

Review

The scope of culture in chimpanzees, humans and ancestral apes

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More studies have focused on aspects of chimpanzee behaviour and cognition relevant to the evolution of culture than on any other species except our own. Accordingly, analysis of the features shared by chimpanzees and humans is here used to infer the scope of cultural phenomena in our last common ancestor, at the same time clarifying the nature of the special characteristics that advanced further in the hominin line. To do this, culture is broken down into three major aspects: the large scale, population-level patterning of traditions; social learning mechanisms; and the behavioural and cognitive contents of culture. Each of these is further dissected into subcomponents. Shared features, as well as differences, are identified in as many as a dozen of these, offering a case study for the comparative analysis of culture across animal taxa and a deeper understanding of the roots of our own cultural capacities.

Keywords: culture; traditions; cultural evolution; social learning; apes; chimpanzees

1. INTRODUCTION

From the perspective of our now-voluminous data [1] it is extraordinary that half a century ago, virtually nothing was known about wild chimpanzees, the animals with whom we share the most recent common ancestry. Today, we have a fund of evidence about the cultural nature of our sister genus that appears unrivalled in animal behaviour and exceeded only by our knowledge of human cultures. Applying the comparative method to reconstruct the scope of culture in the common ancestors of humans and chimpanzees may thus offer a more comprehensive analysis than is yet feasible for other animal groups. This is a prime aim of the current paper. However, no less important are the conceptual and empirical tools developed in doing this, which should be applicable to similar exercises across the animal kingdom, as the necessary data accumulate.

Both the popular and scientific press often ask whether a particular species ‘has culture’. Rather than assume the unitary conception of culture this implies, I dissect cultural phenomena into several major and subsidiary subcomponents organized within a hierarchically structured taxonomy, so as to compare species on each component. This leaves open for empirical investigation whether certain subcomponents vary together in systematic ways across species, or instead evolve in mosaic-like fashion, shaped perhaps by different phylogenetic and ecological factors.

Explorations of this approach in recent years have themselves evolved [2–4] and continue to do so here. However, distinguishing three main classes of variation among cultural phenomena has emerged as a resilient taxonomic approach. The first of these three classes concerns the patterned distribution of traditions in space and time. For this I adopt Frigaszy & Perry’s [5, p. xiii] definition of a tradition, namely ‘A distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning’. As noted in this Issue’s introduction [6], this definition can and should accommodate at least two continua, whereby traditions become more *substantial* as they spread from a minimum of two individuals, across potentially large communities or populations, and more *enduring* as they last longer, potentially persisting across generations. Such variance is inherent in this first class of analyses. In the present paper, my emphasis is on traditions that have spread to become common in a community and are relatively enduring.

The second category in my taxonomy concerns the varied processes by which social learning can occur, such as imitation or teaching. The third class focuses on the content of cultural phenomena, such as action-types (e.g. ‘tool use’), ideas and beliefs.

If we imagine comparing the scope of culture in two or more species, we can appreciate that a high degree of independent variation in each of these three classes may, in principle, be found. Thus, the two species might exhibit similar patterns in the distribution of their traditions (for example, displaying minimal cultural overlap between communities), whatever the transmission mechanisms and particular cultural contents involved. Likewise, they might or might not

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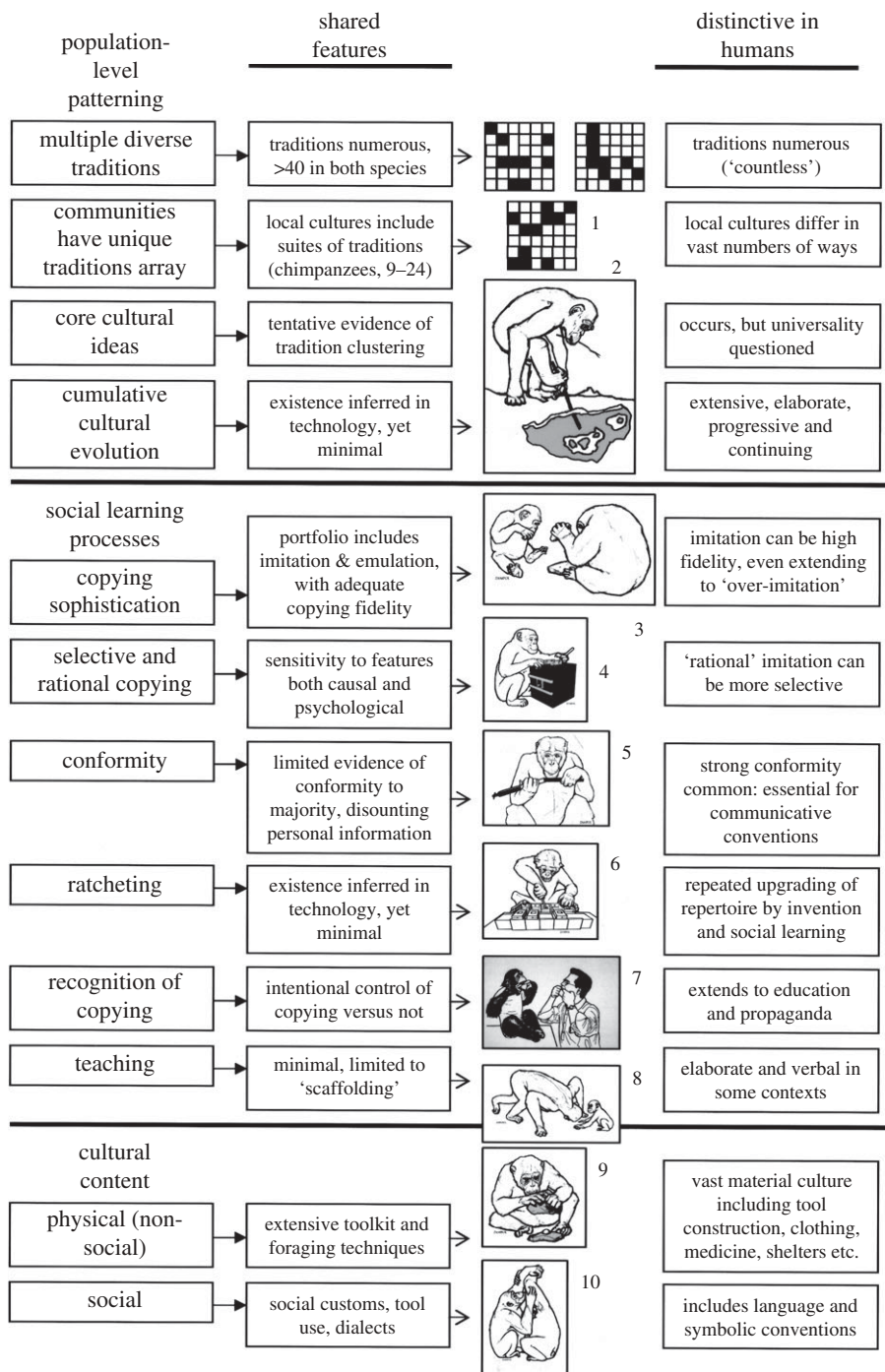


Figure 1. Features of culture shared by chimpanzees, humans and (by inference) their common ancestor, and features of culture distinctive in humans. Features (rows) are nested under three main headings (see text for extended discussion). Images represent examples discussed in the text: further explanation for each numbered image is given in the electronic supplementary material.

share certain processes like teaching, irrespective of the distribution of traditions and their content. Finally, specific cultural contents, such as tool use, might vary independently of the other two classes.

Although it would be relevant for more wide-ranging comparisons across the animal kingdom to assess evidence for the very existence of traditions in each taxon, for economy I here take the existence of tradition *per se* (and thence some kind of social learning) for the species of interest (i.e. humans and chimpanzees) as a well-established given [4,7]. This means that each subcomponent of the three major classes

dissected here (figure 1) is selected to address some way in which human culture clearly goes beyond the mere existence of a tradition, and about which recent empirical discoveries about similar cultural phenomena in chimpanzees and human children allow comparisons with real interest to be made. A central goal of doing this is to establish both the shared features parsimoniously attributed to our common ancestry, and those which differ, reflecting changes since the ancestral divergence about 6–7 Myr ago.

Note that in this procedure, it is not being assumed that the common ancestor was particularly chimpanzee-

like [8]; the crucial inferences about ancestry instead rely upon cultural features that are shared by the descendant taxa. Of course, species may share features because of convergent evolution rather than common descent, but when the features are shared by a closely related group of species, the parsimonious inference is that this is due to shared ancestry—the underlying logic of the comparative method in biology. Such inferences can be argued to be stronger the larger the related clade of taxa becomes; feathers and wings are confidently attributed to the common avian ancestor. From this perspective, inferences about the common ancestor of just two sister species (human and chimpanzee) must be viewed as more tentative. In some of what follows, it is possible to go beyond this to stronger inferences about the common cultural ancestry of the whole great ape clade (henceforth ‘apes’), but at present a greater range of data is available to explore human–chimpanzee commonalities specifically.

2. COMPARING CHIMPANZEE AND HUMAN CULTURES

In the following, I address the three major classes of cultural variation outlined above in turn, and within each, a series of nested subcomponents.

(a) *Variation among traditions in time and space*

Culture is by its very nature a community-level phenomenon, minimally defined above by traditions shared by at least two individuals, but typically many more. When we talk of different human cultures we refer to attributes of communities, typically contrasted either regionally (e.g. Scottish versus Chinese) or across historical time (e.g. Scottish culture in the twentieth century versus the tenth century). Within the first of these contrasts, note that different (sub)cultures may coexist within a larger local population [9]. Four aspects of variation in the patterning of traditions in time and space are distinguished.

(i) *Existence of multiple and diverse traditions*

Many of the published examples of traditions in fishes, birds and mammals concern only a single pattern of behaviour, such as birdsong dialect [10] or pine-cone stripping in black rats [11]. Human culture differs from this in encompassing countless variations, spanning a huge diversity of behaviour, technology, ideas and much else. No other species comes close to this. However, multiple traditions have been identified in some species, and chimpanzees have provided evidence for the greatest number, which also span a diversity of behavioural domains including foraging techniques, tool use, social behaviour and sexual courtship. Systematically identifying these by pooling data across field sites and excluding environmental and genetic explanations for the differences led to an initial count of 39 traditions [12], since significantly expanded by supplementary studies [3,7,13–15], although a formal synthesis of these accumulating cases remains in progress.

So far, it has not proved possible to contrive field experiments to test the social learning inferred to underlie these putative traditions. Indeed, only recently

was the first such field experiment achieved for any wild primate, with alternative techniques for opening ‘artificial fruits’ introduced into different vervet monkey groups. The subsequent spread of these techniques in their respective groups clearly implicated social learning [16]. However, it was with captive chimpanzees that an extensive battery of these primate ‘diffusion experiments’ was first developed [17–20]¹. These experiments confirmed that chimpanzees can sustain multiple traditions transmitted from group to group, each spreading across over 20 individuals ([20]; figure 2), a finding consistent with the inferences drawn about the cultural nature of wild chimpanzees.

The number and diversity of behavioural traditions described for chimpanzees are of course more than matched among humans. Among non-human species, it has only been significantly approached by another great ape, the orangutan, for whom over 30 different traditions have been described, again spanning behavioural diversity that ranges from tool use to social communication [21]. Among other species, it is other primates, notably capuchin monkeys [22], that have revealed multiple and diverse traditions, but enumeration of these suggests less-rich cultures than in orangutans and chimpanzees [23]. Accordingly, on the basis of the comparisons described above, the scope of culture in the chimpanzee–human common ancestor is inferred as incorporating numerous and diverse traditions.² The orangutan data additionally suggest the principal evolutionary step towards this complexity existed already in the common ancestor of all the great apes, approximately 14 Ma (equivalent studies for gorillas have yet to be published, and remain limited for bonobos [24]).

(ii) *Local cultures incorporating, and differentiated by, multiple traditions*

Not only do chimpanzees as a species evidence numerous traditions, but also each community displays its own unique cultural profile, defined by a subset of traditions. Accordingly, as for humans, if enough of a chimpanzee’s behaviour is observed, that individual can be assigned to its community on the basis of its cultural profile. Importantly, this has been replicated in the experimental studies noted above, where four different chimpanzee ‘cultures’ emerged, each defined by multiple, experimentally initiated traditions shown to spread by social learning (figure 2). Local cultures incorporating and differentiated by multiple traditions are thus also inferred in the chimpanzee–human common ancestor.

Although the adaptive significance of many such patterns in living chimpanzees remains to be formally established, the majority that involve food processing manifestly yield access to sources not otherwise available, in many cases through tool use. For some of the latter, there is evidence this carries the community through seasonal nutritional bottlenecks [25]. A potentially important implication of the cultural richness outlined above is thus that there should be a significant selection pressure on the underlying cultural abilities. These have clearly been massively selected for in the cultural learning capacities of our own species [26–29], but Whiten & van Schaik [23] suggested

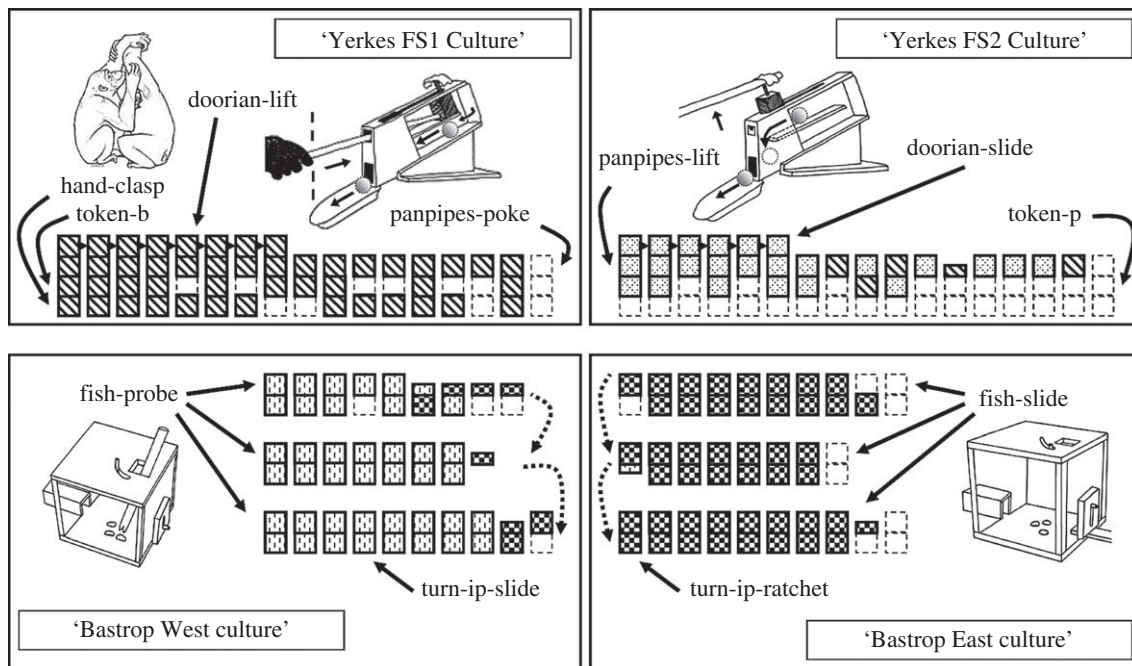


Figure 2. Spread of experimentally seeded, multiple traditions generating four chimpanzee ‘cultures’. At each pair of locations, alternative techniques were experimentally seeded in a single individual and spread locally. Each column represents a single chimpanzee, with hatching corresponding to the alternative techniques seeded in the leftmost individual in each case. At Yerkes, row 1 = *lift* versus *slide* methods to open door in ‘doorian fruit’, run as a diffusion chain [18]; row 2 = *poke* versus *lift* panpipes techniques spread in an open (unconstrained) diffusion [17]; row 3 = *bucket* versus *pipe* posting option for tokens in an open diffusion [19]; row 4 = hand-clasp grooming, which arose and spread spontaneously in only Yerkes FS1 community. At Bastrop, row 1 = *fish-probe* versus *fish-slide* techniques; row 2 = *turn-ip-slide* versus *turn-ip-ratchet* techniques, used to extract food from two different devices; each technique spread to a second group (middle) and then a third (bottom) [20].

that selection for cultural knowledge acquisition and storage may also help explain great apes’ distinctively high degree of encephalisation among primates (the ‘cultural intelligence’ hypothesis [23,30]).

A further implication of chimpanzees’ cultural niche is that more often than in other species, immigrating adolescents or adults (most typically females, in apes) from other communities may be the bearers of cultural variants not yet known locally, from which residents may learn. Conversely, immigrants may observe cultural variants new to them, and learn them. For example, when T. Matsuzawa and co-workers introduced novel nuts into a community in West Africa that uses hammer stones and anvils to crack nuts, just one female was quick to crack these new nuts, inferred to be a known habit in the community from which she had emigrated. Over several years, the new nuts came to be routinely cracked by most of the population [31]. Studies of subtly different grooming techniques in adjacent communities have also shown immigrant females adopting the local approach of their new community, with one female adapting her existing technique and in turn eliciting some corresponding adaptation in the residents who groomed with her [32].

(iii) *Linkage of traditions through core cultural ideas*

The above analyses view cultures in terms of multiple independent traditions that can be enumerated to facilitate species comparisons. Although this basic approach was also used in the earliest twentieth-century analyses of human cultures by anthropologists,

this was later challenged by the view that a set of core ideas links together suites of local cultural phenomena, such that a culture is ‘an organization of ideas rather than aggregate of independent traits’ [33]. Examples include an individualistic and analytic world view in the west, contrasted with more holistic and collective orientations in eastern cultures that pervade many different aspects of cognition and behaviour [34]. This view, although challenged by others in turn [35], is sufficiently central to many cultural anthropologists’ conception of culture (see ‘core principles’ in [36]) that it begs to be addressed from the comparative perspective.

Doing so is clearly a challenge, since much of the evidence for ‘cultural cores’ in the human case appears fundamentally verbal, even if sometimes constrained by sanctions that can include non-verbal actions [36]. Whiten *et al.* [2] suggested that the central hypothesis can perhaps be best addressed for non-verbal animals like chimpanzees by testing whether particular local communities have underlying cognitive representations that steer them towards particular cultural options. It was suggested that differences between some West African chimpanzee communities that display extensive and varied tool use, and others in East Africa that display a poverty of tool use, might reflect an underlying cognitive orientation in the former to see new problems as calling for a variant on their tool repertoire. The alternative that the East/West difference is primarily genetic [37] is countered by a recent experiment showing that East African, non-nutcracking chimpanzees can become proficient

in cracking nuts by observing existing experts [38]. Lycett *et al.* [39] have also completed a series of numerical phylogenetic analyses of the distribution of behavioural variation among chimpanzee communities that they conclude is incompatible with genetic explanations.

A recent experiment that may address the hypothesis of cultural ‘cores’ more directly presented a novel experimental situation—honey in a vertically drilled hole in a fallen log—to two different chimpanzee communities in Uganda [40]. One community habitually uses sticks and stems for gaining water from tree holes, and they applied a similar technique to the new honey source. A second community that does not use sticks as tools, but does make masticated leaf-sponges to gain water from tree-holes, instead applied this method (with less success) to the new problem. The interpretation of Gruber *et al.* [40], summarized in their title, is that ‘Wild chimpanzees rely on [their] cultural knowledge to solve an experimental honey acquisition task’. More evidence is required to test this interpretation, but it is consistent with the essence of the ‘core cultural ideas’ principle, in which certain behavioural variants are proposed to be cognitively linked, rather than mere cultural ‘beans in a bag’.

(iv) *Cumulative cultural evolution*

Human cultural achievements have progressively and repeatedly built upon earlier ones to create the vast complexity and variety in our cultures of today, including technologies, languages and social institutions [41,42]. In the view of some, such cumulative cultural evolution is essentially absent in other species [43]. Others argue for the existence of cumulative culture in animals [7], but the cases discussed appear rudimentary compared with the achievements of humans [41,42,44].

A good example that implies accumulation but at the same time illustrates the ‘rudimentary’ epithet comes from recent studies of tool use by chimpanzees in the Goualougo locality of central Africa. Sanz *et al.* [45] described how these chimpanzees first drive a stout stick deep into the earth (often aided by combined foot and hand pressure), puncturing a channel into a subterranean termite nest. They then modify one of several stems they have brought to the site, fraying the end by drawing it through their teeth to create a brush tip, then carefully inserting this down the channel to fish for termites. The brush tip makes fishing more efficient. This multi-stage procedure is unknown in other communities, where termite-fishing chimpanzees often bite off the ends of used probes, rather than fraying them. Sanz *et al.* therefore conclude that the Goualougo technique must have been elaborated by cumulative modification of the more basic technique observed elsewhere. This conclusion seems compelling. Indeed, the first evidence of hominins exceeding such cumulative achievements did not become apparent until the manufacture of bifaced Acheulian stone tools around 1.6 Ma [46].

Why cumulative culture is so minimal in non-human species remains poorly understood. It is possible that no

particular kinds of accumulation could significantly enhance their technologies and their reproductive success in the ecological niches they successfully exploit. Recent experimental work that focuses instead on the possible role of biases in social learning of chimpanzees versus humans is discussed in §2b(iv), below.

(b) *Social learning processes*

Galef [47] urged that unless processes as sophisticated as those assumed to transmit human culture (notably imitation and teaching) could be shown to underlie a species’ traditions, the term ‘culture’ should be eschewed in favour of talk of ‘traditions’ only. Over the last century, a considerable range of social learning processes has been identified and those available to any one species are likely to shape the scope of culture in that species. For example, if a species is limited only to stimulus enhancement, where an observer simply has its attention drawn to certain objects or locations by another, it may be able to sustain traditions favouring such foci, but it will not be able to acquire novel behavioural techniques that require imitative copying. In the following, I compare chimpanzee social learning to some of the more sophisticated forms such learning can take in the human case.

(i) *Copying sophistication and fidelity*

Over the last two decades a debate has unfolded, fuelled by numerous ingenious and revealing studies, about whether social learning in chimpanzees can accurately be described as imitation or emulation, and how this may constrain their cultures. Imitation and emulation have been defined, respectively, as the copying of others’ actions, versus copying of only the results of those actions, with chimpanzees characterized as dependent on emulation, in contrast with the high imitative competence of children [44,48]. Such a difference could have important implications for the nature of culture in the two species. If chimpanzees rely only on emulation, there should be little scope for the transmission of behavioural techniques or gestural communication. Indeed, the fidelity of copying that distinguishes imitation has been argued to be crucial to facilitate cumulative cultural evolution, which first requires accurate copying across generations, on which progressive elaborations can be built. Accordingly, humanity’s unique capacity for cumulative culture has been linked to imitative prowess, suggested to be lacking in chimpanzees [25].

Accumulating studies have converged towards a consensus across research groups that the imitative ability and motivation of children are indeed typically superior to that of chimpanzees [43,49]. However, several lines of evidence have led our research group to question whether this represents the stark species dichotomy outlined above. First, the chimpanzee diffusion experiments (figure 2) have demonstrated a capacity to sustain different traditional techniques applied to the same foraging task, in different groups. For example, Whiten *et al.* [20] found that for each of two different tasks, one dependent on tool use, the other on a sequence of two separate sets of manipulations, alternative techniques seeded in different groups were

maintained not only in the original groups but also were transmitted by observational learning across two further groups. To be sure, the copying fidelity involved (figure 2) does not match the perfect transmission of ‘panpipes’ techniques along a chain of 20 individuals that we recorded in children [50]. Nevertheless, the differential spread of techniques across two sets of three groups [20] shows that chimpanzees have sufficient copying fidelity for the inter-community spread of complex behavioural techniques, consistent with the picture for African chimpanzees inferred from field observations. Moreover, our first replications of ‘open’ diffusion experiments with groups of young children revealed patterns more similar to those seen in chimpanzees: initial differentiation of traditional techniques was followed by a degree of corruption as some children discovered the technique seeded in the other group [51].

These experimental results for chimpanzees can aptly be described in terms of ‘copying’, because quite elaborate techniques are being replicated as they spread across communities. However, that might still rely on high-fidelity *emulation*, with learning focusing on the way the foraging devices operate to deliver food rewards. One approach to testing this hypothesis has been through ‘ghost’ experiments, which remove the model from the scene and display only the object movements the model would normally cause, which is what an emulation hypothesis suggests the apes are actually learning from. When this was done with the panpipes (figure 2), using fishing line to create the normal effects of tool use in delivering food rewards, chimpanzees showed a stark absence of learning [52]. This contrasts markedly with the learning evidenced in the earlier open diffusion study, where chimpanzees could observe existing tool users in action [17]. This implies copying actions is important. With a much simpler task that involved only a small door being slid to one side or the other to reveal a food reward, Hopper *et al.* [53] elicited the first evidence for emulation in such a ghost experiment with primates, but the effect was fleeting (trial-1 only) and subjects then explored either way to slide the door. This contrasted strikingly with a condition in which a chimpanzee acted as the model, when the direction in which the model slid the door was copied in 99 per cent of trials. Hopper *et al.* [53] concluded that emulation evidenced in this ghost context may operate with respect to the simpler tasks, but for those more challenging to chimpanzee intelligence, observing individuals need to gain information on how another individual actually performs the crucial actions, together with its desirable outcome.

(ii) *Selective and ‘rational’ copying*

One way in which human imitation evidences sophistication is in selectivity, which has been identified in a number of different guises. These include what has been called ‘rational imitation’. In one example, even infants tended to copy a model’s novel and bizarre action of using their head to butt a noise-making device so long as the model’s hands were free, but not if the hands were occupied, such as in holding a blanket round one’s shoulders [54]. Buttelmann *et al.* [55] have subsequently demonstrated a similar phenomenon

in what they call ‘enculturated’ chimpanzees (having extensive interaction with human caretakers), although the effect was weaker than in child studies, consistent with child/chimpanzee contrasts in social learning outlined above. The same authors failed to find such selective copying in non-enculturated (mother-reared) chimpanzees, although they did record it in non-enculturated orangutans [56].

Selectivity has also been identified in relation to evidence for physical causality in what children witness. For example, Lyons *et al.* [28] have shown that children would not copy an adult’s actions on an object physically separate from another where the adult then achieved a desirable goal. Similarly, Horner & Whiten [57] showed that young chimpanzees were significantly less likely to copy aspects of tool use that could be seen to be physically separate from desirable outcomes compared with those displaying contact with such outcomes (gaining food). When an apparatus was used that was identical except that it was opaque, masking the lack of physical connection between tool and outcome, chimpanzees instead tended to incorporate such actions into a more complete imitation of the elaborate sequence they witnessed. This demonstrated a flexible capacity to switch between imitative and emulative modes of social learning, according to context.

Laland [58] has described selective social learning in terms of different learning ‘strategies’ concerning when and from whom to learn. Such flexibility appears increasingly to be widespread in the animal kingdom [59]. The child and chimpanzee studies described above illustrate selectivity resting on relatively complex cognitive distinctions in relation to rationality of actions in others, and plausibility of physical causation. These illustrate selectivity in what Laland distinguishes as ‘when’ to copy, in relation to structural aspects of what the observer witnesses. We have recently completed an experiment ([60], see also [29,61] that focuses instead on ‘whom’ to copy [58]). In an earlier diffusion experiment we noted that one low-ranking individual generated an action different from the rest of her group—yet she was not copied by others [19]. To further explore this apparent selectivity in copying, we tested the preference of chimpanzees to copy the behaviour of a model that was either high ranking, with a strong track record of being a useful model to copy, or low ranking with no such record [60]. In each of two groups, chimpanzees showed a significant preference to copy the first of these two options. In humans, similar effects are described as a bias to copy individuals with high prestige [62]. The preference displayed by the chimpanzees does not imply that exactly the same cognitive processes are involved,³ but it does demonstrate a basic bias shared between the two species. Its function in chimpanzees is not known, but Horner *et al.* [60] note that the preference demonstrated is likely to involve learning from a model who often achieves particularly beneficial outcomes.

(iii) *Conformity*

In humans, the motivation to be like others can lead to extreme degrees of conformity, long studied by social

psychologists [63]. Such conformity can take various forms, such as following the majority, or copying others despite personal experience favouring an alternative course of action.

Whiten *et al.* [17] first attached the term ‘conformity’ to chimpanzee social learning on finding that, after some individuals discovered the non-seeded behavioural option in a diffusion experiment, they showed a significant tendency to ‘return to the fold’ and match the behaviour of the majority of their group (the experimentally seeded technique) at a later time. An allied effect was obtained in a recent study in which we tested chimpanzees’ ability to learn from conspecific models how to combine two sticks into a long tool that could be used to rake in distant food [64]. Most subjects could learn this only from others, but a few achieved the combination by their own individual efforts. The surprising later finding was that when flexibility of action was tested by arranging problems in which the tool was not needed (target within manual reach), chimpanzees who had learned individually did not make a long tool, whereas those who had learned socially tended to persist in making and using the now-redundant long tool. Price *et al.* [64] described this as a particularly ‘potent’ effect of social learning.

Whether such potency, as suggested by these studies, is special among chimpanzees, as well as humans, remains to be established. Galef & Whiskin [65], responding to the chimpanzee conformity study [17], showed that in rats, such potency appears sufficiently strong that individual experience, even the consequences of eating highly noxious foods, will be rejected in favour of others’ observed preferences for the food. What we are seeing in the above chimpanzee and human results may not be a special potency of social learning *per se* (perhaps widespread among animals in certain ecological conditions), but rather its interaction with the more elaborate forms of social learning, notably copying complex forms of action such as tool use.

(iv) Ratcheting versus conservatism

In §2a, it was noted that a major contrast between human and non-human cultures lies in the inflated role of progressive accumulation in humans. Tomasello *et al.* [48] suggested that the contrast is explained by chimpanzees’ tendency to emulate rather than imitate.

However, the diffusion experiments outlined above cast doubt on whether copying fidelity constrains cumulative culture in chimpanzees. A recent experiment [66] accordingly attempted to directly test chimpanzees’ capacity for cumulative social learning. Young chimpanzees first learned, by observation, to open a cover in a honey dispenser and extract honey using a probe. They then observed a more complex approach in which the probe was first used to free a lid, so the probe could be inserted into the usual hole to lever open the lid and gain access to both nuts and honey. Despite this greater payoff, the second, cumulative step was not learned, although control conditions showed it was within chimpanzees’ capability. Young children, by contrast, were later shown to acquire the

second step [49]. It may be, then, that a cognitive capacity for progressive social learning of the kind needed in this study arose only much later in the hominin line, and was limited in our common ancestors. Other experimental studies have identified a similar conservatism in chimpanzee social learning, convergent with that described above [67].

(v) Recognition of copying

Older children become increasingly able to play copying games (‘Simon says’) that rely on knowing what imitation is. Evidence that chimpanzees have an appreciation of the same kind comes from their ability to learn, and be tested in a ‘Do-as-I-do’ paradigm in which having grasped the rule to copy on a command like ‘Do this!’, they evidence copying of novel actions. Apes (both chimpanzees and orangutans) have shown a proficiency in mastering this, where extensive parallel efforts with monkeys failed [2,68]. This apparently meta-cognitive grasp of the nature of copying may accordingly represent a significant achievement that appeared only in the common ancestor of the great ape clade.

(vi) Teaching

Galef [48] expressed a common view that teaching may be a distinctive characteristic of social learning in humans. To the extent that much human teaching is verbal, that is probably correct, although it has been suggested that a lack of teaching in hunter–gatherer societies may mean that teaching has not figured as much in the evolution of human cultures as those of us living in societies with formal schooling might assume ([2], but see [27,69]).

We tend to think of teaching in humans in intentional terms—as based upon an intent to inform or educate a person in the role of pupil. However, if this intentional element is replaced as a criterion by its functional equivalent—actions that serve to support the development of competencies in a pupil, at some cost to the teacher—then we find that recent studies offer evidence of teaching in a wide variety of species [9,70]. Such behaviour is little in evidence in chimpanzees and other apes. At most it seems to extend to tolerant support of difficult skills like nutcracking, where mothers donate tools and nuts to their offspring [71]. Arguably better evidence for such functional teaching in primates comes from callitrichid monkeys, which like meerkats [9] may draw the attention of youngsters to prey and make it available to them [72]. The contrast may appear strange from the socio-cognitive perspective, since recent evidence suggests chimpanzees have a sufficiently sophisticated ‘theory of mind’ to recognize ignorance in others [73], supporting intentional teaching. However, from a functional and ecological perspective the contrast may make more sense. Functional-level teaching appears often to be found in species for whom such challenges as hunting live prey is obligatory, and may help young make the leap from incompetence to the highly skilled abilities required for success. By contrast, a more gradual transition to adult competence is feasible for an animal with the dietary profile of a

chimpanzee, including all the forms of tool use employed in this quest. Hoppitt *et al.* [70] suggest that particularly well-developed observational learning capacities in chimpanzees may counter pressures for teaching that are more significant in some other taxa.

(c) *Cultural content*

From the perspective of biocultural anthropology, Hill [44] suggests two major differences between human culture and its closest matches in non-humans. The first is cumulative culture, discussed in §2a(iv) above. The second concerns what I shall refer to as the specific *contents* of culture, where Hill picks out human ‘symbolic reinforcement of particular systems of rules and institutions that regulate behaviour’ (p. 285) as distinctive. But one can list a considerable range of other cultural contents that are special even to those human cultures in which the total material contents can be carried on nomadic hunter–gatherers’ backs. These include such aspects of material culture as hafted and other, multi-component weapons and other tools, clothing, fire and medicines; and social components ranging from language itself to ceremonial behaviour, dance, music and religion. Murdock *et al.* [74] distinguished 569 subcategories of cultural contents used to compile the data of the human relations area files (HRAFs), including such examples (under a heading ‘leather, textiles and fabrics’) as work in skins, knots and lashings, mats and basketry and woven fabrics. Most of these 569 will not apply to chimpanzees, a measure of the species-gulf in cultural content. However, some chimpanzee cultural content may be absent in humans, such as certain grooming customs and forms of sexual courtship-like oral ‘leaf-clipping’ and other kinds of noisy vegetation-manipulation used to attract a potential partner’s attention.⁴

Nevertheless, it is possible to start to identify features of cultural content that chimpanzees and humans share. These are probably most aptly described at some intermediate level of abstraction. For example, we shall not expect to see an act as specific as chimpanzee ‘pestle pounding’ of the growing points of palm trees in humans; what is shared is rather a tool culture that includes a range of such pounding tools as well as puncturing, probing and wiping tools, used for a diversity of functions that include aiding foraging (e.g. nut-cracking), comfort (e.g. leaf seats on wet ground) and hygiene (e.g. leaf wipes for blood, faeces or semen on the body). Shared contents of social behaviour appear less easy to identify, but include vocal differences between communities [75].

However, one might question whether such questions about content really address the core of cultural phenomena. Content differences in culture appear rather more to do with the range of behaviours that humans and chimpanzees, respectively (the first with brains three times larger than the latter’s) can generate, and which are assimilated into those category (a) and (b) type cultural phenomena analysed earlier. Nevertheless, such content differences suggest some of the most striking differences when we compare the scope of cultures in the two species. They merit more systematic studies and comparisons in future.

3. DISCUSSION

This paper began by noting how little we knew of our closest relatives just a half century ago. Now we know so much that the scope of the three categories of findings summarized in figure 1 is extensive indeed and based upon many scores of publications. I have aimed to illustrate some of the most significant of these discoveries, but it is important to stress that the depth and detail of our knowledge goes far beyond what can be summarized here, as perusal of the more extensive literature reviewed in the publications cited will demonstrate.

A central objective of this paper is to identify significant similarities and differences between chimpanzee and human cultures in the categories indicated, using the similarities to make inferences about our common ancestor, and the differences to identify what has evolved after the split occurred. From this perspective we can distinguish two levels at which to assess the scientific robustness of the conclusions drawn. The first level concerns the facts of the matter in respect of present day humans, chimpanzees and the other reference species compared with them. The next level concerns second-order inferences to ancestral states, and these inferences must logically be viewed as inherently more tentative than the first-order ones upon which they are based. This makes it important to recognize that, although we now possess a vast archive of relevant chimpanzee (and human) observation and experiments, the conclusions about cultural ancestry that should properly be drawn from these remain contentious [76].

Acknowledging this, figure 1 offers a summary of the conclusions I currently draw. At the level of population-level patterning, the shared features are principally the first two of the four listed, which reflect two aspects of cultural richness in terms of multiplicity of traditions. Insofar as this state of affairs is shared with orangutans but not, according to present data, so much with old world monkeys, inferences about its occurrence in our ancestry appears to be most probably attributable to the common ancestor of the great ape clade of about 14 Ma, rather than the earlier ancestor of these old world primates. Evidence for the second two features is minimal, but not non-existent, which suggests corresponding foundations on which later evolving cumulative culture and cognitive inter-linking could have built.

Two potential anomalies in this picture should be noted, however. One is that evidence to date has outlined only a much smaller set of multiple-tradition cultures in chimpanzees’ sister species, the bonobo, especially concerning tool use [24]. Similarly there remains a dearth of information about potential gorilla culture. Both cases may, however, reflect relatively limited field studies, and/or lack of focused attention to the topic by the field workers concerned.

Turning to social learning processes, most of the features listed in figure 1 necessarily remain focused upon human characteristics shared with chimpanzees, rather than apes as a group, because so many more studies have focused upon chimpanzees [68]. One apparently qualitatively distinct feature that has been documented in children, chimpanzees and orangutans

but not in monkeys is the recognition of copying (§2*b*(iv)). Perhaps, the more quantitatively distinct features, notably sophistication in copying, may be related to this. In such copying, it is not so much bodily imitation that is distinctive—that has been shown in birds [77]—but rather the complexity of manipulative techniques, both in the wild and that have been shown to be transmissible in the diffusion experiments summarized above. Indeed, the tool use copying shown in these has not been found in experiments with other taxa, including capuchin monkeys, despite the tool use this genus shows in the wild [72].

This may be of particular significance in relation to the cultural innovations documented in the papers that follow this one, concerning early hominin stone tool making. Although the present paper was at pains to distinguish several quasi-independent aspects of culture (figure 1), their significance for our own cultural ancestry may have lain in specific links between them. In particular, we may infer a shared ancestor that used varied forms of ‘power’ tool (e.g. clubbing and pounding [78]), possibly extending to the unique style of percussive nut-cracking we still see socially learned in local chimpanzee cultures, or at least a special propensity to develop such a culture that evolving hominins took to such world-changing heights [41,42,46].

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ENDNOTES

¹Later field experiments of this kind with other mammals are described in Thornton & Clutton-Brock [9].

²Langergraber *et al.* [37] have shown a correlation between variation in chimpanzees’ behaviour patterns across Africa, and genetic variation, that they suggest weakens the inference that the variations are traditions. However, such a correlation would be expected for even as cultural a species as humans, at least before recent levels of migration and mixing (e.g. before 100 Ka) A fuller analysis of Langergraber *et al.* [37] is in the electronic supplementary material.

³Henrich & Gil-White [62] note that prestige in humans is not to be simply equated with dominance rank. Consistent with this, the demonstration that chimpanzees preferentially copied higher-ranked, experienced models [62], as well as treating these individuals with the respect in agonistic conflicts that defines high rank, suggests the kind of convergence in deference across contexts that signify prestige. Of course, this does not imply identical underlying cognitive mechanisms.

⁴An anthropologist reader of this paper noted that the hunter–gatherer peoples he works with also ‘sit in rows and groom each other and use vegetation noises to attract a potential partner’. Much remains to be systematically compared between the species, concerning the behavioural contents of cultures.

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