

# Evolutionary origins of the human cultural mind

Thibaud Gruber and Klaus Zuberbühler look to non-human primates for clues

**Which components of our cognitive architecture are part of our primate heritage, and what is uniquely human? Comparative studies of non-human primates can provide insights into earlier stages of human evolution by revealing the ancestral states. We address one pillar of what it means to be human, the capacity for culture. Overall, there is good evidence – from both laboratory groups and more recent field studies – that primates possess the key ingredients for culture to various degrees. But can a chimpanzee disregard current cultural norms in order to find optimal solutions to a novel problem, or is this an ability that emerged more recently in human evolution?**

How is it possible to investigate what it was like to be an early human, considering that mental capacities leave no direct traces in the archaeological record? One promising avenue is the study of ancient DNA. A draft sequence of the Neanderthal genome is now available (Green et al., 2010), which will allow comparisons of genetic sequences of modern humans with their sister species, the Neanderthals, and with other closely related primates. Unfortunately, however, very little is still known about how genes relate to the development and regulation of normal behaviour and cognitive functioning. Advances in describing the cognitive capacities of early humans will thus depend on progress made in understanding how genetic variation and cognitive differences are linked. In the meantime, other disciplines will have to provide the brunt of evidence.

A particularly successful approach has been to compare the behaviour and cognitive capacities of animal species that are closely related to humans. The comparative approach engenders inferences about ancestral states by contrasting the cognitive capacities of humans with chimpanzees and bonobos, our closest living relatives. The obvious drawback is that humans and modern apes derived from a shared ancestor that lived several million years ago (Gagneux et al., 1999; Stone et al., 2010), preventing conclusions about the more recent evolutionary history of humans.

With this in mind, we will address one key feature of what it means to be human,

the capacity for culture. By describing how the world looks through the eyes of our closest living relatives, the chimpanzees, we seek to generate insights into the cognitive apparatus of the common primate ancestor. Our goal is to determine what parts of the human cultural mind have shared primate roots and what has evolved more recently in the human lineage.

Back in 2008 in *The Psychologist*, Rachel Kendal provided a comprehensive overview of the question of animal culture and outlined the main lines of argument in this controversial debate. We first summarise the major points before reviewing some recent developments based on field experiments with free-ranging chimpanzees that shed new light on the question of how humans evolved the capacity for culture.

## The biological roots of culture

Modern humans understand themselves as cultural beings, but little is known about how and why the capacity for culture has evolved. Perhaps for this reason, there has been long-standing interest in the study of behavioural traditions in animals, particularly primates. Early work by Japanese primatologists suggested that non-human primates could develop simple forms of behavioural traditions, or 'culture' (Imanishi, 1952). According to these reports, a female Japanese macaque living on Koshima Island invented a novel food processing technique, washing potatoes in water, a behaviour that first spread to immediate family members and then other group individuals (Hirata et al., 2001; Kawai, 1965). Further behavioural innovations were subsequently observed to spread, which led to the notion that non-human primates can develop group-specific behavioural traditions. Is it adequate to describe such phenomena as 'culture'?

Surprisingly, it has been extraordinarily difficult to define 'culture' in a way that is not too narrow (only useful to describe

human behaviour) or too loose (encompassing any non-genetically acquired trait). One solution has been to dissect and define culture as the product of a range of cognitive skills and motivations, which may have their own independent evolutionary histories. But what exactly are the key components? Amongst biologically oriented researchers the following features appear to be particularly relevant: the behaviour in question must be socially acquired from an innovator, then propagate in a group, and subsequently remain stable across generations. If more than one such behaviour is present, preferably in different domains, then the conglomerate qualifies as a culture (Whiten & van Schaik, 2007). In this view, the capacity for culture is not a monolithic phenomenon, but the product of a multitude of cognitive abilities and motivational propensities, particularly to socially learn behaviours and to transmit them to others with or without improvements.

## Do chimpanzees have culture?

Food washing of Japanese macaques still features regularly in textbooks as a classic example of animal culture, although the relevance of these observations has been questioned in the more recent literature (Galef, 1992; Visalberghi & Fragaszy, 1990). Food washing is relatively common in various monkey species, suggesting that the behaviour seen on Koshima may not be an invention, but part of natural macaque behaviour. This is not necessarily a deep problem because cognitively sophisticated animals, including humans, often only realise a proportion of their full behavioural capacity. For example, humans are capable of more than a hundred discrete speech sounds but speakers of different languages only produce fractions of them. A more serious critique is that the transmission speed of potato washing within the group was very slow. This fact is more consistent

with the hypothesis that each group member acquired the potato washing behaviour on its own, rather than by observing others (Galef, 1992).

For chimpanzees, the notion of 'culture' appeared soon after researchers began to study them in their natural habitats in Africa (Goodall, 1973). Chimpanzees are gifted tool users, and it was soon found that different study groups used different tool techniques to solve similar problems (Boesch, 1996; McGrew, 1992). Nut cracking, termite fishing, honey dipping, water sponging are just some of the behaviours seen in the wild. Although this diversity is undisputed, the question of chimpanzee culture has continued to remain controversial. The debate has largely to do with whether the key criteria for culture, as outlined before, are met (Laland & Galef, 2009). In particular, the main point of contention concerns the learning mechanism responsible for the observed behavioural differences. East and West African

chimpanzees differ substantially in the range of tools they use to gain access to difficult foods. For example, West African chimpanzees use hammers and anvils to crack nuts, but this behaviour is not seen in East Africa (Laland & Janik, 2006).

Although such patterns are intriguing, and indicative of cultural differences, they could be the product of genetic or ecological factors, rather than socially learned behaviour. Biologically, West African chimpanzees are a subspecies that is genetically slightly different from the East African population (Goldberg & Ruvo, 1997). Although the genetics hypothesis is difficult to rule out, it is not very plausible that genetic variation is responsible for the observed behavioural differences across groups. Captive chimpanzees or bonobos can acquire nut-cracking and other tool-use techniques with relatively little effort, regardless of their genetic background (Gruber et al., 2010). A more serious critique concerns the role of the environment. For instance,

it is possible that there is something special about West African forests that makes it more likely for chimpanzees to discover nut-cracking individually and regardless of what others are doing (Tennie et al., 2009). Acquired behaviour, in other words, could be the product of trial-and-error learning, and this would not qualify as cultural behaviour. How can such critique be addressed?

## Experiments with wild primates

Other researchers have advocated the use of field experiments to produce more compelling evidence for animal culture (e.g. Kendal, 2008). Until very recently, fieldwork with great apes has almost exclusively been observational (Reader & Biro,



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questions

How much cognitive is primate culture?  
Do chimpanzees disapprove if another does not follow a cultural norm?

resources

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2010). Although this commitment to observe and report on the natural behaviour of our closest relatives has produced much progress (e.g. Lonsdorf, 2010) observational data are often unsuitable for strong conclusions about the causality of behavioural phenomena. Experiments are necessary to clarify the causes and consequences of behaviour, but they tend to be difficult to carry out with free-ranging animals. What type of experiments would discriminate between the main hypotheses, i.e. whether behaviour has been culturally transmitted rather than discovered by individual learning in response to a specific environment?

Meaningful results have been obtained with translocation experiments of individuals between populations or of populations between sites (reviewed in Laland & Hoppitt, 2003). This way, a subject in possession of a novel behaviour can be introduced to a naive population to investigate whether the behaviour spreads. Conversely, exchanging populations between habitats will allow one to assess the impact of the environment on the behavioural repertoire of individuals. Although such experiments have been done successfully with fish, for logistic and ethical reasons they are not feasible with wild chimpanzees.

To address these issues, we carried out a series of field experiments with several East African chimpanzee communities. We first chose two groups in Uganda, the Sonso community of Budongo Forest and the Kanyawara community of neighbouring Kibale Forest. Both forests have similar histories and were connected until about 10,000 years ago but are now separated by about 200 km (Gruber et al., 2009; Reynolds, 2005). The experiment built on previous reports, which had revealed that the two communities differed in their tool-use behaviour. The Kanyawara chimpanzees regularly use sticks to extract food from cavities, but stick use has never been recorded in the Sonso community, despite two decades of continuous careful observations (Gruber et

al., 2009; Whiten et al., 1999). However, both Sonso and Kanyawara chimpanzees sometimes produce leaf sponges to retrieve water from tree holes. The sponges are made by ripping a bunch of leaves from a nearby bramble, putting them into the mouth, and chewing them into a wadge, which is then used to absorb liquids (Quiatt, 1994). By choosing these two groups that belonged to the same subspecies, any explanation based on differences in genetic endowment could be ruled out from the beginning. Our experiments were thus designed to address the second foundation upon which the chimpanzee culture claim rests, the influence of the environment.

In the experiment, members of both communities were exposed to an identical, but novel foraging task; liquid honey trapped in a hole drilled vertically into a large and naturally fallen horizontal tree trunk. The hole was wide enough for chimpanzees to insert two fingers, but not shallow enough to retrieve any honey.

Results were clear-cut. The Sonso individuals tried to access the honey by (unsuccessfully) inserting fingers into the hole, and most soon gave up. However, a few individuals persisted and proceeded to manufacture a leaf sponge. They then inserted this newly manufactured tool into the cavity, which allowed them to extract substantial amounts of honey. The behaviour observed in the Kanyawara community of neighbouring Kibale Forest was very different. Upon encountering the



For the first 10 years of their lives, wild chimpanzees live in permanent associations with their biological mothers and other siblings, providing myriads of social learning opportunities

artificial beehive, most individuals almost immediately manufactured a stick, which allowed them to retrieve honey without much difficulty. No individuals ever produced a leaf sponge, even though this was also part of their natural tool repertoire. The most likely explanation for this behavioural difference was that individuals resorted to their already existing knowledge, rather than to individualistic ad hoc solutions to the problem.

Has this experiment resolved the controversy surrounding chimpanzee culture? Although we have demonstrated that chimpanzees will recruit previously stored knowledge when confronted with novel problems, it is not clear whether this knowledge has been acquired by individual or social learning. Chimpanzees spend the first 10 years of their lives in almost constant contact with their mothers and siblings (Goodall, 1986), suggesting that social influences are strong and social learning opportunities omnipresent.

In captive groups, a wealth of experimental evidence has shown that primates are prone to and capable of various forms of social learning (Whiten, 2010). For example, long-tailed macaques are more likely to manipulate wooden material than other objects after observing a group member raking apples into the enclosure with a wooden stick, a form of 'stimulus enhancement' (Zuberbühler et al., 1996).

Interestingly, individuals affected more strongly by this simple form of social learning were also more likely to learn the tool-use technique themselves. Laboratory chimpanzees can learn new tool techniques, not only by watching other group members, but also by observing human demonstrators (Herrmann et al., 2008). Although such results are relevant, it is imperative to eventually obtain evidence from free-ranging individuals. One way to address this is to artificially seed a novel behaviour in a free-ranging primate group, monitor whether it will spread both horizontally within the group and vertically across generations. Such study efforts are currently under way.

### Culture and cognition

Culture has a substantial impact on the daily lives and behavioural decisions of humans (Tennie, et al., 2009). Human cognition, in other words, is 'overridden' by culture, but it is not clear whether similar effects also govern chimpanzee behaviour. To address this possibility, we revisited members of the two communities at Sonso and Kanyawara and presented them with the same basic task, honey trapped in small hole of a fallen branch (Gruber et al., 2011). This time, however, we also provided a suitable tool, a 40cm branch of an alstonia shrub, with all leaves removed for half of its length, the 'leafy stick'. This tool could thus function in three different ways, as a 'stick' (by inserting the bare end), 'brush' (by inserting the leafy end)

or 'leaf sponge' (by removing and chewing its leaves and inserting the resulting sponge).

We found that, at Sonso, all subjects who seized the tool proceeded to detach the leaves with their lips, discard the stick afterwards, and produce a sponge. Most, however, ignored the tool, although two manufactured a leaf-sponge from the surrounding vegetation. At Kanyawara, all subjects who seized the tool proceeded to insert its bare end into the cavity to retrieve honey. No one manufactured a leaf sponge and no one used it as a brush. From those who ignored the tool, a majority manufactured a stick tool from the surrounding vegetation.

We then tested whether the Sonso chimpanzees could learn stick use if they encountered the test tool already inserted into the hole. From a human perspective, this made one functional feature of this tool particularly obvious. Although many individuals interacted with the provisioned tool, no one used it to extract honey. Individuals either simply touched the tool or they retrieved and discarded it without further interest, sometimes after smelling or consuming residual honey off it. Some others completely ignored the stick and inserted their fingers into the hole, although one individual proceeded to manufacture a leaf-sponge to extract honey.

In sum, although we presented the tool so that its functional properties were particularly evident, no Sonso chimpanzee was able to perceive these features. Much to our surprise, these results do not support the widespread notion of chimpanzees possessing advanced capabilities in the physical realm. What is even more startling is that in captivity, chimpanzees generally perform very well in tasks requiring physical cognition, equivalent to both orang-utans and human infants (Herrmann et al., 2007). How do we interpret this puzzling difference between wild and captive chimpanzees? We think that wild chimpanzees appear to rely heavily on previously acquired knowledge, and this may restrict them

from experimenting with new techniques, a kind of cognitive conservatism (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008). Cognitive conservatism may also explain why evidence for cumulative culture, the ability to improve existing techniques which is a landmark of human culture, currently only consists of insubstantial anecdotal reports in wild chimpanzees.

This is not to say that chimpanzee tool use cannot be very complex. Observations in the Goulougo Forest of the Congo Republic have shown that, when fishing for termites, individuals can use one tool to break into the nest, before using another tool that is more suitable for fishing, raising the possibility that chimpanzees can alter existing techniques to increase complexity (Sanz & Morgan, 2007). Despite such observations, chimpanzee cultures may generally lock their carriers into group-specific behaviours, which may prevent them from developing further improvements to existing problems.

### Primate origins of the human cultural mind

Our review has shown that evidence for culture, if defined in more general terms, is abundant in non-human animals. However, human cultures are not just conglomerates of socially learned behavioural traditions. Instead, humans attach meanings to socially learned activities, which can become part of social norms that are enforced and policed by other group members. With culture being mentally entrenched, external events can be perceived in culturally specific ways with profound impacts on daily decisions. Humans are cognitively channelled by their culture, and seemingly rational and objective analyses can be biased by the specifics of a cultural background (Casasanto, 2008; Chiao & Ambady, 2007; Haun & Rapold, 2009; Haun et al., 2006; Levinson et al., 2002). Whether similar processes take place in non-human primates is an equally open question.

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It has been argued that the human capacity for culture is the product of advanced social cognition, particularly the ability to perceive others' mental states (Tomasello et al., 2005). In humans, this ability is also directly linked to language, a communication device that appears to facilitate the formation of categories of mental states, but may as well be useful to become conscious of their existence (Carruthers, 2002). Although chimpanzees understand others' goals and can make basic inferences, there is no evidence that they are also able to reflect upon their own mental states or even understand others' beliefs, abilities that emerge in humans during childhood (for a review, see Call & Tomasello, 2008; but see also Crockford et al., 2012). Being conscious of others' mental states, however, appears to be a key component for successful pedagogy (Csibra & Gergely, 2011), a process that plays a key role in the transmission of cultural knowledge in humans.

In humans, cultural practices often serve as powerful identity markers. Members of both hunter-gatherer and industrialised societies have strong views on how to do things the 'right' way, often in contrast to what other groups do (Henrich et al., 2010). Would a Kanyawara chimpanzee be surprised when watching a Sonso individual producing a leaf-sponge to retrieve honey? Would she be motivated to propose her own solution, stick use, as the most appropriate response to this problem? Whether or not non-human primates notice when other group members carry out group-specific behavioural traditions and whether they are motivated to act on individuals that deviate from such group-specific norms is one of the current hot topics in primate research (Perry, 2009). If results are negative, then certainly this is not due to a lack of group identity. Like most other primates, chimpanzees can be very hostile towards members of other communities, with sometimes lethal consequences. This extreme xenophobia may effectively



Illustration of the 'leafy stick', the tool provided to subjects, which could function in three different ways to extract honey: as a 'stick (by inserting the bare end)', 'brush' (by inserting the leafy end) or 'leaf sponge', by removing and chewing its leaves and inserting the resulting sponge

prevent them from observing members of other groups, apart from during intergroup conflicts. Arguably, humans are much more tolerant towards outgroup members than chimpanzees, presumably as the result of an evolutionary trend towards more cooperativeness with non-kin-related individuals (Boyd & Richerson, 2006). Although this enables human groups to interact with each other more freely and notice cultural differences, it is sometimes precisely because of such cultural differences that intergroup hostilities can emerge.

As Darwin already suggested in 1871, human and animal minds are unlikely to differ fundamentally in kind. The studies reviewed here are in line with this stance by suggesting that Darwin's hypothesis should include the 'cultural mind', at least



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of chimpanzees. Additionally, we have argued that addressing questions of animal culture in purely behavioural terms is in severe danger of neglecting a key feature of the phenomenon, the cognitive experience of the individual. Our results suggest that there is a deep cognitive side to chimpanzee culture, a point that has yet to be empirically explored. Current evidence suggests that cultural behaviours in chimpanzees is governed by conglomerates of socially acquired 'ideas'; that is, mental representations derived from experience

with others that are used to generate actions (Bryson, 2009). As a result, chimpanzees appear to view the world through a cultural filter, and this will further determine what youngsters will be exposed to during ontogeny.

Finally, although good progress has been made to close the gap between chimpanzee and human cultures, much is still not understood. Future research needs to focus on the role and nature of social learning in the wild. We have argued that the focus should not be limited to documenting the acquisition of behaviour patterns, but should try to describe the mental representations that individuals acquire during the process. Answers to these questions are likely to reveal how our own cultural mind has emerged from its primate roots.

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