable technological advances [47].

We began by noting, along with the mainstream of cultural evolutionary theorists, that much of what we know we learn from others. We then noted, along with more reflective thinkers in that same cultural evolution community, that there are ways for the collective actions of one generation to enhance, facilitate or otherwise influence what further generations learn in ways that do not require any special form of learning: the collective structuring of the environment can also do the trick. And then, once we allow that ‘culture’ might encompass that which is explained via learning in a collectively structured environment—in other words, the traditions sustained and explained by the social actions of previous generations—it seems we have no particular grounds to exclude from the scope of ‘culture’ the ways in which the social actions of past generations enhance or facilitate downstream development through mechanisms other

than learning. Once we reach that point, though, the culture concept itself has become empty.

Laland *et al.* remark that:

We ... inherit a world of our making, complete with dogs, wheat, dairy cows, nectarines, and countless genetically modified types of grapes and without dodos, woolly mammoths, and the numerous other species left extinct by human activities. This is both our ecological and our cultural inheritance [41].

There are myriad ways in which the collective actions of previous generations influence how we develop: indeed, at the limit, social facts about how populations are divided into heterogeneous subgroups, and other such demographic facts, can affect who reproduces with whom, and ultimately the sorts of genotypes that come to exist in future generations. In that sense, genotypic combinations, and their downstream developmental effects, might also be considered elements of ‘culture’. That is precisely why people like Toren deny the value of the culture concept, and it is also precisely why the developmental systems theorists have expressed scepticism about our abilities to pull nature and culture apart. The culture concept is so elastic that it threatens to stretch much too far: far enough to encompass all aspects of human and animal behaviour that owe themselves, in some way or another, to the collective practices of earlier generations.

Once again though, it is (perhaps) surprising to see how robust work in cultural evolution is in the face of these worries about whether—and how—we might decide what counts as ‘culture’. Kim Sterelny [10], for example, stresses, in his recent work on what he calls ‘apprentice learning’, the ways in which novice learners can enjoy very significant epistemic leg-ups in much the same way as Hobaiter *et al.*’s chimps: by spending time in environments rich with the detritus of an adept’s activities, novices end up having access to felicitously prepared raw materials, half-constructed elements of completed tools and so forth [10]. The consequence is that they learn for themselves in ways that are already significantly ‘scaffolded’. For Sterelny, this is part of a natural historical narrative in which increasingly elaborate forms of teaching, and the maintenance of large storehouses of know-how, emerge from more rudimentary beginnings.

While Sterelny’s work falls squarely within the general cultural evolutionary project of asking what processes underpin our accumulation and maintenance of bodies of knowledge, and how and why those varied processes emerged over time, that project does not require that we give any principled answer to the question ‘what is culture?’. It is simply not a threat to Sterelny’s work that we might want to count those simple forms of scaffolded learning as facilitating ‘culture’; and it would not be a problem if we began to be convinced that ultimately there is no good answer to the question of how to pick out ‘culture’ from the broader mess of ways in which social interactions help to explain the reasonably reliable transmission of forms of behaviour, modes of thinking and so forth.

## 5. Getting back to Earth

If we set ourselves the very general project of asking what is nature, what is culture and how we should distinguish the two, then we will inevitably fail. DST, and the niche construction perspective, remind us that there are many ways in which the collective practices of parental generations—of

humans, and of other species, too—can influence offspring generations, and hence that simple distinctions between ‘individual’ and ‘social’ learning are often inadequate. They also remind us that, if we wanted to, it would not be an outrage to attribute a form of ‘culture’ to very ‘low’ forms of animal life, even to plants: for here, too, the activities of earlier generations in modifying environments end up affecting the manner in which later generations develop. These very abstract worries still leave intact the project of asking how different forms of learning, and how different contexts for learning, first emerged in our own species, how they differ in the capacities they confer on populations and why they persist. In that respect, too, the cultural evolutionary project survives any scepticism we might have about ‘culture’, and whether ‘culture’ is best thought of as a moving evolutionary target.

We can offer, then, an irenic resolution of the debate between sceptics of the cultural evolutionary project and its proponents. Social anthropologists, among others, are right to cast doubt on the propriety of distinctions between nature and culture, between individual and social learning, and ultimately they are right to point out the potential of the very idea of ‘culture’ to encourage an overly narrow approach to the question of how such things as traditions, bodies of practice and so forth are sustained from one time to another. But the very same concerns that motivate these worries about the culture concept are also beginning to inform cultural evolutionary investigations themselves.

We can also suggest an ironic resolution to these debates. As we have seen, it is true of all species that the interactions of organisms of one generation leave behind a structured set of developmental resources that combine in later generations to bring about new organisms, whose dispositions resemble those of the previous generation. These are the sorts of themes long suggested in social scientific contexts by thinkers such as Bourdieu [48] and Vygotsky [49]. In the most liberal sense, then, social relations are always responsible for patterns of reproduction, and any choice over exactly which of these relational processes we choose to call ‘culture’ will be to some degree arbitrary. At one extreme, we have rare processes such as teaching, in which demonstrators model behaviours—often in unusually slow, segmented or exaggerated ways—with the explicit goal of assisting novices in acquiring skills or know-how. Towards the other extreme,

we have those much more widespread cases of ‘socially biased individual learning’, where the activities of one group of organisms give rise to by-products that enhance the learning of others. In answering the question ‘What is to count as “culture”?’ we must make choices as investigators; the answer is not something given to us by the world itself. It turns out that cultural evolutionists, for the most part, use ‘culture’ in ways that are reasonable given their aims: they understand, for example, that learning from others is not the only way in which traditions can be sustained across generations; and they understand that our collective ability to sustain elaborate bodies of know-how depends on a very wide variety of processes. This fact becomes clear when we take time to examine the pragmatic goals and explanatory practices of cultural evolutionists themselves.

In recent years, some prominent social anthropologists have urged that we should not dismiss the ontologies of alien communities simply because they differ from our own; more specifically, we should not try to accommodate or explain those alien ontologies by showing how they might arise as *their* projections onto the true world—i.e. the world as *we* understand it. Instead, those who advocate an ‘ontological turn’ have stressed the need to take these others more ‘seriously’. The variety of ways in which we might inadvertently *not* take alternative ontologies with suitable seriousness is a theme in the work of people like Eduardo Viveiros de Castro [50] and Martin Holbraad [51], for example. As this mode of thinking predicts, when the natives in question are cultural evolutionists themselves, we can also see how the particular manners in which they construct ‘culture’ can be justified, by taking their practical lives—their investigative and explanatory lives—seriously, too.

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## References

- Cavalli-Sforza L, Feldman M. 1981 *Cultural transmission and evolution: a quantitative approach*. Princeton, NJ: Princeton University Press.
- Boyd R, Richerson P. 1985 *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Richerson P, Boyd R. 2005 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: University of Chicago Press.
- Avital E, Jablonka E. 2000 *Animal traditions: behavioural inheritance in evolution*. Cambridge, UK: Cambridge University Press.
- Homer V, Proctor D, Bonnie K, Whiten A, de Waal F. 2010 Prestige affects cultural learning in chimpanzees. *PLoS ONE* **5**, e10625. (doi:10.1371/journal.pone.0010625)
- Danchin E, Charmantier A, Champagne F, Mesoudi A, Pujol B, Blanchet S. 2011 Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nat. Rev. Genet.* **12**, 475–486. (doi:10.1038/nrg3028)
- Henrich J. 2001 Cultural transmission and the diffusion of innovations: adoption dynamics indicate that biased cultural transmission is the predominate force in behavioral change. *Am. Anthropol.* **103**, 992–1013. (doi:10.1525/aa.2001.103.4.992)
- Henrich J, Boyd R. 1998 The evolution of conformist transmission and the emergence of between-group differences. *Evol. Hum. Behav.* **19**, 215–241. (doi:10.1016/S1090-5138(98)00018-X)
- Henrich J, Gil-White F. 2001 The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* **22**, 165–196. (doi:10.1016/S1090-5138(00)00071-4)
- Sterelny K. 2012 *The evolved apprentice: how evolution made humans unique*. Cambridge, MA: MIT Press.
- Henrich J. 2015 *The secret of our success*. Princeton, NJ: Princeton University Press.
- Henrich J, Boyd R. 2002 On modelling culture and cognition: why cultural evolution does not require

- replication of representations. *Cult. Cogn.* **2**, 87–112. (doi:10.1163/156853702320281836)
13. Griffiths PE. 2009 Reconstructing human nature. *Arts* **31**, 30–57.
  14. Lewens T. 2012 Human nature: the very idea. *Philos. Technol.* **25**, 459–474. (doi:10.1007/s13347-012-0063-x)
  15. Heyes C. 2001 Causes and consequences of imitation. *Trends Cogn. Sci.* **5**, 253–261. (doi:10.1016/S1364-6613(00)01661-2)
  16. Heyes C. 2010 Where do mirror neurons come from? *Neurosci. Biobehav. Rev.* **34**, 575–583. (doi:10.1016/j.neubiorev.2009.11.007)
  17. Heyes C. 2012 Grist and mills: on the cultural origins of cultural learning. *Philos. Trans. R. Soc. B* **367**, 2181–2191. (doi:10.1098/rstb.2012.0120)
  18. Heyes C. In press. Human nature, natural pedagogy, and evolutionary causal essentialism. In *Why we disagree about human nature* (eds T Lewens, E Hannon). Oxford, UK: Oxford University Press.
  19. Smith R. 2007 *Being human: historical knowledge and the creation of human nature*. New York, NY: Columbia University Press.
  20. Laland K, Brown G. In press. The social construction of human nature. In *Why we disagree about human nature* (eds T Lewens, E Hannon). Oxford, UK: Oxford University Press.
  21. Oyama S. 1985 *The ontogeny of information: developmental systems and evolution*. Durham, NC: Duke University Press.
  22. Gray RD. 1992 Death of the gene: developmental systems strike back. In *Trees of life: essays on the philosophy of biology* (ed. PE Griffiths), pp. 165–209. Dordrecht, The Netherlands: Kluwer.
  23. Griffiths PE, Gray RD. 1994 Developmental systems and evolutionary explanation. *J. Philos.* **91**, 277–304. (doi:10.2307/2940982)
  24. Griffiths PE, Gray RD. 1997 Replicator II—judgement day. *Biol. Phil.* **12**, 471–492. (doi:10.1023/A:1006551516090)
  25. Oyama S. 2000 *The ontogeny of information: developmental systems and evolution*, 2nd edn. Durham, NC: Duke University Press.
  26. Griffiths PE, Gray RD. 2001 Darwinism and developmental systems. In *Cycles of contingency: developmental systems and evolution* (eds RD Gray, PE Griffiths, S Oyama), pp. 195–218. Cambridge, MA: MIT Press.
  27. Toren C. 2012 Anthropology and psychology. In *The Sage handbook of social anthropology* (eds R Fardon, O Harris, THJ Marchand, C Shore, V Stang, RA Wilson, M Nuttall), vol. 1, pp. 27–41. Los Angeles, CA: Sage.
  28. Bloch M. 2012 *Anthropology and the cognitive challenge*. Cambridge, UK: Cambridge University Press.
  29. Ingold T. 2013 Prospect. In *Biosocial becomings: integrating social and biological anthropology* (eds T Ingold, G Pálsson), pp. 1–21. Cambridge, UK: Cambridge University Press.
  30. Feldman MW, Cavalli-Sforza LL. 1989 On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem. In *Mathematical evolutionary theory* (ed. MW Feldman), pp. 145–173. Princeton, NJ: Princeton University Press.
  31. Holden C, Mace R. 1997 Phylogenetic analysis of the evolution of lactose digestion in adults. *Hum. Biol.* **69**, 605–628.
  32. Itan Y, Jones B, Ingram C, Swallow D, Thomas M. 2010 A worldwide correlation of lactase persistence phenotypes and genotypes. *BMC Evol. Biol.* **10**, 36. (doi:10.1186/1471-2148-10-36)
  33. Laland KN, Sterelny K, Odling-Smee J, Hoppitt W, Uller T. 2011 Cause and effect in biology revisited: is Mayr's proximate-ultimate dichotomy still useful? *Science* **334**, 1512–1516. (doi:10.1126/science.1210879)
  34. Lewens T. 2015 *Cultural evolution: conceptual challenges*. Oxford, UK: Oxford University Press.
  35. Swallow D. 2003 Genetics of lactase persistence and lactose intolerance. *Annu. Rev. Genet.* **37**, 197–219. (doi:10.1146/annurev.genet.37.110801.143820)
  36. Ingram C, Mulcare C, Itan Y, Thomas M, Swallow D. 2009 Lactose digestion and the evolutionary genetics of lactase persistence. *Hum. Genet.* **124**, 579–591. (doi:10.1007/s00439-008-0593-6)
  37. Mace R. 2010 Update to Holden and Mace's 'Phylogenetic analysis of the evolution of lactose digestion in adults'. *Hum. Biol.* **81**, 621–624. (doi:10.3378/027.081.0610)
  38. Whiten A. 2000 Primate culture and social learning. *Cogn. Sci.* **24**, 477–508. (doi:10.1207/s15516709cog2403\_6)
  39. Heyes, C. 1994 Social learning in animals: categories and mechanisms. *Biol. Rev.* **69**, 207–231. (doi:10.1111/j.1469-185X.1994.tb01506.x)
  40. Odling-Smee J, Laland K, Feldman M. 2003 *Niche construction: the neglected process in evolution*. Princeton, NJ: Princeton University Press.
  41. Laland KN, Odling-Smee J, Feldman M. 2001 Niche construction, biological evolution, and cultural change. *Behav. Brain Sci.* **23**, 131–146. (doi:10.1017/S0140525X00002417)
  42. Perreault C, Moya C, Boyd R. 2012 A Bayesian approach to the evolution of social learning. *Evol. Hum. Behav.* **33**, 449–459. (doi:10.1016/j.evolhumbehav.2011.12.007)
  43. Hobaiter C, Poisot T, Zuberbühler K, Hoppitt W, Gruber T. 2014 Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biol.* **12**, e1001960. (doi:10.1371/journal.pbio.1001960)
  44. Frigaszy D. 2011 Community resources for learning: how Capuchin monkeys construct technical traditions. *Biol. Theory* **6**, 231–240. (doi:10.1007/s13752-012-0032-8)
  45. Humle T, Snowdon C, Matsuzawa T. 2009 Social influences on ant-dipping acquisition in the wild chimpanzee (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim. Cogn.* **12**, S37–S48. (doi:10.1007/s10071-009-0272-6)
  46. Visalberghi E, Frigaszy D. 2012 Learning how to forage: socially biased learning and 'niche construction' in wild Capuchin monkeys. In *The primate mind* (eds F de Waal, P Ferrari). Cambridge, MA: Harvard University Press.
  47. Toren C. In press. Human ontogenies as historical processes: an anthropological perspective. In *Why we disagree about human nature* (eds T Lewens, E Hannon). Oxford, UK: Oxford University Press.
  48. Bourdieu P. 1977 *Outline of a theory of practice*. Cambridge, UK: Cambridge University Press.
  49. Vygotsky L. 1986 *Thought and language*. Cambridge, MA: MIT Press.
  50. Viveiros de Castro E. 2013 The relative native. *Hau: J. Ethnographic Theory* **3**, 469–471. (doi:10.14318/hau3.3.032)
  51. Henare AJM, Holbraad M, Wastell S. 2007 Introduction: thinking through things. In *Thinking through things: theorising artefacts ethnographically* (eds AJM Henare, M Holbraad, S Wastell). Oxford, UK: Routledge.