PROGRESS

The second inheritance system of chimpanzees and humans

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Half a century of dedicated field research has brought us from ignorance of our closest relatives to the discovery that chimpanzee communities resemble human cultures in possessing suites of local traditions that uniquely identify them. The collaborative effort required to establish this picture parallels the one set up to sequence the chimpanzee genome, and has revealed a complex social inheritance system that complements the genetic picture we are now developing.

In the first decade of the twenty-first century, we find ourselves at a point that future generations will probably reflect on as unique in the scientific relationship between humans and chimpanzees. In historical—let alone evolutionary—time frames, this window has only just opened. We have progressed from a position of almost complete ignorance about wild chimpanzees just decades ago[1], to having gathered very detailed knowledge through hundreds of field and laboratory studies[2–9]. Tragically, however, just as new levels of integrative analysis appear on the horizon, including comparative genomics[10] and the parallel analysis of culture outlined below, the scientific window so recently opened has already started to close as the human species inexorably exterminates its closest relatives. The very material of interest—genetic and cultural diversity—is melting away[11]. This state of affairs adds urgency to our attempts to grasp the big picture of what it means to be a chimpanzee, and thus, by comparison, what it means to be the human ape.

When we focus our comparative lens on culture, the evidence is all around us that a gulf separates humans from all other animals. Nevertheless, recent studies of great apes suggest that they resemble us culturally to an extent unmatched by other species[8,12–17]. Many species of fish, birds and mammals have been shown to have 'traditions', but if we follow those authors who reserve the term 'culture' for the more particular manifestations of tradition that characterize our own species (Box 1), we are increasingly finding marked cultural similarities between ourselves and other apes.

The following sections will examine three aspects of culture that go beyond the existence of tradition *per se*. These are (1) the population-level patterning of traditions, (2) the mechanisms facilitating transmission of traditions, and (3) the specific behavioural content of traditions. Comparison among chimpanzees, humans and other species in each of these dimensions helps to delineate what chimpanzees share with humans and just where the differences begin.

Population-level cultural complexity

As observations accumulated in the 1980s and 1990s, researchers began to compile a growing list of putative traditional variations among wild chimpanzees[2,18]. More recently, research directors of the longest-running chimpanzee study sites have pooled their hard-earned data to create the first systematic overview of behavioural variation. Identifying no fewer than 39 different traditions[12,13] (Fig. 1), the collaborative effort of this international project parallels that which made possible the chimpanzee genome project.

A collaborative exercise applying precisely the same systematic method to orangutans subsequently identified 19 clearly defined traditions, with an additional five more tentatively classified[14]. In contrast, studies of traditions in other primates, other mammals,

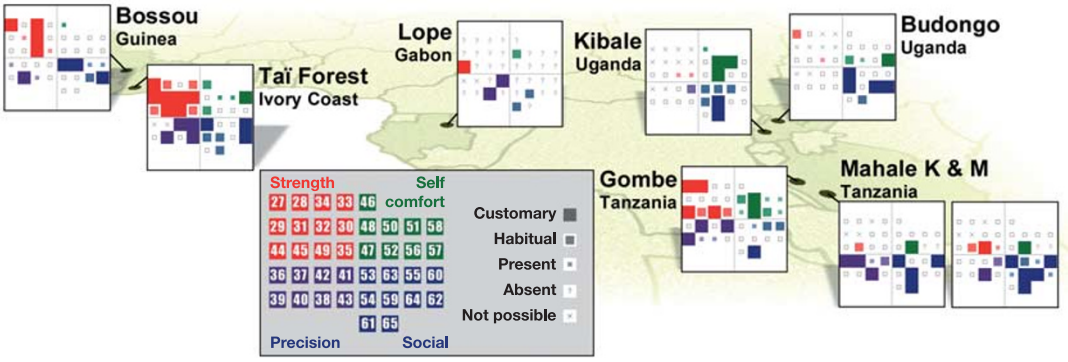

Figure 1 | The cultures of wild chimpanzees. Each chimpanzee community has its own unique array of traditions that together constitute the local 'culture'. 'Customary' acts are those typical in the community, 'habitual' ones are less common but consistent with social transmission, and 'absent' acts are those missing with no apparent straightforward environmental explanation. Traditions are defined as behaviour patterns that are customary or habitual in at least one site but absent elsewhere. Transmission is attributed to social learning on the basis of a complex of circumstantial evidence, ranging from intense observation by juveniles to distributions inconsistent with alternative explanations[12,13,15]. The numbers in cells refer to behaviour patterns in the catalogue of ref. 13, illustrated at http://culture.st-and.ac.uk/chimp.

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birds and fish have most commonly identified no more than a single tradition, and in no such species has the number of behavioural variants reached double figures[16,17,19,20]. A working hypothesis is thus that in the ancestors of the great ape clade, there occurred a distinctive step towards reliance on a relatively rich cultural repertoire that incorporates both technological and social elements[14].

Figure 1 suggests an additional way in which a distinction between tradition and culture can be made. Each local chimpanzee community has a unique array of specific traditions, representing a 'package' that can be described as its local culture, in the same way that we might distinguish between Scottish and English culture, which are defined by distinctive arrays of traditions. In contrast, studies have yet to identify cultures defined by multiple traditions in species other than primates and cetaceans.

Every year now sees new putative traditions added to the chimpanzee catalogue, and a research consortium, recently formalized as the Collaborative Chimpanzee Cultures Project, Round 2 (CCCP-2), has embarked on a new collation of the accumulated records. Recent investigations address more fine-grained phenomena, such as subtle contrasts in social conventions between neighbouring communities[21]. This is nicely illustrated by recent work on the 'grooming hand-clasp' (Box 2). Data from new study sites have identified additional behavioural variants, such as the recently described 'social scratch': for example, chimpanzees at Ngogo in Uganda will scratch each other's backs using a short jabbing technique, in contrast with the long, raking style observed at Mahale[22]. Perhaps the most remarkable recent discovery comes from the young study site at Goualougo, where chimpanzees prepare a two-part tool set for termite fishing[23], unlike the simpler technologies well known at other sites[12,13] (Box 3).

Ape culture may be particularly complex among non-human animals, yet it clearly falls far short of human culture. An influential contemporary view is that the key difference lies in the human capacity for cumulative culture[24,25], whereby the achievements of successive generations have built on previous developments to create complex structures such as languages and technologies. Chimpanzees have accumulated many traditions, but each remains sufficiently simple that there is little scope for it to have developed significant complexity compared to its original form. Hints of cumulation exist[15], such as the refinement of using prop stones to stabilize stone anvils during nut-cracking[7], but these remain primitive and fleeting by human standards. One possible explanation that has been offered for this human–chimpanzee difference lies in the social learning mechanisms available to each species[25], an issue that new genetic approaches based on the complete chimpanzee genome sequence may help to unravel.

The psychological bases of cultural transmission

The circumstantial evidence for traditions among wild chimpanzees is strong, but experiments are required to identify the different social and non-social learning processes involved. Field researchers have been understandably resistant to experimental interventions that might seriously perturb the naturalness of the behavioural ecology they study. Matsuzawa and his colleagues have pioneered subtle field experiments, for example introducing to a community of nut-cracking chimpanzees at Bossou various new nuts that are cracked by chimpanzees at more distant locations[26,27]. When this introduction coincided with the immigration of a female already expert in dealing with the new (*Coula*) nuts, close observation of this female by other chimpanzees was followed by the gradual spread of *Coula*-cracking to a majority of the community.

Box 1 | Animal traditions, human cultures?

Some authors, particularly in the biological sciences, draw no distinction between the terms 'tradition' and 'culture'[16]. Others discriminate between the two in a variety of ways, typically driven by a perceived need to recognize that there is more to culture (human culture in particular) than the existence of tradition alone[24,25,37]. These terminological differences must be recognized before any sensible comparative analysis can be made of the diverse claims to have identified 'cultural' phenomena across the animal kingdom. Of the two terms, 'tradition' is used with the greatest consistency. Most would probably be content with the definition in a recent survey of the biology of traditions: "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"[17]. Accordingly, for those happy to treat culture as a synonym for tradition, a phrase such as 'cultural evolution in chaffinch song' will sit unproblematically alongside hundreds of others identifying behavioural traditions in a variety of vertebrate (and perhaps invertebrate) species. For others, human culture involves so much that cannot be reduced to the existence of a tradition that they prefer to define culture more restrictively, at one extreme applying criteria such as language and symbolism, which limit culture to humans alone: animals have traditions—humans have culture.

Of more interest from an evolutionary perspective is a focus on characteristics that are shared to a greater or lesser extent with other species, including particular transmission mechanisms such as imitation or teaching, which apply to a smaller set of species than those shown to display traditions[24,25,37]. When tradition and culture are distinguished in this way, it is common to regard tradition as the more basic and widespread phenomenon that, in certain restricted contexts, has evolved into more refined forms worth distinguishing as culture. This offers more scope for comparative analysis than simply equating tradition and culture, but can leave us with a simplistic debate over which species do or do not have culture. As the available data become richer, a more productive approach might be to dissect culture into multiple elements for comparative analysis[15,38], accepting that the resulting picture might indicate mosaic-like evolutionary patterns rather than a unitary pathway of cultural elaboration. This review outlines a compressed analysis of this kind, focusing on three aspects of cultural complexity.

Box 2 | The different social conventions of neighbours

The 'grooming hand-clasp' was the first social custom to be identified in chimpanzees, routine at Mahale but absent at Gombe, just 100 km away. Recently, it was discovered that although the Mahale K community (photographed, but now extinct) used the originally described palm-to-palm convention (left), members of the neighbouring M community typically show a different, wrist-to-wrist hand-clasp (right)[39]. Moreover, the relative status of the groomers is apparent in the placement of the hands. Gwekulo, an adult female that transferred from the K to the M community, was observed to adopt the preferred wrist-to-wrist pattern of her new partners some of the time, but also to influence them to occasionally make palm-to-palm contact; however, she made delicate adjustments to do so, flexing her elbow in the local customary way, rather than keeping it straight, which was the norm in K community[40].

Box 2 Figure | Hand-clasp styles. Left, palm-to-palm (drawing by D. Bygott). Right, wrist-to-wrist (courtesy of M. Nakamura).

Constraints on such experimentation in the wild, such as the addition of conditions to control for individual learning in cases like the spread of *Coula*-cracking, has meant that social learning has been studied more extensively in captivity. However, the first such experiment seeding an expert tool-user into a naive community found surprisingly little evidence of imitation[28]. After a flurry of similar findings, doubters soon began to ask: "Do apes ape?"[29] after all. A raft of more focused experiments ensued, and a recent review of ape studies over the past 15 years (ref. 30) concluded that, perhaps as a consequence of greater diversity in methodological approaches, the pendulum has swung back: out of 31 experiments, 22 involved chimpanzees and of these, 10 reported imitative behaviour and another 5 reported 'emulation', in which learning is focused on the outcomes of what the model achieved rather than precisely how it was done. The emerging picture is that apes do ape, but that imitation is just one of a 'portfolio' of varied social learning processes[31], and perhaps most interestingly of all, it is applied selectively (Box 4).

This selectivity is one probable explanation for the curious mixture of both impressive and negative findings that now co-exist in the burgeoning literature on social learning in apes[31]. Among the impressive qualities are the ability to recognize what it means to be asked to imitate a new action and to do so with significant success ('do-as-I-do'), and to recognize and test that one's own actions are being imitated by others[30]—abilities that primates other than apes have failed to demonstrate. This echoes a similar and well-established difference between primates in the ability to use one's image in a mirror[5]. This correlation may reflect a fundamental aspect of ape cognition that underlies the translation of perceived actions into one's own actions[31]. Turning to the imitation of functional actions such as foraging techniques, experiments have demonstrated the copying of alternative sequential organizations applied to a series of actions used to open up complex 'artificial fruits'[31].

Nevertheless, when chimpanzees and children are compared on similar versions of the same task, children typically show higher copying fidelity. The findings summarized in Box 4 illustrate a common difference found in such studies. The observational learning of chimpanzees is highly pragmatic, subjugated to individual efforts wherever this gets results. In contrast, children are more prone to copy the actions of others just because others are doing them, betraying an extreme form of reliance on cultural convention. This difference was highlighted in a recent study in which chimpanzees and children observed conspecific models struggling to open two parts of an artificial food item: the children later targeted the part struggled with, perhaps seeing this as the one the model aimed to open, whereas chimpanzees tended to choose the other part, pragmatically avoiding the one already shown to be problematic[32].

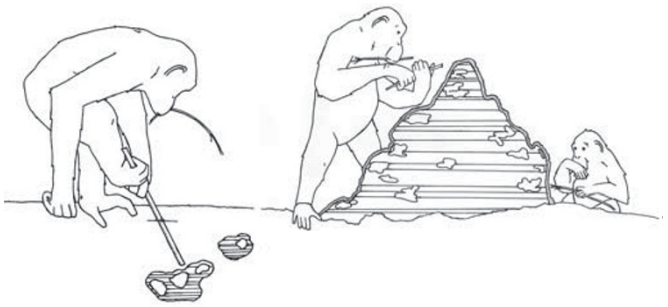
The contents of culture

Whatever the similarities and differences between chimpanzees, humans and other taxa in terms of the population-level patterning of traditions and underlying transmission mechanisms, a further set of comparative questions exists concerning the contents of those traditions. Again, there are significant overlaps as well as profound differences between human and chimpanzee behaviour. An example of overlap is the use of a wide range of types of tools; for example, chimpanzees use natural hammers, anvils, probes, sponges, clubs and seats. Key differences between the species in this domain include the construction of tools from complementary parts (as when hunter–gatherers construct even the simplest animal traps) and the use of weapons for hunting, both of which are found in humans but not chimpanzees. Chimpanzees fashion tools, but only by removing and modifying subcomponents[15] (see Box 3).

Other overlaps and differences beyond the scope of this piece can be dissected into such domains as foraging, grooming, courtship and social behaviour[15]. An interesting example that has now been

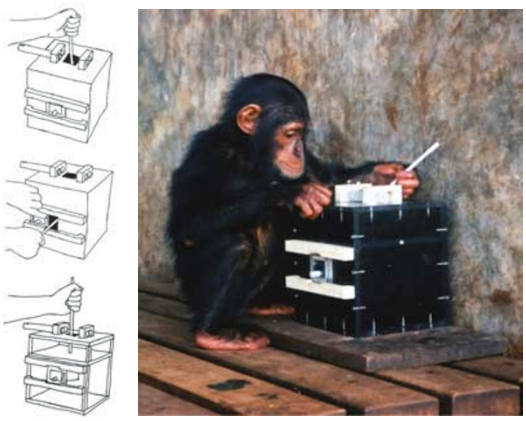
Box 3 | A tool-set for harvesting termites

At many study sites, chimpanzees harvest termites using a single probing tool inserted into the sides of the insects' mounds. This skill has recently been shown to be acquired much earlier in young females, which spend more time than males closely observing the proficient fishing of their mothers[41]. Such evidence suggests that this skill is acquired by social learning. Recently, a study in the Goualougo Triangle, Republic of Congo, described chimpanzees approaching termite mounds already armed with appropriate tools, sometimes two different ones[23]. The first is a stout stick (left), which is thrust into the ground using both hands and often a foot, puncturing a tunnel into the nest about 30 cm beneath the ground. A more delicate probe is then inserted into the tunnel to extract termites; this probe is first prepared by biting it to length, manually stripping the leaves and pulling it through the teeth to create an effective 'brush-tip'. This brush-tip method, like the use of the puncturing stick, is not known for chimpanzees harvesting termites elsewhere in Africa. The drawing on the right shows a female ready with such a probe in her mouth, and holding a third tool-type used for perforating termite mounds. Images drawn by D. Morgan from a video by C. Sanz and D. Morgan.



Box 4 | Selective copying: are chimpanzees more rational imitators than children?

In a recent experiment[42], young children and chimpanzees watched a familiar human first stab a tool into a small hole in the top of an opaque box (top diagram), then remove it and apply it to a second, lower hole to recover food (middle diagram). When allowed their turn (photo), youngsters in both groups typically tackled both holes in the sequence demonstrated. In a second condition, the box was transparent and revealed that the first stabbing action from the top was in fact ineffectual (bottom diagram). Now, the chimpanzees switched from the imitative approach they had used with the opaque box to a relatively emulative strategy that focused on the crucial terminal work around the lower hole. In contrast, the children continued to 'blindly' imitate the original stabbing sequence, which although apparently less rational in this particular context, emphasizes the extremes of conformity to which our own, super-cultural species is often subject.



comprehensively analysed is self-medication, which involves swallowing whole, rough-surfaced leaves (chimpanzees only) and chewing bitter piths (both chimpanzees and humans)[33]. Extensive correlational evidence suggests that these actions counter intestinal worm infections, and recent additional experimental evidence[33] implies that innate predispositions in chimpanzees to indulge in such behaviour are refined by observational learning—an adaptive package given the requirement in the wild to discriminate specific local items from highly poisonous alternatives. Both the function of such self-medication and its social mode of acquisition appear to be common to chimpanzees and humans, although the human repertoire is more extensive.

Conclusions, controversies and the future

The emerging picture outlined here is significant for both chimpanzees and humans. With regards to chimpanzees, we now know that not only are chimpanzees as a species endangered, but unique local cultures are being destroyed at an even faster pace, much like some contemporary small-scale human cultures. A more positive effect of this research is that as increasing links between chimpanzee and human behaviour are discovered, people may become more motivated in their conservation efforts. Among the many implications for humans is a deeper understanding of both the shared and unique mental heritage that underlies our cultural capacity. A challenge for comparative genomics will be to help explain these similarities and differences. Of particular interest is the sheer scale of chimpanzee culture. Although all animals that acquire traditions may benefit from this second kind of inheritance system, the richness of chimpanzee culture outlined here suggests that this system may be particularly significant in this species and might interact with processes of genetic inheritance in interesting ways.

The synthesis of recent work on this topic has generated much new knowledge, along with a number controversies that will drive future research. One of the fundamental controversies concerns the explanation for the evolution of distinctive cumulative culture in humans. A dominant view has been that deficits in the social learning capacity of chimpanzees, coupled with other aspects of social cognition (see reviews 34, 35), account for this difference[24,25]. However, if chimpanzee social learning is as sophisticated as some of the recent work reviewed above suggests, this view becomes less tenable[15]. An alternative hypothesis is that the important differences lie in the cognitive complexity of the relevant cultural contents: the capacity to knap an Acheulian biface, for example, as much as the capacity to copy the skills of others[15]. Experimental programmes are now underway that may help to resolve this controversy by tracking the cultural dynamics of whole groups of chimpanzees[36], joining full-circle with the knowledge that continues to be garnered from the African forests.

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