

## Social learning and teaching in chimpanzees

Richard Moore

Received: 5 April 2013 / Accepted: 28 June 2013 / Published online: 3 July 2013  
© Springer Science+Business Media Dordrecht 2013

**Abstract** There is increasing evidence that some behavioural differences between groups of chimpanzees can be attributed neither to genetic nor to ecological variation. Such differences are likely to be maintained by social learning. While humans teach their offspring, and acquire cultural traits through imitative learning, there is little evidence of such behaviours in chimpanzees. However, by appealing only to incremental changes in motivation, attention and attention-soliciting behaviour, and without expensive changes in cognition, we can hypothesise the possible emergence of imitation and pedagogy in evolutionary history.

**Keywords** Chimpanzees · Social learning · Imitation · Pedagogy

Human beings both teach their young, and have an unrivalled capacity to learn from others. Indeed, many behaviours thought of as characteristically human—for example, our learning the words of a language—could only be acquired socially (Moore 2013a, b). Given the fundamental importance of social learning to human cognitive development, the question of whether and in what ways animals learn from one another has received a great deal of attention. This attention often takes the form of the question: is culture uniquely human? The appeal to culture is relevant because, while the term has been used in numerous ways, it's generally agreed upon that cultural behaviours are learned behaviours that differ between groups of similar populations, where these differences cannot be explained either by individual learning, genetic inheritance, or by ecological differences between group habitats. Rather, cultural behaviours are those that, having emerged within a

---

R. Moore (✉)

Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany  
e-mail: r.t.moore@gmail.com

community, come to persist because the members of each new generation acquire the behaviour from their peers. The issues of culture and social learning are, then, intimately linked.<sup>1</sup>

Along with the bonobo (*Pan paniscus*), chimpanzees (*Pan troglodytes*) are the closest living relatives of *Homo sapiens*; we shared a common hominin ancestor around 6 million years ago. To ask about whether, and in what ways, chimpanzees teach skills to and learn from others is to ask about how similar to us they are in a respect that is likely to have shaped profoundly the human lineage. The answer can therefore provide us with valuable insights into the evolutionary routes by which our ancestors became modern. Since the question of chimpanzee social learning is intimately tied to the question of culture, I start with a review of the highlights of 15 years research on this subject.<sup>2</sup> I'll argue that while the evidence for some varieties of chimpanzee social learning is robust, the mechanisms of human and chimpanzee social learning are likely to be different. Nonetheless, the nature of these differences may have been overstated, and seem unrelated to cognition. Finally, I'll turn to the question of whether chimpanzees engage in pedagogy. I'll finish by sketching some valuable directions that future research in this area could take, and sketching a possible trajectory for the emergence of uniquely human social learning capacities.

## Group differences in populations of wild chimpanzees

Initial claims about primate culture were justified using the 'method of exclusion' (Whiten et al. 1999; Van Schaik et al. 2003; for discussion see Sterelny 2009; Langergraber et al. 2010). The starting point of this method is to gather behavioural data from geographically diverse groups of the same species. Where between-group behavioural differences are identified, if genetic and ecological explanations of these differences can be ruled out, the presence of culture—and consequently of social learning—can be inferred.

This method was adopted in the first large-scale comparison of data concerning putatively cultural chimpanzee behaviours, published as the result of collaboration between researchers at seven long-term research field sites (Whiten et al. 1999). The authors of this report identified 39 behaviours that were habitually observed in some chimpanzee communities, but absent from others, and where this behaviour was not explained by any obvious ecological difference; and so concluded that these behaviours must be 'cultural'. The behaviours included both material aspects of culture (including

---

<sup>1</sup> Some have argued that social learning is insufficient for the presence of culture, because culture also involves issues like group identity, conformity, and normativity (e.g., Perry 2009). These claims fall outside the scope of this review, and won't be discussed here. It might also be objected that insisting on a boundary between culture and ecology neglects that many intuitive cases of human cultural difference are grounded in ecological factors. For example, different types of human dwelling place—from igloos to mud huts—often reflect differences in climate. This shows that the term 'culture' is used in a more restricted sense in comparative psychology than in common parlance.

<sup>2</sup> For reasons of space alone, I restrict discussion here to chimpanzees. See Laland and Galef (eds) (2009) for an overview of debates about culture in other species of animal.

the use of tools) and social behaviours (like grooming). For example, chimpanzees at some but not all sites were observed to use sticks to gather army ants (*Dorylus anomma*) to eat (a foraging behaviour first reported by McGrew (1974)). Additionally, the techniques used for catching ants differed between populations. At Mahale in Tanzania, apes insert long ‘wands’ into the nests of ants, before swiping gathered ants from the stick with their closed hands and inserting them into their mouths. In the Tai forest in the Ivory Coast, however, apes use a shorter stick, which they raise directly to the mouth to eat. While neither behaviour was observed at either Budongo or Kibale in Uganda, despite the presence of army ants, both behaviours were observed at Bossou in Guinea, and in the Gombe community in Tanzania.

Analogous differences were noticed for nut-cracking behaviour, in which chimpanzees use heavy ‘hammers’ to crack hard nuts (for example, the *Coula edulis*) against solid ‘anvils’. Chimpanzees at Bossou were observed to use stone hammers with stone anvils. However, at Tai apes were observed to crack nuts using both wooden and stone hammers, and wooden and stone anvils (in all possible combinations). Meanwhile, no nut cracking behaviour was observed at any of the sites in Tanzania or Uganda. While this absence is explicable by the absence of appropriate nuts in the Ugandan sites, these nuts are present in Tanzania.

In addition to tool cultures, social behaviours were also found to vary between groups. These are harder to explain ecologically, since they are largely independent of environmental constraints. For example, in the grooming handclasp (first described by McGrew and Tutin 1978) pairs of individuals each raise one hand above their head and, while grasping each other’s raised arm with their own, groom the partner’s under-arm with their free hand. This behaviour was observed at Mahale (Tanzania), Tai (Ivory Coast) and Kibale (Uganda), but not Gombe (Tanzania), Budongo (Uganda) or Bossou (Guinea).

A central question is whether the different between-group behaviours really are the result of social learning, and not a consequence of either genetic or ecological features (or their interaction). After all, the chimpanzee populations reported by Whiten et al. came from two distinct sub-populations of chimpanzee: the western *Pan troglodytes* versus (in Guinea and the Ivory Coast), and the eastern *Pan troglodytes schweinfurthii* (in Tanzania and Uganda). It may be that genetic explanations of some reported differences—for example, in the nut-cracking tendencies of eastern and western chimpanzees—cannot be ruled out (Galef 2009).<sup>3</sup> Additionally, the ecological measures used in the Whiten et al. (1999) comparison were fairly crude. It may be that subtler and previously unidentified ecological factors could also explain some of the reported differences (Galef 1992, 2009).

## Ecological differences

Follow-up studies of chimpanzees at Bossou showed that at least some of the factors determining their ant-foraging behaviour were ecological and not, after all, cultural:

<sup>3</sup> Although nut-cracking has yet to be observed in eastern chimpanzees, it has been observed in *Pan troglodytes vellerosus*, in the Ebo forest in Cameroon (Morgan and Abwe 2006; Wrangham 2006).

Humble and Matsuzawa (2002) reported that different techniques used during ant-eating were reliably correlated with the aggressiveness of the ant prey. The ants present at Bossou, and at numerous other sites, can loosely be classified into two sub-species: *Dorylus nigricans*, which are epigaeic, black and belligerent; and the less aggressive red *Dorylus*. Both species are found in denser populations and are more aggressive at their nests than when travelling in columns. For both species, it was found that chimpanzees at Bossou were more likely to use long sticks (>50 cm) when feeding at nests than at columns. Additionally, when dipping at black ant nests the chimpanzees tended to use significantly longer tools than at red ant nests. Longer sticks reduced apes' chances of being bitten. Chimpanzees were also more likely to use their hands to sweep ants directly from long sticks into their mouths. When using shorter sticks (<50 cm) to fish for red ants, they ate ants directly from the stick. In other words, choice of wand length was reliably predicted by the aggressiveness of ants, and eating technique by the length of stick—such that both putatively cultural behaviours were found to have an ecological explanation.

While these ecological factors do seem to explain the within-group foraging strategies employed in Bossou, they do not account for all differences between sites. Two later comparisons (Schöning et al. 2008; Möbius et al. 2008) found (among other things) that although the same species of *Dorylus* are present and hunted at Taï as at Bossou, the Ivorian chimpanzees do not use long tools, and eat ants from the stick only by holding them directly up to their mouths. Additionally, they never dip at the nests of black ants, but forage at them by opening the nests and removing brood by hand (Schöning et al. 2008). In experimental comparisons of (again, among other things) the ease of access to nutritious brood (which might reduce the need to dip for ants at nests), and the comparative ant yield from black ant nests at Bossou and Taï, no ecological explanations of these differences could be found (Möbius et al. 2008). The (overlapping) authors of the Schöning and Möbius studies therefore suggest a cultural explanation. The 'hand-swipe' technique of removing ants from a stick, which greatly facilitates the use of longer sticks, may be a culturally acquired innovation. To the extent that it has not emerged in Taï, its absence may prohibit apes from using a longer stick to dip at the nest of more aggressive ants; and so restrict them to foraging by hand. In that case, the emergence of long-wand dipping at Bossou may be the consequence of an interaction between cultural and ecological factors.

### Genetic explanations of behaviour

Even if not all between-group differences can be explained by ecology, some may be explained by differences in genetic inheritance. In recent years some putatively cultural differences have been shown to be consistent with a genetic explanation. In a ground-breaking paper, Langergraber et al. (2010) showed that behavioural dissimilarity and genetic dissimilarity in nine chimpanzee groups across Africa (including all seven sites described by Whiten et al. 1999) were strongly correlated,

such that genetic explanations of between-group differences could not be ruled out. The thrust of this paper was not to deny the existence of chimpanzee social learning, but to undermine both the credibility of the method of exclusion for identifying it and the correlated assumption that genetic similarity could be taken for granted among members of the same subspecies. Its effect motivated researchers to prioritise looking for behavioural differences among neighbouring communities. Since female chimpanzees disperse to nearby groups when they reach sexual maturity, neighbouring chimpanzee groups frequently exchange genetic material in ways that distant groups do not. Genetic explanations of behavioural differences between neighbouring groups can consequently be more confidently ruled out.

In this respect, 2012 saw the publication of an important paper recording different behaviours between neighbouring populations. Luncz et al. (2012) found that while the South group of three neighbouring groups of chimpanzees in the Tai forest preferred to (although did not always) use stone tools to crack coula nuts, irrespective of the stage of the nut-cracking season, chimpanzees in the North and East groups tended to switch to using more wooden tools as the dry season wore on, and the shells of coula nuts became easier to crack. Additionally, while all chimpanzees in all three groups chose relatively small tools early in the season, the size of wooden hammers in the East and South groups increased as the season wore on; with a particularly large hammers being used by the East group. Very detailed analysis of the microecology of the neighbouring communities showed that these patterns could not be explained by readily identifiable ecological differences, including the relative hardness of the nuts in the neighbouring habitats, and the availability of wooden and stone tools.

In a similar vein, van Leeuwen et al. (2012) identified different grooming handclasp techniques between neighbouring communities of chimpanzees at the Chimfunshi wildlife sanctuary in Zambia. Here the absence of genetic differences between groups was not a consequence of mixing due to female migration. Rather, since Chimfunshi houses rescued captive apes, the pattern of genetic diversity within and between groups is the consequence of the chronological allocation of newly arriving individuals from diverse regions in and around Zambia to existing groups. The grooming handclasp was initially identified in only two out of the four studied groups at Chimfunshi (although it emerged later in a third). Furthermore, different populations of chimpanzees gripped the hands of partners in different ways: whereas in one group partners gripped hands using a palm to palm technique, in the second group they were more likely to groom wrist to wrist. These differences were not correlated with the relative arm-lengths of grooming individuals (Fig. 1).

The existence of different techniques between nearby groups is stronger evidence for cultural transmission than simply the presence or absence of a behaviour, since the latter is consistent with a genetically coded behaviour that has simply failed to be expressed in some populations (perhaps because of the absence of a trigger). The Luncz et al. and van Leeuwen et al. findings therefore constitute robust evidence that there exist behavioural differences between groups of neighbouring apes that can be explained by neither ecological variation, nor genetic inheritance. Such behaviours are, by definition, cultural.



**Fig. 1** The grooming handclasp. While chimpanzees of group one at Chimfunshi Wildlife Orphanage groom most often wrist-to-wrist, members of group two groom almost exclusively palm-to-palm. Photographs taken by Mark Bodamer (*top*) and Edwin van Leeuwen (*bottom*), used with permission

### The diffusion of social traditions

Further support for the presence of socially transmitted behaviours in chimpanzees can be drawn from experimental data collected in laboratories, and from innovative field experiments. If cultural behaviours really are the product of social learning, then once introduced into a community they should spread. (In the literature, within-generation learning is known as ‘horizontal’ transmission; ‘vertical’ transmission

takes place across generations.) Moreover, the patterns of transmission should reflect the roles of individuals within the transmission process.

To explore questions about the diffusion of behaviours within a community, Biro et al. (2003) introduced a new nut-cracking technique to the Bossou community, who had previously cracked and eaten only oil palm nuts (*Elaeis guineensis*). By collecting locally unavailable coula (*Coula edulis*) and panda (*Panda oleasa*) nuts from neighbouring regions and leaving them in small piles in a clearing, they were able to observe whether or not the tendency to crack coula and panda nuts would emerge. With one exception, after the coula nuts were first presented (in 1993), adults did not attempt to crack them, and only half even investigated them. The exception among the adults was one adult female, who seemed to show familiarity with the coula nuts—perhaps because she had migrated from a neighbouring group where such nuts were cracked and consumed. She immediately cracked and ate the nuts. The juvenile chimpanzees showed a greater degree of interest; all were observed either to investigate or to attempt to crack the new nuts. Despite their initial lack of interest, over the four series of coula nut presentations (in 1993, 1996, 2000 and 2002), the number of adults who cracked coula nuts rose to 67 %. This increase was not attributable only to the ageing of nut-cracking juveniles.

Unlike the coula nut, when the panda nut was introduced in 2000, the behaviour failed to seed—perhaps because no member of the group was familiar with the behaviour. Of the thirteen apes who cracked palm oil nuts in 2000, only four (two adult females and two juveniles) cracked panda nuts upon their introduction. However, after tentatively tasting the nuts, both adult females abandoned the activity. While the two juveniles continued to try to crack the panda nuts, they did not succeed in doing so.

The Biro et al. study is particularly valuable because it presents evidence for both the emergence of a behaviour within a community, and for the pattern of its transmission. When individuals experimented with the cracking of individuals nuts, they were often surrounded by curious others who were observed to watch them intently. Analysis of these observations found that apes observed others in the same age class or older than themselves (adults > juveniles > infants), but not younger apes. Furthermore, infants were particularly attentive to the nut-cracking behaviour of their mothers. This is consistent with Frans de Waal's hypothesis that young apes acquire behaviours through observational learning of particularly influential individuals (de Waal 2001).<sup>4</sup>

In a further study on social learning, this time conducted in a laboratory, Whiten et al. (2005) tested three groups of chimpanzees' ability to retrieve food from a piece of apparatus that could be operated in either of two ways. The same stick could be used either to poke aside a blockage in a pipe, or to lift it out of the way. Both techniques released food to the ape. In each of two groups, one 'expert' (in both cases a high ranking female) was trained to operate the apparatus using one of

---

<sup>4</sup> De Waal calls this 'bonding-and-identification-based observational learning' ('BIOL'). His hypothesis includes further aspects that are not directly supported by the evidence described here—namely, that chimpanzees imitate older individuals, and that they do so in order to be like them. Issues of chimpanzee imitation will be discussed in later sections. For discussion of affiliative conformity see van Schaik (2012), Over and Carpenter (2013) and van Leeuwen and Haun (2013).

the techniques, which others from her group could then observe. In a third group no expert was trained; individuals were left to figure out the apparatus for themselves. In the ‘poke’ group, the vast majority of individuals learned the poke technique and adopted it almost exclusively, while in the ‘lift’ group most individuals learned and continued to use the ‘lift’ technique—although several chimpanzees independently discovered the poke. No individuals in the control group succeeded in retrieving food at all. This suggests that tool use techniques were acquired through observation of the trained expert, and not learned individually. In a further study Horner and colleagues (Horner et al. 2006) used a similar paradigm, but now only a single chimpanzee (per condition) observed the trained demonstrators. Upon successful retrieval of the food, this observer took over as the demonstrator for a new ape. In both seeded groups, ‘transmission chains’ developed, showing that behaviours were readily transmitted within groups, and within-group differences persevered across generations (‘lift door’ group,  $n = 6$  ‘generations’; ‘slide door’ group,  $n = 5$ ). Again, members of a control group who did not have the opportunity to observe an expert were unable to solve the task.

These studies show that seeded behaviours spread within groups of chimpanzees, and that they do so both horizontally and vertically. They also suggest an important role for observational learning, reinforcing the findings drawn from wild populations. However, a weakness is that the demonstrated behaviours all corresponded to features of the equipment with which chimpanzees interacted. As such, behaviours could be learned both through attention to the apparatus (stimulus enhancement and affordance learning), and by attention to the particular techniques used by demonstrators (imitative learning). Consequently, the studies leave unanswered important questions about the particular varieties of social and observational learning in which chimpanzees engage. This is significant, because even if it is accepted that chimpanzees do learn from one another, they may differ from humans in the methods by which cultural behaviours are transmitted.

### **The cognitive mechanisms of cultural learning**

Differences between the various forms of social learning can be illustrated with examples. Suppose that one day, in a forest somewhere in west Africa, a juvenile male, Kofi, sees an older chimpanzee, Robert, gather coula nuts from the ground and then select a rock from the forest floor. Placing one coula nut at a time into a small crater in the root of a tree, Robert takes his rock, lifts it, and strikes down hard onto the shell. After six or seven strikes the nut cracks and reveals a fruit, which Robert eats. In the course of watching this scene unfold, Kofi might learn many things. For one thing, he could learn that coula nuts can be cracked to produce fruit. This would be a form of *affordance learning*—of learning about the properties of objects in the environment, and the relationships in which they might stand to other objects in the environment. Affordance learning can be more or less detailed. For example, Kofi might learn that nuts can be cracked; or that nuts can be cracked by rocks, or by heavy objects; or that nuts can be cracked only when placed on appropriate anvils. (Perhaps when Robert doesn’t use the tree root as an anvil, the nuts either roll away,

or sink into the soft mud.) Such cases are all forms of learning about the environment. However, since these affordance properties become salient only because of Robert's behaviour, this is nonetheless a form of social learning.

In the process of watching Robert, Kofi's attention might be drawn to particular features of the environment in ways conducive to further learning. For example, Robert's actions might make the hammers, nuts, or anvil with which he interacts particularly salient. These instances of *stimulus enhancement* (or, in the case of locations *local enhancement*) might motivate Kofi to investigate these features further. Perhaps in conjunction with trial and error learning, these investigations would lead him to acquire causal knowledge that would support his learning. Or, without his even being aware of it, they might subtly predispose him to act in some ways rather than others. For example, if Kofi sees Robert cracking more often with wooden than stone hammers, he might assume that such hammers are superior even if they are not, or just develop an unconscious preference for them.

On classical accounts of social learning, the varieties just described have been considered relatively cognitively undemanding. For example, local enhancement might figure in accounts of associative learning, in which causally efficacious patterns of tool selection are acquired through a process of repeated observation. These learning processes are also consistent with the received wisdom that, at least in comparison to humans, chimpanzees understand little about the minds of others. On these routes to learning, while Robert's actions draw attention to relevant features of the environment, little engagement with his mental life is required for Kofi to acquire the behaviours that he observes.

While these varieties of social learning make comparatively weak claims on an agent's social cognition, others may be more complex. For example, it may be that Kofi recognises that Robert intends to crack the nuts. If on this basis Kofi also forms an intention to crack nuts, this would be a form of *end-state emulation*: Kofi acts in order to realise the same state of affairs that he has seen Robert intend to bring about. Furthermore, Kofi might also see that when Robert cracks nuts, he does so by performing particular actions. If Kofi knowingly tries to replicate the actions—like gripping techniques, or striking manoeuvres—he has seen Robert perform, he would have tried to *imitate* him. In imitation, an agent grasps both the goal of another's action, and the means pursued to achieve that goal, and acts intending to reproduce both. Both imitation and emulation require some understanding of the intentions, beliefs and desires of others, which may not be possible to those who lack knowledge of other minds.

### **The importance of imitation**

For those who emphasise the discontinuity between human and chimpanzee culture, considerations about the mechanisms that support social learning are tantamount. Richerson and Boyd emphasise the importance not only of cultural transmission, but particular—and characteristically human—varieties of transmission:

Culture is information capable of affecting individuals' behaviour that they acquire from other members of their species through teaching, imitation, and other forms of social transmission. (Richerson and Boyd 2005, p. 5)

While this definition remains consistent with non-imitative forms of cultural learning, other accounts are less inclusive. Galef (2009) writes only of ape 'traditions', preferring to reserve the term 'culture' for human cases. He argues that:

If ... tradition in chimpanzees is the expression of fundamentally different behavioural processes than is human culture, then culture in the two species is analogous [not homologous] and tells us nothing about the evolutionary origins of human culture. (*ibid.*, p. 245)

Galef and Tomasello have been consistent and vocal critics of the attribution of human-like culture to animals. They argue that the primary mechanisms of social learning in apes and human children differ (Galef 1992, 2009; Tomasello 1994/2009)—because while humans consistently imitate those whose behaviour they observe, apes do not. Rather, what they acquire from observational learning is information about the sorts of action possibility that an environment affords. In Tomasello's early work (e.g., Tomasello 1994), the claim that chimpanzees do not imitate was motivated in part by the belief that chimpanzees fail to understand or do not attend to the intentions of others. While he has subsequently argued that chimpanzees do understand intentions (Call et al. 2005; Call and Tomasello 2008), and that they are capable of emulation, the claim that chimpanzees are unmotivated or unable to imitate others remains (Tomasello 1994/2009, postscript).

The emphasis on imitation is significant for the evolution of human cognition and culture, because, in conjunction with teaching, imitation enables—or greatly facilitates—a particular variety of culture foundational in *Homo sapiens*' transition to modernity: *cumulative culture*. Cumulative culture is characterised by technological traditions (including tool use and language) that not only persist through time but become more complex, as new generations build on the innovations of their forefathers (Galef 1992; Tomasello 1999). For cumulative culture to be possible, learners must be able to master existing technologies quickly and efficiently, so that they can devote their finite stock of cognitive capital to the refinement of existing technologies and the development of new ones. Tomasello and colleagues have called this the 'ratchet' effect (Tomasello 1999; Tennie et al. 2009): through social learning, naïve individuals acquire the latest innovations of their predecessors and refine them, thereby raising the entry level for subsequent generations. Imitation and teaching facilitate this accelerated learning because they enable faithful acquisition of complex behaviours, and so free learners from the need to reinvent earlier innovations for themselves.

### **In what varieties of social learning do chimpanzees engage?**

Currently our best empirical evidence supports the conclusion that the primary mechanisms of chimpanzee social learning are not imitation, but combinations of

affordance learning, local and stimulus enhancement, and emulation. Matsuzawa et al. (2001) have defended this conclusion on the basis of extended observations of nut-cracking behaviour at Bossou. They argue that young chimpanzees do not imitate, because for the first few years of their lives infant chimpanzees (<4 years) do not try to crack nuts. Rather, they watch intently as others crack nuts, and explore the nuts and tools. Only between the ages of three and five do they start to combine stones, nuts and anvils in sequences that are appropriate for cracking. Consequently, according to Biro et al. (2003, p. 220):

Detailed accounts at Bossou of the developmental processes involved in infant chimpanzees' acquisition of the nut-cracking skill ... do not point towards imitative learning as the underlying mechanism. Young chimpanzees go through several stages of manipulating nuts and stones, first as single objects then in various combinations, and only gradually come to approximate the correct sequence of actions. Hence, the observed models' role is likely to lie in providing the observer with information about the objects necessary and/or about the outcome of a successful bout of nut cracking – the former an example of stimulus or local enhancement, the latter a more sophisticated “emulation” learning.

This finding is partly supported by research on the ontogeny of termite fishing at Gombe conducted by Lonsdorf and collaborators (Lonsdorf et al. 2004; Lonsdorf 2005, 2006). Lonsdorf found that juvenile females mastered termite fishing substantially younger than males. This difference was best explained by the fact that while females spent more time at termite mounds watching their mothers fish, males spent more time playing (Lonsdorf et al. 2004; Lonsdorf 2005). While this is consistent with the claims made by Biro et al. Lonsdorf also makes the stronger claim that female but not male juveniles imitated their mothers—because while females dipped their tools into the mound to the same depth as their mothers, males did not. In her words (2005, p. 681):

Male and female offspring learn from their mother that the termite mound is the object to which attention should be directed (stimulus enhancement). Once the mother starts to termite-fish, male and female offspring learn that the goal of the behaviour is to capture termites (goal emulation). Male offspring then develop their own method of achieving this goal, while female offspring learn something about the form of the behaviour, namely how deep to insert the tool (imitation).

While the possibility that females learn imitatively should not be ruled out, in fact the same behaviour patterns can be explained without invoking imitation. In this case, females may not have been copying not their mothers' grip on the tool, so much as learning about affordances of their environment—namely that sticks retrieve more termites when dipped to a certain length (namely, one corresponding to the mother's dip). Such information could be learned by attending only to the movements and/or properties of the tool.

Further findings from experimental paradigms support the conclusion that while chimpanzees are very good at observational learning of tool functions, they do not

typically copy the precise techniques with which the tools are used. Nagell et al. (1993) presented 2-year-old children and chimpanzees with an experimenter who used a rake tool to retrieve an inaccessible reward. The tool was demonstrated with one of two functionally equivalent but visually different techniques. Unlike in the aforementioned Whiten studies, the differences related not to affordance properties of the apparatus, but only to the style with which the tool was used. When given the opportunity to retrieve the reward for themselves, children and chimpanzee subjects were equally competent, and performed better than control subjects who received no demonstration. However, whereas children reliably reproduced the demonstrated technique, chimpanzees did not: participants in both ape groups performed identically.

This pattern of findings has been replicated in a number of more recent studies (Call et al. 2005; Tennie et al. 2006). Together they suggest that chimpanzees' default social learning strategies are a mixture of end-state emulation and observational learning of environmental affordances (perhaps facilitated by local and stimulus enhancement effects); and that even if imitation is not cognitively too difficult for chimpanzees, for the most part they are not motivated to do it.

Particularly robust evidence for this hypothesis comes from a study by Whiten et al. (2005). They presented chimpanzees and three and four year old children with a puzzle box containing food. In different conditions, the box was either transparent, so that its internal workings were visible, or opaque. In both conditions a human experimenter performed an identical demonstration in which she used a tool to retrieve food from the box. However, only some of her actions were causally necessary for retrieval. Subjects in the clear but not in the opaque condition could see this. While in both conditions children performed the same actions as the demonstrator, the chimpanzees did so only in the opaque condition. In the clear condition, they performed only those actions necessary for removing food from the box. In other words, where chimpanzees could see a solution themselves, they did things their own way. Note that in both conditions participants could have been attending only to the tool, and not to the technique with which the experimenter manipulated it. Nevertheless, children reproduced the same actions as the experimenter regardless—perhaps because they assume that all aspects of adults' actions are significant, even if they don't understand why (Gergely and Csibra 2005).

The non-imitation strategy is by no means irrational, since it minimises wasted effort. However, where one pursues a strategy of reproducing only actions that one identifies as a pre-requisite of success, then one effectively limits oneself to performing actions the causal basis of which can readily be understood. Unlike children, chimpanzees should therefore perform poorly in tasks that cannot easily be solved by causal reasoning and attention to the environment, and where success is greatly facilitated or made possible only by the careful copying of a demonstrator's technique. In support of this hypothesis, Tennie et al. (2009) found that human children but not chimpanzees were able to construct a straw loop with which to lasso and reel in an out-of-reach reward. The test action was chosen precisely because it could not easily be constructed without careful attention to the action performed by the experimenter to create the required loop. In a no-demonstration control, neither

children nor chimpanzees created a loop. However, following the demonstration, nine out of twelve children succeeded in doing so, and eight then tried to use it to retrieve the reward (four succeeded). No apes either recreated the loop or retrieved the reward.

The most persuasive evidence that chimpanzees imitate would come in the form of evidence that they participate in conventional, learned behaviours. Conventional behaviours—including, for example, the communicative use of words—are arbitrary. That is, they are not intrinsically well suited to realising the states of affairs in pursuit of which they are used as means. Individuals within a community therefore perform these behaviours only because their peers do (Millikan 2005; Moore 2013a, b). These properties make conventional behaviours an excellent candidate to test for the presence of imitative learning, since they are highly unlikely to be acquired through trial and error learning and cannot be inferred from the causal properties of the environment. Luck aside, they can be learned only by attention to and faithful reproduction of others' behaviour. In a recent study, Tennie et al. (2012) tested chimpanzees' ability to recreate an arbitrary gesture performed by a conspecific demonstrator. They found that while one chimpanzee (out of fifteen) was able to reproduce a familiar gesture in exchange for a reward, the same individual did not learn a new behaviour in the same circumstances. This suggests that while some chimpanzees may be inspired to perform familiar actions after watching others, they may not learn new actions in this way.

Better evidence of imitation comes from a study of the vocal behaviour of wild chimpanzees. Crockford et al. (2004) found audible structural differences between the pant hoots of males in three neighbouring groups at Taï. Since the pant hoots of these groups do not differ acoustically from the pant hoots of males in a fourth community 70 km away, this suggests that chimpanzees in neighbouring groups actively modified their calls to make them acoustically discriminable from those of neighbouring groups. (Given the existence of between-group conflicts, there are good reasons to make oneself identifiable to both in- and out-group members.) Since the differences relate to the pitch, tone and speed of production of different parts of the calls, this provides compelling evidence of group specific conventions. Moreover, the active matching of calls by individuals to the calls of their group (or to the calls of a dominant individual within a group) is suggestive of vocal imitation. The possibility of vocal imitation in chimpanzees has often been dismissed (e.g., Tomasello 2008), not least because vocalisations are thought to reflect arousal, such that they are not under intentional control. However, recent findings indicate that chimpanzee vocalisations may be subject to more intentional control than has been supposed (Slocombe and Zuberbühler 2007; Slocombe et al. 2010; Crockford et al. 2011). Moreover, Crockford and colleagues found that variation between group calls was not correlated only with call features correlated with respiratory pressure, which has been thought to be a consequence of excitation. This exciting finding therefore holds open the possibility that wild chimpanzees do imitate, at least in the vocal modality. Further research—not least on the ontogeny of chimpanzee calls, and on intentional control of vocal behaviour—would be needed to confirm this possibility, though.

The general absence of evidence of chimpanzee imitation shows neither that chimpanzees could not imitate, nor even that they do not. It may be, for example, that they imitate only particular individuals (in line with de Waal's BIOL hypothesis; see footnote 3). This possibility gains credibility from reports of cases in which a social custom has emerged after others copied the idiosyncratic behaviour of one individual (Hobaiter and Byrne 2010),<sup>5</sup> and from evidence that chimpanzees preferentially copy high-ranking individuals (Horner et al. 2010). If chimpanzee imitation were highly selective, then studies might simply fail to isolate this competence. Another possibility is that chimpanzees just prefer to solve problems by engaging causal reasoning than by copying others. Since the repertoire of tool-use behaviours that chimpanzees need to survive in the wild could all be acquired in this way, they may simply lack motivation to pay close attention to others' actions. This hypothesis is consistent with experimental evidence that enculturated chimpanzees are capable imitators (Tomasello et al. 1993)—showing that the absence of imitation in un-enculturated apes is not the consequence of an insurmountable cognitive limitation. A further possibility is that chimpanzees find it harder to map actions observed in others to their own bodies than do humans (the 'correspondence problem'—see, e.g., Heyes 2013). This would explain why they prefer to develop their own techniques for action, rather than copy those of others. It is also consistent with the possibility of their being better at vocal than sensorimotor imitation. Future research should try to disambiguate these possibilities. In the meantime it should be emphasised that while chimpanzees seem not to imitate, its absence may be unrelated to cognition.

Among those who doubt the existence of chimpanzee imitation, the existence of arbitrary but learned behaviours would constitute the most robust form of evidence. If arbitrary behaviours—like conventional sign use—could be found in chimpanzee communities, this would support the conclusion that they do imitate. However, aside from Crockford et al. (2004), such behaviours have not yet been well documented. In the meantime, the cultural differences that have been identified between groups of chimpanzees can all be explained without appeal to imitative learning. For example, the grooming handclasp might be learned through a process of ritualisation, in which more experienced groomers simply manoeuvre the hands of their partners into the desired position. Differences in tool-use behaviours, like those documented by Luncz et al. (2012), could also be attributable to salience effects: seeing some apes use stone and not wooden hammers might unreflectively incline observers to follow suit.

### **Cumulative culture in chimpanzees**

In contrast to chimpanzees, children's willingness to imitate even actions that they don't understand enables them to learn skills that they could not figure out for themselves—and so prepares them for cumulative culture. There is currently little evidence that ape culture is in any substantial respect cumulative. Indeed, chimpanzee

---

<sup>5</sup> A similar example has recently emerged at Chimfunshi, where others have followed one high-ranking female by inserting long strands of grass into their ear (Edwin van Leeuwen, in conversation).

nut-cracking technology has remained largely unchanged for 4,300 years (Mercader et al. 2007). At the same time, the identification of cumulative culture is not straightforward—because its attribution typically depends on judgement calls about whether observed behaviours could have been invented by isolated individuals, or only through the incremental improvements of generations.

Yamamoto et al. (2013) recently found that chimpanzees who could retrieve juice from a box only by dipping a straw into it, and then licking the straw, learned to suck on the straw (a more effective technique) after observing a conspecific or human do the same thing. In contrast to previous findings (Marshall-Pescini and Whiten 2008), this suggests that chimpanzees can refine tool-use techniques already in their repertoire through observational learning. While this finding is valuable, the theoretical gloss with which the authors present it is not. Following Marshall-Pescini and Whiten, Yamamoto et al. conclude that their finding is evidence of a “basis for cumulative culture in chimpanzees”. However, since the results can readily be explained by observational learning of new affordance properties of the straw, the study does not challenge any previous findings about the mechanisms of chimpanzee social learning. Moreover, even if it’s conceded that cumulative culture should not be identified too closely with particular learning mechanisms (Caldwell and Millen 2009), this demonstrated behaviour is not a case of cumulative culture. While the ability of individuals to refine techniques through social learning may be necessary for cumulative culture, it certainly isn’t sufficient, since it is consistent with the absence of a ratchet-effect. Ratchet-effect behaviours require that the contributions of later generations surpass the technology of earlier generations, and don’t merely match them; such that cultural accumulations are too sophisticated to result from the efforts of an individual learner. This is clearly not the case for Yamamoto et al.’s straw-sucking technique: the fact that it was discovered independently by four of the tested chimpanzees makes it a poor candidate for evaluating the presence or absence of cumulative culture.

A more plausible candidate for cumulative culture in chimpanzees are the complex, multi-tool honey-foraging techniques used by chimpanzees in the Goulougo triangle and in the Loango National Park in Gabon to retrieve honey from the nests of bees (Morgan and Abwe 2006; Boesch et al. 2009; Boesch 2012). However, even these impressive technologies could potentially be acquired through non-social processes of affordance learning and causal cognition, such that it’s not easy to judge whether they are the technological product of one generation or many. Future studies would do well to investigate the learning processes implicated in the use of these more complex tool sets. One way in which this could be discerned is through the use of Tennie’s ‘latent solutions’ paradigms, which seek to identify which species-specific behaviours are part of a repertoire that need not be learned from others.

## Latent solutions

In an important study of all ape species, Tennie et al. (2008) found that a behaviour previously attributed to social learning may be the unlearned product of a genetic adaptation, perhaps operating in conjunction with individual learning. Mountain

gorillas (*Gorilla beringei beringei*) feed on the stinging nettle *Laportea alatis* by means of an elaborate processing technique that largely protects them from its sting (Byrne and Byrne 1993). Byrne (2003) has claimed that this skill is likely to be acquired through imitation—albeit a ‘behaviour-parsing’ variety that does not require intention understanding. To test this hypothesis, Tennie et al. presented similar nettles (*Urtica dioica*) to three captive groups of Western lowland gorillas (*Gorilla gorilla gorilla*) who are not known to eat nettles in the wild, and to orang-utans, chimpanzees and bonobos. Individuals in all gorilla groups both ate the nettles and produced the targeted processing technique, and fed on similar-looking but harmless willow leaves without using the technique. No individual from the other species ate the nettles, except one orang-utan who used a different technique. From its spontaneous appearance in naïve groups, the authors concluded that social learning was likely to play only a limited role in the gorillas’ mastery of the skill.

Such paradigms provide a valuable test for the absence of social learning: if identified behaviours appear in apes isolated from other practitioners of that behaviour, then clearly one need not appeal to social learning to explain their diffusion with a group. Nonetheless, the theoretical elaboration of the nature of ‘latent solutions’ remains unsatisfying.

To characterise the combinations of genetic predisposition and individual learning that they invoked to explain the nettle feeding behaviour of captive gorillas, Tennie and Hedwig (2009) introduced the term ‘latent solutions’. They hypothesise that numerous ape behaviours may be latent solutions—including the tendency of chimpanzees to swallow medicinal hispid leaves without chewing them (Huffman and Hirata 2004; Menzel et al. in press) and the grooming handclasp. According to Tennie and Hedwig, a species’ zone of latent solutions “encompasses the sum of potential solutions acquired by individual learning and constrained by the learners’ problem solving skills” (p. 99). In other words, the zone of latent solutions includes any behaviour that, in at least some individuals, was not learned socially. This includes unlearned adaptations, exaptations (Gould and Lewontin 1979), and behaviours that are learned individually. In other words, the zone of latent solutions includes behaviours that are neither ‘latent’ (in the sense of unlearned), nor ‘solutions’ to any evolutionarily problem. (While the grooming handclasp may emerge spontaneously in different groups of chimpanzees, there is no clear evolutionary hurdle to which it would constitute a solution.) Given this extension of the term, while the phrase concisely classifies a subset of behaviours that are relevantly similar for some issues in the study of comparative ontogeny, it runs together different sources of behaviour that might usefully be distinguished—no least, innate and learned behaviours. To say that a behaviour is a latent solution is therefore not, on current formulation, to extend the culture debate beyond the claim that apes do not learn through imitation.

## Teaching

To finish, I turn to the question of whether chimpanzees engage in teaching. Like imitation, teaching has been thought to be a cornerstone of the possibility of

cumulative culture (Tomasello 1999). In recent years the subject of pedagogy has received renewed attention from cognitive scientists, following the proposal from Gergely and Csibra that human children are hardwired to learn from the teaching of others (e.g., Gergely and Csibra 2005), facilitating their learning the accumulated wisdom of successive generations. A central assumption of this hypothesis is that the motivation to teach is uniquely human (Csibra 2007). Nonetheless, teaching might be valuable for chimpanzees because there appears to be a critical learning window within which tool techniques can be learned. For example, chimpanzees who do not learn to crack nuts between the ages of three and five do not subsequently do so (Matsuzawa et al. 2001; Biro et al. 2003), and will obtain nuts later in life only by scrounging from others. Given this critical learning period, and the likely decreased fitness and increased dependence of unskilled offspring, mothers might have an incentive (which need not be altruistic) to ensure that their children learn required skills.

Boesch (1991, 2012) has consistently argued that chimpanzee mothers at Tai teach their young. For example, they are said to facilitate their offspring's nut-cracking by leaving suitable hammers and un-cracked nuts in the vicinity of anvils—sometimes even leaving them arranged for juveniles to crack. Boesch also reports two cases of active teaching—one mother demonstrated the correct way to position a panda nut on the anvil; and a second demonstrated to her daughter the correct way to hold an irregular shaped hammer.

Despite these observations, researchers at other field sites have found no evidence of teaching. In her work on the ontogeny of termite fishing at Gombe, Lonsdorf reports that while mothers tolerated offspring watching their termite fishing, and even some instances of interference or termite theft, they did not actively teach:

In no instance did I see a mother actively facilitate her offspring's learning in any way. Mothers were oriented completely to the task of termite-fishing and rarely even made eye contact with offspring. A mother never offered a termite to her offspring, never handed her offspring a tool and never molded the offspring's behavior while fishing. (Lonsdorf 2006, p. 44)

Similarly, Matsuzawa et al. (2001) report that while mothers at Bossou are highly tolerant of juveniles' observation, they neither teach nor donate tools or nuts. A further recent laboratory study failed to find any evidence of teaching in chimpanzees, in a paradigm in which children were quick to provide instructions for one another (Dean et al. 2012).

A possible explanation of these differences is that cases of active teaching have been misidentified. However, this would not explain the provisioning of tools and nuts in the context of which teaching was observed. Boesch (2012) suggests that the differences may be explained by the fact that chimpanzees at Tai but not Bossou eat the harder panda nut, the cracking of which juveniles rarely master before they are 8 years old. Since female chimpanzees give birth every 5 years, the demands of having two dependent offspring may push them to accelerate their offspring's learning. However, this hypothesis is less likely to be true if the panda nut is not a vital part of the Tai diet. Furthermore, the extended dependency of young

chimpanzees might also decrease the likelihood of teaching, since opportunities for observational learning will be plentiful (Hoppitt et al. 2008).

In the absence of consensus, some researchers have come to adopt a more conservative analogy to characterise the form of teaching that predominates among wild chimpanzees. The analogy first used by Matsuzawa (Matsuzawa et al. 2001; Matsuzawa 2011) and subsequently adopted by others (de Waal 2001; Boesch 2012) is the master-apprentice model employed in the art of Japanese sushi making. Here apprentices spend several years watching their master, without explicit instruction, before making sushi themselves. Silent—but tolerated—observation takes the place of active teaching. These authors (and others, e.g., Sterelny 2009) have argued for the importance of tolerance to being watched as crucial for facilitating observational learning. Boesch (2012) has also defended the claim that explicit teaching is a predominantly Western phenomenon, absent from the hunter-gather communities whose ecological niche most resembles that of chimpanzees. However Hewlett and co-authors (2011) argue that while teaching is less common in hunter-gatherer communities than in Western cultures, it is present; and that existing anthropological data may under-estimate its presence by over-looking non-verbal and implicit forms of pedagogy.

The same may also be true of chimpanzee data: by identifying teaching with active behaviour-moulding, Lonsdorf may have set the bar for pedagogy too high. It's therefore worth considering the question of what a minimal form of teaching could look like.

The most basic form of human pedagogy takes the form of a communicative act (Csibra 2007). Its content might specify information that the teacher intends the pupil to learn: “Do *this!*” or, in more discriminating cases, “Do *this* like *this!*”—where the demonstratives would pick out either undifferentiated action sequences, or differentiated means and ends. This act could be performed consistently with criteria for teaching previously given by Caro and Hauser (1992), according to which a behaviour would count as teaching only if (1) it occurs only in the presence of naïve (or appropriately inexperienced) observers, (2) it is costly and does not provide any immediate and direct benefit to the teacher, and (3) facilitates knowledge acquisition or skill learning in the observer.

How might such pedagogical messages be enacted? The answer is perhaps surprisingly simple. In practice one could intend to communicate a message with the content “Do *this!*” simply by demonstrating the action to be performed; and one could demonstrate that action just by performing it while addressing one's performance to an intended audience (Moore 2013b, c). This address can be achieved through a variety of attention soliciting acts, including eye contact, touch, and vocalisation. In addition to this attention solicitation, the action should be performed in an open manner, so as not to block visual access of the intended audience (Byrne and Rapaport 2011). To make particular aspects of the performance particularly salient—for example, the motion of a nut cracking technique, or the placement of the nut—particular aspects of an act could be exaggerated by being performed particularly slowly or ostensively.<sup>6</sup> However, such

---

<sup>6</sup> In fact, similar behaviour has already been identified in free-ranging macaques (*Macaca fascicularis*), who floss their teeth more often and more slowly when observed by infants (Masataka et al. 2009).

elaborations need not be present in the basic case. This form of ‘minimal pedagogy’ therefore mitigates against one possible objection—raised by Sutton (2013) in response to Sterelny (2012)—to thinking that pedagogy could have emerged early in hominin phylogeny. The objection states that if pedagogy requires “performances that are stylized and accompanied by meta-commentary” (Sterelny 2012: 145–146), it places very strong demands on the ability of teachers to break down and represent to others parts of ordinarily fluid action sequences. The account of pedagogy sketched here makes no such representational demands but could nonetheless facilitate knowledge transfer between teacher and pupil. Furthermore, while Boesch (2012) has claimed that pedagogy presupposes the ability to engage in sophisticated reasoning about a prospective student’s lack of ability, this need not be the case. In interactions around the tool site, a juvenile’s lack of skill is likely to be visually evident.

On the account sketched here, minimal pedagogy would require only the ability to judge the incompetence of an action performed in pursuit of a goal, operating in conjunction with an intention to inform, and the ability to address a demonstrated behaviour to its intended audience. That chimpanzees understand inadequate goal-directed behaviour has been established (Call et al. 2005). Furthermore, while it has often been taken for granted that chimpanzees do not communicate to share information (Tomasello 2008), Crockford and colleagues have gathered compelling evidence that chimpanzees do vocalise for one another the presence of snakes. These vocalisations are not emotionally charged, and are produced differentially for knowledgeable and ignorant others. Consequently, they seem to be under intentional control—and thereby cases of intentional, informative communication. Since chimpanzees also direct their communicative acts appropriately to an intended audience (Tomasello 2008; Moore 2013c), then even if they are not motivated to teach, they should nonetheless be cognitively capable of doing so.

Aside from Lonsdorf’s comment that chimpanzee mothers “rarely even made eye contact with offspring” I know of no work in which mother–child interactions in learning contexts have been analysed for attention-soliciting behaviours. If they are present, they may be subtle—for example, touches to solicit the juvenile’s attention prior to cracking, perhaps combined with postural shifts to facilitate observation, or pauses to wait for attention. It may be that none of these behaviours are present; that the attention of juveniles is just taken for granted. Nonetheless, exploratory analysis, to rule in or rule out the possibility of minimal pedagogy, would be a worthwhile undertaking.

Whether or not chimpanzees engage in teaching, its minimal form has been worth elaborating for a further reason: by seeing that the act of demonstration is not cognitively sophisticated, we can see a cognitively inexpensive route from animal to human culture. This gives the lie to Galef’s claim (quoted above) that culture in chimpanzees “tells us nothing about the evolutionary origins of human culture”. It may be that the transition from early hominin to human culture took place through two subtle shifts in the attentional play of individuals. In the case of imitation, individuals who previously emulated the actions of others came to spend more time attending to the precise techniques they used—either because they came to appreciate the importance of these techniques, or for other reasons. Haun and Over

(in press) have argued that the transition from emulation to imitation was driven by the desire to be like other group members, which motivated more precise behaviour matching. Alternatively, as Gergely and Csibra have maintained (2005), selection for imitation may have been driven by pressure for the social transmission of causally opaque or conventional behaviours.

In the case of teaching it may be that, perhaps as skills necessary for individual or group survival became more complex, caregivers came under pressure to pass on their skills to offspring. This might motivate them to direct their instrumental actions pedagogically, in the first instance through the small and incremental changes of attention soliciting, and later through exaggerated performance of key elements of the instructed behaviour. In this way, recognisably human forms of teaching could have emerged against the background of a more minimal pedagogy. Alternatively, intentional teaching might have emerged not because of pressure for improved social learning, but fortuitously—on the back of a more general selection for pro-social motivations, perhaps as a consequence of selection for cooperative breeding (Burkart et al. 2009).

The behavioural changes that mark the transition from chimpanzee to human culture—from self-absorbed activity to pedagogy; and from emulation to imitation—need not be cognitively expensive. They implicate no changes in cognition, but only changes in attention direction and solicitation, and accompanying motivations (and perhaps, in the case of imitation, a more fluid ability to map others' bodily actions to one's own). In that case, studying the culture of chimpanzees may already have told us a great deal about the possible evolutionary pathways and selection pressures that culminated in human social learning.

**Acknowledgments** Thanks to Matthias Allritz, Cathy Crockford, Gergely Csibra, Edwin van Leeuwen, Lydia Luncz, Claudio Tennie, Roman Wittig, and two anonymous reviewers for comments on and discussions relating to drafts of this material; and to Edwin van Leeuwen, Mark Bodamer, and the Chimfunshi Wildlife Orphanage Trust for photographs of the grooming handclasp in Fig. 1.

## References

- Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T (2003) Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim Cogn* 6:213–223
- Boesch C (1991) Teaching among wild chimpanzees. *Anim Behav* 41:530–532
- Boesch C (2012) *Wild cultures: A comparison between chimpanzee and human cultures*. Cambridge University Press, Cambridge
- Boesch C, Head J, Robbins MM (2009) Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *J Hum Evol* 56(6):560–569
- Burkart JM, Hrdy SB, van Schaik CP (2009) Cooperative breeding and human cognitive evolution. *Evol Anthropol* 18:175–186
- Byrne RW (2003) Imitation as behaviour parsing. *Philos Trans R Soc Lond B Biol Sci* 358(1341): 529–536
- Byrne RW, Byrne JME (1993) Complex leaf-gathering skills of mountain gorillas (*Gorilla gorilla beringei*): variability and standardization. *Am J Primatol* 31:241–261
- Byrne RW, Rapaport LG (2011) What are we learning from teaching? *Anim Behav* 82:1207–1211
- Caldwell CA, Millen AE (2009) Social learning mechanisms and cumulative cultural evolution: is imitation necessary? *Psychol Sci* 20:1478–1483

- Call J, Tomasello M (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn Sci* 12:187–192
- 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
- Caro TM, Hauser MD (1992) Is there teaching in nonhuman animals? *Q Rev Biol* 67:151–174
- Crockford C, Herbinger I, Vigilant L, Boesch C (2004) Wild chimpanzees have group specific calls: a case for vocal learning? *Ethology* 110:221–243
- Crockford C, Wittig RM, Mundry R, Zuberbuehler K (2011) Wild chimpanzees inform ignorant group members of danger. *Curr Biol* 22:142–146
- Csibra G (2007) Teachers in the wild. *Trends Cogn Sci* 11(3):95–96
- De Waal F (2001) The ape and the sushi master. Basic Books, New York, NY
- Dean LG, Kendal RL, Schapiro SJ, Thierry B, Laland KN (2012) Identification of the social and cognitive processes underlying human cumulative culture. *Science* 335(6072):1114–1118
- Galef BG (1992) The question of animal culture. *Hum Nat* 3:157–178
- Galef BG (2009) Culture in animals? In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, MA
- Gergely G, Csibra G (2005) The social construction of the cultural mind: imitative learning as a mechanism of human pedagogy. *Interact Stud* 6(3):463–481
- Gould SJ, Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc R Soc B Biol Sci* 205:581–598
- Haun DBM, Over H (in press) Like me: a homophily-based account of human culture. In: Christiansen MH, Richerson PJ (eds) *Cultural evolution, a Strungmann Forum Report*. MIT Press, Cambridge, MA
- Hewlett BS, Fouts HN, Boyette AH, Hewlett BL (2011) Social learning among Congo Basin hunter-gatherers. *Philos Trans R Soc Lond B Biol Sci* 366(1567):1168–1178
- Heyes C (2013) What can imitation do for cooperation? In: Sterelny Joyce, Calcott Fraser (eds) *Cooperation and its evolution*. MIT Press, Cambridge, MA
- Hobaiter C, Byrne RW (2010) Able-bodied wild chimpanzees imitate a motor procedure used by a disabled individual to overcome handicap. *PLoS One* 5(8):e11959
- Hoppitt WJE, Brown GR, Kendal R, Rendell L, Thornton A, Webster MW, Laland KN (2008) Lessons from animal teaching. *Trends Ecol Evol* 23:486–493
- Horner V, Whiten A (2005) Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Anim Cogn* 8:164–181
- Horner V, Whiten A, Flynn E, de Waal F (2006) Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proc Natl Acad Sci USA* 103(37):13878–13883
- Horner V, Proctor D, Bonnie KE, Whiten A, de Waal FBM (2010) Prestige affects cultural learning in chimpanzees. *PLoS ONE* 5(5):e10625
- Huffman MA, 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(2):113–118
- Humble T, Matsuzawa T (2002) Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *Am J Primatol* 58(3):133–148
- Laland KN, Galef BG (eds) (2009) *The question of animal culture*. Harvard University Press, Cambridge, MA
- Langergraber KE, Boesch C, Inoue E, Inoue-Murayama M, Mitani J, Nishida T, Pusey A, Reynolds V, Schubert G, Wrangham R, Wroblewski E, Vigilant L (2010) Genetic and ‘cultural’ similarity in wild chimpanzees. *Proc R Soc Lond B* 278(1704):408–416
- Lonsdorf EV (2005) Sex differences in the development of termite-fishing skills in wild chimpanzees (*Pan troglodytes schweinfurthii*) of Gombe National Park, Tanzania. *Anim Behav* 70:673–683
- Lonsdorf EV (2006) What is the role of the mother in the acquisition of tool-use skills in wild chimpanzees? *Anim Cogn* 9:36–46
- Lonsdorf EV, Pusey AE, Eberly L (2004) Sex differences in learning in chimpanzees. *Nature* 428(6984): 715–716
- Luncz LV, Mundry R, Boesch C (2012) Evidence for cultural differences between neighboring chimpanzee communities. *Curr Biol* 22(10):922–926
- Marshall-Pescini S, Whiten A (2008) Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Anim Cogn* 11:449–456

- Masataka N, Koda H, Urasopon N, Watanabe K (2009) Free-ranging macaque mothers exaggerate tool-using behavior when observed by offspring. *PLoS ONE* 4(3):e4768
- Matsuzawa T (2011) Education by master-apprenticeship. In: Matsuzawa T et al (eds) *The chimpanzees of Bossou and Nimba*. Springer, Tokyo, pp 201–209
- Matsuzawa T, Biro D, Humle T, Inoue-Nakamura N, Tonooka R, Yamakoshi G (2001) Emergence of culture in wild chimpanzees: education by master-apprenticeship. In: Matsuzawa T (ed) *Primate origins of human cognition and behavior*. Springer, Tokyo, pp 557–574
- McGrew W (1974) Tool use by wild chimpanzees in feeding upon driver ants. *J Hum Evol* 3(6):501–508
- McGrew WC, Tutin CEG (1978) Evidence for a social custom in wild chimpanzees? *Man* 13:234–251
- Menzel C, Fowler A, Tennie C, Call J (in press) Leaf surface roughness elicits leaf-swallowing behavior in captive chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), but not in gorillas (*Gorilla gorilla*) or orangutans (*Pongo abelii*). *Am J Primatol* 70:584–593
- Mercader J, Barton H, Gillespie J, Harris J, Kuhn S, Tyler R, Boesch C (2007) 4,300-Year-old chimpanzee sites and the origins of percussive stone technology. *PNAS* 104(9):3043–3048
- Millikan RG (2005) *Language: a biological model*. OUP, Oxford
- 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(1):37–45
- Moore R (2013a) Imitation and conventional communication. *Biol Philos* 28(3):481–500
- Moore R (2013b) Evidence and interpretation in great ape gestural communication. In Cappuccio ML (ed) *Pointing: where embodied cognition meets the symbolic mind*. *Humana Mente* (in press)
- Moore R (2013c) Enacting and understanding communicative intent. *Mind and Lang* (in press)
- Morgan BJ, Abwe EE (2006) Chimpanzees use stone tools in Cameroon. *Curr Biol* 16(16):632–633
- Nagell K, Olguin K, Tomasello M (1993) Processes of social learning in the tool use of chimpanzees and human children. *J Comp Psychol* 107(2):174–186
- Over H, Carpenter M (2013) The social side of imitation. *Child Dev Perspect* 7(1):6–11
- Perry S (2009) Are nonhuman primates likely to exhibit cultural capacities like those of humans? In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, MA, pp 247–268
- Richerson PJ, Boyd R (2005) *Not by genes alone: how culture transformed human evolution*. Chicago University Press, Chicago
- Sanz C, Morgan D (2007) Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *J Hum Evol* 52(4):420–433
- Schöning C, Humle T, Möbius Y, McGrew WC (2008) The nature of culture: technological variation in chimpanzee predation on army ants. *J Hum Evol* 55:48–59
- Slocombe KE, Zuberbühler K (2007) Chimpanzees modify recruitment screams as a function of audience composition. *PNAS* 104(43):17228–17233
- Slocombe KE, Kaller T, Turman L, Townsend SW, Papworth S, Zuberbühler K (2010) Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behav Ecol Sociobiol* 64(12):1959–1966
- Sterelny K (2009) Peacekeeping in the culture wars. In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, MA, pp 288–304
- Sterelny K (2012) *The evolved apprentice: how evolution made humans unique*. MIT, Cambridge, MA
- Sutton J (2013) Collaboration and skill in the evolution of human cognition. *Biol Theory*. doi:10.1007/s13752-013-0097-z
- Tennie C, Hedwig D (2009) How latent solution experiments can help to study differences between human culture and primate traditions. In: Potocki E, Krasinski J (eds) *Primateology: theories, methods and research*. Nova Publishers, New York, pp 95–112
- Tennie C, Call J, Tomasello M (2006) Push or pull: emulation versus imitation in great apes and human children. *Ethology* 112:1159–1169
- Tennie C, Hedwig D, Call J, Tomasello M (2008) An experimental study of nettle feeding in captive gorillas. *Am J Primatol* 70:584–593
- Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. *Philos Trans R Soc Lond B Biol Sci* 364(1528):2405–2415
- Tennie C, Call J, Tomasello M (2012) Untrained chimpanzees (*Pan troglodytes schweinfurthii*) fail to imitate novel actions. *PLoS ONE* 7:e41548
- Tomasello M (1994) The question of chimpanzee culture. In: Wrangham R, McGrew W, de Waal F, Heltne P (eds) *Chimpanzee cultures*. Harvard University Press, Cambridge, MA, pp 301–317.

- [Reprinted (2009, with new postscript) in Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, MA, pp 198–221]
- Tomasello M (1999) *The cultural origins of human cognition*. Harvard University Press, Cambridge, MA
- Tomasello M (2008) *Origins of human communication*. MIT, Cambridge, MA
- Tomasello M, Savage-Rumbaugh S, Kruger AC (1993) Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Dev* 64(6):1688–1705
- Van Leeuwen EJC, Haun DBM (2013) Conformity in nonhuman primates: fad or fact? *Evol Hum Behav* 34:1–7
- Van Leeuwen EJC, Cronin KA, Haun DBM, Mundry R, Bodamer MD (2012) Neighbouring chimpanzee communities show different preferences in social grooming behaviour. *Proc R Soc B Biol Sci* 279: 4362–4367
- Van Schaik C (2012) Animal culture: chimpanzee conformity? *Curr Biol* 22(10):402–404
- Van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill MY (2003) Orangutan cultures and the evolution of material culture. *Science* 299:102–105
- Whiten A (2009) The identification and differentiation of culture in chimpanzees and other animals: from natural history to diffusion experiments. In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, MA, pp 99–124
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399(6737):682–685
- Whiten A, Horner V, de Waal FBM (2005) Conformity to cultural norms of tool use in chimpanzees. *Nature* 437(7059):737–740
- Wrangham R (2006) The culture zone becomes untidy. *Curr Biol* 16(16):634–635
- Yamamoto S, Humle T, Tanaka M (2013) Basis for cumulative cultural evolution in chimpanzees: social learning of a more efficient tool-use technique. *PLoS ONE* 8(1):e55768