

## Ratcheting up the ratchet: on the evolution of cumulative culture

Claudio Tennie, Josep Call and Michael Tomasello

*Phil. Trans. R. Soc. B* 2009 **364**, 2405-2415

doi: 10.1098/rstb.2009.0052

---

### References

[This article cites 58 articles, 3 of which can be accessed free](#)

<http://rstb.royalsocietypublishing.org/content/364/1528/2405.full.html#ref-list-1>

### Rapid response

[Respond to this article](#)

<http://rstb.royalsocietypublishing.org/letters/submit/royptb;364/1528/2405>

### Subject collections

Articles on similar topics can be found in the following collections

[behaviour](#) (621 articles)

[cognition](#) (166 articles)

[ecology](#) (737 articles)

### Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

---

To subscribe to *Phil. Trans. R. Soc. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

---

# Ratcheting up the ratchet: on the evolution of cumulative culture

Claudio Tennie\*, Josep Call and Michael Tomasello

*Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany*

Some researchers have claimed that chimpanzee and human culture rest on homologous cognitive and learning mechanisms. While clearly there are some homologous mechanisms, we argue here that there are some different mechanisms at work as well. Chimpanzee cultural traditions represent behavioural biases of different populations, all within the species' existing cognitive repertoire (what we call the 'zone of latent solutions') that are generated by founder effects, individual learning and mostly product-oriented (rather than process-oriented) copying. Human culture, in contrast, has the distinctive characteristic that it accumulates modifications over time (what we call the 'ratchet effect'). This difference results from the facts that (i) human social learning is more oriented towards process than product and (ii) unique forms of human cooperation lead to active teaching, social motivations for conformity and normative sanctions against non-conformity. Together, these unique processes of social learning and cooperation lead to humans' unique form of cumulative cultural evolution.

**Keywords:** cumulative culture; ratchet effect; imitation; emulation; zone of latent solutions; teaching

## 1. INTRODUCTION

In recent years, researchers have claimed that a variety of different animal species have some form of culture or cultural transmission. Culture has been claimed, for example, for dolphins and whales (Rendell & Whitehead 2001), New Caledonian crows (Hunt & Gray 2003), chimpanzees (Whiten *et al.* 1999), orangutans (van Schaik *et al.* 2003), Japanese macaques (Huffman 1996) and capuchin monkeys (Perry *et al.* 2003; Frigaszy *et al.* 2004). Assuming that these claims are to some degree valid, this means that cultural transmission as an evolutionary process may arise in a wide variety of species given the right ecological and social conditions.

In the case of primates, the further claim is sometimes made that chimpanzee culture and human culture are homologous, that is, that their common ancestor some 6 million years ago passed on to both species the same basic skills of cultural transmission (Boesch 2003; Whiten *et al.* 2003; Byrne 2007). Although this may be true for some aspects of the process, for others it is clearly suspect, as chimpanzees' sister species, bonobos, who shared that same common ancestor, have so far provided little evidence of cultural traditions or transmission in natural populations (though of course they have not been observed nearly as closely as have chimpanzees). The other possibility is that chimpanzee culture has evolved on its own, perhaps even after the split from bonobos,

and represents simply one more among many different kinds of animal culture.

Regardless of whether chimpanzee and human culture share some common mechanisms, which they almost certainly do, what is undeniable, we would claim, is that human culture is an evolutionarily unique phenomenon. *Prima facie* evidence of this uniqueness is the kind of products human cultures produce: material and symbolic artefacts from industrialized technologies to language, to money and to symbolic mathematics. These cultural products suggest the possibility of some unique types of cultural transmission processes in humans. Also important in a full assessment of human culture are humans' many unique forms of cooperative social practices and institutions from marriage to religions to governments.

Tomasello *et al.* (1993a) claimed that from the point of view of process, a key feature of uniquely human cultural products and practices is that they are cumulative. One generation does things in a certain way, and the next generation then does them in that same way—except that perhaps they add some modification or improvement. The generation after that then learns the modified or improved version, which then persists across generations until further changes are made. Human cultural transmission is thus characterized by the so-called 'ratchet effect', in which modifications and improvements stay in the population fairly readily (with relatively little loss or backward slippage) until further changes ratchet things up again. This process obviously relies both on inventiveness, for the cultural novelties, and on faithful transmission across generations to keep the novelties in place until other novelties come along. The claim in the original paper was that while inventiveness is fairly widespread

\* Author for correspondence ([tennie@eva.mpg.de](mailto:tennie@eva.mpg.de)).

One contribution of 13 to a Theme Issue 'Evolution, development and intentional control of imitation'.

among primates, humans transmit cultural items across generations much more faithfully, and it is this faithful transmission (the ratchet) that explains why human culture accumulates modifications over time in a way that chimpanzee and other animal cultures do not.

In this paper, we would like to update our characterization of the ratchet effect in light of recent studies and discussions on the topic of chimpanzee and human culture. Much more is known now about the nature of chimpanzee cultural traditions in the wild, and recent experimental studies, especially by Whiten *et al.*, have provided new and important data on chimpanzee cultural transmission. At the same time, new empirical and theoretical research with human children has demonstrated some potentially species-unique processes of cooperation, social imitation, pedagogy and social norms of conformity, which might plausibly be linked to the human cultural ratchet.

## 2. CHIMPANZEE CULTURAL TRADITIONS

Whiten *et al.* (1999) reported the results of observations and discussions among the major chimpanzee fieldworkers relevant to the question of chimpanzee culture. These fieldworkers reported observations of interesting chimpanzee behaviours and checked whether they occurred at other field sites. Based on these discussions, and some systematic published data, several dozen population-specific behavioural traditions were identified as ‘cultural’—meaning that they were used by most members of a population, not used by most other populations, and most likely due to some form of social learning (because they did not seem to be due to ecological factors).

Ecological surveys such as this are an important first step, but to determine the nature of chimpanzee traditions in detail, more systematic studies are needed (see also Galef & Giraldeau 2001). One of the most systematic field studies to date is that of Humle & Matsuzawa (2002) on the ant-dipping of the Bossou chimpanzees. Ant-dipping was at one time used by many fieldworkers as the best example of chimpanzee culture because it involves different groups engaging in the same basic foraging activity—poking sticks into ant nests to capture and eat ants—but each group seems to do this in its own way (Boesch & Boesch 1990). Thus, chimpanzees in the Tai Forest dip for ants using short wands and bite the ants off the wand directly (Boesch & Boesch 1990), whereas at Gombe National Park they use longer wands and typically (though not always) pull the ants off it with their other hand before eating them (McGrew 1974). Humle & Matsuzawa observed that the chimpanzees at Bossou sometimes use both techniques. They found that the choice of technique is driven in the first instance by the length of the wand: biting from shorter ones and pulling ants off with longer ones. In turn, the length of the wand is driven mainly by the aggressiveness of the ants—with different species of ants being differentially aggressive, and all ants being more aggressive at the nest than when on the move—and longer tools are used (to avoid being bitten) when the ants are more aggressive.<sup>1</sup> It may thus be that different levels of

aggressiveness on the part of different ant species, and whether ants are either at the nest or on the trail, drive the group differences of behaviour—with social learning playing no or only an assisting role. Indeed, in a survey of ant-dipping in all of the chimpanzee populations in Africa in which it has been observed, Schöning *et al.* (2008, p. 10) conclude ‘Our data do not show that variation in army-ant-eating is sociocultural...’<sup>2</sup>

Even though the systematic study of ant-dipping has undermined to some degree the claim of its cultural status (though see Möbius *et al.* 2008 for a different view), it may well turn out that some chimpanzee behavioural traditions will survive close scrutiny. But this must be demonstrated systematically and quantitatively for each case independently. Another important method is exposing naive captive individuals to materials from the wild and seeing what they do with them. Thus, Huffman & Hirata (2004) found that giving medicinal leaves—whose use was thought to be socially transmitted in the wild—to naive individuals in captivity resulted in several using them in ways similar to wild chimpanzees, thus, in our view, undermining the social transmission hypothesis to some degree in this case as well (see Tennie *et al.* 2008 for a similar study undermining the idea that programme-level imitation is key for the acquisition of gorilla nettle eating). A related issue is potentially cultural behaviours that seem to have multiple origins, which turns out to be true for two of the best-known chimpanzee traditions. First, the so-called grooming hand-clasp (McGrew & Tutin 1978) has arisen in several populations independently, including at least one in captivity not even on the African continent (de Waal & Seres 1997). Second, nut cracking was always thought to occur only in West Africa on the west side of the Sassandra river, but it has recently been found 1700 km to the east, with many non-nut-cracking populations in between (Morgan & Abwe 2006).

The most plausible explanation of chimpanzees’ cultural traditions in the wild, then, relies on the fact that we are dealing here with behaviours that are inevitable by individuals, perhaps particularly gifted individuals. After individual invention, a novel behaviour may spread within groups by some form of learning, with the within-group spreading being made possible by the ease of individual invention. We may thus envision here a kind of ‘zone of latent solutions’ (ZLS). Some latent solutions then are things that individual chimpanzees could easily invent on their own, whereas others might arise rarely and only if all conditions are right. In the easy cases, we would expect almost all chimpanzee groups to have the behaviour, whereas in the more externally and internally (e.g. physiological or motivational) dependent cases, the presence of the behaviour across populations would be more scattered (e.g. nut cracking). But once an individual in a group has invented the behaviour, its activities make it easier for others to learn. Thus, nut crackers and termite fishers leave their tools and detritus behind, and in the right place, which makes the learning of their offspring and others much easier. In addition, there could be several processes of social

learning at work—such as stimulus enhancement and emulation learning (see below)—that facilitate the spread of an individually invented behaviour in a group as well.

Our claim is thus that the behaviours one sees as part of chimpanzee culture are all things that individual chimpanzees could invent on their own fairly readily if all of the external and internal conditions are right. While some such behaviours will be highly likely for all groups (like making nests), others will need more environmental input (which sometimes can take an indirect route via physiology) in order to develop—perhaps even in the right order and at the right time—and these will then necessarily be relatively rare behaviours or ‘inventions’. But once an individual in a group has invented one of these rarer types of behaviour, its activities, or resulting products, make it considerably easier for others to repeat the behaviour—and this they do basically on their own by mostly re-inventing it (e.g. by ‘product copying’ or emulation learning; Tomasello *et al.* 1987). What this means is that non-human ape (ape henceforth) cultures are restricted by the upper boundaries of their species’ ZLS, i.e. their physical cognition skills (see also Richerson & Boyd 2008 for a related theoretical and general discussion consistent with our view). Whether a given behaviour within these boundaries is then actually exhibited is determined by: (i) the species’ cognitive and learning skills; (ii) the ecologies to which they are exposed; and (iii) the social situation in terms of the age and rank and number of practitioners that are potentially observable, as well as the general ‘sociability’ of the species (see van Schaik & Pradhan 2003).

Given this general view, we may then account for different traditions in different chimpanzee groups often by different local ecologies, as in the case of ant-dipping and many other tool use behaviours. The other main possibility is basically random ‘founder effects’. Thus, if an individual in a given chimpanzee population, by chance, invents a way to crack nuts with a wooden stick, then the others in its group—by virtue of their exposure to sticks and open nuts in close proximity—will be exposed to learning conditions favouring the individual discovery of stick use (perhaps influenced by stimulus enhancement and emulation learning). In another population, the whole process might proceed in the same way but with a stone tool, thus generating different traditions within the different populations, depending mainly on the different first steps in the process. In both cases, the populations are copying products that are within their species’ ZLS.

### 3. CHIMPANZEE AND HUMAN SOCIAL LEARNING

In none of the reports of behavioural traditions in wild chimpanzee groups has anyone claimed to observe a behavioural tradition that seemed to accumulate modifications over time (though see Matsuzawa 1994 for a related claim of chimpanzees using human-provided tools). This is not because of the fact that we have not been observing chimpanzees in the wild for so very long, as even a brief observation of almost any

human group will reveal tools (and also symbols and other artefacts) that could be as they are only if they have accumulated modifications over time. This accumulation is presumably due, or at least plausibly due, to some unique processes of social learning and transmission.<sup>3</sup>

Based on extensive reviews of experimental literature, Tomasello (1990, 1996) and Tomasello & Call (1997) proposed that one important factor leading to the ratchet effect in human culture, but not chimpanzee culture, is that human social learners focus in on different information. Specifically, when chimpanzees observe someone using a tool, for example, they tend to focus on the effect being produced in the environment, and they pay little attention to the actual bodily actions of the tool user. They then use their own behavioural strategies to produce that environmental effect. Thus, they re-construct the product rather than copy the process leading to it. Thus, if they have to ‘re-invent the wheel’ at each transmission step, the result will always be recognizable as the same, unchanging type of wheel—since, importantly, the resulting wheel’s designs will always be independent realizations drawn from the same ZLS. This re-invention is emulation learning. Although humans in many situations rely on emulation learning as well, they also sometimes pay attention to the actual behaviour or behavioural strategies of a demonstrator. This means that the fidelity of copying in the case of humans is much greater and includes a wider range of activities, since the focus of the learning is not just on the environment but rather on the intentional actions of others. And better copying by individuals enables ratcheting across generations, since cultural artefacts and practices can evolve only if the added modifications do not degenerate beyond recognition (Richerson & Boyd 2005).

Recently, Whiten *et al.* have performed a series of experiments demonstrating that chimpanzees do learn some aspects of demonstrations from one another, and this they do also across ‘transmission chains’. Whiten *et al.* (2005) taught two chimpanzees—each from a different captive group—different ways to open a food box, one by poking a stick into it and the other by lifting a kind of door. Each was then placed back into its home group. The main finding was that the individuals of each group tended to use the technique demonstrated by the trained individual. Importantly, some individuals discovered the method not demonstrated in their group, and then later switched over to the method that everyone else in their group was using (actually, only one individual did so clearly). While this is certainly powerful evidence that social learning of some kind may potentially underlie the behavioural traditions of chimpanzees in the wild, it is entirely consistent with our ZLS view: the apes did not learn anything radically new or improbable, but rather had their attention drawn to things by the demonstrators, and then solved the problem for themselves. And they were not learning about actions but rather about how or where the box works—without attending much or at all to the behavioural techniques used<sup>4</sup> (emulation learning). Hopper *et al.* (2007) argue

that the chimpanzees in their study were not using emulation learning because they failed to learn in a condition in which the box simply operated itself (called a ghost condition; Heyes & Ray 2000; see also Tennie *et al.* 2006). But it is not at all clear that chimpanzees attend to a moving box in the same way they attend to the results of others' actions, and the food in the Hopper *et al.* (2007) ghost condition was sometimes dispensed to the observers after the box's actions, creating a potential distraction (see also Byrne 2002 for a general critique of ghost conditions). Note, however, that chimpanzees evidenced at least some emulation in a subsequent study (Hopper *et al.* 2008). And we know from a number of other studies that apes do indeed engage in emulation learning with regularity, in the sense that they reproduce results and ignore actions (see Tomasello 1996 for a review).

Another important fact is that when these same investigators attempted to duplicate the results of Whiten *et al.* (2005) on another pair of captive chimpanzee groups, the results were not as clear-cut (Hopper *et al.* 2007). Indeed, in the group that saw the lifting action, many individuals nevertheless poked (presumably because poking may be a preferred strategy). This does not mean that chimpanzees in the first study were not learning socially, it just means that social learning in chimpanzees is a fairly fragile phenomenon, which can be fairly easily overridden by individual preferences (Tennie *et al.* 2006). This is further support, in our view, for our ZLS account. Chimpanzees will socially learn something if, and only if, it is something they (i.e. some individuals—even if only very few) could in principle learn for themselves (and this can be tested by presenting naive individuals with all necessary raw material; for examples of such 'latent solution experiments', see Huffman & Hirata 2004; Tennie *et al.* 2008). Tasks outside their ZLS are not copied, but it would be misleading to think that the underlying processes to derive the solution are merely too difficult to copy (Whiten *et al.* 2009, but compare Tennie *et al.* 2006). As we have argued: these processes are simply not readily copied by the apes. Rather, what happens in these cases is that the observer cannot re-invent the solution on her own. Thus, the behaviour cannot spread (and in fact it could not have been invented in the first place).

Additionally, two recent studies have shown that chimpanzees also are reluctant to adopt any new behavioural strategy if they already have one that works (Hrubesch *et al.* 2008; Marshall-Pescini & Whiten 2008). In sum, it is still possible that apes in the Whiten *et al.* diffusion experiments are learning behavioural outcomes (products) via emulation learning, not behavioural processes via action copying. Product copying can lead to changes in behavioural traditions, but for the accumulation of useful modifications process copying is required.

An especially telling additional fact is: chimpanzees have never shown evidence for socially learning communicative gestures. This is important because communicative gestures cannot in most cases be acquired by emulation learning, and the ZLS is not

really applicable—since gestures produce no effects on the environment (other than sometimes noise). Of most direct relevance, Tomasello *et al.* (1997) performed an experiment of the general type performed by Whiten *et al.* (2005), but with gestures. One chimpanzee was taught a novel gesture and put back in the group to demonstrate it (on two different occasions using two different gestures and demonstrators). But the other members of the group did not pick up this gesture (chimpanzees very likely learn their gestures individually via ritualization). Failures have many potential explanations, of course, but it is relevant that to learn to mimic bodily actions in the so-called 'do as I do' paradigm, human-raised chimpanzees need several weeks of training (Hayes & Hayes 1952; Custance *et al.* 1995), which suggests that copying actions is not something that they do with special skill or ease (or fidelity; see review in Huber *et al.* 2009).

What about human children? The first important fact is that whenever experimental studies have included a comparison between chimpanzees and human children, the children are much more inclined to copy actions. For example, in the studies of Nagell *et al.* (1993) and Whiten *et al.* (1996), 3-year-old human children reproduced demonstrated actions in problem-solving tasks much more faithfully than did chimpanzees. This result was corroborated by Call *et al.* (2005), who found more particularly that chimpanzees preferentially focused on the outcomes of problem-solving activities (product copying), whereas human children preferentially focused on the actions of the demonstrator (process copying). Importantly, Horner & Whiten (2005) found that observer chimpanzees tended to ignore irrelevant actions on a box when their causal ineffectiveness was clear, but tended to produce them when their causal effectiveness was unclear—again suggesting that chimpanzees are focused in the first instance on the desired outcome and only secondarily on the demonstrator's actions. In contrast, in this study, as well as that of Nagell *et al.* (1993), the human children paid much more attention to the actions of the demonstrator, even ignoring the apparent causal relations governing the problem in order to imitate the adult's behavioural strategies—not an intelligent approach, perhaps, but one more focused on demonstrator actions. In general, in all of the studies in which chimpanzees and human children have been compared, the clear result is that the human children are much more focused on the actual actions of the demonstrator, whereas the chimpanzees are much more focused on the outcome of the demonstrator's actions. The one potential exception is some human-raised chimpanzees, that seem to focus more on actions (Tomasello *et al.* 1993b; Bjorklund *et al.* 2000; Tomasello & Carpenter 2005), which may suggest, possibly, that the issue is more one of motivation than competence. Further evidence for the motivational hypothesis comes from recent evidence for action copying in marmosets which even lack material culture but may simply be more motivated to copy actions than are chimpanzees (but they might also be more skilled (Voelkl & Huber 2007); see review in Huber *et al.* 2009).

And so, a reasonable hypothesis to explain all of the recent data on chimpanzee social learning might be as follows (Tomasello & Carpenter 2005; see also Call & Carpenter 2002). Chimpanzees are able to understand to some degree the goal of a demonstrator's action, and as observers they tend to focus on that goal, or else the actual outcome—with little attention to the actions designed to achieve that goal. Being raised and/or trained by humans can lead chimpanzees to focus more on actions. In all cases, chimpanzees only attend to outcomes and actions that are in the chimpanzee's ZLS, and only when they do not have another effective strategy already. Human children—perhaps through some kind of adaptation for cultural learning in general, especially for 'arbitrary' actions such as communicative conventions for which reproducing exact behaviours is crucial—focus much more on the actions involved (process copying). It is important to note, however, that children also focus quite a bit on outcomes in concrete problem-solving situations (Nagell *et al.* 1993; Tennie *et al.* 2006), and so one might actually say it this way. In observing instrumental actions, apes in general, including humans, tend to focus on the outcome, either produced or intended, but in some cases they analyse the action backward to the behavioural technique used to discern how that outcome was achieved; human children engage in such analysis more naturally, more frequently and perhaps more skillfully, than do chimpanzees and other non-human primates.

Putting together the observations of chimpanzees in the wild with recent experimental results, then, we may thus provide an explanation of chimpanzee cultural traditions comprising four major elements. First is the ZLS, reflecting in a probabilistic way the latent capacities of individuals to invent novel solutions to novel ecological problems on their own—given the appropriate learning conditions. Second is the social environment in terms of who, how and how often a tradition is practised with opportunities for potential learners to observe, setting the conditions for learning. Third is the social learning capacities of individuals in terms of such things as stimulus enhancement, emulation learning and imitation or process-oriented copying. And fourth is the founder effects, because of serendipitous circumstances of various kinds, that set particular populations down a particular behavioural pathway.

#### 4. EXPERIMENTAL STUDY: THE LOOP TASK

We believe that, in order to test our ZLS hypothesis, it is best to move away from using tasks that apes can solve on their own, or can solve with only minimal information (e.g. local or stimulus enhancement). And so, as further evidence for differences between apes and children in social learning abilities, we recently conducted a comparative study of social learning using a task that would require them to learn something new. Thus, we included a baseline condition to see if the behaviour to be learned was already in the repertoire of the examined species, that is, if it was in their ZLS before the demonstration. The rationale was that we tested whether apes could learn something outside their ZLS, which we hypothesize that they cannot.

#### (a) *Method*

##### (i) *Participants*

Twenty-six great apes, based in Leipzig Zoo (seven chimpanzees, six gorillas, eight orangutans and five bonobos) and 27 human children (age 4 years, sex ratio balanced) participated in this study, resulting in a dataset of 25 ape subjects and 24 children subjects.

##### (ii) *Materials*

We used a small, plastic platform that had a protruding screw. The ape and child platforms were calibrated to their relative sizes. Prior to test, the rewards (apes: two grapes, split in halves; children: two small stickers) were placed on the platform. The attached screw then protruded upwards, near the broad front (figure 1). Subjects were handed pieces of straightened, slightly moistened (so that the material would be more flexible) wooden wool (also calibrated to their relative sizes: 25 cm long pieces for children and 40 cm long pieces for apes). Subjects could form a loop with the wooden wool, push the whole loop through the mesh and put it over the screw (figure 1). They then could pull the baited platform towards themselves, to collect the rewards.

##### (iii) *Procedure*

Each subject was first tested in a baseline, to check for spontaneous loop productions. Then each subject participated in only one of two conditions: object movement demonstration or social demonstration. Subjects were distributed among the two conditions counterbalanced as much as possible for age, species and sex. This resulted in 12 apes and 12 children in the social demonstration condition and 13 apes and 12 children in the object movement demonstration condition. Apes were tested three times, once per day: on the first day, they received the baseline trial, then the respective demonstration trial, and only the latter demonstration was repeated on days 2 and 3. Altogether, this resulted in one baseline and three experimental trials. Children were tested on 1 day (resulting in one baseline and one experimental trial per child).

For the apes, testing took place in their sleeping rooms, while children were tested in a separate room at their daycare centre. Apes stood or sat facing E through the mesh. Children were seated facing E, with a mesh-box on a table in between the subject and E. The children's mesh-box's front was 40 cm high, and its upper part was made of Plexiglas (30 cm), while the lower part was made of mesh (10 cm). All subjects were tested individually and out of sight of other subjects. Children received a warm-up phase before testing to make sure that they were unafraid to put their fingers or objects through the mesh. All subjects were verbally encouraged to solve the task, with language such as 'Look! Try to get it'.

*Baseline.* All subjects, regardless of experimental condition, received a baseline trial before they were given any demonstrations. Here, the platform was baited and then placed in position. Then the subject was given one piece of wooden wool through the lower right corner of the mesh. If subjects pushed out the

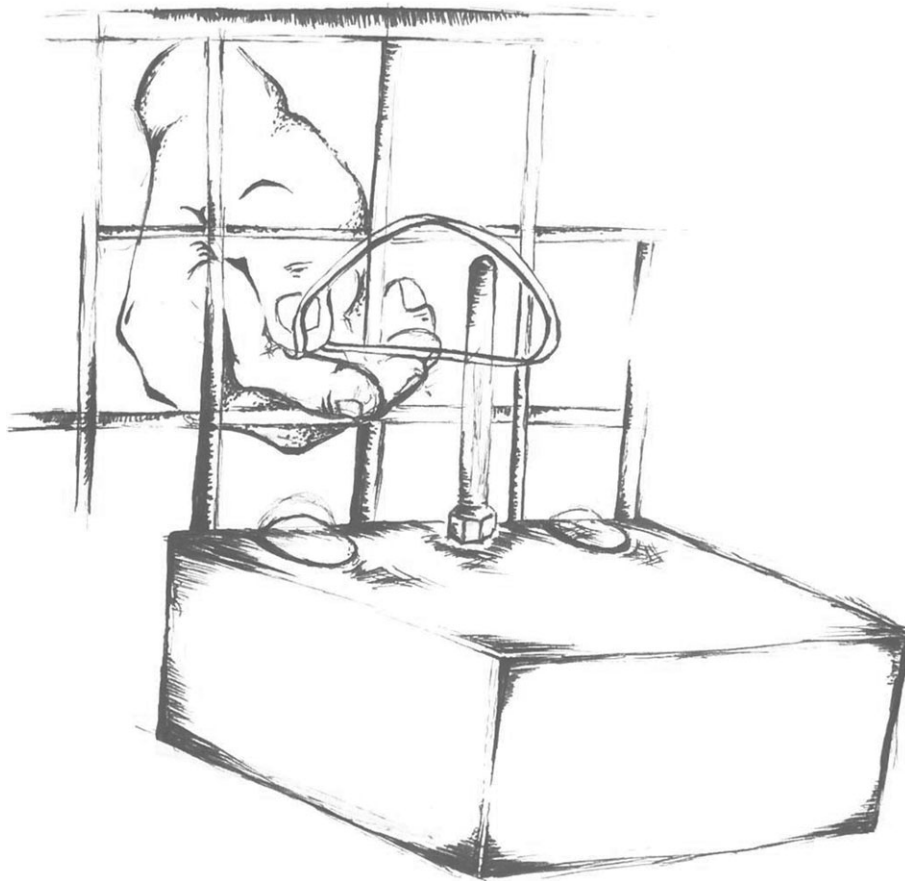


Figure 1. Schematic drawing of human setup and loop usage.

filament, they were given it back for a maximum of three times (otherwise they would have been excluded). No other information was provided, i.e. the platform was not moved in any way after placement by E. Then the subject was free to interact with the setup (5 min for apes, 2 min for children).

*Social demonstration condition.* Same as baseline, except that here, before the subject was given the filament, E demonstrated loop production and usage. For this, E took a small piece of wooden wool (20 cm long in all cases), slowly formed a loop in full sight of the subject and used it with one hand to slowly pull the platform towards the mesh, reaching over his body to do so. Once the platform reached the mesh, it was pulled back to its original position, by pressing down one finger on the back of the platform.

Children were required to see fewer demonstrations than apes (pilot tests suggested that children would otherwise become bored). Apes were required to watch at least five full demonstrations defined as watching a demonstration from the beginning till the end during a 10 min period. However, if an ape had already seen five demonstrations after 6 min, the demo phase was concluded. Children were required to observe at least two full demonstrations to a maximum of six.

*Object movement condition.* Same as demonstration condition, except that E did not form and use a loop to solve the task. Instead, E used one of his fingers, pressed onto the side of the platform facing him, to move the platform slowly towards the mesh, as well

as back again. Thus, here only the potential object movement was demonstrated.

*Coding.* We videotaped (and live coded) all the trials and scored whether a subject ever formed a loop ('loop production'), tried to push it through the mesh ('attempt loop usage') and further, whether a subject was successful in getting the rewards with such a loop ('loop success'). To assess inter-observer reliability, two naive coders coded all behavioural categories for apes and human children from videotape. Reliability was nearly perfect (only one mismatch in total).

### (b) *Results*

No great ape in any condition (including the baseline) produced a loop. Similarly, no child produced a loop during the baseline. After object movement demonstrations, 1 out of 12 children produced a loop and succeeded in getting the reward. After social demonstrations, 9 out of 12 children produced a loop, 8 attempted to use this loop to get the platform and 4 were successful. Children who observed the social demonstration were significantly more likely to produce a loop and try to use it (Fisher's exact  $p < 0.01$  in both cases) than children who only observed the object movement. Apes and children did not differ significantly in the number of loops produced in the object movement condition (Fisher's exact  $p = 1.0$ ) but children produced more loops and also attempted to use them more often than apes did in the social demonstration condition (Fisher's exact  $p < 0.01$  in both cases).

**(c) Discussion**

No ape ever produced a loop in the baseline or in the object movement demonstration condition, which suggests that loop usage is indeed outside their species' ZLS. No ape ever learned to produce loops after social demonstrations, which lends further support to our ZLS hypothesis. We do not believe that the reason the great apes failed in this task was because of a general inability of gripping and producing loops, as one gorilla (apparently by chance) was once observed to produce a loop (Kathrin Greve, personal communication, 2005).

In contrast, human children were greatly influenced by social demonstrations, but object movement demonstration alone also enabled one child to invent the solution on its own. The findings on human children can be best explained by reference to culture: the cultural adaptation of humans enabled the children to copy the process to solve the task, but also allowed one child to find the solution on its own (enabled by cultural intelligence, see below). Owing to the success of this one child, we currently cannot discount the possibility that the loop task lies within the human ZLS. We suspect, however, that younger children (who are more close to our own species' ZLS) would fail to produce loops on their own, yet would also have no problem to imitate them.

## 5. COOPERATION AND SOCIAL TRANSMISSION

A major dimension of human culture that makes it stand out relative to that of chimpanzees and other non-human primates is cooperation. Humans cooperate in large groups with non-kin, even strangers, to an unprecedented degree, based on species-unique skills and motivations. Such cooperation is necessary for participation in all kinds of cultural institutions, from marriage to government, that seem to be unique to humans, and it is also necessary for the kind of cooperative communication uniquely characteristic of the human species as well (Tomasello, *in press*). Cooperative activities are thus an essential component in a full characterization of human and chimpanzee culture.

But in addition, uniquely human cooperation also plays a role in the process of cultural transmission, both in terms of innovation and transmission. In terms of innovation, it is obvious that in human cultural groups many behavioural novelties are not created by individuals but rather by groups of individuals working together. Improved ways of hunting large prey, for example, would almost certainly be invented by multiple individuals in the process of their collaboration. Even more broadly, when individuals use the cultural artefacts and practices invented by others before them they are, in a sense, collaborating indirectly with those others—so that any improvements they make are owing to a kind of indirect collaboration, as they build on the products of previous inventors. This means that the cultural intelligence that individual human beings build up is much more of a collaborative enterprise, either directly or indirectly, than is that of non-human primates (van Schaik & Pradhan 2003). Whiten & van Schaik

(2007) have argued that ape culture makes individuals smarter than they would otherwise be. Although we agree that culture can potentially make an individual smarter by extending its ZLS, we disagree that ape culture actually accomplishes this for individual apes. Owing to the current excitement generated by chimpanzee social learning studies, it is easy to forget the crucial contribution of individual learning to ape problem solving (see above). Unlike ape culture, human culture can extend the ZLS by providing knowledge accumulated across many generations that an individual alone could never produce.

Uniquely human forms of cooperation also play a fundamental role in human cultural transmission. They do this, we think, in three main ways. First is teaching. Teaching is of course a form of altruism—though it may often be directed at kin—and so presupposes cooperative motives. An instructor expends some time and energy making sure that a pupil gains a certain piece of knowledge or skill (Caro & Hauser 1992; Tomasello *et al.* 1993a; Thornton & Raihani 2008). Teaching is present in all human societies we know of (Kruger & Tomasello 1996), and it is clearly not an everyday activity among chimpanzees or other non-human primates—though something in this direction may occur occasionally (e.g. see the two single observations of Boesch 1991, though these have multiple interpretations (Maestripieri 1995)).

Teaching may be especially important for those kinds of cultural conventions—for example, communicative gestures or linguistic items—that cannot be invented on one's own but can only be imitated from others (Tomasello 1999; Hoppitt *et al.* 2008). Indeed, Gergely & Csibra (2006) have recently elaborated an account explaining why the existence of relatively 'opaque' cultural conventions (there is no causal structure or else it is difficult to see this structure) requires both that human adults be specifically adapted for pedagogy toward children and that human children be specifically adapted for recognizing when adults are being pedagogical—which is typically indicated by the same behavioural signs as cooperative communication in general, such things as eye contact, special tones of voice and so forth (and indeed teaching may be seen as one manifestation of human cooperative communication in general; Tomasello 2008). Gergely and Csibra emphasize that when children detect pedagogy, they assume that they are supposed to be learning something otherwise opaque to them that applies to the world in a general way.

The tendency of adults and children to engage with one another pedagogically means that at least some human cultural traditions are passed on through teaching. The main point is that teaching from adults and sensitivity to teaching from children provides much additional strength to the cultural ratchet. Specifically, if adults have the proximate goal that children learn—and they will do whatever is necessary to make sure that they learn—this strengthens immensely the cultural ratchet. Children, for their part, must trust adult teaching and be ready to change behavioural strategies—in a way that chimpanzees apparently are not (Hrubesch *et al.* 2008; Marshall-Pescini & Whiten 2008)—as soon as they see a better one.



The second way in which cooperation feeds into cultural transmission involves a special kind of imitation or, more precisely, a special kind of motivation for imitation, or even conformity. Uzgiris (1981) noted that human children not only imitate in order to acquire more effective behavioural strategies in instrumental situations—as has been the main focus of research so far—but they also sometimes imitate for purely social reasons. That is to say, human beings often imitate others simply in order to be like them. The tendency of humans to follow fads and fashions in their cultural group for no apparent instrumental reason—to conform to the group in all kinds of non-instrumental ways—are well known and well documented (see any social psychology textbook). The evolutionary basis of this behaviour is very likely to be identification with the group, in the context of cultural group selection (Cavalli-Sforza & Feldman 1973)—which requires, as its fundamental component, very strongly conformist cultural transmission (Laland *et al.* 2000; Richerson & Boyd 2005). Although there have been some anecdotal reports of things that some people might want to call fads and fashions in some non-human primate species (e.g. de Waal 2001), to our knowledge, there is no systematic documentation of anything like this in non-human primate groups that could not more parsimoniously be explained with reference to simpler learning mechanisms.

The proposal here, following Carpenter (2006), is that this represents a different and important motivation for social learning that may produce more group conformity. For example, human infants have a greater tendency than do chimpanzees for copying the unnecessary ‘style’ of an instrumental action (Tomasello & Carpenter 2005; see also Whiten *et al.* 2009; Nielsen *in press*), and in acquiring linguistic conventions, children are not just driven by communicative efficacy but also by the desire to do it like others do (Tomasello 2003). This analysis would also explain why children in the studies cited above sometimes tended to imitate poor demonstrators when it would have been to their advantage to ignore them, and, in general, why children copy the actual actions of others more readily than do other apes. This so-called social function of imitation—simply to be like others in the group—is clearly an important part of human culture and cultural transmission and enables much more faithful reproduction of behaviour in the process of cultural ratcheting.

Third and finally is the normative dimension of human cultural transmission. Bruner (1993) emphasizes that human culture persists and has the character that it does, not just because human children do what others do, but also because adults expect and even demand that they behave in certain ways. Children understand that this is not just the way that something is often done, but rather the way it *should* be done. In a recent study, Rakoczy *et al.* (2008) found that 3-year-old human children not only copied the way that others did things, but when they observed a third party doing them in some other way they objected and told them they were doing it ‘wrong’—and even taught them the ‘right’ way. Kelemen (1999) has also shown that young children learn very quickly that a particular artefact is ‘for’ a particular function, and its

other uses may be considered wrong. Although there is very little direct research, at the moment there would seem to be no evidence that any non-human primates engage in any kind of third-party punishment of non-conforming behaviour (Fehr & Fischbacher 2004), much less any kinds of normative judgements about what oneself and others ‘ought’ to do.

This normative dimension to human cultural traditions may be seen again as deriving from teaching, in this case adults teaching children how to and how not to do things. But this is not totally accurate, as it was not the case in either the Rakoczy *et al.* or the Kelemen study that children observed adults making normative judgements about the right and wrong actions involved. So they were not copying adults teaching others what not to do; the children spontaneously jumped to the conclusion that the way the adults were showing them how to do it was the right way, to which everyone should conform. The evolutionary source of this normative dimension to human activities is not immediately clear, although it is surely bound up in general, one would think, with group identity and conformist transmission (this is how we, the members of this group, do things—even if others do them differently)—as enforced by punishment, including third-party punishment. But in the current context, the main point is simply that the normative dimension of human social learning in some contexts serves to further guarantee an unusual degree of faithful transmission across generations—one is punished for not doing it the right way, after all—in a way that supports the further ratcheting up in complexity of cultural artefacts and practices across historical time.

These three additional processes—teaching, social imitation and normativity—represent the contribution of humans’ special forms of cooperation to the process of cultural transmission across generations. They all assume cooperative motives and group identity, conformity and even morality of a type not typically attributed to other primate species. The key point here, again, is simply that it may be these three cooperative processes—along with the tendency of human learners to focus on actions as well as outcomes—that give human cultural traditions their extraordinary stability, cohesion and cumulativeness. They ratchet up the ratchet.

## 6. CONCLUSION

One way to focus the question is to ask whether chimpanzee culture is more similar to that of other non-human primates—for example, orangutans and capuchin monkeys—or more similar to that of humans. To our mind, chimpanzee culture is clearly of the same general type as that of their ape and monkey cousins. What distinguishes the chimpanzee version is mainly quantitative: many more traditions have been identified. This may have something to do with observation time, but it may also result from the fact that chimpanzees use such a wide array of tools when compared with other non-human primate species (i.e. their ZLS may be wider). Different uses of tools are quite salient to observers, but more

important is the fact that emulation learning and other low-fidelity social learning mechanisms can be used to socially learn tool use activities (whereas it is of much less use in most social behaviours). The key point in the current context is that the cultural traditions of non-human primate species, including those of chimpanzees, do not seem to accumulate modifications over time with any kind of ratchet effect. Rather, they represent behavioural biases of different populations—all within the respective species' ZLS—generated by founder effects, individual learning, and product-oriented (rather than process-oriented) copying.

Human cultural traditions can and do accumulate modifications over time, thus producing improbable design that survives over multiple generations. Our explanation of this phenomenon for many years has focused on the fact that human social learners focus to a much greater degree than other non-human primates on the actual actions performed by others (process copying), not just the results produced on the environment (product copying). But added to that we believe that uniquely human forms of cooperation make human social organization in many ways different as well, as things such as teaching and norms of conformity contribute to the cultural ratchet.

As always, it may be that we have underestimated chimpanzees' skills and motivations for social learning and cooperation. The studies of Whiten *et al.* (2009) have shown at the very least that emulation learning can lead to the cultural transmission of instrumental tasks in much more powerful ways than many people, including us, would have suspected. But we still see no solid evidence of accumulating culture in chimpanzees, or any kind of ratchet effect. Our hypothesis at the moment is thus that this is owing to quantitative differences with humans in the attention paid to the actions of others and to qualitative differences with humans in the way that cooperative skills and motives lead to extreme cultural inventiveness, along with teaching, social imitation and norms of conformity. These differences create in human societies a uniquely powerful cultural ratchet.

We thank Kathrin Greve, Anika Bürgermeister, Eva Siegert, Raik Pieszek, Liane Jorschik and Eva Kretschmann. We are grateful to Keith Jensen, Cecilia Heyes, Ludwig Huber and two anonymous reviewers for comments on an earlier version of the manuscript. We thank the Kindergartens of Leipzig and Leipzig Zoo. We also thank Rodney Lematia for his drawing.

## ENDNOTES

<sup>1</sup>Importantly, to determine the source of these behaviours, when investigators compared the techniques used by three mother–infant pairs in different situations, there was no relationship.

<sup>2</sup>The end of the quote is: '... but our findings are consistent with the interpretation that army ant eating by chimpanzees varies culturally'. We take this to mean that, in their opinion, there are population differences (cultural variation) in the behaviour, but that the process by which this variation is maintained is not based on sociocultural processes (such as imitation).

<sup>3</sup>There are, of course, special situations like the island of Tasmania, where the early inhabitants seem to have dropped some of their cultural complexities. The reasons for this are not completely clear (although see Henrich 2004 for a promising approach), but the claim is not

that human cultures always ratchet up in complexity inevitably, but only that they are capable of doing so under the right conditions.

<sup>4</sup>Underlying learning mechanisms matter, and this is best demonstrated with an invented example: a thirsty animal might only rarely find a hidden water hole alone, but it may do so reliably after having observed another animal moving towards the hidden water. Yet, it did not have to learn how to approach the hole (it was adept at running and drinking before), instead it had to remember a new location. Let us suppose this process repeats itself for a few more times, and our animal retains memory of the best water holes—then eventually our observer animal might have 'upgraded' its knowledge so that it now knows the whereabouts of an extremely well hidden, yet vast, crystal-clear and predator-free water hole. Would this constitute a case of cumulative culture? We do not think so. Relative rarity of behaviour alone is not a sufficient criterion, and neither are mere changes. We would rather like to reserve this term to those cases where actual processes are being copied—and to show this requires special control conditions (like in our loop task). For this reason, we would not have been convinced of cumulative culture even if the chimpanzees tested by Marshall-Pescini & Whiten (2008) had shown an upgrade of technique (and the same is in principal true for the positive findings in human children of Whiten *et al.* (2009)). Instead, we would have called it a step-wise tradition, subsumed under our ZLS concept.

## REFERENCES

- Bjorklund, D. F., Bering, J. M. & Ragan, P. 2000 A two-year longitudinal study of deferred imitation of object manipulation in a juvenile chimpanzee (*Pan troglodytes*) and orangutan (*Pongo pygmaeus*). *Dev. Psychobiol.* **37**, 229–237. (doi:10.1002/1098-2302(2000)37:4<229::AID-DEV3>3.0.CO;2-K)
- Boesch, C. 1991 Teaching among wild chimpanzees. *Anim. Behav.* **41**, 530–532. (doi:10.1016/S0003-3472(05)80857-7)
- Boesch, C. 2003 Is culture a golden barrier between human and chimpanzee? *Evol. Anthropol.* **12**, 82–91. (doi:10.1002/evan.10106)
- Boesch, C. & Boesch, H. 1990 Tool use and tool making in wild chimpanzees. *Folia Primatol.* **54**, 86–99. (doi:10.1159/000156428)
- Bruner, J. 1993 Commentary on Tomasello *et al.* 'Cultural learning'. *Behav. Brain Sci.* **16**, 515–516.
- Byrne, R. W. 2002 Imitation of novel complex actions: what does the evidence from animals mean? *Adv. Study Behav.* **31**, 77–105. (doi:10.1016/S0065-3454(02)80006-7)
- Byrne, R. W. 2007 Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Phil. Trans. R. Soc. B* **362**, 577–585. (doi:10.1098/rstb.2006.1996)
- Call, J. & Carpenter, M. 2002 Three sources of information in social learning. In *Imitation in animals and artifacts* (eds K. Dautenhahn & C. L. Nehaniv), pp. 211–228. Cambridge, MA: MIT Press.
- Call, J., Carpenter, M. & Tomasello, M. 2005 Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Anim. Cogn.* **8**, 151–163. (doi:10.1007/s10071-004-0237-8)
- Caro, T. M. & Hauser, M. D. 1992 Is there teaching in non-human animals? *Quart. Rev. Biol.* **67**, 151–174. (doi:10.1086/417553)
- Carpenter, M. 2006 Instrumental, social, and shared goals and intentions in imitation. In *Imitation and the social mind: autism and typical development* (eds S. J. Rogers & J. H. G. Williams), pp. 48–70. New York, NY: Guilford Press.
- Cavalli-Sforza, L. L. & Feldman, M. W. 1973 Models for cultural inheritance. I. Group mean and within group variation. *Theor. Popul. Biol.* **4**, 42–55. (doi:10.1016/0040-5809(73)90005-1)

- Custance, D. M., Whiten, A. & Bard, K. A. 1995 Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes and Hayes (1952) revisited. *Behaviour* **132**, 837–859. (doi:10.1163/156853995X00036)
- de Waal, F. B. M. 2001 *The ape and the Sushi Master: cultural reflections by a primatologist*. New York, NY: Basic Books.
- de Waal, F. B. M. & Seres, M. 1997 Propagation of hand-clasp grooming among captive chimpanzees. *Am. J. Primatol.* **43**, 339–346. (doi:10.1002/(SICI)1098-2345(1997)43:4<339::AID-AJP5>3.0.CO;2-Y)
- Fehr, E. & Fischbacher, U. 2004 Third-party punishment and social norms. *Evol. Hum. Behav.* **25**, 63–87. (doi:10.1016/S1090-5138(04)00005-4)
- Fragaszy, D. M., Izar, P., Visalberghi, E., Ottoni, E. B. & De Oliveira, M. G. 2004 Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *Am. J. Prim.* **64**, 359–366. (doi:10.1002/ajp.20085)
- Galef Jr, B. G. & Giraldeau, A. 2001 Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim. Behav.* **61**, 3–15. (doi:10.1006/anbe.2000.1557)
- Gergely, G. & Csibra, G. 2006 Sylvia's recipe: the role of imitation and pedagogy in the transmission of cultural knowledge. In *Roots of human sociality: culture, cognition, and human interaction* (eds N. J. Enfield & S. C. Levenson), pp. 229–255. Oxford, UK: Berg Publishers.
- Hayes, K. J. & Hayes, C. 1952 Imitation in a home-raised chimpanzee. *Quart. J. Exp. Psychol. Sect. B Comp. Physiol. Psychol.* **45**, 450–459. (doi:10.1037/h0053609)
- Henrich, J. 2004 Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the Tasmanian case. *Am. Antiq.* **69**, 197–214. (doi:10.2307/4128416)
- Heyes, C. M. & Ray, E. D. 2000 What is the significance of imitation in animals? *Adv. Stud. Behav.* **29**, 215–245. (doi:10.1016/S0065-3454(08)60106-0)
- Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V. & Whiten, A. 2007 Experimental studies of traditions and underlying transmission processes in chimpanzees. *Anim. Behav.* **73**, 1021–1032. (doi:10.1016/j.anbehav.2006.07.016)
- Hopper, L. M., Lambeth, S. P., Schapiro, S. J. & Whiten, A. 2008 Observational learning in chimpanzees and children studied through 'ghost' conditions. *Proc. R. Soc. B* **275**, 835–840. (doi:10.1098/rspb.2007.1542)
- Hoppitt, W. J. E., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M. & Laland, K. N. 2008 Lessons from animal teaching. *Trends Ecol. Evol.* **23**, 486–493. (doi:10.1016/j.tree.2008.05.008)
- Horner, V. & Whiten, A. 2005 Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Anim. Cogn.* **8**, 164–181. (doi:10.1007/s10071-004-0239-6)
- Hrubesch, C., Preuschoft, S. & van Schaik, C. P. 2008 Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Anim. Cogn.* (doi:10.1007/s10071-008-0183-y)
- Huber, L., Range, F., Voelkl, B., Szucsich, A., Virányi, Z. & Miklósi, A. 2009 The evolution of imitation: what do the capacities of non-human animals tell us about the mechanisms of imitation? *Phil. Trans. R. Soc. B* **364**, 2299–2309. (doi:10.1098/rstb.2009.0060)
- Huffman, M. A. 1996 Acquisition of innovative cultural behaviors in nonhuman primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques. In *Social learning in animals: the roots of culture* (eds C. M. Heyes & B. G. Galef), pp. 267–289. San Diego, CA: Academic Press, Inc.
- Huffman, M. A. & Hirata, S. 2004 An experimental study of leaf swallowing in captive chimpanzees: insights into the origin of a self-medicative behavior and the role of social learning. *Primates* **45**, 113–118. (doi:10.1007/s10329-003-0065-5)
- Humle, T. & Matsuzawa, T. 2002 Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *Am. J. Primatol.* **58**, 133–148. (doi:10.1002/ajp.10055)
- Hunt, G. R. & Gray, R. D. 2003 Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc. R. Soc. Lond. B* **270**, 867–874. (doi:10.1098/rspb.2002.2302)
- Kelemen, D. 1999 The scope of teleological thinking in pre-school children. *Cognition* **70**, 241–272. (doi:10.1016/S0010-0277(99)00010-4)
- Kruger, A. C. & Tomasello, M. 1996 Cultural learning and learning culture. In *The handbook of education and human development: new models of learning, teaching and schooling* (eds D. R. Olson & N. Torrance), pp. 369–387. Oxford, UK: Blackwell Publishers, Inc.
- Laland, K. N., Odling-Smee, J. & Feldman, M. W. 2000 Niche construction, biological evolution, and cultural change. *Behav. Brain Sci.* **23**, 131–146. (doi:10.1017/S0140525X00002417)
- Maestriperi, D. 1995 First steps in the macaque world: do rhesus mothers encourage their infants' independent locomotion? *Anim. Behav.* **49**, 1541–1549. (doi:10.1016/0003-3472(95)90075-6)
- Marshall-Pescini, S. & Whiten, A. 2008 Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Anim. Cogn.* **11**, 449–456. (doi:10.1007/s10071-007-0135-y)
- Matsuzawa, T. 1994 Field experiments on use of stone tools by chimpanzees in the wild. In *Chimpanzee cultures* (eds R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. G. Heltne), pp. 351–370. Cambridge, MA: Harvard University Press in coop. with The Chicago Academy of Science.
- McGrew, W. C. 1974 Tool use by wild chimpanzees in feeding upon driver ants. *J. Hum. Evol.* **3**, 501–508. (doi:10.1016/0047-2484(74)90010-4)
- McGrew, W. C. & Tutin, C. E. G. 1978 Evidence for a social custom in wild chimpanzees. *Man* **13**, 234–251. (doi:10.2307/2800247)
- Möbius, Y., Boesch, C., Koops, K., Matsuzawa, T. & Humle, T. 2008 Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Anim. Behav.* **76**, 37–45. (doi:10.1016/j.anbehav.2008.01.008)
- Morgan, B. J. & Abwe, E. E. 2006 Chimpanzees use stone hammers in Cameroon. *Curr. Biol.* **16**, R632–R633. (doi:10.1016/j.cub.2006.07.045)
- Nagell, K., Olguin, R. S. & Tomasello, M. 1993 Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J. Comp. Psychol.* **107**, 174–186. (doi:10.1037/0735-7036.107.2.174)
- Nielsen, M. In press. The imitative behaviour of children and chimpanzees: a window on the transmission of cultural traditions. *Primatologie*.
- Perry, S. *et al.* 2003 Social conventions in wild white-faced capuchin monkeys: evidence for traditions in a neotropical primate. *Curr. Anthropol.* **44**, 241–268. (doi:10.1086/345825)
- Rakoczy, H., Warneken, F. & Tomasello, M. 2008 The sources of normativity: young children's awareness of the normative structure of games. *Dev. Psychol.* **44**, 875–881. (doi:10.1037/0012-1649.44.3.875)
- Rendell, L. & Whitehead, H. 2001 Culture in whales and dolphins. *Behav. Brain Sci.* **24**, 309–324. (doi:10.1017/S0140525X0100396X)
- Richerson, P. J. & Boyd, R. 2005 Not by genes alone: how culture transformed human evolution. Chicago, USA: University of Chicago Press.

- Richerson, P. & Boyd, R. 2008 Response to our critics. *Biol. Phil.* **23**, 301–315. (doi:10.1086/417553)
- Schöning, C., Humle, T., Möbius, Y. & McGrew, W. C. 2008 The nature of culture: technological variation in chimpanzee predation on army ants revisited. *J. Hum. Evol.* **55**, 48–59. (doi:10.1016/j.jhevol.2007.12.002)
- Tennie, C., Call, J. & Tomasello, M. 2006 Push or pull: imitation vs. emulation in great apes and human children. *Ethology* **112**, 1159–1169. (doi:10.1111/j.1439-0310.2006.01269.x)
- Tennie, C., Hedwig, D., Call, J. & Tomasello, M. 2008 An experimental study of nettle feeding in captive gorillas. *Am. J. Primatol.* **70**, 584–593. (doi:10.1002/ajp.20532)
- Thornton, A. & Raihani, N. J. 2008 The evolution of teaching. *Anim. Behav.* **75**, 1823–1836. (doi:10.1016/j.anbehav.2007.12.014)
- Tomasello, M. 1990 Cultural transmission in the tool use and communicatory signaling of chimpanzees? In *'Language' and intelligence in monkeys and apes: comparative developmental perspectives* (eds S. T. Parker & K. R. Gibson), pp. 274–311. New York, NY: Cambridge University Press.
- Tomasello, M. 1996 Do apes ape? In *Social learning in animals: the roots of culture* (eds C. M. Heyes & B. G. Galef), pp. 319–346. San Diego, CA: Academic Press, Inc.
- Tomasello, M. 1999 *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M. 2003 In *Constructing a language: a usage-based theory of language acquisition*. Cambridge, MA: Harvard University Press.
- Tomasello, M. 2008 *Origins of human communication. Jean-Nicod lectures*. Cambridge, MA: MIT Press
- Tomasello, M. In press. *Why we cooperate*. Cambridge, MA: MIT Press.
- Tomasello, M. & Call, J. 1997 *Primate cognition*. New York, NY: Oxford University Press.
- Tomasello, M. & Carpenter, M. 2005 The emergence of social cognition in three young chimpanzees. *Monogr. Soc. Res. Child Dev.* **70**, 1–132.
- Tomasello, M., Davis-Dasilva, M., Camak, L. & Bard, K. A. 1987 Observational learning of tool-use by young chimpanzees. *Hum. Evol.* **2**, 175–183. (doi:10.1007/BF02436405)
- Tomasello, M., Kruger, A. C. & Ratner, H. H. 1993a Cultural learning. *Behav. Brain Sci.* **16**, 495–511.
- Tomasello, M., Savage-Rumbaugh, S. & Kruger, A. C. 1993b Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Dev.* **64**, 1688–1705. (doi:10.2307/1131463)
- Tomasello, M., Call, J., Warren, J., Frost, G. T., Carpenter, M. & Nagell, K. 1997 The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. *Evol. Commun.* **1**, 223–253.
- Uzgiris, I. C. 1981 Two functions of imitation during infancy. *Int. J. Behav. Dev.* **4**, 1–12.
- van Schaik, C. P. & Pradhan, G. R. 2003 A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *J. Hum. Evol.* **44**, 645–664. (doi:10.1016/S0047-2484(03)00041-1)
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. 2003 Orangutan cultures and the evolution of material culture. *Science* **299**, 102–105. (doi:10.1126/science.1078004)
- Voelkl, B. & Huber, L. 2007 Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE* **2**, e611. (doi:10.1371/journal.pone.0000611)
- Whiten, A. & van Schaik, C. P. 2007 The evolution of animal 'cultures' and social intelligence. *Phil. Trans. R. Soc. B* **362**, 603–620. (doi:10.1098/rstb.2006.1998)
- Whiten, A., Custance, D. M., Gómez, J.-C., Teixidor, P. & Bard, K. A. 1996 Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **110**, 3–14. (doi:10.1037/0735-7036.110.1.3)
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999 Cultures in chimpanzees. *Nature* **399**, 682–685. (doi:10.1038/21415)
- Whiten, A., Horner, V. & Marshall-Pescini, S. 2003 Cultural panthropology. *Evol. Anthropol.* **12**, 92–105. (doi:10.1002/evan.10107)
- Whiten, A., Horner, V. & de Waal, F. B. M. 2005 Conformity to cultural norms of tool use in chimpanzees. *Nature* **437**, 737–740. (doi:10.1038/nature04047)
- Whiten, A., McGuigan, N., Marshall-Pescini, S. & Hopper, L. M. 2009 Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Phil. Trans. R. Soc. B* **364**, 2417–2428. (doi:10.1098/rstb.2009.0069)