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Understanding culture across species

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Recent claims of culture in great apes have provoked fervent argument about the 'true' definition of culture, most of which has been unhelpful. Instead, a range of definitions should be used to explore different aspects of the cognitive processes that together result in human culture, many of which can be productively studied in non-humans. A richer cognitive account of the contents of culture needs to be developed and used to compare animal and human cultures, instead of sterile searching for a cognitive Rubicon between them. Exploring six views of culture, this article highlights the fundamental contrast of whether culture evolves as a by-product of cumulative change in cognitive mechanisms, or whether it is actively selected for its advantages.

Culture makes humans unique. But if we ask most scholars how to recognize culture, the answer is likely to be a list of things that humans do and animals don't. With this circular logic in the background, it is unsurprising that attempts to understand the evolution of culture become polarized. At one extreme, a single magic ingredient – such as speech, syntax, symbol-use, causal belief, teaching, theory of mind, or representational ability – appeared during recent human evolution and enabled culture to begin [1,2]. At the other, by suitably redefining culture, it becomes something shared with other species, such as great apes, capuchin monkeys, cetaceans, rats, or even fish [3–9].

Although such debate is fascinating, arguments about 'the critical ingredient' are likely to inhibit interdisciplinary analysis of any larger evolutionary pattern. Human culture is reflected in an intricate 'package' of capabilities, behaviours and artefacts. That package undoubtedly differs from that of other species – so human evolution *was* evidently affected by one or more unique adaptations. Equally, the mind, society and culture of humans cannot have arisen *de novo*. Understanding the behavioural and cognitive precursors to the complete human cultural package requires experimental study of social learning and comparative phylogenetic analysis of living species, as well as evidence from extinct hominins (fossil animals more closely related to modern humans than to living non-human apes) and modern ethnography.

In the quarter century since the first serious claim of 'culture' in animals [10], lamentably little interdisciplinary consensus has emerged. Debates have pivoted on the championing by various scholars of their definition of culture as the 'true' one, but this has thwarted progress because they are seldom talking about quite the same thing [8]. Even within anthropology, no single view of culture has gained universal acceptance, and most discourage evolutionary theorizing [11]. Here, we attempt to tease apart six different ways in which culture has been construed, to answer specific questions. These fall naturally into pairs (see Figure 1): pattern of variation versus psychological mechanism, adaptive value versus potential inefficiency, and physical objects versus underlying meaning. Each pair might at first appear diametrically opposed, but these contrasts are better thought of as two sides of the same coin.

Culture as pattern

Adaptive value need not be crucial in generating cultural patterns. One can therefore take social learning as a starting point and ask what kinds of shared behavioural patterns arise simply because individuals learn from each other. Studies of bird song [12] provide some direct answers, including evidence of local dialects and regional clines, measurable cultural mutation rates, and even cultural boundaries promoted by geographic features [13].

Theorists have modelled the patterns of cultural traits produced by social information transmission in the absence of adaptive variation in traits. Importantly, the transmission mechanism itself has little influence on the pattern of traits, within or between populations [14]. Instead, the main variables of influence are the direction of information transmission (between parents and offspring, between successive generations, or among individuals of the same generation), the stability of the environment, and genetic constraints. Furthermore, individuals of social species often show a conformity bias [15], and it is advantageous for individuals to enforce local conformity by

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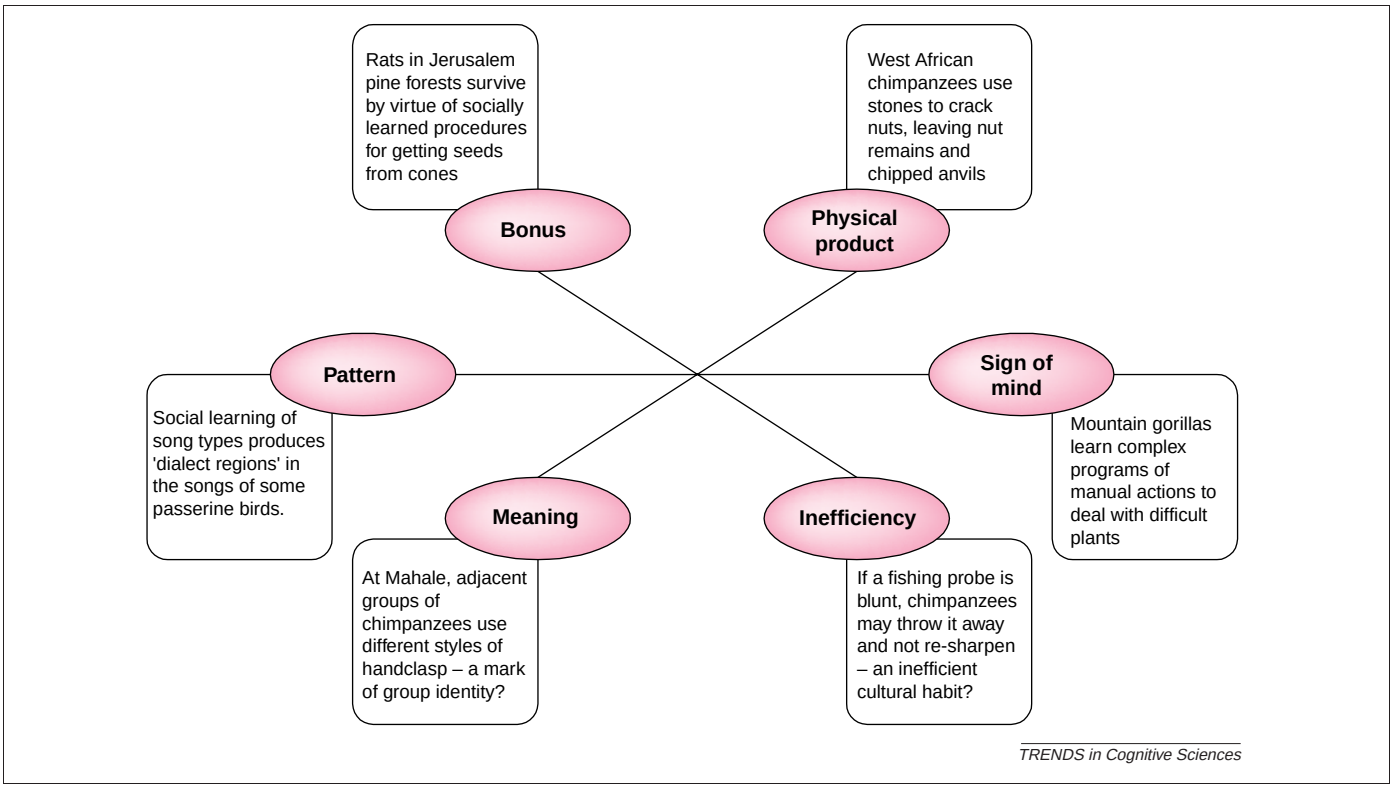

Figure 1. **Six views of culture**. Schematic illustration, showing that each view can be seen, to some extent, as complementary to another view, forming three pairs. For each axis, an illustrative example of animal behaviour is given that might, from the viewpoint in question, be considered as culture. Our examples are chosen to illustrate the dimensions, and we are not concerned with whether or not they are 'valid' or 'true' cases of culture in animals. At present, many putative cases of culture cannot exclude genetic and environmental factors, and doing so is no trivial task. Indeed, social transmission is unproven even for those chimpanzee habits frequently discussed as cultural [29]. Our aim here is to jump ahead to the next step in the analysis of culture, and illustrate the way in which cultural patterns can be analysed to shed light on cognitive evolution.

directing aggression at anyone who is different from everyone else. This 'xenophobia' benefits most group members, who learned their traits from each other and so are unlikely to be targeted as outsiders [16]. Lachlan and Slater showed that on an evolutionary time scale, social learning is likely to persist once it has evolved even if cultural traits later become adaptively neutral, an effect they called the 'cultural trap' [17]. Their simulations show that complex effects, including in-group/out-group biases and xenophobia, can arise from relatively simple mechanisms. Culture can be exhibited by any animal with a mind that allows social learning; conversely, finding cultural variation is no guarantee of unusual cognitive capacity.

Culture as a sign of mind

Although cultural patterning can emerge from social transmission alone, cognitive capabilities might determine the nature of the information transmitted. Debates about the relationship between culture and cognition have developed a rather black-and-white character, because attention is inevitably drawn to the presumed apex of the cultural pyramid – the human mind. The lack of local behavioural variation in most animals is then taken to reflect cognitive simplicity, and human cultures are attributed to more sophisticated or higher fidelity mechanisms [18]: imitation, creative ideation, theory of mind, teaching dependent upon joint attention, or even deliberate instruction. Each such proposal is an empirical challenge to animal researchers, leading to repeated testing of boundaries between animal and human cognition. But to advance our understanding of how the minds of a wide range of species deal with cultural knowledge we need to frame questions in rather less absolute terms, and concentrate on the substantive *content* of the information involved and how that relates to transmission mechanisms.

Most higher animals are able to differentiate categories. Although the precise distinctions made by rats, dogs and monkeys probably vary, human meaning systems might only be making *explicit* a process that is universal among higher mammals [19]. Table 1 provides a concrete illustration of how semantic roles, precursors of those expressed in language, are implicit in animal cognition. Furthermore, the contrasts encoded by a species might determine its cultural content: fish learn socially to use particular locations for particular behaviours [20], dolphins 'see' the landscape using sonar thus allowing richer coding, and human groups add symbolic meanings to locations. A similar gradient in the complexity of semantic content exists in socially transmitted foraging methods: from simple food choices, to the elaborate procedure of pine-cone processing in black rats [21], to the repeated detachment of flakes from a stone core by early hominins [22]. Differences in the content of cultural information across species might reflect a small number of distinguishable semantic roles [23]. Moreover, semantic systems could exhibit both graded progression and discontinuities in different species. The current focus on one-dimensional contrasts – presence vs. absence, simple vs. complex, human vs. animal – carries

Table 1. Case roles for chimpanzees

Semantic role	Fillmore's definition [23]	Linguistic example	Implicit counterpart for chimpanzees
Agent	*Instigator* of an event	**John** opens the door	Chimpanzee, '**Mike**', climbs a tree
Counter-agent	Force or resistance *against which* the action is carried out	John hit **the desk**	A chimpanzee strikes a *Strychnos* fruit against **a stone** to break it open
Object	Entity that *moves* or *changes* or whose position or existence is *under consideration*	**Mary** is seven years old	Chimpanzee, '**Figan**', is now alpha male
Result	Entity that comes *into existence* as a result of the action	Mary made **a cake**	Chimpanzee makes a **fishing probe** by stripping leaves from a grass stem
Instrument	Inanimate *stimulus* or immediate *physical cause* of an event	**The key** unlocked the door	**Spherical stone**, used as a hammer by a chimpanzee to crack nuts
Dative	Animate being *affected* by the action named by the verb	I gave my sweets to **Mary**	Female chimpanzee, '**Flora**', is being groomed by another chimp
Experiencer	Animate being having a given *experience* or *mental state*	**Daddy** is cross	Piloerection and *waa* barks show that chimpanzee '**Frodo**' is angry
Locative	*Location* or *spatial orientation* of the state or action named by the verb	Toby sits by **the fire**	A group of male chimpanzees goes to the group's **periphery** and looks for intruders

The above activities are everyday ones for chimpanzees, and in most cases for many other animal species. Nevertheless, they can only be understood in terms of the relationship between the action itself and the animate and inanimate entities that stand in different semantic roles to the action. Therefore, to the extent that a chimpanzee can understand these actions and their meaning, and not merely perform them, it must possess some way of coding the semantic relationship. In the past few years, a start has been made into discovering how non-human primates encode the broadest categories, including physical properties of objects, everyday causality and mental states [47–49]. A very much more detailed analysis will be needed to understand the evolution of the categorizations that eventually led to human semantic meaning.

the risk of obscuring variation in semantic categories that would more clearly illuminate cultural differences.

Culture as a bonus

Part of the excitement about culture in animals is based on culture's potential to allow access to information not available otherwise. With useful, socially learnt traditions, a local population can 'punch above its weight', and thus gain a critical survival advantage. Elephants can learn of the location of water sources merely by following their elders. Without this social guidance they could not survive in the Namib [24]; with it, individuals gain valuable knowledge for nothing. If each generation adds something to what they learnt, then 'ratcheting' of cultural knowledge can occur – a sort of cultural 'compound interest' [18]. In Japanese macaques, the progressive changes over decades in the techniques of sweet potato washing and wheat sluicing strongly suggest a ratchet effect [25], although the origin of the local tradition in this case was the result of human influence [26].

Viewing culture as 'knowledge scrounging' has interesting consequences. First, allowing such scrounging is altruistic, and evolutionary theory predicts that compliance should be limited by kin relatedness [27]. Individuals benefit by allowing relatives to learn from them but actively preventing non-kin from acquiring their knowledge, unless reciprocation can be negotiated [15]. Therefore, when social learning depends on demonstrator co-operation, culture will seldom spread beyond genetical lineage except under special conditions that allow group selection to be evolutionarily stable [28]. Second, if a skill is copied from others, its mechanism need not be understood. Rich cultural traditions can therefore give a false impression that agents understand what they are doing.

Often, discussion of human culture and the animal/human divide is couched in terms of formidable advantages that culture can bestow, by allowing rapid adaptation to a changing environment. We should also remember that these benefits are often selfishly limited to kin-based groups, and that they ultimately reflect a way of circumventing cognitive *limitations* rather than a display of advanced cognitive mechanisms or differentiated control of actions.

Culture as inefficiency

If social learning is needed to acquire a difficult skill, individuals are likely to copy whatever behaviour is demonstrated – even if it is not the most efficient means of achieving a result. This might seem to be a 'glass is half-empty' view – after all, inefficient methods are better than none. But compare instrumental conditioning as a learning mechanism. Because solutions produced by trial-and-error learning are the 'survivors' of much greater variation, selected on the basis of efficient consequences, acquisition of a difficult skill is a hill-climbing process that tracks inexorably towards locally optimal solutions and increased efficiency.

Researchers have therefore used inefficiency as diagnostic of cultural origin. Different chimpanzee populations employ tool-use methods that vary in efficiency, and this has been cited as strong evidence that these skills are cultural [29]. To give a specific example, when ant-dipping, Taï chimpanzees use a one-handed method that gathers ants at a quarter of the rate of Gombe chimpanzees' two-handed method [30]. But can we be sure their behaviour is really inefficient? At Bossou, it has now been discovered that both one-handed and two-handed methods of ant-dipping are used by the same individuals – but for different kinds of ants [31]. Immediately, one can explain the local variations in method by ecological differences in ant species. This has been used to argue against ant-dipping being cultural, anywhere [32], but dismissal is premature: skills can be culturally learnt, even if local variation is environmentally determined. Rather, the logic of 'inefficient' equating with 'cultural' needs re-examining.

When new and valuable methods of getting food become available for social learning they will be copied, however imperfect the method. As knowledge spreads, however, individuals will show slight variations of the model, and variation provides grist to the mill of instrumental learning. Individuals with the best versions are more likely to be

copied than those seen to do poorly (and they might also gain greater fitness). Cultural spread provides the rough-and-ready version, but selective copying will gradually shape individuals' actions towards the most efficient style. Thus, highly stable cultural information will be hard to detect, and culture will be more readily noticed where change is rapid or efficiency has few consequences for survival. The focus on local population variation has resulted in even the most complex plant-eating skills of apes – those of mountain gorillas – being overlooked as potential animal culture [33]. Culturally transmitted skills are unlikely to remain inefficient, generation after generation: for long-established cultural traditions, optimality is precisely what we should expect.

Culture as physical products

The earliest durable products of human culture, stone tools, are not just convenient artefacts for museums to label as 'Oldowan culture' or whatever it might be. Because they endure long after the lifetime of the knappers they form potential resources for those who come after, opening up new opportunities for tool making and tool use. These artefacts could be used both as a source of stone for re-fashioning, and as a lasting mnemonic of the best choice of material or knapping technique. As a result, the world in which the species survives becomes a new, more differentiated one. Ever since hominins began flaking stone, at least 2.6 million years ago [34], niche construction of this simple, unintentional kind has been happening [35]. Forms produced accidentally when flaking stone might later be achieved deliberately, leading to increasingly specialized products [15], which can in turn create a larger space of possible actions from which to learn and select. Finally, culture itself can affect genetic evolution [36,37]. For a mind capable of recognizing the potential of accidental solutions and producing them at will, observing their production provides real creative possibility.

Increasing complexity brings potential for cognitive advance. Chimpanzee termite-fishing probes and human digging sticks both consist of single elements used in food procurement [38]; but whereas the probe is formed by a simple process of stripping a stem, the preparation of the digging stick requires a chain of actions including use of a stone flake. Two superficially similar tool forms thus have different underlying cognitive requirements, involving at least two variables: the seriation of action elements, and the objects with specific properties required in that sequence. As requirements grow, more advanced mechanisms of acquisition gain competitive edge over simple associative learning, and the result can be a relatively domain-specific learning mechanism. It has recently been noted that a variety of human cultural artefacts take advantage of domain-specific cognitive adaptations [39]: for example, masks and caricatures exploit pattern invariants in human face recognition. The physical products of hominin culture give us the best evidence of the evolutionary origins of these invariants. Cultural traditions that involve complex sequences of skilled action, such as crafts or dance, are likely to be steered towards the pattern invariants in this domain, involving movement contingencies over time as well as space.

Culture as meaning

Meaning is central to human culture and its very nature a matter of extensive debate [40]. Human relationships are governed by shared rules and values expressed in rituals, language and other symbols [41]. To examine, in comparative perspective, how that expands the potential effects of socially transmitted knowledge, we focus on the formation of risk-sharing networks [42].

Long-distance networks, linking individuals into an expanded support group that consequently has reduced risk, might have emerged 60 000 years ago [43,44], although only by 30–35 000 BP is there evidence that cultural technology was sufficiently complex to forge co-operation and competition between larger social groups. In the modern era, a Kalahari !Kung (Ju/'hoansi) poisoned arrow – already a formidable technological product – takes on cultural meaning when given as a gift [45]. Exchange of arrows between non-biological 'kin' in villages up to 200 km apart marks a relationship in one of the mutual assistance networks that constitute risk-sharing systems for the !Kung. Delayed exchange of arrows and other gifts, such as ostrich eggshell beads, carries information about mutual obligations: one person can visit the other and seek help whenever there is need. In addition, stylistic attributes of arrows indicate self-identity as belonging to a dialect group with shared conventions, values, rituals, and ability to classify one another as kin.

Compared with animal cultures, certain differences are obvious. Agents that can represent abstract categories such as obligation and risk, and coordinate information-flow through a social landscape of large distances and long timescales, are crucial to understanding !Kung gift-exchange networks. Obviously, then, the package of human culture is unique – but when viewed in terms of component variables, important common themes in human and animal cultures are emphasized. As we have seen, the tolerance required to build risk-sharing systems, and the xenophobia associated with hierarchy and ethnic boundaries – as suggested by local stylistic variation in late Upper Palaeolithic projectile points and other artefacts [46] – might both have evolutionary origins in patterns of culture that emerge inevitably from social transmission. When augmented by cultural meaning, human groups can also become fertile ground for the development of ethnic conflict and of acts of selfless humanity.

Any culture is a complex system, with emergent properties that cannot be described by adding up its component elements, any more than a molecule can be understood by reference only to its atoms. We look to comparative studies, therefore, to go beyond debates about whether 'meaning' or 'culture' is exclusively human or not. We need to target the systems of interacting variables underlying increasingly differentiated culture across species, from fish, through apes, to humans (see Box 1 for other questions for future research).

Conclusions

So what can we hope for, in putting aside simple yes/no questions about animal culture? Cultural '**pattern**' can emerge as a near-automatic product of social learning, whereas transmission of richer information reveals a

Box 1. Questions for future research

- Animal species vary both in the sophistication of their cognitive mechanisms and in the content of information that is subject to cultural spread. Are particular transmission mechanisms necessary to propagate certain types of information content?
- We humans might be over-generous to ourselves in routinely attributing our behavioural patterns to higher cognitive mechanisms. To what extent do patterns of human culture emerge automatically as by-products of constraints on the rate, direction and accuracy of information transmission?
- From theoretical considerations, when social learning depends upon demonstrator cooperation it is expected that cultural spread should be limited to kin. To what extent does this occur, and are other individuals, thereby deprived of valuable cultural information, able to overcome the restriction?
- We have predicted that inefficient methods of achieving valuable ends should be unstable as cultural traits, tending to 'creep' towards the most efficient style (unless that would require major behavioural reorganization). This should be studied experimentally, by introducing more or less inefficient behavioural solutions into captive animal groups and measuring their persistence and rate of change.
- In human society, interactions outside an individual's regular social group are often made predictable by knowledge of cultural norms and rules. Is there evidence that other species attach *meaning* to cultural traits, or treat unfamiliar conspecifics according to their cultural habits?

distinctive '**sign of mind**' in certain species. Culture can overcome cognitive limitations, and the **bonus** may be valuable enough to encourage limitation to close kin. When transmission is rapid, cultural traits might temporarily exhibit **inefficiency**, which will gradually become optimal as a result of individual learning and natural selection. The **physical products** of culture are a sign of niche construction, a reservoir of knowledge with potential to aid the ratchet of cumulative change; and investment of **meaning** in physical objects transforms them into tokens of societal obligation, changing the culture itself and thus the environment of cultural learning. By construing culture as three pairs of issues, our analysis reveals two distinct opportunities for advancing our debate, guided in both cases by classic evolutionary concerns with differentiation and adaptiveness.

Differentiation

Human culture and its physical products are undeniably far more differentiated behaviourally and cognitively than those seen in apes, cetaceans or birds. However, only by identifying which aspects of cognition *vary* across species – unique semantic categorizations, in relation to particular adaptive niches – can we understand how the culture of *Homo sapiens* attained its special form. We can sensibly ask what sets of distinctions might underlie each species' package of socially learned behaviour, including those inferred from the archaeological record (see Table 1 for a flavour of what this might look like).

Adaptiveness

Is culture the primary adaptation, or a by-product of something else? In one scenario, challenges from the environment of particular species selected directly for culture-promoting cognitive traits, because culture paid off in Darwinian terms. The slogan, 'mind is a product of culture', encapsulates this hypothesis, in which cognitive advances such as theory of mind, syntactic structuring, cause–effect reasoning, or co-operative action, are viewed as favoured in evolution because of their cultural effects. Conversely, each cognitive advance can be seen as an adaptive response directly to environmental or social challenges – involving food procurement, predator defence, collaborative hunting or cooperative breeding, competing in Machiavellian ways to minimize the costs of group living, and so on. Because these cognitive mechanisms promote efficient social learning, there is an automatic consequence: 'culture as a by-product'. Culture's effects can be large for some species, but on this view they are secondary results of adaptation to more utilitarian functions. We would not necessarily expect one of these two opposing hypotheses to apply to all species, and both might affect the evolution of culture in a single species.

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